New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada and Washington State, USA)¹

S. Bruce Archibald

Abstract: Six new species of the extinct family Dinopanorpidae (Mecoptera) are described in the new genus **Dinokanaga** gen. nov. from five Early (and early Middle?) Eocene Okanagan Highlands localities in British Columbia and Washington State. These are **Dinokanaga hillsi** sp. nov., **D. wilsoni** sp. nov., **D. dowsonae** sp. nov., **D. andersoni** sp. nov., **D. sternbergi** sp. nov., and **D. webbi** sp. nov. The family Dinopanorpidae is previously known only from a hind wing of **Dinopanorpa megarche** Cockerell, and an undescribed species of **Dinopanorpa**, both from the Paleogene of Primorye (Maritime Province) in Pacific coastal far-eastern Russia. The family includes mostly large species, with forewings up to 43 mm in length. Dinopanorpidae is particularly distinguished by a long R₁ vein in both the fore- and hind wings, extending almost to the wing apex and bending posteriad distally. Their wings are mostly dark with light bands and spots; have many to extremely dense crossveins; and an expanded costal space in the basal quarter of the forewing, which is more developed in larger species. The rostrum is extended; the medigynium is without tongue-shaped structures.

Résumé: Six nouvelles espèces de la famille disparue des Dinopanorpidae (Mecoptera) sont décrites dans le nouveau genre *Dinokanaga* gen. nov.; elles proviennent de cinq localités dans les terres hautes de l'Oganagan en Colombie-Britannique et dans l'État de Washington et elles datent de l'Éocène précoce (et moyen précoce?). Ces novelles espèces sont: *Dinokanaga hillsi* sp. nov., *D. wilsoni* sp. nov., *D. dowsonae* sp. nov., *D. andersoni* sp. nov., *D. sternbergi* sp. nov. et *D. webbi* sp. nov. La famille des Dinopanorpidae était connue antérieurement seulement à partir d'une aile arrière de *Dinopanorpa megarche* Cockerell et d'une espèce non décrite de *Dinapanorpa*, les deux provenant du Paléogène de Primorye (une province maritime) sur la côte du Pacifique dans l'extrême est de la Russie. La famille comprend surtout de grandes espèces, les ailes antérieures pouvant atteindre une longueur de 43 mm. Les Dinopanorpidae se distinguent surtout par une longue veine R₁ dans les ailes antérieures et postérieures, s'étendant presque jusqu'au sommet de l'aile et pliant vers l'arrière distal. Leurs ailes sont surtout foncées avec des bandes et des taches pâles; elles ont des veines transversales de nombreuses à très denses et un espace costal dans le quart basal de l'aile antérieure, laquelle est plus développée dans les espèces plus grandes. Le rostre est étendu; le médigynium ne présente pas de structure en forme de langue.

[Traduit par la Rédaction]

Introduction

In recent years, a number of fossils of a large, enigmatic insect group have been recovered from five localities of the Eocene Okanagan Highland deposits of southern British Columbia, Canada, and northern Washington State, USA (Fig. 1). Close examination of well-preserved specimens reveals these insects to be mecopterans, a determination made certain by the presence of an extended rostrum in combination with the following wing characters: four wings, similar in size and shape; Sc not extending the to apex; one branch of Rs from R; CuA simple (Penny 1975).

Within this order, the wings of these new insects bear a distinctive character state, an extended R_1 that almost reaches the wing apex, bending posteriad to reach the margin. This form of R_1 has heretofore been found only in the extinct *Dinopanorpa megarche* Cockerell, 1924 (Figs. 2, 3F). Carpenter (1972, p. 86) found this to be "unique in the known Mecoptera, extinct and Recent, as noted by Cockerell [1924]; in other members of the order, R_1 is much shorter and is curved anteriorly at its termination". *Dinopanorpa megarche* is known only from a hind wing collected by A. Kuznetzov at the Late Eocene – Early Oligocene (but see later in the text) locality of the Khutsin Formation on the

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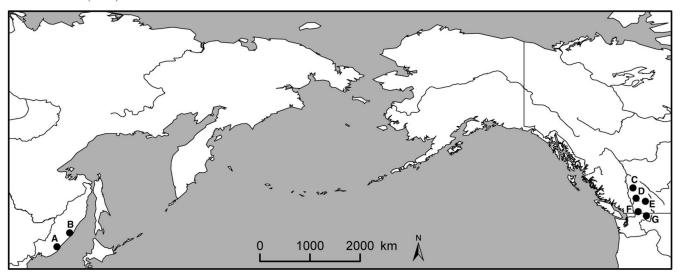
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Fig. 1. Map of localities containing Dinopanorpidae (A–B) Primorye, Russia; (C–G) Okanagan Highlands, British Columbia, Canada and Washington State, USA. (A), Zerkalnaya; (B), Amgu; (C), Horsefly; (D), McAbee; (E), Falkland; (F), Whipsaw Creek; (G), Republic. For a larger scale map of the Okanagan Highlands, and location of other Okanagan Highlands sites mentioned in the text, see Greenwood et al. (2005).

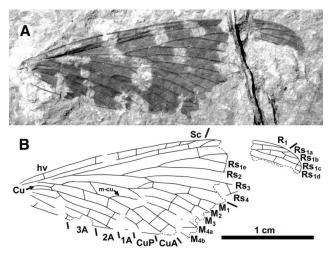


Kudya River, a tributary of the Amgu River (sometimes "Amugu" or "Amagu") in Primorye (Maritime Province) on the Pacific coast of Siberia (Rasnitsyn and Zherikhin 2002). This insect was described and placed in the family Panorpidae by Cockerell (1924, p. 2) stating simply that the venation "is nearly as in *Dinopanorpa megarche*...", except for the long, oblique first basal crossvein between M and Cu (m-cu) (Carpenter 1972: fig. 6, here seen to be the second basal crossvein between M and Cu, Fig. 2B), and the "remarkable" form of R₁. Carpenter (1931, p. 412) stated that this insect is "certainly not a member of the Panorpidae, and may not even be a scorpion-fly". Tillyard (1933) moved it to "Orthophlebiidae" (paraphyletic: Willmann 1987), through a combination of the five-branched M (although Tillyard mentioned this specifically as a forewing character state—the hind wings of orthophlebiids have a four-branched M (Willmann 1989)) with a pectinately branched Rs. Later, Martynova (1962) placed D. megarche in the genus Orthophlebia, extending its range from the Mesozoic into the Paleogene. She based this on Rs_{1+2} and Rs_{3+4} branched at almost the same distance from the wing-base, combined with Rs₁ having more than three branches.

Carpenter (1972) later erected the monotypic family Dinopanorpidae for this species, particularly noting the distinctive form of R_1 , together with the five-branched M of the hind wing (both of these characters evident in all complete specimens of the new species described here) and the long, oblique m-cu (not found in the new species). He stated the opinion that this family is close to both "Orthophlebiidae" and Panorpidae.

Zherikhin (1974, p. 216) published a "drawing from a photograph of the holotype" of "Orthophlebia" megarche Cockerell; this was presumably a production error, as this figure is of a trichopteran from the same locality that is discussed immediately following Dinopanorpa megarche in the text. In addition, Zherikhin (1978) reported (but did not figure) a new, undescribed species of Dinopanorpa from an

Fig. 2. *Dinopanorpa megarche* Holotype, NMNH69173: (A) photograph, (B) drawing. See section "Terms and abbreviation". (A, B) to scale.



outcrop of the Paleocene Tadushi Formation on the Zerkalnaya (also called Tadushi) River, also in Primorye, Russia.

The fossil insects described here constitute six new species in a new genus. Although these insects may be confidently associated with *Dinopanorpa* in Dinopanorpidae, they differ from the type genus *Dinopanorpa*, and thus Carpenter's (1972) diagnosis of the family. A revised diagnosis is presented to update the family concept in light of the new information presented by these specimens.

Materials and methods

The lacustrine shales within which these new specimens were preserved are composed of volcanogenic and organic matter, and at times (Horsefly, McAbee) diatoms or diatom-derived silica (Wilson 1993; Mustoe 2002; Wolfe and

Edlund in press). They are often thinly bedded and fine grained, usually splitting easily along even planes. The fossils were excavated with light hand tools, and some specimens were lightly prepared with an insect pin held in a pin-vise when required (or by similar tools at the respective institutions from which they were borrowed, and in some cases by their collectors). Most were examined and drawn at times while wetted with distilled water, although the matrix of some fossils (particularly some from Horsefly) precludes the use of water, which may degrade those specimens.

