

Wheeler's dilemma

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Abstract. We identify certain biota as "tropical" and others as "temperate" in the modern world, yet this distinction was not as clear in the early Tertiary. Indeed, many authors have commented upon the well-documented co-occurrence of tropical and temperate biotas in early Tertiary deposits; REID and CHANDLER (1933) called this "one of the most vexed of climatological problems." Almost a century ago, William Morton WHEELER (1910) noted the surprising mix of warm and cool-adapted ant genera found together in Baltic amber. We review some other warm/cool assemblages of insects, plants and vertebrates, which occur at Eocene extra-tropical localities worldwide. Explanations of time averaging, transitional assemblages between climatic regimes and mixing of biocoenoses are unsatisfying. Instead, these seemingly anomalous mixtures are consistent with hypothesized low temperature seasonality in early Tertiary temperate regions. The sorting of biota into temperate and tropical-identified may be a later Cenozoic phenomenon that reflects our specific modern climatic regime of high seasonality in extra-tropical regions, rather than an innate and historical biogeographic association of these organisms with their present latitudinal ranges. Thus, the presence of clearly thermophilic organisms outside of low latitudes in early Tertiary assemblages may indicate milder winters, not necessarily tropical or subtropical climate.

Key words: paleoclimate, paleoecology, fossil insects, seasonality, equability, Eocene.

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I. INTRODUCTION

Almost a century ago, William Morton WHEELER (1910) noted the strange co-occurrence of thermophilic and temperate ant genera in Baltic amber: "The mixture of arctic and tropical forms in the amber, a peculiarity which characterises other insects and plants no less than the Formicidae, has not been satisfactorily explained". WHEELER described the Paleotropical ant genera *Sima* ROGER, 1863 (now known as *Tetraponera* SMITH, 1852) and *Plagiolepis* MAYR, 1861, the Malaysian *Gesomyrmex* MAYR, 1868 and the pantropical *Oligomyrmex* MAYR, 1867 (called *Erebomyrma* by WHEELER) as co-occurring with circumpolar taxa such as *Leptothorax* MAYR, 1855, *Stenammina* WESTWOOD, 1839, *Liometopum* MAYR, 1861, and *Lasius* FABRICIUS, 1804. "The foregoing considerations suggest several questions that are not easily answered," he concluded (WHEELER 1914).

WHEELER (1910, 1914) discussed two hypotheses: 1) that these anomalous assemblages had resulted from time averaging of assemblages from both early warm and later cool episodes; and 2) HEER's conjecture (1860) that cool-adapted allochthonous highland ants co-mingled with autochthonous thermophilic lowland ants in a common depositional basin, episodically carried (within easily transportable resin) by streams from mountainous regions.

A b b r e v i a t i o n s

CMM – cold month mean

MAT – mean annual temperature

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II. WHEELER'S HYPOTHESES

T r a n s p o r t. WHEELER (1910) found the mixture of biocoenoses hypothesis unsatisfactory, as the boreal component of the ant fauna greatly outnumbered the tropical element in number of specimens, unlikely if cool-adapted ants were occasionally transported to a tropical depositional setting. The presence of both tropical and boreal extant ant genera as syninclusions further precludes explanations of post-mortem mixing of upland and lowland taxa, and of amber deposits being reworked into the same beds.

T i m e A v e r a g i n g. Baltic amber from the Kaliningrad region is dated Late Eocene, with amber deposits in other Baltic regions possibly Oligocene (POPOV et al. 2001). We now know that WHEELER was correct in his inference that the Early Oligocene was characterised by climatic cooling (see GRAHAM 1999 for a review), although the problem of syninclusions remained. WHEELER suggested that syninclusions could be explained by a period of transitional community assembly as the climate was changing from warm to cool. This does not seem likely, however, as insect communities respond to climate rapidly (COOPE 1970).

III. FURTHER PROBLEMS

O t h e r i n s e c t s. The tropical/temperate mix in Baltic amber is not a problem confined to ants. Thermophilic insects present in the amber include Mantodea (possibly close to extant South American taxa), Phasmatodea, and Embioptera, as well as taxa of Orthoptera, Isoptera, Psocoptera, Hemiptera, Neuroptera, Coleoptera, Diptera, and Hymenoptera that are today associated with warm climates (POPOV et al. 2001). These are found together with many insects of Palearctic and Holarctic modern affinities, such as Raphidioptera (Inocelliidae and Raphidiidae). Furthermore, Baltic amber contains a diversity of aphids and ichneumon wasps, which today are depauperate in the tropics (HEIE 1967; JANZEN 1981; DIXON et al. 1987; HEIE 1994; POPOV et al. 2001).

