

Fossil palm beetles refine upland winter temperatures in the Early Eocene Climatic Optimum

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Eocene climate and associated biotic patterns provide an analog system to understand their modern interactions. The relationship between mean annual temperatures and winter temperatures—temperature seasonality—may be an important factor in this dynamic. Fossils of frost-intolerant palms imply low Eocene temperature seasonality into high latitudes, constraining average winter temperatures there to >8 °C. However, their presence in a paleo-community may be obscured by taphonomic and identification factors for macrofossils and pollen. We circumvented these problems by establishing the presence of obligate palm-feeding beetles (Chrysomelidae: Pachymerina) at three localities (a fourth, tentatively) in microthermal to lower mesothermal Early Eocene upland communities in Washington and British Columbia. This provides support for warmer winter Eocene climates extending northward into cooler Canadian uplands.

palm bruchines | paleoclimate | Okanagan Highlands | palm pollen

Eocene climates have received intense scrutiny in recent decades, providing an increasingly detailed analog system with which to assess the dynamics of modern global climate change, thereby allowing prediction of its long-term trends and biotic consequences. It was a time of increased global temperatures associated with elevated atmospheric carbon levels, particularly during episodic hyperthermal events such as the Early Eocene Climatic Optimum (EEOC) (1, 2). The Eocene was also notable for greater climatic homogeneity, with low latitudinal temperature gradients coupled with low temperature seasonality extending to the poles, creating a global climate type unknown today outside of restricted regions. This is thought to have had far-ranging biological consequences, e.g., for intercontinental dispersal, global biodiversity patterns, community structures, and evolutionary trajectories (e.g., refs. 2–6). Here, we use the presence of insects that have obligate associations with floral climatic indicators to refine characterization of winter climate in a cool higher midlatitude upland during the EEOC, and therefore the environmental context of these biotic patterns during an interval of global warmth.

A key factor in these dynamics may have been warmer winter temperatures [coldest month mean temperature (CMMT)] relative to mean annual temperature (MAT) even in mid- and higher latitude regions of cooler MAT (3). Consequently—as in the modern tropics and some southern hemisphere midlatitude coastal areas—Eocene organisms across the globe would not have been burdened by the necessity to allocate resources to endure hostile extreme winter climates with its costs for metabolic and insulation adaptations, or escape its effects by an annual period of dormancy or expenditure of large amounts of energy in migration. This would allow the potential of near year-round reproduction, feeding, and growth, providing an explanatory context for observed differential Eocene diversity patterns. In the geologically brief time scale of our modern interval of global climate change, the partial release of such constraints by warming winters is seen to have had a large influence on natural communities, with resulting high economic and social impact,

e.g., the current dramatic mountain pine beetle infestations of western North America (7, 8).

Palms as Indicators of Winter Temperatures

Eocene temperature seasonality has been characterized using proxy thermometers such as palms (Arecaceae), whose seeds and seedlings cannot survive sustained freezing, today limiting their natural distribution to regions of CMMT >5 °C (3, 9), although some palms may tolerate CMMT ~2.5 °C (Fig. 1). Freezing tolerance is reduced under high atmospheric CO₂, so Eocene records of palms may indicate CMMT >8 °C (10, 11).

Consequently, the overwhelming greatest diversity of genera and species of palms is now restricted to the tropics, with only a few genera occurring outside of it and the subtropics (12). The most cold-tolerant of all living palms, inhabiting the limits of this range, are almost exclusively members of the tribes Trachycarpeae (e.g., *Rhapidophyllum hystrix*, *Serenoa repens*, *Trachycarpus fortunei*, and *Washingtonia filifera*), Cryosophileae (e.g., *Trihrinax* spp.), and Sabaleae (i.e., *Sabal minor*), all in the subfamily Coryphoideae, with only the New Zealand arecoid palm *Rhopalostylis sapida* matching their cold-tolerance (Fig. 1).