Drawings represent information taken from both part and counterpart, therefore, morphology may be present on the drawing that is not on the photograph of the part (e.g., Figs. 11A, 11B; 16A-16C). Dotted lines indicate faintly preserved veins and dashed lines indicate boundaries beyond which portions of the fossil are missing or obscured in all drawings, except Fig. 9E (see caption); there is no representation of hypothesized missing morphology. The dense net of crossvenation is only drawn where it may be rendered with precision; these crossveins may be seen on specimens (e.g., D. hillsi) to grade from distinctiveness in the anterior portion of the wing to a weak "quilting" in the apical midwing (Figs. 5B, 5C). Surprisingly, in some cases these crossveins may be more easily seen in the photograph than can be drawn under the microscope. Wings are drawn both with and without crossveins, so as not to obscure morphology of the main veins. All wing images are represented in standard aspect (apex to the right).

Terms and abbreviations

Venational terminology used is as in Carpenter (1992); abbreviations used are hv, humeral vein; C, costa; Sc, subcosta; R, radius; Rs, radial sector; M, media; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; A, anal vein; m-cu, second basal crossvein between the media and cubitus (*Dinopanorpa*). Institution abbreviations: BMNH, Burke Museum of Natural History and Culture, Seattle, Washington (USA); CDM, Courtenay and District Museum, Courtenay, British Columbia (Canada); ROM, Royal Ontario Museum, Toronto, Ontario (Canada); RTM, Royal Tyrrell Museum, Drumheller, Alberta (Canada); SRIC, Stonerose Interpretive Center, Republic, Washington (USA); UA, University of Alberta, Edmonton, Alberta (Canada); UCC, University College of the Cariboo, Kamloops, British Columbia (Canada); UW, University of Washington, Seattle, Washington (USA).

Localities

The fossils described here were found in lacustrine shales of five localities in the Eocene Okanagan Highlands series that range through about 450 km from northernmost Washington State, USA, to the central Cariboo region of British Columbia, Canada (see map, Fig. 1, and fig. 1 in Greenwood et al. this issue). The Okanagan Highlands series as a whole stretch about 1000 kilometres from Republic to Driftwood Canyon, near the town of Smithers in west-central British Columbia (see other papers, this issue).

Localities include the following:

(1) The town of Republic, Ferry County, in northeastern Washington: Tom Thumb Tuff Member of the Klondike

- Mountain Formation; UW–BMNH localities A0307, A0307B, B4131; 49.42 ± 0.54 Ma (Wolfe et al. 2003), Early Eocene (Ypresian).
- (2) Whipsaw Creek, British Columbia: an exposure of the Vermillion Bluffs Shale Unit of the Allenby Formation (Princeton Group) on Highway 3 about 10 km south of the town of Princeton. The Vermillion Bluffs Shale Unit exposure at the Hospital Hill locality is dated Early Eocene (52.08 ± 0.12 Ma by preliminary U-Pb zircon ages by Mortensen and Archibald, work in progress), indicating an Early Eocene age for Whipsaw Creek, although an early Middle Eocene age cannot be ruled out for this exposure, pending further results.
- (3) The McAbee locality: an exposure of shales of an unnamed formation of the Kamloops Group near Cache Creek, in the Thompson–Okanagan region of south-central British Columbia; ~51 Ma, Early Eocene (Ewing 1981).
- (4) Falkland, in the Columbia–Shuswap region of south-central British Columbia: unnamed sediments of the Kamloops Group; 50.61 ± 0.16 Ma (preliminary U–Pb zircon ages by Mortensen and Archibald, work in progress), Early Eocene.
- (5) Horsefly River, in the Cariboo region of south-central British Columbia, unnamed shale beds of unnamed regional sediments and volcanics. This locality is Horsefly 2 of Greenwood et al. (2005) and Moss et al. (2005), and matches descriptions of UA locality H2 (= ROM locality L88). A radiometric age has not been given for the Horsefly beds, although it is considered coeval with other fossiliferous shales of the Okanagan Highlands; therefore, here it is considered Early (or possibly early Middle) Eocene pending radiometric dating in progress (Mortensen and Archibald, current research).

These five sites represent an upland region with mean annual temperatures of about 9–10 °C as determined by leaf margin analysis or about 13–14 °C by bioclimatic analysis (nearest living relatives of flora), yet mild winters with few if any freezing days, in which the hypothesized antecedent of the eastern North America deciduous forests grew (Greenwood et al. 2005). Further locality descriptions and detailed discussion of paleoecology and paleoclimate are found in Greenwood et al. (2005) and Moss et al. (this issue).

Twenty-two specimens were examined. Of these, ten are assigned to one species, five (and two further tentatively) to one species, and one is too fragmentary to determine below genus level. The remaining four specimens represent four species. This specimen species-count indicates both high species richness and the likelihood of new species being uncovered in ongoing fieldwork. The Republic locality has three species, McAbee two, Horsefly River two, Whipsaw Creek one, and Falkland one. The locality species-count seems to mostly reflect the collecting intensity that has been curated in museum collections. Republic, and then McAbee, have had by far the most such collecting; at the other extreme, very little collecting has been done at the Falkland locality. Fossil insects from Whipsaw Creek and the locally surrounding area have been reported and described since Scudder (1879), yet this has likely been the result of comparatively little fieldwork. Although the Okanagan Highlands Driftwood Canyon locality has been steadily collected for many decades,

no specimens of this family are known from this locality; relatively few of the insects from this site have been accessioned into museum collections. The Quilchena locality, however, does seem anomalous: it has been steadily collected for ~30 years for a research collection (R. Mathewes, personal communication, 2003), yet no dinopanorpid has yet been recovered there, in spite of a rich insect fossil record (Archibald and Mathewes 2000). Quilchena differs from these other sites in that it is inferred to have had the warmest mean annual temperature (Mathewes 2003; Greenwood et al. 2005).

How close in age are the Russian localities (Fig. 1) containing Dinopanorpidae to the Okanagan Highlands? Based on floral and insect assemblages, Zherikhin (1998) determined an age for the Amgu locality similar to that of the shales at Florissant, Colorado (referred to as early Oligocene, now determined to be Late Eocene), and to the Bembridge Marls of the Isle of Wight (also see Dlussky and Rasnitsyn 2002). The Amgu insect assemblage that Zherikhin (1998) cited as similar to Florissant includes bruchid seed weevils (Chrysomelidae: Pachymerinae), dolichoderine ants, and unnamed common genera. Bruchids are now known from Early Eocene Quilchena (Archibald and Mathewes 2000) and other Okanagan Highlands localities (current research); dolichoderine ants have been discovered in the Okanagan Highlands Hat Creek amber, ~30 km east of McAbee (Poinar et al. 1999). Further, the Amgu locality is notable for its rich Bibionidae (Diptera) assemblage, with six species named of Plecia and Penthetria (although Zherikhin expressed the opinion that they may be over-split). Twenty-two species in these two genera have been named from the Okanagan Highlands (Rice 1959). Increasing numbers of insect taxa are found in common between Florissant and the Okanagan Highlands, in cases extending their range some 18 Ma or so. The Bembridge Marls are considered quite close to Florissant in age, somewhere near the Eocene-Oligocene boundary (Rasnitsyn and Zherikhin 2002) and Late Eocene (Priabonian) by Jarzembowski (1999) based on comparative insect assemblage. Although a Late Eocene age remains a possibility for the Amgu locality, an age closer to, or even coeval with the Early – early Middle Eocene Okanagan Highlands is also consistent with these insect data. Floral assemblages, however, are not compared here, and may indicate otherwise.

The undescribed species of *Dinopanorpa* mentioned by Zherikhin (1978) is from the Paleocene Tadushi Formation exposure on the Zerkalnaya (Tadushi) River in Primorye. This locality is possibly Thanetian (Rasnitsyn and Zherikhin 2002), if so, indicating about 4–8 million years between Zerkalnaya and Okanagan Highland times, e.g., McAbee (~51 Ma)

Patterns of the distributions of mammals (Beard and Dawson 1999; Bowen et al. 2002) and plants (Tiffney and Manchester 2001) suggest dispersal between East Asia and North America across the Bering Land Bridge, which connected these continents in the Eocene.

Systematic paleontology

Family Dinopanorpidae Carpenter, 1972 (revised)

Dinopanorpidae Carpenter, 1972, p. 83.

DIAGNOSIS: May be distinguished from all other Mecoptera by R_1 long, bending posteriad distally, extending almost to apex.

DESCRIPTION:

Head: Rostrum elongate.

