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FOSSIL MAYFLY LARVAE (EPHEMEROPTERA, CF. HEPTAGENIIDAE) FROM THE LATE CRETACEOUS WAPITI FORMATION, ALBERTA, CANADA

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ABSTRACT—Fossil mayfly larvae (cf. Heptageniidae) are reported for the first time in the Cretaceous of Canada. The new fossils come from the latest Campanian part of the Wapiti Formation, which crops out in west-central Alberta, near the British Columbia border. These sediments represent mixed lentic and lotic fluvial environments consistent with modern heptageniid ecology. This discovery helps fill a significant temporal gap in heptageniid evolution between the Eocene and their earliest appearance in the Turonian.

INTRODUCTION

ALTHOUGH THE fossil record of mayflies (Ephemeroptera Hyatt and Arms, 1890) is relatively complete compared to many other insect orders, Mesozoic records are comparatively poor. Late Cretaceous occurrences of mayflies are restricted to amber inclusions from the Taymr Peninsula, North Siberia (Kluge, 1993) and New Jersey, U.S.A. (Sinitshenkova, 2000) and tuffaceous mudstones from Jakutia, Russia (Zherikhin, 1978) and Kzyl-Dzhar, Kazakhstan (Zherikhin, 1978). In contrast, Early Cretaceous, principally lacustrine, occurrences are widespread across Asia (Zherikhin, 1978; Huang et al. 2011), Australia (Jell and Duncan 1986), Europe (Martinez-Declòs, 1991), and South America (McCafferty, 1990) with a single record from Burma (Myanmar) (McCafferty and Santiago-Blay, 2008).

In North America, Late Cretaceous mayflies have been documented only in the Turonian amber deposits at Sayreville, New Jersey (Sinitshenkova, 2000). This locality has yielded representatives of the families Ametropodidae Bengtsson, 1913, Australiphemeridae McCafferty, 1991, Heptageniidae Needham, 1901, and Polymitarcyidae Banks, 1900. Moreover, this locality represents the oldest occurrences of the extant families Ametropodidae and Heptageniidae. Until now, mayflies were unknown from the Mesozoic of Canada despite several insect-rich amber localities (McKellar et al., 2008; McKellar and Wolfe, 2010; McKellar and Engel, 2011). The oldest Canadian record of Ephemeroptera is a single larva of indeterminate family from the Eocene Paskapoo Formation of Alberta (Mitchell and Wighton, 1979).

Few fossil heptageniid larvae have been described, all of which come from the Cenozoic. These include *Heptagenia* sp. Walsh, 1963 (upper Miocene, Shandong Province; Zhang, 1989), *Miocoenogia gorbunovi* Tshernova, 1962 (Oligocene, West Siberia, Russia; Tshernova, 1962), *Pseudokageronia thomasi* Masselot and Nel, 1999 (uppermost Miocene, France), and *Succinogenia larssoni* Demoulin, 1965 (upper Eocene, Baltic amber; Demoulin, 1965). Here we report on an important new Canadian locality that has yielded body fossils of larval mayflies from the Late Cretaceous Wapiti Formation. Insects in amber from the Wapiti Formation have been noted previously (Tanke, 2004; McKellar and Wolfe, 2010); however, these have yet to be described in detail.

GEOLOGICAL SETTING

The Wapiti Formation consists of interbedded fluvial sandstone, siltstone and mudstone, with subordinate coal and lacustrine sediments that were deposited during the early Campanian to the late Maastrichtian (Fanti and Catuneanu, 2009). As with other well-known coeval deposits of the Western Interior Basin of Canada and United States, the Wapiti Formation is represented exclusively by non-marine deposition, thus playing a role in understanding terrestrial biota during the latest Cretaceous. Deposits exposed at the Red Willow Falls locality are representative of the upper unit four of the Wapiti Formation (equivalent to the lower part of the Horseshoe Canyon Formation in southern Alberta), which accumulated during the latest Campanian some 400 km west of the paleo-shoreline of the Western Interior Seaway (represented by the Bearpaw Formation deposits) and is therefore representative of freshwater conditions. The occurrence of the hadrosaurid dinosaur *Edmontosaurus regalis* Lambe, 1917, confirms a latest Campanian age for the upper unit four (Campione and Evans, 2011). In addition, sediments of unit four of the Wapiti Formation accumulated at a paleolatitude of approximately 65° N and are therefore representative of a high latitude ecosystem (Fanti and Miyashita, 2009).