In the Eocene, the range of palms extended into regions of cooler MAT well outside their modern latitudinal limits (3, 11, 13, 14), supporting the reconstruction of globally more equable climates, i.e., milder winters in cooler regions. For example, in the Early Eocene Okanagan Highlands series of montane localities of far-western North America (Fig. 2), the vegetative

Significance

Elevated CO₂ combined with globally warm temperatures in the Eocene make its climate ideal for understanding modern global warming and its biotic consequences. Globally low temperature seasonality—the relationship between winter and mean annual temperatures—has been proposed as key to differential Eocene biodiversity and community patterns. Palms are important winter temperature indicators by their sensitivity to frost; however, their presence in paleocommunities may be masked by taphonomic constraints and identification difficulties. We used fossil obligate palm-feeding beetles to establish the presence of palms in a cool upland in midlatitude western North America. In this way, we provide a more precise characterization of climate during an important interval of the emergence of modern ecosystems.

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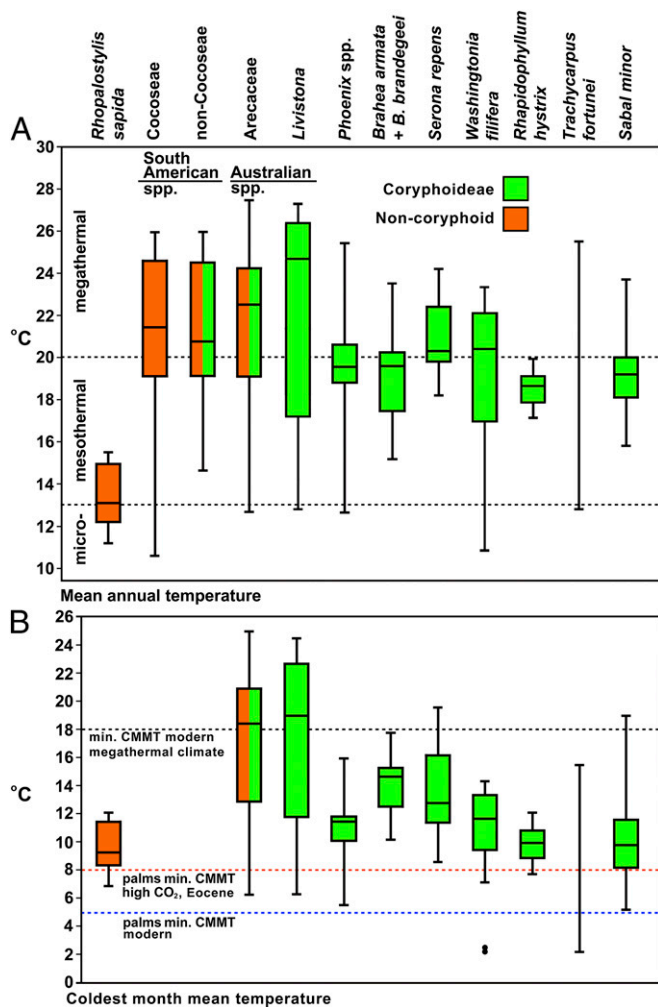


Fig. 1. Climatic profile of palms (median, quartile, and maximum and minimum values), with an emphasis on cold tolerant clades (principally Coryphoids). (A) MAT profiles of selected extant palm taxa. (B) CMMT profiles of selected extant palm taxa with key thresholds for megathermal (tropical) climates and for palms: CMMT >5 °C for modern palms (with few exceptions: Two outlier occurrences shown as dots are for *W. filifera*) (3); CMMT >8 °C for palms under Eocene levels of atmospheric CO₂ (10). Systematics follows Baker et al. (43).

organs of the extinct coryphoid palm *Uhlia allenbyensis* are common in the Princeton Chert (Allenby Formation, BC, Canada), with their anatomy indicating a close affinity to the modern Coryphoideae genera *Brahea*, *Rhapidophyllum*, and *Serenoa* of the tribe Trachycarpeae (15). Palm macrofossils have not been reported from any of the other Okanagan Highlands Eocene floras (16, 17).