Forewing: Costal space narrow basal-most then broadening (C bowed out) near humeral vein in basal quarter, tapering apicad to termination; Sc, R₁ slightly or strongly curving together opposite to outward bow of C basally, increasing costal space; R₁ long, extending almost to apex, curving posteriad near termination; Rs with 5–8 branches; M fivebranched; Cu free at base; CuA joins M for short distance; CuP bends towards and almost joins with 1A; 1A long, ending after first branch of Rs; light maculations on predominantly dark wing membrane; crossveins numerous.

Hind wing: As forewing, except: costal space narrower in basal quarter (C not bowed out, Sc not bowed in).

Dinokanaga gen. nov.

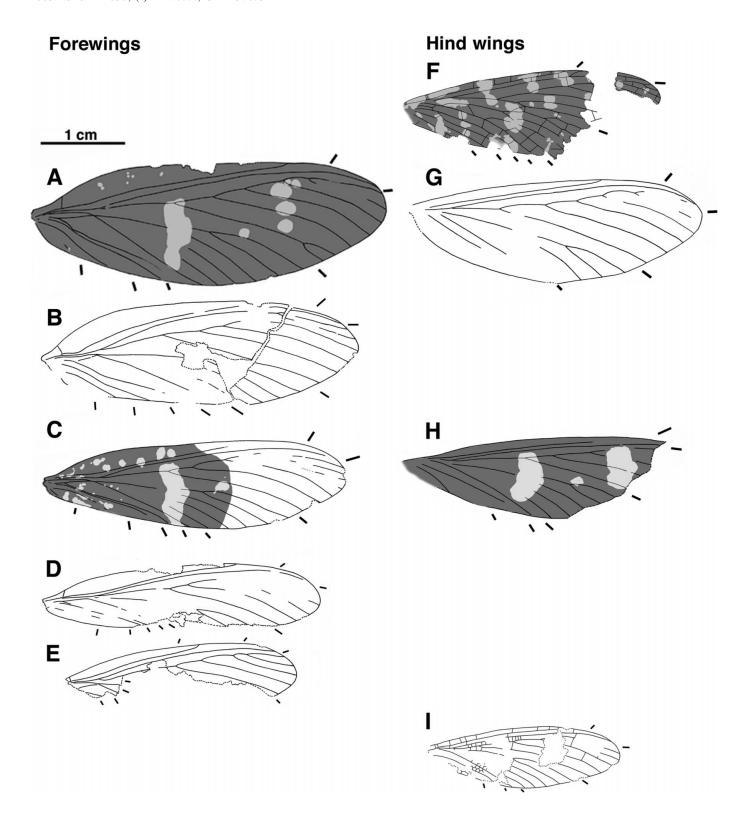
TYPE SPECIES: D. hillsi sp. nov.

DIAGNOSIS: Wings of *Dinokanaga* may be easily distinguished from those of *Dinopanorpa* by the following character states: (1) crossveins mostly developed to fine, dense reticulate venation throughout most of wing in larger species, in smaller species large numbers of simple crossveins in parts of wing, branching to reticulate in other areas; (2) 5–7 branches of Rs; (3) pectinate branching of Rs₃, Rs₄ (*Dinopanorpa*: joined as Rs₃₊₄ for distance); (4) joining of M + CuA extremely brief (\leq 0.5 mm) or only touching; (5) M straight or almost through brief joining with CuA; (6) 1A straight or gently curved, not bent sharply by crossveins near base; (7) no strong, oblique, m-cu crossvein; area filled with densely reticulate crossvenation; (8) colouration (see detailed description of *Dinokanaga* colouration in the following text, vs. *Dinopanorpa* colouration in Figs. 2, 3F).

DESCRIPTION:

Forewing: Length 28-43 mm, width (7?) 8-14 mm; C bowed outward in basal quarter (amount varying among spp.), costal region wide at base; humeral vein crossvein-like; Sc unbranched, joining C in apical half to third quarter (most spp.), bowed inward basally; R₁, Rs fork in basal quarter of wing, R₁ long, extending almost to, curving posteriad near, apex; Rs pectinately branched 5-7 times, apicalmost 2-3 often weak; M five-branched; Cu free at base; CuA joining, immediately separating from M or for ≤0.5 mm, then almost straight to posterior margin; CuP curving toward 1A, perhaps (poor preservation) touching in some spp.; anal veins subparallel, straight or gently sigmoid; crossveins numerous, extremely developed, branched, reticulate, throughout wing, particularly in larger species (well-preserved specimens), well developed in costal region, in smaller species many simple crossveins, some branching to reticulate. Membrane dark, with colouration organized as light fascia across width at ~1st branch of Rs; light spot near branching of M₁, M₂;

Fig. 3. Comparison of wings of Dinopanorpidae. Colour patterning, where preserved, simplified as two shades, darker and lighter grey. Wings aligned horizontally within columns to forking of Rs, R₁. All to scale. (A–E) forewings; (F–I) hind wings. (A) *Dinokanaga hillsi*, UCCIPR L-18 F-1036; (B) *D. wilsoni*, UAFIC5004; (C) *D. dowsonae*, 2003.2.5 CDM 030; (D) *D. andersoni*, SR01-06-01; (E) *D. sternbergi*, UWBM95361; (F) *Dinopanorpa megarche*, (G) *Dinokanaga hillsi*, UCCIPR L-18 F-1037/8; (H) *D. dowsonae*, 2003.2.5 CDM 030; (I) *D. webbi*, UAFIC7075.



2nd fascia or row of 3 spots at ~4th branch; few scattered small light spots, particularly in basal area, costal region.

Hind wing: As in diagnosis, forewing, but: length, width several mm smaller than forewing when associated; smallest species (*D. webbi*) length 24 mm, width 8 mm; C not bowed basally, rather straight to near apex; costal space narrower than forewing.

DISTRIBUTION AND AGE: Okanagan Highlands sediments of British Columbia (Canada): McAbee, Early Eocene; Whipsaw Creek, Early (or early Middle?) Eocene; Falkland, Early Eocene; and Horsefly River, Early (or early Middle?) Eocene; and Washington State (USA): Republic, Early Eocene.

INCLUDED SPECIES: (1) *D. hillsi* sp. nov. (type species), McAbee, British Columbia, Early Eocene; (2) *D. wilsoni* sp. nov., Whipsaw Creek, British Columbia, Early (or early Middle) Eocene; (3) *D. dowsonae* sp. nov., Horsefly, Falkland, British Columbia, Early Eocene; McAbee, British Columbia, Early Eocene; Republic, Washington, Early Eocene; (4) *D. andersoni* sp. nov., Republic, Washington, Early Eocene; (5) *D. sternbergi* sp. nov., Republic, Washington, Early Eocene; (6) *D. webbi* sp. nov., Horsefly River, British Columbia, Early (or early Middle) Eocene.

ETYMOLOGY: From the Greek *deino* ("terrible, monstrous") referring to the large size of dinosaurs, as well as to Dinopanorpidae; and the suffix — *okanaga*, alluding to the Okanagan Highlands. Gender: feminine.

DISCUSSION: The wings of Mecoptera may show considerable intra-specific variation in size, and details of venation (Ohm 1961; Willmann 1989). It is possible that some of the wing character states listed later in the text may be found to be intra-specific variation when larger numbers of specimens are known. For example, see variation in branches of Rs within *D. hillsi* and of size in *D. dowsonae*. Wing venation is similar throughout this genus, yet the range of wing morphology throughout the sample (Fig. 3) reasonably precludes lumping into fewer species. As all specimens were collected fairly recently, mostly within the last decade, and fieldwork is ongoing, undoubtedly greater numbers of specimens recovered in the future will either provide support for these species, as defined here, or suggest revisions.

The general colour patterning appears consistent in all well-preserved specimens of the genus (but see finer scale differences among species later in the text). Particularly exceptional preservation of a specimen of *D. dowsonae* (2003.2.6 CDM 030, Fig. 10D) allows fine-level examination of colouration. Although hue is not preserved in any of these fossils, colour value, preserved in gradation on this specimen, as well as the sharply defined light fascia and spots present on most other wings, indicates a greater complexity of colouration, at least in this species. It is possible that in other cases, diagenetic processes allowed only for preservation of high contrast patterns.

The multiple specimens examined of *Dinokanaga hillsi* show that not only are veins faintly preserved within light spots and fascia, but also in some cases, the matrix does not separate from light regions cleanly when splitting, adhering to these areas, leaving a coating of rock over the light por-

tion. In specimens of other species, where colouration is not ("overtly") preserved, there are regions where the matrix has similarly adhered to the wing; these regions are precisely where a light spot or fascia might be expected (e.g., *D. dowsonae*, Fig. 12; *D. sternbergi*, Fig. 18).