O t h e r o c c u r r e n c e s. We now know that the occurrences of similar tropical/temperate mixtures are widespread in the world throughout the Eocene – unlike HEER, who called it: “this exceptional appearance, which is seen nowhere else in the plants and animals of the ancient world” (undated translation in WHEELER 1910).

The Late Eocene Bembridge marls of the Isle of Wight contain an even stronger thermophilic insect component, including termites of the families Mastotermitidae and Termitidae, the ant genus *Oecophylla* SMITH, 1860, the wasp genus *Polybia* LEPELETIER, 1836, as well as thermophilic dragonflies, orthopterans, cicadas and moths (JARZEMBOWSKI 1980; POPOV et al. 2001). These co-occur

with a more characteristically temperate fauna of diverse ichneumonid wasps and aphids, as well as the cool-adapted termite *Reticulitermes* HOLMGREN, 1913 (ibid.).

Similarly, Eocene deposits in Yellowstone Park, Wyoming, USA contain both tropical and temperate-associated plant taxa (WING 1987). This has also been interpreted as a mixture of biocoenoses from multiple source altitudes, even including the upright transport of stumps in mudflows downhill to mix with autochthonous lowland stumps (COFFIN 1976). However, the depositional setting of many such climatically mixed floras in western North America argues against transport; furthermore at least some taxa with mutually exclusive climatic tolerances (in the modern world) co-occur in *almost all* western North American Early Eocene floras (WING 1987).

C l i m a t e a n d m i x t u r e. In the Canadian Arctic, Eocene crocodylians, varanid lizards, large non-burrowing tortoises, and a suite of mammals have been described on Ellesmere Island, paleolatitude 78°N (ESTES & HUTCHINSON 1980; MCKENNA 1980). The range of modern crocodylians extends to a northern limit of about 4.4°C cold month mean (CMM), and varanid lizards are almost entirely tropical today. Although turtles may range into areas of colder winters, they never reach shell sizes of larger than 30 cm today in regions with CMM <13°C (HUTCHINSON 1982). The fossil tortoise *Geochleone* from Ellesmere Island had an estimated shell of up to 64 cm, indicating cold month average temperatures well above freezing (ESTES & HUTCHINSON 1980). At least 41 species of mammals have been found, including two species of paromyid primates, five plagiomenid dermopterans ("flying lemurs"), and four perissodactyles (MCKENNA 1980). Possible lack of winter hardening in Eocene "mummified" wood from the arctic fossil forests of Axel Heiberg Island (immediately west of Ellesmere) similarly suggest that freezing days were minimal if present at all at high paleolatitudes (BASINGER 1991).

A suite of conifers from the Late Paleocene or Early Eocene sediments of Spitsbergen Island whose modern analogues do poorly or cannot withstand frost similarly indicate few if any freezing days (SCHWEITZER 1980; but see WOLFE 1980).

In the northeast Pacific, the Eocene Kamchatka flora exhibited a "curious mix" of temperate (e.g. *Alnus*, *Acer*, *Ulmus*) and thermophilic (e.g. palms) elements (BUDANTSEV 1992) (for other Eocene northern occurrences of palms, see GREENWOOD & WING 1995).

The Eocene London Clay flora includes 11% extra-tropical, e.g. *Alnus*, *Betula*, *Cedrus*, *Corylus*, and 43% exclusively or mainly lowland tropical (e.g. palms, Icacinaceae) taxa associated today with the Indo-Malayan region (REID & CHANDLER 1933). REID and CHANDLER called the presence of the tropical element "disquieting" and "one of the most vexed of climatological problems" (ibid.). DALEY (1972) rejected hypotheses that this anomalous assemblage was due either to transport of temperate-associated taxa downhill from cool uplands, or to a cool-adapted relictual flora from the Paleocene transitionally coterminous with a dominant thermophilic Eocene flora. Mountains containing this temperate flora would have required altitudes exceeding 2000 meters, and local terrain lacked the high topography required for transport of a significant component of the flora over very large distances. Similarly, persistence of a relict cool-adapted flora during hundreds of thousands or millions of years of much warmer climate seems unparsimonious (ibid.).

IV. SEASONAL EQUABILITY

DALEY (1972) speculated that a possible explanation lay in a hypothesis of different climatic structure, one with no modern analogue. If the Eocene of southern Britain was characterised by low seasonality such that there were few or no frost days even at cool mean annual temperature (MAT), and if the present range of the Indo-Malayan flora is delimited by CMM, not MAT, then such a flora could well inhabit higher latitudes, mixing with a temperate flora (ibid.). Higher equability would result in such assemblages.