Palm pollen (as *Sabal granopollenites*) has been reported in the Allenby Formation and other Okanagan Highlands sites at Driftwood Canyon, Falkland, Hat Creek, and McAbee (18, 19), although not at others of this series, e.g., Quilchena or Republic. Searches of Quilchena slides prepared by R.W.M. have so far identified only one possible palm pollen grain (Fig. 3) of the *Sabal* type; it is, however, larger (length = 40 μm) than the size range defined by Rouse (20) (28–32 μm) for *S. granopollenites*, and should be referred to *Liliacidites* (21). Harley and Baker (22, 23) reviewed the record of fossil palm-like pollen and express caution in identification, based on its similarity to nonpalm monosulcate monocots and some fossil form genera of nonangiosperm origin. Evidence other than pollen is needed to confirm that palms were distributed widely in the Eocene Okanagan Highlands.

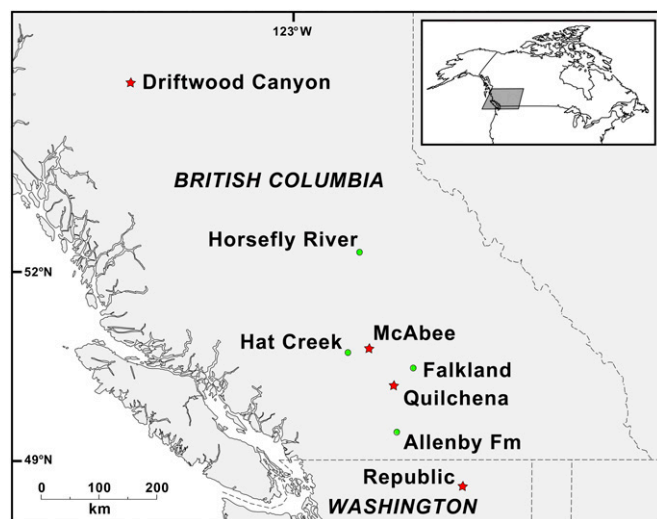


Fig. 2. Map of Early Eocene Okanagan Highland fossil sites. Red stars represent beetle sites: Republic, Quilchena, and McAbee, with confirmed Pachymerina; Republic and McAbee, including beetles assigned to *Caryobruchus* + *Speciomerus*; and Driftwood Canyon with likely Pachymerina. Green dots represent other Okanagan Highlands sites: Allenby Formation with palm macrofossils in chert, *Uhlia allenbyensis* (15); putative palm pollen reported from the Allenby Formation, Quilchena, Falkland, McAbee, Hat Creek, and Driftwood Canyon (for Quilchena, see *Palms as Indicators of Winter Temperatures*; for others, see ref. 18 and references therein). No evidence of palms has been reported from Okanagan Highlands localities at Republic or Horsefly River.

The lack of palm macrofossils from any Okanagan Highlands locality other than the Princeton Chert may reflect that the others are all lacustrine shale localities (except Hat Creek: coal), which might at least in part explain this absence by taphonomic bias. The Chert preserves an in situ aquatic community, and all of the vegetative organs of *U. allenbyensis* are preserved. In lake sediments, however, the persistence of leaves on the trunk after death in many low-statured monocot plants, including coryphoid palms such as most *S. minor*, *S. repens*, and to a limited extent *Trachycarpus* spp., greatly restrict leaf



Fig. 3. Fossil palm-like pollen. Early Eocene pollen from the Quilchena (BC, Canada) locality of the Okanagan Highlands resembling palm pollen, but assigned to *Liliacidites*.

fossilization (24). *U. allenbyensis* is reconstructed as a low-statured rhizomatous plant similar in ecology to *S. repens* (15) (Fig. S1). Palms were only recently confirmed at the Florissant locality (Colorado: late Eocene, lacustrine shale) by a single coryphoid palm leaf; long-standing fruit and pollen evidence had been considered controversial (25).