The number of crossveins in *Dinokanaga* is developed to a great degree, even in smaller species, and to a surprising degree in larger species. In these, they form a dense reticulation of veinlets seen throughout much of the wing (crossveins numerous and simple in remaining portions) in well-preserved (many) specimens, and visible in at least some regions, usually the costal space, even in those more poorly preserved. They create a fine net of polygons throughout broader areas between veins in the wings, particularly in larger species. In smaller species, crossveins may form a series of pentagonal cells in some areas, separated by a zig-zag series of crossvein elements. In both large and small wings of this genus, these are expressed as large numbers of simple crossveins between close, subparallel main veins, e.g., Sc and R₁.

The extensive reticulation of veins in this genus is fundamentally different than that seen in some other Mecoptera, such as the extant *Merope* Newman, 1838 and *Austromerope* Killington, 1933 (both Meropeidae), and *Notiothauma* MacLachlan, 1877 and the Eocene *Eomerope* Cockerell, 1909 (both Eomeropidae). There, although crossvein development forms reticulation in some areas, i.e., the costal space, in general it is the branching of the main veins (e.g., Rs may have up to 19 branches, and M is about 10-branched in *Notiothauma* (Willmann 1981)), which may be extensively zig-zagged by the many simple crossveins between them that together form the venational reticulation; in *Dinokanaga*, the main veins play no role in this.

Austromerope, Merope, and Notiothauma live a cockroach-like existence on the forest floor, and their extensive venation (along with heavier sclerotization) may strengthen and protect wings from damage as they crawl amongst detritus and into tight spaces under logs and rocks (Penny 1975). A similar life for Dinokanaga would be consistent with this morphology, primarily amongst leaf litter and underbrush in the Eocene forests of the Okanagan Highlands. If this were so, then we would expect to see a particular strengthening of the expanded costal region in larger forewings (D. hillsi and D. wilsoni), as these areas would presumably bear the brunt of impact (protruding "shoulder-like"), when moving through debris with wings folded. In these wings, the crossvenation in this region is indeed stronger.

Dinokanaga hillsi sp. nov.

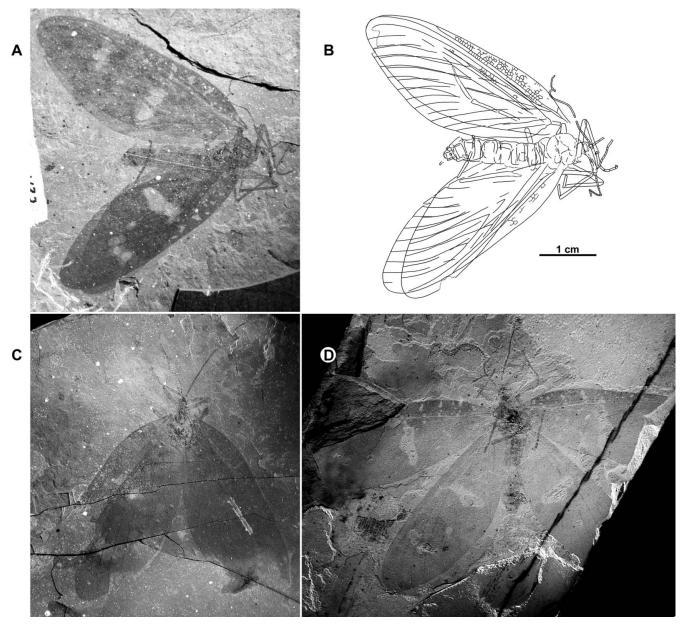
(Figs. 3A, 4–8)

DIAGNOSIS: Wings distinguished from all other *Dinokanaga* species by a combination of wide, subtriangular shape, widest at middle, with posterior margin curved deeply from base to apex, light colouration at ~4th branching of Rs as three distinct spots (Figs. 3A, 5C, 8A), completely separated, or just touching (spots convergent to form fascia where known in other species), and apical margin smoothly curved, not pointed.

DESCRIPTION:

Female: Body. Length 26 mm preserved (likely close to

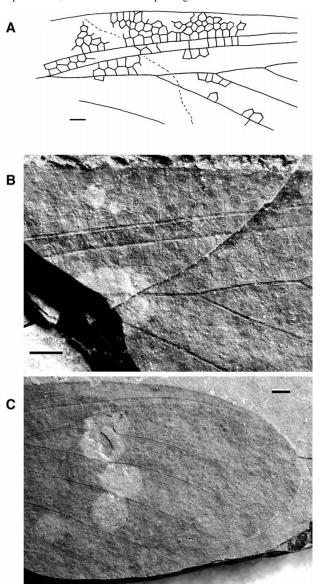
Fig. 4. Habitus of *Dinokanaga hillsi*, sp. nov. All to scale. (A) photograph of holotype TMP8339.1132; (B) drawing of holotype; (C) UWBM97365A; (D) UCCIPR L-18 F-1034.



life length); values of mid-dark brown throughout as preserved, presumably indicating sclerotization, not original colouration. **Head.** Extended rostrum (Figs. 6A, 6B); ovate compound eyes; ocelli not detected; antennae long, filiform (distalmost portion missing in all examined specimens). **Thorax.** Poorly preserved, posterior portion obscured, length about 5–6 mm, apparently just over 5 mm greatest width (exaggerated as artefact?). **Legs.** (Figs. 6A–6D) Covered in short, no longer hairs, irregularly arranged (Fig. 6C); tibial spurs detected: hindleg, 2; foreleg, 1. Foreleg: basitarsus > 2 × length of other tarsomeres. **Abdomen.** Proximad of A4 rather obscured, A4–A8 roughly equally wide, ~4 mm (possibly slightly distorted post-mortem), T4–T8 rectangular, sub-equal in size; genitalia indistinctly preserved. Dark, circular structure on A9 is interpreted as the medigynium.

Forewing: Length: 39–43 mm (average 41 mm, n=4); maximum width: 13–14 mm (average 13 mm, n=5). Venation as for genus, except: C strongly bowed outward at base, humeral vein terminating apicad of right angle to C; Sc terminates at ~4th branch of Rs, gently curved anteriad to meet C; R₁ curved gently posteriad after termination of Sc; Rs 6–7 pectinately branched (one specimen: 1st again branched near margin); M straight or nearly to branching, only touching CuA; M₁, M₂ forked at middle wing length; Cu base free, close to 1A; CuA meets M, immediately separating, almost straight before touching M, sharply angled at M + CuA, then almost straight to margin near mid-wing; CuP (usually weakly preserved) immediately curves toward 1A, but does not actually join, then diverges away from 1A at low angle, follows 1A closely; 1A, 2A, 3A curved gently,

Fig. 5. Reticulate crossvenation in forewing of *Dinokanaga hillsi* (2003.2.7 CDM 031a, b): (A) Drawing from part and counterpart, mid-anterior region; (B) photograph of part, mid-anterior portion, crossveins visible in costal, subcostal areas, becoming less distinctly preserved posteriad, (C) photograph of part, weak crossvenation in apical half, visible as faint "quilting." Scale bars = 1 mm.



sigmoidally; crossveins numerous, weak, finely reticulate throughout, invariably well preserved in anterior region.

Hind wing: As forewing, but a few millimetres shorter, narrower than associated forewing (in three known articulated specimens) — length: 33-37 mm (average 36 mm, n = 5); maximum width: 11-13 mm (average 12 mm, n = 5); costal area not expanded basally; C rather straight until apical quarter.