The Red Willow Falls strata include repeating fining-upward successions of channel fills, crevasse-splay, and organic-rich overbank deposits with rare and discontinuous bentonitic beds. Fluvial-body stacking patterns, together with common coal seams, also suggest high-water table conditions and highly vegetated, poorly drained grounds. In particular, the ephemeropteran fossils reported here come from a discrete stratigraphic interval (three meters in overall thickness) characterized by repeating alternation of tabular to lenticular overbank strata. Each bed consists of a lower sandy/silty interval that fines into dark gray, organic rich mudstone and ranges in thickness between 3 and 35 cm. Strata display a fine, horizontal lamination, with minor ripples and other water traction indicators. The contact with overlying sandy/silty deposits is sharp and erosive with evidence of abundant natural casts (scale 2 to 20 cm). An accurate lithostratigraphic composite section clearly indicates that both lotic and lentic water environments are represented in the strata exposed at the Red Willow Falls locality. In addition to ephemeropterans, the sandy/silty beds are replete with diverse invertebrate trace fossils including nematode and bivalve (cf. Unionidae) traces. Such fossils (including the ephemeropterans described here) are preserved in positive epirelief on the lower surfaces of the sandy/silty intervals.

SYSTEMATIC PALEONTOLOGY

Order Ephemeroptera Hyatt and Arms, 1890
cf. Family HEPTAGENIIDAE Needham, 1901

Description.—Two larval mayflies (University of Alberta

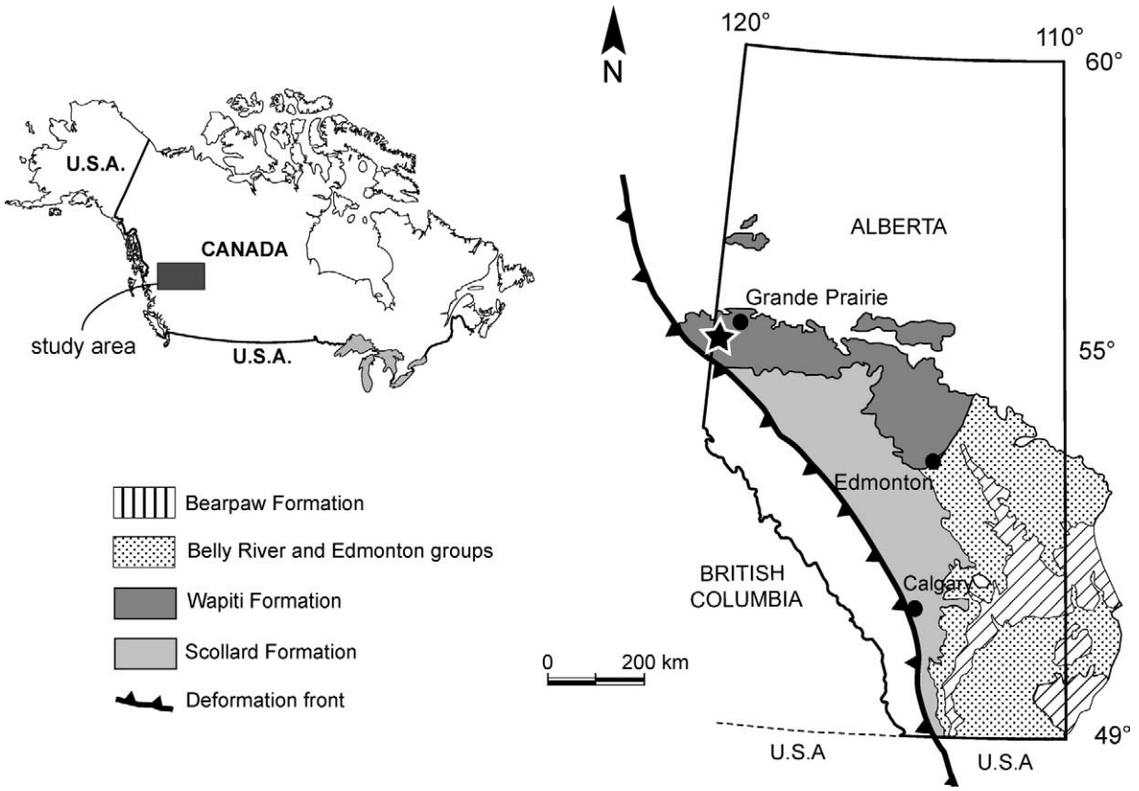

FIGURE *1*—Reference map of Alberta (Canada) showing the geographic extension of the Campanian-Maastrichtian Wapiti Formation and correlative deposits. UALVP 53483 was recovered approximately 1 km east of the Alberta-British Columbia border.

Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; UALVP 53483) were found as three-dimensional impressions in fine-grained sandstone exposed at Red Willow Falls on the Red Willow River, near the Alberta-British Columbia border (Fig. 1). Both specimens were preserved on the same bedding plane, one in much greater detail than the other. The best-preserved larva measures 15 mm long excluding the cerci, which are incompletely preserved (see following description).

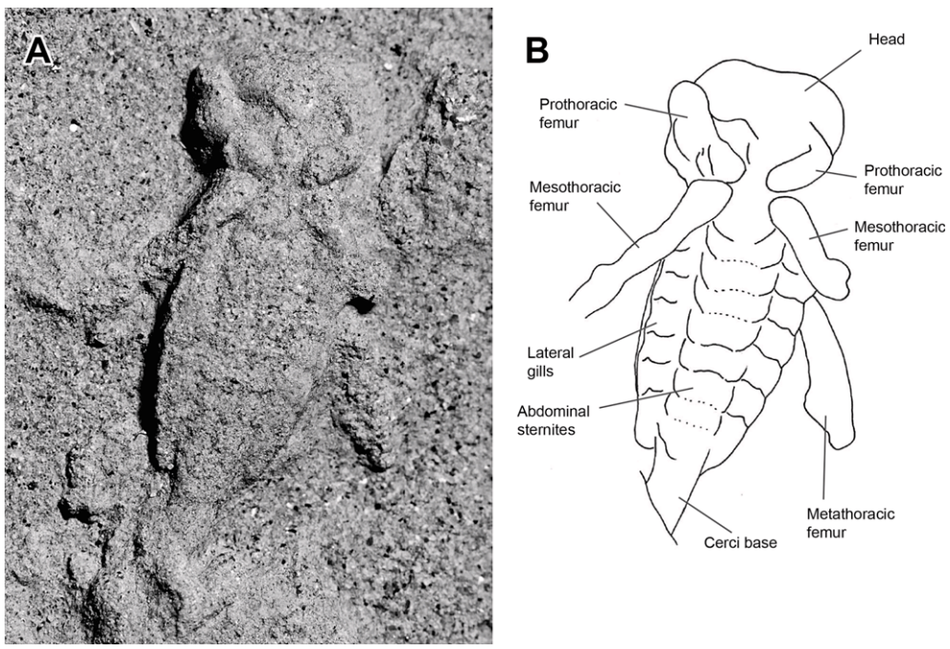

FIGURE *2*—Fossil mayfly (cf. Heptageniidae) from the late Campanian Wapiti Formation, UALVP 53483: *1, 2,* late-instar larva in ventral view.

FIGURE 3—Geographic and temporal distribution of Heptageniid fossils. Data sources explained in text.

From their sizes, it is assumed that they were well developed, late-instar individuals.

The head is large, elliptical, and wider than long, although no details of the eyes or cephalic anatomy could be discerned.