Palm Beetles

Here, we evaluate the Eocene upland winter temperature in the Okanagan Highlands using fossil palm bruchines, beetles of the obligate palm-feeding chrysomelid subtribe Pachymerina as an indicator for the presence of palms where direct macrofossil

evidence may be obscured by these factors. In the Eocene, the tribe Pachymerini (bruchines, which includes legume as well as palm feeders) is known from the Early Eocene Okanagan Highlands locality at Quilchena, BC (26), the late Eocene Florissant (27), and an apparently coeval locality in Primorye, Pacific coastal Russia (28); all tentatively assumed to either belong to legume feeding taxa or not associated with host plants. Here, we reexamine the Quilchena beetle and eight new fossils from Okanagan Highlands localities at Driftwood Canyon and McAbee, BC; and Republic, WA (Figs. 2, 4, and 5).

We assign these beetles to the Pachymerini by the following (see terminology in *Materials and Methods*; Figs. S2–S4):

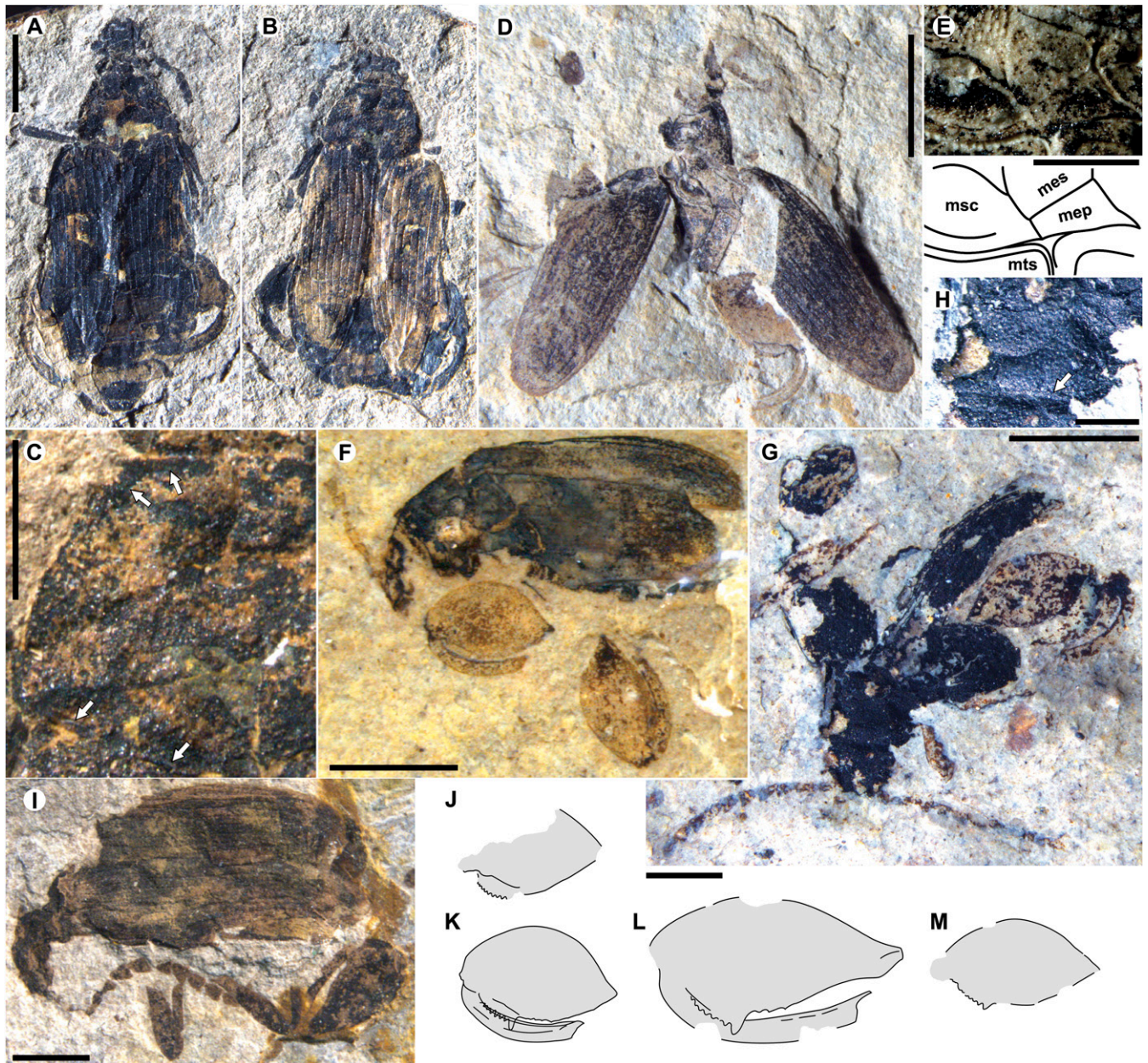


Fig. 4. Quilchena, Republic, and Driftwood Canyon Pachymerina. Specimens from (A–C) Quilchena, (D–H, J, K, and M) Republic, and (I and L) Driftwood Canyon. (A) Q-0061a part and (B) counterpart. (C) Q-0061b, showing impressed marginal line (arrows) surrounding pronotum; (top) anterior margin. (D) SR 05-03-10. (E) Detail (photograph and drawing) of SR 05-03-10 showing mesepimeron, extending and broad mesally. mep, mesepimeron; mes, mesopleuron; msc, mesocoxal cavity; mts, metasternum. (F) SR 99-78-71. (G) SRUI 00-94-80, (H) Detail showing impressed line on anterior margin (arrow). (I) RBCM.EH2013.031.0001.001. (J–M) Drawings of metafemora of SR 05-03-10, SR 99-78-71, RBCM.EH2013.031.0001.001, and SRUI 00-94-80 respectively. Metatibiae also on K and L. (Scale bars: 2 mm in A, D, F, G, and I; B is the same scale as in A; and 1 mm in C and J–M; 500 μ m in E and H.) (E–G) Wetted with ethanol.