TYPE MATERIAL: Holotype: TMP8339.1132 (part; counterpart) (Figs. 4A, 4B, 6A–6D, 7A, 7B), deposited in the RTM collection. McAbee beds, unnamed formation of the Kamloops Group, south-central British Columbia, Canada; Early

Eocene. Labelled: Holotype *Dinokanaga hillsi* Archibald. A well-preserved female, with all four wings (fore- and hind wings mostly overlapping), only slightly disarticulated. Collected by Len Hills in May-June 1984. Paratypes (All labelled: Paratype Dinokanaga hillsi Archibald): (1) UCCIPR L-18 F-1036, a well-preserved, almost complete forewing (part only), also from the McAbee; deposited in the UCC collection; collected by unknown visitor to the McAbee within the last few years, donated by David Langevin; (2) UWBM97365A (Figs. 4C, 8E), a mostly complete insect, but lacking the abdomen, collected by Rick Dillhoff at the McAbee, April 1996, deposited in the BMNH collection (part only in collection); (3) UCCIPR L-18 F-1034 (part), UCCIPR L-18 F-1035 (counterpart) (Figs. 4D, 8F), a faintly preserved specimen, entire body (undetermined sex due to preservation) and four wings; part: forewings, right hind wing missing apical quarter, left hind wing complete; counterpart: all four wings with apical quarter missing, abdomen missing; deposited in the UCC collection; collected at McAbee within the last few years, donated by David Langevin; (4) UWBM97366, three disarticulated wings in close association: UWBM97366.1 (Fig. 8C), a mostly complete, well-preserved, but somewhat laterally compressed, forewing; UWBM97366.2, a hind wing with the posterior region crumpled and apicalmost portion torn; UWBM97366.3, a forewing with the apical third missing, and somewhat deformed basal anterior region, collected by Rick Dillhoff at the McAbee, September 1999: deposited in the BMNH collection (part only in collection); (5) 2003.2.7 CDM 031a, b, a well-preserved forewing, part with mid-portion missing, counterpart with basal-most portion missing, collected by Rick Dillhoff at McAbee, July 1998, in the CDM collection (Fig. 5); (6) UCCIPR L-18 F-1039/40 (part, counterpart), A mostly well-preserved but bent hind wing; deposited in the UCC collection; collected at McAbee within the last few years, donated by David Langevin.

SUPPLEMENTARY MATERIAL: UCCIPR L-18 F-1037 (part), UCCIPR L-18 F-1038 (counterpart), a faintly preserved hind wing (Fig. 8G); 2003.2.2 CDM 026 (part only) (likely) forewing, well preserved, but missing basal quarter. All from McAbee, Early Eocene.

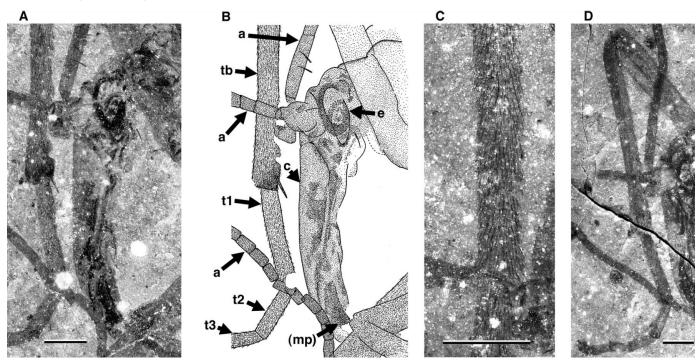
DISTRIBUTION AND AGE: McAbee, British Columbia; Early Eocene.

ETYMOLOGY: The specific epithet is from the surname of Len Hills, paleontologist at the University of Calgary, in honour of his work in the Eocene of British Columbia, including his pioneering work at the McAbee site.

DISCUSSION: The large number of specimens of *D. hillsi* provides an opportunity to gauge intra-specific morphological plasticity of wings. A six-branched Rs is clear in some specimens (e.g., 2003.2.2 CDM 026), seven-branched in others (e.g., 2003.2.7 CDM 031). UCCIPR L-18 F-1036 is unusual in that the first branch again branches near the margin, an individual oddity.

There are more specimens of this species known than of any other Dinopanorpidae. They are not common, but are found periodically at the McAbee locality.

Fig. 6. Head and leg of *Dinokanaga hillsi* (holotype). Scale bars = 1 mm. (A, B) to scale; (A–C) part, (D), counterpart (counterpart image reversed). (A) head and partial foreleg (all leg images same foreleg); (B) drawing of (A) — a, antenna; c, clypeus; e, eye; (mp), position of mouthparts, not clearly preserved here; t1, first tarsomere; t2, second tarsomere; t3, third tarsomere; tb, tibia; (C) detail of hairs of foreleg; (D) foreleg.



Dinokanaga wilsoni sp. nov. (Figs. 3B, 9)

DIAGNOSIS: Forewing distinguished from all other *Dinokanaga* by apex slightly or almost pointed, not gently rounded; from all *Dinokanaga* spp. but *D. hillsi* by wing widest in middle. Distinguished from *D. hillsi* (Fig. 9E) by anterior, posterior margins rather parallel through middle third; elongate-oval, not subtriangular as in *D. hillsi* (see "Discussion"); CuA and M each with shallower angle to margin distad to separation (M almost on mid-line of wing).

DESCRIPTION:

Forewing: Length 38 mm, maximum width 13 mm; membrane dark with light maculation, pattern not discernable by poor preservation; wing widens sharply at base (anterior and posterior margins), C bowed strongly basally, Sc strongly curved away from bow of C, increasing costal area near base; termination not preserved, apparently ~2/3 wing length; humeral vein terminating at right angle to C; R₁ space wide; Rs branched six times; M in mid-point of wing width until 1/2 wing length, in straight line, hardly bent at M + CuA; stem of Cu not preserved; CuP not preserved (poorly preserved region, presumed weak); anal veins sub-parallel, 1A, 2A angled slightly apicad at ~1/2 length.

Hind wing: Little known (small portions preserved).

TYPE MATERIAL: Holotype: UAFIC5004a, b (part and counterpart) (Figs. 3B, 9); deposited in the UA fossil insect collection. Labelled: Holotype *Dinokanaga wilsoni* Archibald. A poorly preserved body with a well-preserved forewing, but

small portions in the centre of the wing missing (more missing on part than counterpart) and portions of the other four wings. Collected by Mark Wilson, 1975.

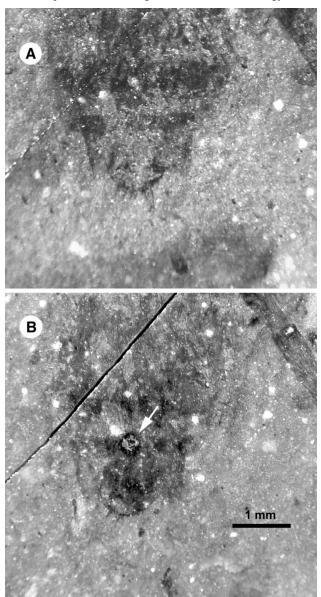
DISTRIBUTION AND AGE: Whipsaw Creek, British Columbia; Early or early Middle Eocene.

ETYMOLOGY: The specific epithet is from the surname of Mark Wilson, a paleontologist at the University of Alberta, in honour of his extensive work in the Eocene Okanagan Highlands, including the first broad, regional studies of its insect fauna (e.g., Wilson 1977).

DISCUSSION: The shape of the forewing of the only known specimen of D. wilsoni (hind wing incomplete and poorly preserved) is distinct from all known specimens of D. hillsi where the margin is preserved (Fig. 9E). Both species have wide wings, widest in the middle, rather than more apicad as in other species of the genus. However, in the forewing of D. wilsoni, the anterior and posterior margins are closer to equal width throughout the middle third (the overall shape is elongate-oval); in D. hillsi, the wing is widest at the midpoint, formed by a deeply curving posterior margin (the overall shape is subtriangular). The holotype of D. hillsi (TMP8339.1132) and paratype 1 (UCCIPR L-18 F-1036) are the only specimens with comparable forewings, as these have complete and undistorted margins. The posterior margin is not preserved in D. hillsi paratype 5 (2003.2.7CDM031, Fig. 8D: note dashed line), and paratype 4 (UWBM97366.1) is somewhat distorted due to compression (note internal breakage lines Fig. 8C); both are unsuitable for comparison.

The differing shape of the forewing results in differences

Fig. 7. *Dinokanaga hillsi*, sp. nov., photographs female abdominal terminalia, holotype TMP8339.1132. Both to scale. (A) part; (B) counterpart, reversed image. Arrow indicates medigynium.



in vein angles, most distinctively of CuA and M distad to their separation. When images of the forewings are aligned (see caption Fig. 8E) (including *D. hillsi* paratype 5, as it is in this case comparable: Fig 8D), these veins curve toward the posterior margin at a distinctly steeper angle in *D. hillsi*.

Further, the humeral vein joins C at a right angle, not at an oblique angle, as it does consistently in all known specimens of *D. hillsi* (Figs. 8B, 8E, 9B), although this may be an individual characteristic of the only specimen of *D. wilsoni* known.

Dinokanaga dowsonae sp. nov. (Figs. 3C, 10–16)

DIAGNOSIS: May be separated from forewings of other Dinokanaga: from D. hillsi and D. wilsoni by penniform

Fig. 8. Wings of *Dinokanaga hillsi* sp. nov. (drawings omit crossveins). (A) photograph of paratype UCCIPR L-18 F-1036 forewing; (B) drawing of paratype UCCIPR L-18 F-1036 forewing; (C) UWBM97366.1, forewing; (D) 2003.2.7 CDM 031 (a, b combined), forewing; (E) left forewing of UWBM97365A; (F) right hind wing of UCCIPR L-18 F-1034/5 (combined); (G) UCCIPR L-18 F-1037/8, hind wing. See section "Terms and abbreviation".