On both specimens, impressions of four prominent legs form an X-shaped arrangement, centered on the thorax. These are likely the pro- and mesothoracic legs, since the better-preserved specimen also possesses a leg impression that appears to extend from behind the abdominal gills, in the usual position for the metathoracic femur. The prothoracic legs extend anterolaterally, whereas the meso- and metathoracic legs extend posterolaterally. All legs are present as indistinct impressions, and all leg impressions are interpreted here as representing femora, although the bases of some tibiae may be present as well. The coxal bases of the pro- and mesothoracic legs lie close to one another on each side, but are well separated from those on the opposite side of the thorax. The arrangement of the legs, as well as the absence of discernible wing pads, all suggest that the fossil preserves the ventral aspect of these larvae. Setae on the legs, and other fine details, are not preserved.

The abdomen is relatively short and broad, less than twice as long as it is wide, and clearly divided longitudinally into a central, segmented region (which we interpret as the abdominal sternites), bordered by two lateral, segmented regions (which we interpret as platelike gills). There are at least eight abdominal segments. The largest individual abdominal segments (sternite plus lateral gills) are up to 1 mm long and 5 mm wide, and the lateral margins are gently convex. There appear to be seven pairs of gills. Only the indistinct bases of the cerci are preserved, and therefore it cannot be determined how many cerci were present.

The condition of these fossils does not allow certain identification but the combination of broad head, robust legs, prominent laterally directed gills, relatively large size, and overall body shape all suggest assignment to the family Heptageniidae.

DISCUSSION

Sinishenkova (2000) noted significant differences in Ephemeroptera diversity between the Late Cretaceous New Jersey (Australiphemeridae, Ametropodidae, Heptageniidae, Polymitarcyidae) and Taymyr (Baetidae Leach, 1815, Palaeoanthidae Kluge, 1993, Siphlonuridae Ulmer, 1920 [1888]) amber deposits, citing zoogeographic differences. The presence of heptageniids in the latest Campanian of Canada is consistent with the evolution and biogeography of this group; the oldest record of heptageniids being from the Turonian of New Jersey (Fig. 3), represented by imago adults of *Amerogenia* Sinitshenkova, 2000. The Wapiti heptageniids also help fill a significant temporal gap in the distribution of Heptageniidae prior to their 'reappearance' in the Eocene of Europe (Kluge, 1986, 1993) and the United States (Lewis and Wehr, 1993).

Present-day heptageniids are widespread across North America, Europe, Africa, and Asia (Webb and McCafferty, 2008) where they principally inhabit streams with abundant firm substrates (such as cobbles, logs, sub-emerged vegetation, and leaf packs), although lacustrine species also exist (Masselot and Nel, 1999). However, lotic and lentic larvae are extremely rare in fossil localities owing to their relatively soft body parts in high-energy paleoenvironments that are not conducive to soft-tissue preservation. Adult (imago and subimago) heptageniids are better represented in Cretaceous and Paleogene amber deposits although they have yet to be identified from Late Cretaceous Canadian insect-bearing amber localities (McKellar et al., 2008; McKellar and Wolfe, 2010; McKellar and Engel, 2011). It is also important to note the stark contrast in preservational environments between the Canadian amber deposits (salt marsh, lagoon, and near-shore swamp; McKellar and Wolfe, 2010) and the lotic environment represented by the Wapiti heptageniid locality reported here. Sinishenkova (2000) suggested that Turonian mayflies (including Heptageniidae)

from New Jersey inhabited a large backwater river although most modern heptageniids are strongly rheophylic, preferring fast moving waters. In the fossil record, mayflies are commonly recovered in amber or lacustrine deposits, with isolated cases referred to fluvial settings and forested backswamps (Mitchell and Wighton, 1979). The discovery of heptageniids in freshwater rivers of the Wapiti Formation underscores the problem of taphonomic biases in the fossil record although their presence in high-latitude (65°N; Fanti and Miyashita, 2009) freshwater ecosystems is consistent, both ecologically and geographically, with known fossil and extant heptageniid distribution.

As part of the drift, mayfly larvae are also important prey to drift-feeding fishes, such as extant salmonids. To date, only rare holostean and esocoid fishes have been identified from unit three of the Wapiti Formation (Fanti and Miyashita, 2009); however, there is little doubt that the Wapiti heptageniids were significant components of the food chain and were far more common and diverse—not only in the Wapiti Formation, but in other contemporaneous fluvially dominated Late Cretaceous formations—than their fossils suggest.

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