By "more equable," we do not mean seasonless, but rather characterized by reduced thermal seasonality when compared with modern extra-tropical regions of similar MAT (see AXELROD

1992). Annual varve pairs of light diatomaceous summer and dark organic winter laminae in the Eocene Okanagan Highlands locality at Horsefly, British Columbia, indicate some degree of seasonality (WILSON 1976). Horsefly, however, may have been further north in the Eocene (closer to 60° N). Certainly strong photoperiod seasonality was a significant factor at high latitudes, as today.

The idea that ancient climates were less seasonal predates both WHEELER and HEER. Without the knowledge that England lay near the equator in the Carboniferous, LYELL (1830) hypothesized that decreased seasonality could have fostered the creation of coal swamps at high latitudes. He described the climate of the Carboniferous as characterised by: “the uniformity of climate, both in the different seasons of the year and at different latitudes” and notes that it was “remarkable for its warmth, moisture, equability and freedom from cold, rather than the intensity of its *tropical heat*” (italics his).

In the early 1990's, the idea of increased equability in continental climates of the Cretaceous and Early Tertiary was challenged by computer climate modelling (SLOAN & BARRON 1990, 1991). However, paleontological evidence that thermophilic plants such as palms, cycads, tree ferns and gingers inhabited interior continental North America demonstrated mild winters in spite of temperate MAT (WING & GREENWOOD 1993). These taxa are particularly suited for nearest living relative analysis, as they display high morphological similarity to closely related modern plants, have large (non-relictual) ranges, and bear clearly climate-limiting structures (ibid.). Few palm genera extend today beyond the tropics into warm-temperate regions. They are limited to regions with CMM >5° C, as frost damages the roots, leaves, and their soft, water-rich manoxylic trunks (SAKAI & LARCHER 1987; GREENWOOD & WING 1995). Crocodylians inhabited the North American continental interior in the Eocene, indicating winters at least as mild as in the modern southeastern and southern United States (MARKWICK 1994). MAT in interior North America and Australia is estimated as <15° C, by both taxon dependent and independent paleobotanical analyses (GREENWOOD & WING 1995).

Eocene Australia, further south than present, was without significant frost days at MAT <15°C, and maintained thermophilic biota such as palms and crocodiles (GREENWOOD & WING 1995). At various sites there was a mixture of tropical rainforest components (e.g. *Cupanaie*, *Anacolosia*, *Santalum*) along with cooler, temperate region flora (*Nothofagus*, *Dacrydium*) (KEMP 1978). “This apparently anomalous mixture of tropical or subtropical rainforest types with those of cool temperate rainforest communities suggests that the early Tertiary vegetation cannot be represented by a single modern forest type”(ibid.).

The Eocene Okanagan Highlands of western North America bear a mixture of tropical and temperate insect taxa (ARCHIBALD & MATHEWES 2000; current research). These series of upland deposits extend about 1000 kilometres through south-central British Columbia and northern Washington State. RICE (1959) described the climate of the Okanagan Highlands as tropical or semitropical, based on the presence of thermophilic plants, and the bionid dipteran *Plecia* WIEDEMANN, 1828. However, these localities are now characterised as having had MAT's ranging from about 9 to 14°C as determined by taxon-independent analysis of leaf physiognomy (WOLFE 1994; GREENWOOD & WING 1995; MATHEWES 2003).

In the Okanagan Highlands, any mixing of climatically distinct biocoenoses by transport would be upslope, more difficult to consistently achieve than would be the downslope transport originally hypothesised for Baltic amber. Thermophilic insects in the Okanagan Highlands include mastotermitid termites, megapodagrionid damselflies, diplopterine cockroaches, *Plecia*, and others (WEHR & BARKSDALE 1996; WEHR 1998; ARCHIBALD & MATHEWES 2000). Thermophilic plants include cycads (HOPKINS & JOHNSON 1997), *Paleophytocrene* (Icacinaceae), and the banana *Ensete* (WEHR & MANCHESTER 1996) at Republic, Washington (MAT 12-13°C: WOLFE & WEHR 1987). Palms are some of the most common monocotyledon fossils in the Princeton chert (ERWIN & STOCKEY 1990) (nearby coeval One-Mile Creek site, also Allenby Formation, estimated MAT 9.3°C: WOLFE 1994). Such mixed tropical/temperate plant and insect assemblages would also fa-

facilitate shifts of tropical insects to feeding on temperate plants without the requirement of synchronous adaptation to the presence of frost (BD FARRELL & MITTER 1993).