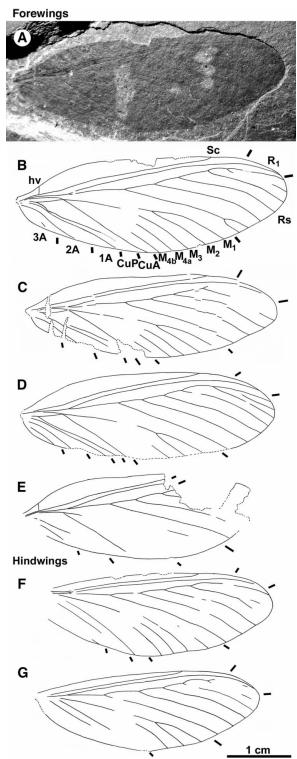


Fig. 9. Dinokanaga wilsoni, sp. nov. UAFIC5004a, b. (A–D) to scale. (A) photograph of forewing of UAFIC5004b; (B) drawing of forewing of UAFIC5004b (crossveins omitted); (C) drawing of crossveins apparent in anterior portion of forewing (part and counterpart combined); (D) habitus photograph of UAFIC5004a; (E) Shape comparison of *D. wilsoni* holotype (shown as dotted lines) and *D. hillsi* holotype TMP8339.1132, UCCIPR L-18 F-1036, 2003.2.7 CDM 031 (solid lines: dashed lines indicating missing margin regions in Fig. 8 omitted, e.g., hind margin area of 2003.2.7 CDM 031); sizes altered to compare shape, not to any scale. a, preserved portion of M from separation with CuA, *D. hillsi*; b, preserved portion of M from separation with CuA, *D. wilsoni*; c, CuA from joining with M, *D. hillsi*; e, hind margin of *D. wilsoni* (see text for explanation). See section "Terms and abbreviation".

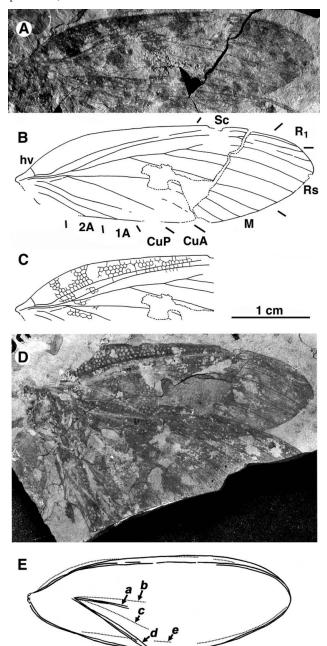
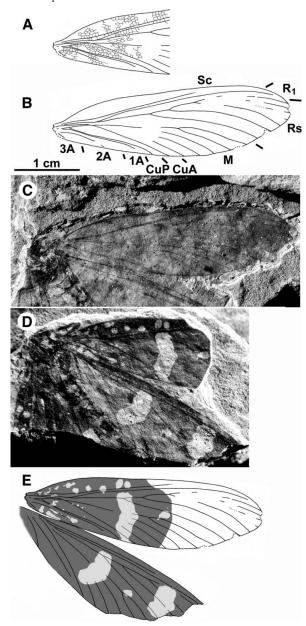


Fig. 10. Dinokanaga dowsonae, sp. nov. Holotype 2003.2.5 CDM 030. All to scale. (A) crossveins apparent in basal portion of forewing; (B) drawing of forewing with crossveins omitted; (C) photograph of part; (D) photograph of counterpart; (E) drawing of forewing, hind wing from part and counterpart combined, with colour pattern. See section "Terms and abbreviation".



shape, narrower in basal region, widest apicad of middle; from *D. andersoni* by greater width; from *D. sternbergi* by longer Sc, larger size; from *D. webbi* by larger size, crossveins more reticulate.

DESCRIPTION:

Forewing: Penniform, length 31–36 mm preserved (see later in the text), maximum width 9–11 mm. Rs six or sevenbranched.

Fig. 11. *Dinokanaga dowsonae*, sp. nov. Forewing, paratype 2003.2.4 CDM 028; A, B to scale: (A) photograph; (B) drawing without crossveins (indistinct). See section "Terms and abbreviation".

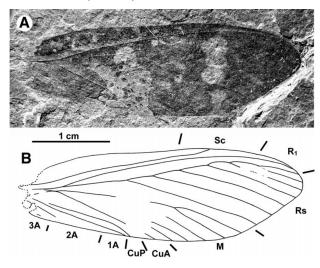
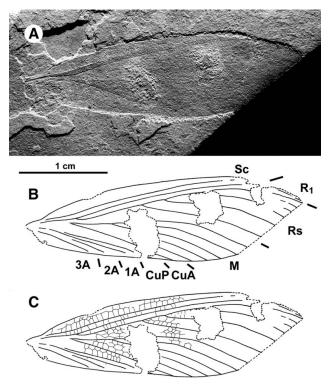


Fig. 12. *Dinokanaga dowsonae*, sp. nov. Forewing, paratype 2003.2.3 CDM 027. All to scale. (A) photograph; (B) drawing without crossveins; (C) drawing with crossveins. See section "Terms and abbreviation".



Hind wing: Known only in 2003.2.6CDM030a, b: length not known; width ~9 mm.

TYPE MATERIAL: Holotype: 2003.2.6CDM030a, b (part, counterpart) (Figs. 3C, 3H; 10; 16A) Part (2003.2.6CDM030a): a partially complete but not distinctly preserved body, articulated with complete right forewing, and basal portions of other three wings, colouration poorly preserved; Counterpart

Fig. 13. *Dinokanaga dowsonae*, sp. nov., forewing, paratype 2003.2.3 CDM 029. Both to scale. (A) photograph; (B) drawing without crossveins (indistinct). See section "Terms and abbreviation".

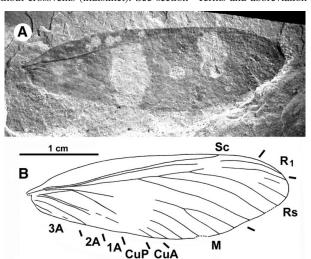
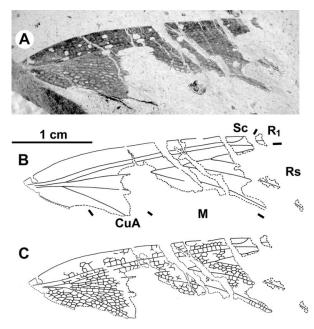
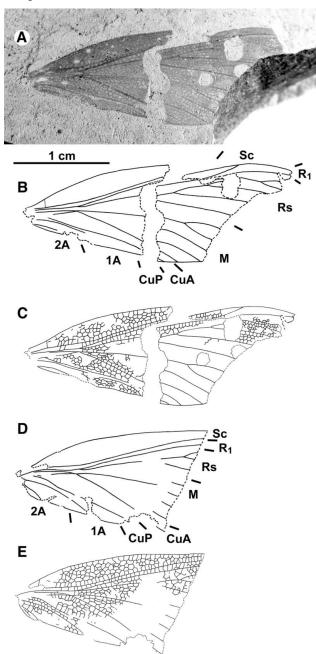


Fig. 14. *Dinokanaga dowsonae*, sp. nov., forewing, paratype SR94–05–09. All to scale. (A) photograph; (B) drawing omitting crossveins; (C) drawing with crossveins. See section "Terms and abbreviation".



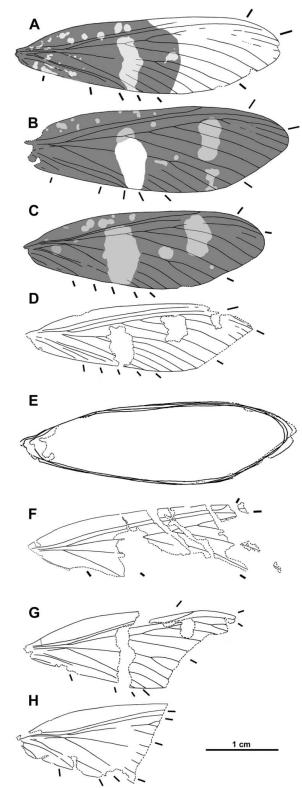
(2003.2.6CDM030b): as part, except right forewing basal half only, finely detailed preservation of colour patterning. Forewing: length 36 mm, maximum width 10 mm; hind wing: length not known, width ~9 mm. Labelled: Holotype *Dinokanaga dowsonae* Archibald. Collected at Horsefly River, British Columbia; by the author, September 2001. Paratypes, all labelled: Paratype *Dinokanaga dowsonae* Archibald: (1) 2003.2.5CDM029a, b (part; counterpart) (Fig. 11). A forewing with portions of the basal-most region missing, but otherwise complete and well preserved: length 34 mm preserved, likely 36 or 37 mm in life, maximum width 11 mm. Curated in the CDM collection. Collected by Shelley Dowson at Falkland, British Columbia, July 2002.