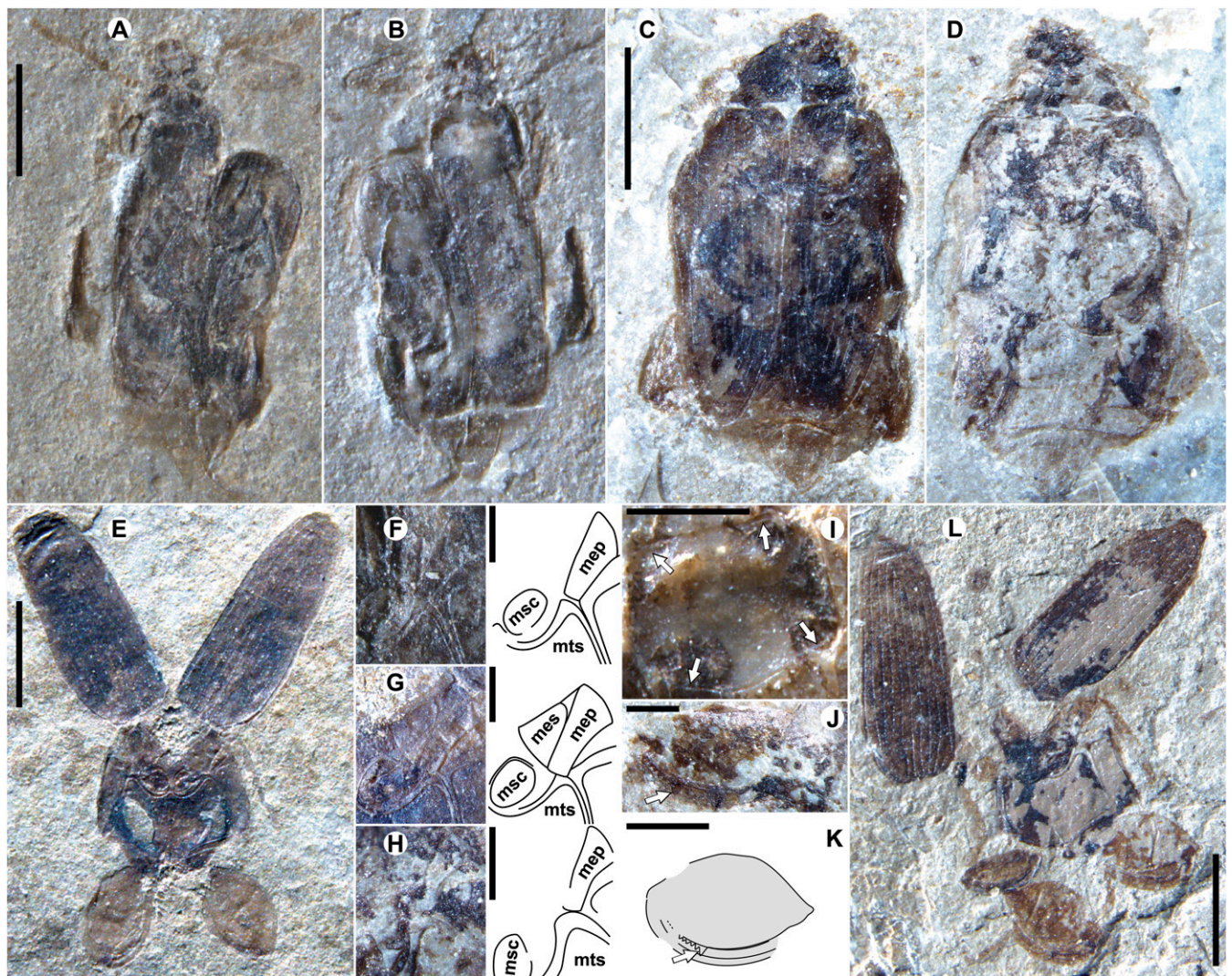


Fig. 5. McAbée *Pachymerina*. (A) F-1542. (B) F-1543, counterpart of F-1542. (C) F-1540, showing dorsal morphology. (D) F-1541, counterpart of F-1540, showing ventral morphology. (E) F-939, ventral, pleural portions of the meso- and metathoracic segments, elytra (top) and hind legs (bottom) preserved. (F–H) Details (photographs and drawings) showing mesepimeron broad mesally (Fig. 4E and abbreviations therein) of F-1542, F-939, and F-1541 respectively. (I) F-1543 showing impressed marginal line (arrows) surrounding pronotum; (top) anterior margin. (J) Hind leg of F-1541, arrow shows position of denticle 1, distal midfemur. (K) Drawing of femur and tibia of F-1544, arrow indicating denticle 1; orientation as in J (distal femur to the left). (L) F-1544, preserved portions mostly as for E. (Scale bars: 2 mm in A, C, E, and L; B is the same scale as A and B, and D as C; 1 mm in I and K; and 500 μ m in F–H and J.)

mesepimeral plate broadly joining the mesocoxa (plesiomorphic for bruchines) combined with metafemora incrassate, with pecten; metatibiae arcuate and mucronate, mucro wedge-shaped; and metacoxa about half-width of metafemur and first sternite (29, 30). We further determined them as palm bruchines, *Pachymerina* (Table 1 and Figs. 4 and 5), by the presence of either an impressed marginal line extending to the lateral/anterior margins of the pronotum, or broadly triangular tarsomeres one and two on the fore- and midlegs (27, 29, 30).

Results

We found all but one (from Driftwood Canyon) to be palm bruchids, including the *Quilchena* beetle; its previous tentative association with the *Caryopemina* (26) was incorrect. In Republic specimens SR 99-94-80 and SRUI 99-78-71 (Fig. 4), and McAbée specimens F-1540/1 and F-1544 (Fig. 5), the pecten positioned *mesad* the metatibia in the flexed hind leg excludes *Pachymerus*, and the pecten placed in the distal portion of the metafemur further excludes *Pachymerus* and also *Caryoborus*, placing these beetles in the *Caryobruchus*–*Speciomerus* group.

Caryobruchus and *Speciomerus* are separated by fine details of morphology not preserved in these specimens. Modern species of *Caryobruchus* show a marked preference for palm seeds of the coryphoid tribes Coryphaea, Phoeniceae, and Hyphorbeae, whereas recorded hosts of *Speciomerus* are found within the Arecoideae (31).