E q u a b i l i t y f o r c i n g m e c h a n i s m s. Three categories of hypotheses have been proposed to model increased latitudinal heat transport, and presumably increased equability: orbital forcing, and differing marine, and atmospheric regimes. The latter two are at times mixed.

Change in the obliquity of the axis of Earth's rotation has received discussion (e.g. WOLFE 1977; SLOAN & MORRILL 1998). However, orbital forcing remains controversial, as mechanisms for changes in the earth's axis of rotation remain unexplained.

Australia was still separating from Antarctica during the Eocene, creating a barrier to circumpolar currents. Presumably, north-south currents would have transferred heat between the equator and high southern latitudes. The initiation of the circumpolar current as a consequence of the separation of these continents in the Late Oligocene would then have isolated Antarctic waters, increasing the latitudinal temperature gradient. There was general high-latitude cooling at this time, and possibly an increase in Antarctic glaciation (e.g. see KENNETT & SHACKLETON 1976; KEMP 1978). Other major oceanic events include the development of the psychrosphere (the modern system of cold ocean bottom waters), which is placed near the Eocene-Oligocene boundary (KENNETT & SHACKLETON 1976). MOLNAR and CANE (2002) modelled "permanent El Niño" conditions for "pre-Ice Age" climates, resulting in increased extra-tropical temperatures. Analysis of Eocene varved lacustrine sediments in Wyoming (USA) and Germany (HUBER & CABALLERO 2003), however, argues against "permanent El Niño," and adds support for the hypothesis that warmer deep ocean temperatures (~10°C higher than today) may have been a significant forcing mechanism for Eocene climatic. The onset of Antarctic glaciation at the Eocene/Oligocene boundary may also have been caused by a drop in atmospheric CO₂ levels (DECONTO & POLLARD 2003). Furthermore, a Cretaceous-Early Tertiary atmospheric regime characterised by extension of the Hadley cell to polar latitudes is proposed to have played the major role in latitudinal heat transport, and thus climatic equability (BF FARRELL 1990).

WHEELER would have undoubtedly been surprised to see an occurrence of the mixture of tropical and temperate ant genera in the modern world. In the mountains of tropical southern Mexico, MAT remains cool in concert with decreased seasonality. In a sample taken at 1,585 meters in Puebla Province (~20° N), the tropical ant genera *Adelomyrmex* EMERY, 1897, *Oligomyrmex*, *Hyponoponera* SANTSCHI, 1938, and a member of a tropical species-group of *Pyramica* ROGER, 1862 coexist with *Stenammas* (seen by WHEELER in Baltic amber) and *Ponera* LATREILLE, 1804, both primarily temperate in the New World (S. COVER, personal communication). This provides anecdotal evidence that tropical and temperate-associated ant genera may coexist under conditions analogous with those hypothesised in Eocene extra-tropical latitudes. Temperate-adapted ants seem to commonly require seasonal low temperatures for diapause, which triggers reproduction; frost days in particular, however, may be by no means necessary, and may represent a hardship that these ants endure as the price of temperate-zone life. If tropical ants are restricted to low latitudes by intolerance to frost, then they would find such equable areas of lower MAT suitable as well.

CONCLUSIONS

The warm/cool organism mixture is seen in Eocene assemblages in distant parts of the world, including the Baltic region, Britain, Spitsbergen, western Canada, interior continental USA, the Arctic, Kamchatka, and Australia, as well as in an example from a modern tropical cool upland. Paleontomological data further confirm work indicating Early Tertiary equability (e.g. WING & GREENWOOD 1993; MARKWICK 1994; GREENWOOD & WING 1995). Such a mixture of organisms presumably persisted until some undetermined time later in the Cenozoic, when thermal seasonality

increased along with dropping MAT, and so colder winters became generally associated with extra-tropical latitudes, resulting in biotic sorting.

The mixture of thermophilic and temperate ants seen in Baltic amber is most likely a direct consequence of more equable temperature seasonality: expectable, not anomalous. The presence of fossil organisms with closely related modern representatives that have clear tropical affinities may be a consequence of raised CMM in cool climates (increased equability), not necessarily an indicator of raised MAT (subtropical or tropical climates). In light of this, ascribing tropical or subtropical climates to early Tertiary sites by the presence of thermophilic organisms should take such considerations into account.

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