Fig. 15. Forewings of specimens tentatively referred to *Dinokanaga dowsonae*. All to scale. (A) SR-01-1-4, photograph; (B) SR-01-1-4, drawing, crossveins omitted; (C) SR-01-1-4 drawing with crossveins; (D) SR-01-01-03 drawing, crossveins omitted; (E) SR-01-1-3 drawing with crossveins.



(2) 2003.2.3CDM027a, b (part; counterpart) (Fig. 12), a mostly preserved forewing with the apical–posterior margin missing, length 31 mm preserved (<32 mm whole?), maximum width 9 mm; deposited in the CDM collection. Collected by the author at McAbee, British Columbia, May 2001). (3) 2003.2.4CDM028a, b (part; counterpart) (Fig. 13), a complete forewing, colouration preserved, length 34 mm, maximum width 11 mm; in the CDM collection. Collected by the author at McAbee, British Columbia, May 2001.

Fig. 16. Forewing comparison of specimens assigned to (and cf.) *Dinokanaga dowsonae*. (A–D) and (F–H) to scale. (A) Holotype 2003.2.5 CDM 030; (B) Paratype 2003.2.4 CDM 028; (C) Paratype 2003.2.3 CDM 029; (D) Paratype 2003.2.3 CDM 027; (E) comparison of shape (only) of specimens (A–D), relative sizes changed; (F) Paratype SR94-05-09; (G) *D.* cf. *dowsonae*: SR-01-1-4; (H) *D.* cf. *dowsonae*: SR-01-1-3.



(4) SR94-05-09 (part only) (Figs. 14, 16F); collected by Standley Lewis, 1993 at Republic, Washington (UW–BMNH locality A0307B). Deposited in the SRIC collection; forewing, basal portion mostly complete except for posterior margin, missing portions of the mid-section, apical portion missing.

DISTRIBUTION AND AGE: McAbee, Early Eocene; Falkland, Early Eocene; and Horsefly River, British Columbia, Early or early Middle Eocene; Republic, Washington, Early Eocene.

ETYMOLOGY: The specific epithet is in honour of Shelley Dowson, who collected and donated a paratype, in recognition of her fieldwork, and long-standing assistance to fieldwork in the Okanagan Highlands.

DISCUSSION: As the shapes of 2003.2.4CDM027, 2003.2.4CDM028, 2003.2.5CDM029, and 2003.2.6CDM030 are very close when images are adjusted for size difference and superimposed (see Fig. 16E), and venational differences are not beyond that demonstrated within some Mecoptera species (Ohm 1961; Willmann 1989), it is most conservative here to place these specimens in the same species.

Although the somewhat damaged nature of SR94-05-09 disallows such overall shape comparison, preserved portions agree closely with the other specimens just listed. This specimen would likely have been the largest of the species when whole, perhaps in the size-range of *D. hillsi*. The possible size difference between this specimen and the smallest of *D. dowsonae*, 2003.2.3CDM027 is still within range seen in species of *Panorpa* (Ohm 1961).

Two partial specimens from Republic are tentatively referred to this species as *Dinokanaga* cf. *dowsonae*: (1) The basal ~1/2 of a forewing from locality B4131 (SR01-01-03, part only, collected by Zach Adamsen, September 1997, deposited in the SRIC collection) (Fig. 15D, 15E; 16H), and (2) SR1-1-4a, b (part and counterpart) (Figs. 15A–15C, 16G), collected by Bill Richards, 1997, UW–BMNH locality B4131, deposited in the SRIC collection; a forewing, with the basal portion, separated mid-portion, broken away anterior mid-portion, missing the apical portion. The preserved portions of these wings show significant similarity to *D. dowsonae* in shape and size.

Dinokanaga dowsonae is the widest ranging species of this genus, the only species known from more than one locality, present at McAbee, Falkland, Horsefly River, and Republic.

Dinokanaga andersoni sp. nov.

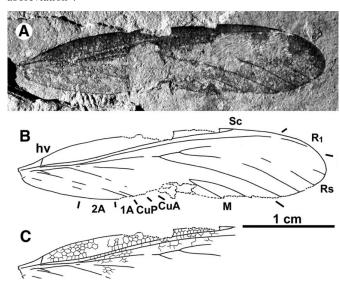
(Figs. 3D, 17)

DIAGNOSIS: May be separated from other *Dinokanaga* by forewing narrow for preserved regions (basal third, apical portion), others widening more rapidly from base.

DESCRIPTION:

Forewing: Length 34 mm; width 7 mm preserved; C moderately bowed outward basally, Sc and R inward, moderately widening costal area; Rs > four-branched (four preserved, either five, six likely). Humeral vein terminating slightly

Fig. 17. *Dinokanaga andersoni*, sp. nov., forewing, holotype SR01-06-01. All to scale. (A) photograph; (B) drawing omitting crossveins; (C) drawing with crossveins. See section "Terms and abbreviation".



apicad of right angle to Sc; Sc, R_1 space narrow. Veins posteriad of R_1 not well preserved.

TYPE MATERIAL: Holotype: SR01–06–01, (part only) (Figs. 3D, 17), deposited in the SRIC collection; forewing, mostly complete, but missing small portions of the posterior and the anterior margins. Labelled: Holotype *Dinokanaga andersoni* Archibald. Collected by Eric Anderson, August 2001.

DISTRIBUTION AND AGE: Republic, Washington (UW–BMNH site B4131); Early Eocene.

ETYMOLOGY: The specific epithet is from the surname of Eric Anderson, in honour of his contribution to paleoentomology in the collecting and donation of this fossil to the Stonerose Interpretive Centre.

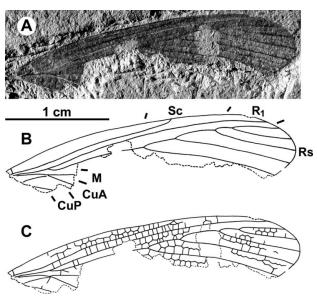
Discussion: This forewing is 34 mm in length and appears distinctively slender. As the middle portion of the posterior margin is slightly damaged and partially folded upward, it is possible that this wing was wider than might be suggested by its preserved habitus, yet this is unlikely, as the curvature of the posterior margin preserved for the basal third viewed with the angle of the curve of the apex together indicate that any reasonable reconstruction of this forewing would be among the narrowest of the genus (cf. *D. sternbergi*, which is, however, only 28 mm long; *D. webbi*, only 24 mm in length). The basal posterior margin is not likely deformed, as the preserved portions of the anal veins appear unbent.

Dinokanaga sternbergi sp. nov.

(Figs. 3E, 18)

DIAGNOSIS: Forewing may be separated from all other *Dinokanaga* by Sc short, joining anterior margin at close to, but just apicad of, 1/2 wing length, anteriad of 2nd (possibly, but less likely 3rd) fork of Rs; by small size from all but

Fig. 18. *Dinokanaga sternbergi*, sp. nov., forewing, holotype UWBM95361. All to scale. (A) photograph; (B) drawing omitting crossveins; (C) drawing with crossveins. See section "Terms and abbreviation".



D. webbi (which is smaller); costal space only slightly expanded in basal quarter.

DESCRIPTION:

Forewing: Length 28 mm, width not known. C gently curved until near apex, hardly bowed out basally; Sc ending just over half wing length; Rs 5 branches preserved (likely total); much of venation posteriad of Rs not preserved.

TYPE MATERIAL: Holotype: UWBM95361 (part only) (Figs. 3E, 18). Housed at the BMNH. Labelled: Holotype *Dinokanaga sternbergi* Archibald. A forewing, missing the posterior midsection, but otherwise well preserved, collected by Michael Sternberg, July 1995.

DISTRIBUTION AND AGE: Republic, Washington (UW-BMNH locality A0307); Early Eocene.