Assignment of the single Driftwood Canyon beetle RBCM.EH2013.031.0001.001 (Fig. 4 I and L) to subtribe level is problematic by preservation, as it bears a damaged and incomplete pronotum and lacks the distal portions of its fore- and middle legs. Its pecten morphology and positioning in the flexed hind leg is, as above, distinctive of *Caryobruchus* and *Speciomerus* when these character states are found within the *Pachymerina*; however, these are also characteristic of some Old World Caryedontina, a possibility that cannot be excluded here. Within the Caryedontina, *Afroredon* is clearly excluded by its distinctively squat shape; *Exoctenophorus* by the pecten *mesad* the tibia in the flexed hind leg; and *Caryotrypes* by antennal morphology (segments slender, 5–10 feebly serrate in *Caryotrypes*). It is possible that it belongs to the tropical *Mimocaryedon*, which is only known

Table 1. Fossil beetle diagnostic characters, localities, ages, and MAT values

Locality	Specimen	Age, Ma	MAT, °C	MW	MP	IL	TM	PS	PT	
Republic	SR 99-94-80	49.4 ± 0.5*	13.5 ± 2.2 [†]							
	SR 05-03-10					X		X		
	SRUI 99-78-71							X		X
Quilchena	Q-0061	51.5 ± 0.4 [‡]	14.8 ± 2.0 [†] –15.0 ± 0.6 [†]				X	X		
McAbee	F-1540/1	52.90 ± 0.83*	9.5 [§] –13.5 ± 2.5 [†]	X	X	X		X	X	
	F-1542/3			X				X	X	
	F-1544					X	X			
	F-939					X			X	
Driftwood Canyon	RBCM.031	51.77 ± 0.34*	6.2 ± 4.7 [†] –12.3 ± 1.9 [†]					X	X	

MAT values are from both leaf physiognomy and nearest living relative analyses, which provide the lower and upper values for each site, respectively. MW and MP are diagnostic of Pachymerini (MP within Bruchinae); IL and TM of Pachymerina; PS of *Caryobruchus* and *Speciomerus* (within Pachymerina), and PT of *Caryobruchus*, *Speciomerus*, and *Caryoborus* (when these character states are found within Pachymerina) (28, 29). IL, impressed marginal line extending to anterior lateral and anterior margins of the pronotum; MW, metacoxae about half width of metafemora and first sternite; MP, mesepimeral plate broad mesally, meets mesocoxa and/or metasternum; PS, pecten short, *distad* midfemur; PT, pecten *mesad* tibia on flexed hind leg; RBCM.031, RBCM.EH2013.031.0001.001; TM, broadly triangular tarsomeres 1 and 2 on the fore- and midleg.

*Moss et al. (18).

[†]Greenwood et al. (16).

[‡]Villeneuve and Mathewes (46).

[§]Dillhoff et al. (47).

from Lake Manyara, Tanzania (3.75° S latitude, 955 m elevation) (32), or to the genus *Caryedon*, which today ranges widely through Africa (best known in the tropics), the eastern Mediterranean, Arabian Peninsula, southern Black Sea to Caspian Sea region, and tropical and subtropical South and Southeast Asia (33).

Discussion

These findings provide robust support for the presence of palms at Quilchena and McAbee previously suggested by tentative pollen evidence, and further at Republic, where evidence of palms has not been recovered. The Driftwood Canyon beetle as Pachymerina would provide support for pollen evidence of palms there; but even a *Caryedontina* affinity would place it in a group with a marked modern preference for tropical to subtropical climates. We also examined beetles from the late Eocene Florissant Formation, confirming their association with the Pachymerina (27), consistent with the recent confirmation of palms there (25). We did not examine the Russian beetle; however, Zherikhin assigned it to the same genus as those from Florissant (28).

All of the Okanagan Highlands localities considered here have estimated microthermal climates (i.e., MAT ≤13 °C) except Quilchena, which is thought to have been lower mesothermal (Table 1).