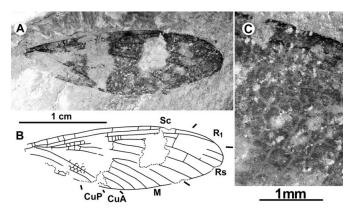
ETYMOLOGY: The specific epithet is in honour of Michael Sternberg, for his service to paleontology in Washington State, particularly in conjunction with the Stonerose Interpretive Centre (Republic) and the Northwest Paleontological Association (Seattle).

DISCUSSION: Although the costal region is only very slightly expanded basally, the curvature of C is consistent with forewing morphology in other species of the genus.

Dinokanaga webbi sp. nov. (Figs. 3I, 19)

DIAGNOSIS: Distinguished from other Dinokanaga by small

Fig. 19. *Dinokanaga webbi* UAFIC7075. (A–B) to scale. (A) photograph; (B) drawing (with strong crossveins); (C) detail of apical portion between R₁ and branches of Rs showing fine reticulate crossvenation. See section "Terms and abbreviation".



size, numerous simple crossveins, branching to reticulate in some areas.

DESCRIPTION:

Hind wing: Length 24 mm, width 8 mm; C; humeral vein crossvein-like; Sc joins margin about 3/4 wing length; R_1 extended near apex, curving posteriad near terminus; Rs: five branches detected (six-branched?); branches of M apparently deep: M_{1+2} branched at mid-wing; M_3 , M_4 apparently originate near R_1 , Rs fork (but poor preservation); base of Cu not preserved; CuA long, straight (from presumed region of CuA +M) to margin; CuP slightly curving to margin; Anal veins: region poorly preserved, one detected near margin; crossveins: simple, well preserved in C, Sc, R_1 areas, also some simple crossveins between branches of Rs, but reticulate in at least apical portion; branching, forming simple pentagons where detected in basal posterior region.

TYPE MATERIAL: Holotype: UAFIC7075, (part only) (Figs. 3I, 19), deposited in the UA fossil insect collection; hind wing, mostly complete, but surface broken (peeling upward) midwing, thin coating of matrix bound to wing in places, basal posterior portion damaged. Labelled: Holotype *Dinokanaga webbi* Archibald. Collected by Mark Wilson, 1987.

DISTRIBUTION AND AGE: Horsefly River, British Columbia; Early or early Middle Eocene.

ETYMOLOGY: The specific epithet is a patronymic in hour of Robin Webb, in recognition of his support of paleontology in British Columbia.

DISCUSSION: This wing is presumed to be a hind wing, as the costal space is not bowed outward at all in the basal quarter. However, this is the smallest wing, and this expansion appears to lessen as a trend with decreasing wing size. Therefore, it is also possible that this specimen is a forewing.

Most well-preserved crossveins in this wing are simple, unlike those of larger species. They are unbranched not only in narrow spaces between veins, but also in some broader areas, such as between branches of Rs, where they would

form polygons in larger wings of other species (as they do here in the basal posterior of the wing). Close examination shows a fine reticulate crossvenation in the apical portion of the wing between branches of Rs (Fig. 19C).

Key to genera and species of Dinopanorpidae

1.	Rs ₃ , Rs ₄ joined Rs ₃₊₄ for a distance, all crossveins simple	Dinopanorpa megarche
1′.	All branching of Rs pectinate, at least some crossveins branching: Dinokanaga	2
2.	Wing wide basally, widest at middle; forewing: costal space greatly expanded in basal quarter	3
2′.	Wing narrow basally; forewing costal space moderately or minimally expanded in basal quarter	4
3.	Forewing subtriangular	D. hillsi
3′.	Forewing elongate-oval	D. wilsoni
4.	Forewing: Sc short, reaching only second (third?) fork of Rs	D. sternbergi
	Forewing: Sc longer, reaching fourth fork of Rs	
5.	Numerous strong, simple crossveins anteriad of M (C, Sc, R1 spaces, but reticulate near apex)	D. webbi
5′.	Forewing not as above	6
6.	Forewing slender-oval	D. andersoni
6′.	Forewing subtriangular	D. dowsonae

Discussion: a revised assessment of the Dinopanorpidae

Ponomarenko and Rasnitsyn (1974) considered the Dinopanorpidae to belong among the more basal Mecoptera; later, Willmann (1987) placed the family in the derived taxon Panorpoidea. The Panorpoidea also include the families Panorpidae, Panorpodidae, Muchoriidae (Jurassic), Austropanorpidae (Paleocene), and the paraphyletic "Orthophlebiidae" (Mesozoic), from which the others presumably arose (Willmann 1987). While some members of this group (Muchoriidae, Austropanorpidae, Panorpidae, Panorpodidae) lost the fifth branch of M in the forewing (M_{4b}), likely as convergence (Willmann 1987), this state was retained in Dinopanorpidae, which gained a fifth branch in the hind wing (M is five-branched in the forewings, four-branched in the hind wing of "Orthophlebiidae": Willmann (1989). Holcorpa, described and often considered as a panorpid, but also discussed in its own family (e.g., Zherikhin 1970; Willmann 1989), also shares a five-branched M in both fore and hind wings). Both five-branched and four-branched M are found elsewhere in Mecoptera.

The form of R_1 (extending almost to the apex, curved posteriad near termination), is the major character state that supports placing Dinokanaga together with Dinopanorpa in this family. This is so distinctive, however, as to strongly support this determination. Other similarities (brief M + CuA, large numbers of crossveins and branches of Rs, biogeography, age, size), while not providing strong support, are not contradictory.

The Russian localities where Dinopanorpidae have been found are apparently close to the Okanagan Highlands in age, the Zerkalnaya locality older and the Amgu locality younger. The family is then known to range from the Late Paleocene possibly to the Late Eocene. The Bering Land Bridge connected these regions at that time, and there is ample evidence of biotic transfer between these continents (see "Localities").

Dinopanorpidae are generally large insects: although a few species of *Dinokanaga* are relatively small, most are

similar to or exceed (hind wings up to 37 mm long) the notably large size of *Dinopanorpa megarche* (hind wing 30 mm long).

The wings of *Dinokanaga* bear a similar number of branches of Rs (6–7) as *Dinopanorpa* (8). This may be related to size only, however, and carry no phylogenetic significance.

As in *Dinopanorpa*, in those specimens where this region is preserved in *Dinokanaga*, the stem of Cu is free at its base. In *D. megarche*, M + CuA is about 1 mm, considered remarkably short (Cockerell 1924; Carpenter 1972). It is shorter yet in *Dinokanaga*, where M and CuA only join for ≤0.5 mm, in some species only touching and immediately separating. *Dinokanaga* differs from *Dinopanorpa*, however, in that M bends very little or not detectably through this joining, unlike in *Dinopanorpa*, where M bends sharply in joining and in separating from CuA.

Both Cockerell (1924) and Carpenter (1972) considered the long, oblique crossvein m-cu in *Dinopanorpa* noteworthy. Carpenter, however, also stated the possibility that this morphology might be an individual peculiarity of the only specimen then known. Crossveins in all *Dinokanaga* are unlike this condition; they are numerous and reticulate through this region, confirming that this form of m-cu in *Dinopanorpa* must be considered a trait below family level.

In *Dinopanorpa megarche* crossveins are numerous, at least twice as many as are found in members of Panorpidae or "Orthophlebiidae" (Carpenter 1972). Even further, extreme development of crossveins is a striking feature of *Dinokanaga* (see earlier discussion of genus). Therefore, unusually large numbers of crossveins for the Panorpoidea are common between these two genera, although exceptionally large numbers, reticulate in many areas, are particular to *Dinokanaga*.

The outward curve of the costa in the basal quarter of the forewings of *Dinokanaga* and associated expanded costal space is a general forewing shape common in Neuroptera but not so often seen in Mecoptera, e.g., Choristidae, some Eomeropidae, and certainly convergent between these instances. It is not known if the forewing of *Dinopanorpa*

shared this morphology, as found in all species of *Dinokanaga* (developed to a greater or lesser extent).

Although the head is only known from *Dinokanaga hillsi*, the extended rostrum in this species is likely a family-level trait, as rostrum size is found to be elsewhere in the Mecoptera.

The dark, circular structure on abdominal segment 9 of TMP8339.1132 (readily visible on the counterpart), the holotype of *Dinokanaga hillsi* (female), is interpreted as the medigynium. This structure appears similar in morphology to those of Panorpodidae and "Orthophlebiidae," i.e., without tongue-shaped structures characteristic of the Panorpidae (Willmann 1989; Willmann and Novokshonov 1998) (*Holcorpa* has a medigynium lacking these tongue-shaped structures (Willmann 1989)).

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