Peak regional tectonic uplift during Okanagan Highlands times resulted in a mountainous topography comparable to the modern British Columbian Coast and Selkirk ranges (34, 35). Floral proxies indicate a considerably warmer climate in coeval nearby coastal lowland formations, with a substantial elevational MAT gradient upslope to the cooler Okanagan Highlands (16, 17, 19, 36–39). It is highly unlikely that all localities bearing Pachymerina were situated at the precise elevation of the coldest limits of palm tolerance. Any deviation would have to be downslope, i.e., warming winters relative to the established MAT estimates, not cooling them, and Okanagan Highland palms would then have been growing in a climate of even narrower temperature seasonality than is suggested by their minimum winter temperature tolerance.

The climates and communities of numerous hot lowland fossil localities deposited in the EECO have been examined, such as the megathermal Green River Formation in the midcontinental United States (for a review of Green River climates, see refs. 5

and 40). The establishment of warmed winters by the presence of palms in such communities does not, however, indicate reduced temperature seasonality as would their presence in the cooler Okanagan Highlands communities, where they constrain winter temperatures closer to microthermal and lower mesothermal MAT values established independently by bioclimatic and leaf physiognomy analyses (16, 40). Previous analysis based on paleobotanical proxies indicates that McAbee summers were not excessively hot (3). High EECO summer temperatures cannot be excluded, however (e.g., see isotopic analyses for the Bighorn Basin) (41), as the physiological limits of warmer summer temperatures on plants and therefore plant-based proxies, is not well constrained (40). General patterns of Okanagan Highlands summer temperatures would, however, follow from the relationship between CMMT and MAT by definition.

The presence of Pachymerina implies mild winters (Figs. S5 and S6) across this cooler montane setting from northern Washington into midlatitude Canadian localities, all a few degrees more northerly in the Eocene (42). This strengthens the supposition of equable Eocene extratropical climates, with the consequent implications for a globally nonmodern climatic context impacting the emergence of modern ecosystems in the late greenhouse world.

Materials and Methods

We examined nine fossil beetles from four localities of the Okanagan Highlands series of Early Eocene fossil localities: three from Republic, WA, on loan from the Stonerose Interpretive Center (SR 05-03-10; SR99-78-71a, b; SRUI 00-94-80); one from Quilchena, BC, in the Simon Fraser University collection (Q-0061a, b); four from McAbee, BC, on loan from Thompson Rivers University (UCCIPR L-18 F-1540/1; F-1542/3; and F-1544); and one from Driftwood Canyon, BC, on loan from BC Parks (RBCM.EH2013.031.0001.001). We follow the palm systematics of Baker et al. (43) and the beetle systematics of Nilsson and Johnson (30). Subtribe Pachymerina (palm bruchines) was previously considered by many authors as the tribe Pachymerini *sensu* Nilsson and Johnson (30), with Bruchinae the family Bruchidae; we treat the Bruchinae as a subfamily of the Chrysomelidae and adjust references to previously published ranks accordingly.

Analyses. Climate range analyses for both the beetles (Tables S1–S4) and palms (Fig. 1) used existing data sources (references in *S1 Text*) or were done using the DIVA-GIS software (www.diva-gis.org) with the WorldClim dataset

(www.worldclim.org) to generate estimates of MAT, winter temperature [coldest quarter mean temperature ~1–2 °C warmer than CMMT, which palm climate ranges are reported in] and mean annual precipitation for modern localities to a 1-km square resolution (44). Climate analyses for palms further used ANUCLIM 6.1 (45) for the Australian records.

Terminology (Figs. S2–S4).

Metafemora incrassate: femora of the hind leg thickened, swollen.

Pecten: comb-like structure on the posterior–ventral portion of metafemora.

Denticles: projections from pecten forming “teeth of the comb.”

Metatibia arcuate: tibia of the hind leg curved.

Metatibia mucronate: projection (mucro) extending from distal surface of the hind tibiae.

Metatibia carinate: with grooves (carinae) running lengthwise along the hind tibiae.

Mesocoxa: basal segment of the middle leg, attaching the leg to the thorax.

Metacoxa: basal segment of the hind leg.

Tarsomeres: subdivisions of the tarsus, portion of the leg *distad* the tibia.

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Mesepimeron: posterior division of the middle thoracic pleuron (exterior, side).

Impressed marginal line on pronotum: a groove on the dorsal surface of the pronotum, just inside its margin.

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