

Life was a beach: a panbiogeographic analysis of the cosmopolitan mayfly genus *Choroterpes* (Ephemeroptera: Leptophlebiidae: Atalophlebiinae)

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Mayflies of the cosmopolitan genus *Choroterpes* have been a systematic and biogeographical puzzle for many years. Currently, the genus is divided into three subgenera (*Choroterpes s.s.*, *Euthraulius*, and *Cryptopenella*) distributed from North America to China, South America, Africa and New Guinea. Most extant species inhabit small lowland coastal streams, often temporary ones. They are generally absent from the diverse mayfly faunas of mid- and high-elevation tropical streams. A panbiogeographic analysis of the distribution of all known species, and a review of published life history observations, suggest that the ancestors of these genera were distributed along both sides of the Tethys Sea during the Mesozoic Era. Their combined distribution is a terrestrial analogue of a shallow water marine biota traversing the Tethys during the late Mesozoic. Ancestors of extant *Choroterpes* and related genera could have spread along the borders of epicontinental seas to reach the current distribution of the group.

Keywords: *Choroterpes*; Ephemeroptera; Tethys; panbiogeography

Introduction

The recent discovery of two new species of *Choroterpes* Eaton along the Pacific rim of Costa Rica (Ávila and Flowers 2006) and its co-occurrence in temporary pools with mayflies of the *Terpides* complex (Savage 1986), along with *Ulmeritoides* Traver, encouraged me to take a closer look at this genus which is apparently widespread everywhere except in Australia and Latin America. The first treatment of the biogeography of *Choroterpes* and its subgenera was in Peters (1988). He gave a map depicting the worldwide distribution of three subgenera but stated that their origins and relations could not be determined. More recently Kluge (2007) mentioned *Choroterpes* as an Arctogean taxon, a classical but uninformative description of its distribution (Arctogaea refers to everywhere but Australia and South America). Although many new species of *Choroterpes s.l.* have been described since Peters' (1988) paper, many of these have been descriptions of larvae or adults only and the biogeography and evolutionary history of the genus remains in the nebulous category of 'cosmopolitan group'.

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Despite the fact that the Ephemeroptera have been around since the Carboniferous Period and occur on all continents (except Antarctica) and many oceanic islands, only a handful of genera can be said to be truly cosmopolitan. *Choroterpes* Eaton and the closely related *Neochoroterpes* Allen form a generic complex – called hereafter the *Choroterpes* complex (= *Choroterpes* group of O'Donnell and Jockusch 2008) – whose distribution stretches from California through southern Europe to the Philippines, and down to the tip of Africa. As currently constituted, *Choroterpes* includes three subgenera: *Choroterpes s.s.* Eaton (14 species), *C. (Euthraulius)* Barnard (27 species), and *C. (Cryptopenella)* Gillies (three species). *Neochoroterpes*, until recently also considered a subgenus of *Choroterpes*, contains four species in southwestern United States and Mexico.

The *Choroterpes* complex can be recognised by the following combination of characters. In the larva: (1) the first abdominal gill is a pair of slender filaments and different in structure from gills 2–6; (2) the apex of the glossae is provided with broad spatulate setae; (3) the posterior row of setae on the labrum arises close to the middle of the labrum (except in some *Neochoroterpes*). In the adult: (1) in the forewing MP1 has a symmetrical fork while in MP2 this fork is asymmetrical; (2) the cubital area of the wing is broad with four (sometimes reduced to three) intercalaries; (3) the forceps of the male are abruptly widened in their basal 1/4–1/3; (4) the penes are two simple lobes which can be very short to elongate and which lack spines or accessory lobes. The subgenus *Choroterpes* is distinguished by a broad terminal lobe on each lamina of gills 2–6. In subgenus *Euthraulius*, gills 2–6 bear three narrow filaments on the apex of each lamina. The subgenus *Cryptopenella* was originally described as a separate genus (Gillies 1951) but Zhou (2006) placed it as a subgenus of *Choroterpes*. It can be distinguished from the other subgenera by the very short penes which do not protrude beyond the styliger plate. *Neochoroterpes* was described by Allen (1974) as a subgenus of *Choroterpes*, but Henry (1993) raised it to generic rank without, however, giving any explanation. Adults of *Neochoroterpes* have short penes lobes (although not as short as in *C. (Cryptopenella)*) while the larvae resemble larvae of *C. (Euthraulius)* but without the row of setae across the middle of the labrum.

Methods

Leon Croizat (1958, 1964, 1976) developed the panbiogeographic method of biogeographic analysis. Despite exaggerated reports of its demise (Briggs 2007) this method continues to elucidate distributions and historical geographies of such diverse subjects as plants (Alzate, Quijano-Abril and Morrone 2008), crustaceans, bugs, and hagfish (Cavalcanti and Gallo 2008). The distributional patterns of *Choroterpes* and *Neochoroterpes* were analysed by the panbiogeographical method of track analysis (Posadas, Crisci and Katinas 2006). Distributions of the four taxa in the *Choroterpes* complex were taken from literature sources (Gillies 1951, 1957; Burian 1995; Puig and Gaino 1996; Thomas and Vitte 1988; Vitte and Thomas 1988; Bauernfeind 1998; Bae, Lee and Yoon 2000; Ávila and Flowers 2006; O'Donnell and Jockusch 2008) and the William L. Peters Museum Collection of Aquatic Insects, and were plotted as exactly as possible on a map of the world (see Figure 1), using the Global Gazetteer 2.1 “*Directory of Cities and Towns in World*” (Falling Rain Genomics Inc. 2008) to obtain coordinates. Map points were then connected by drawing lines between nearest neighbours and continuing until all localities for each of the four generic and subgeneric taxa were connected (Figure 2).

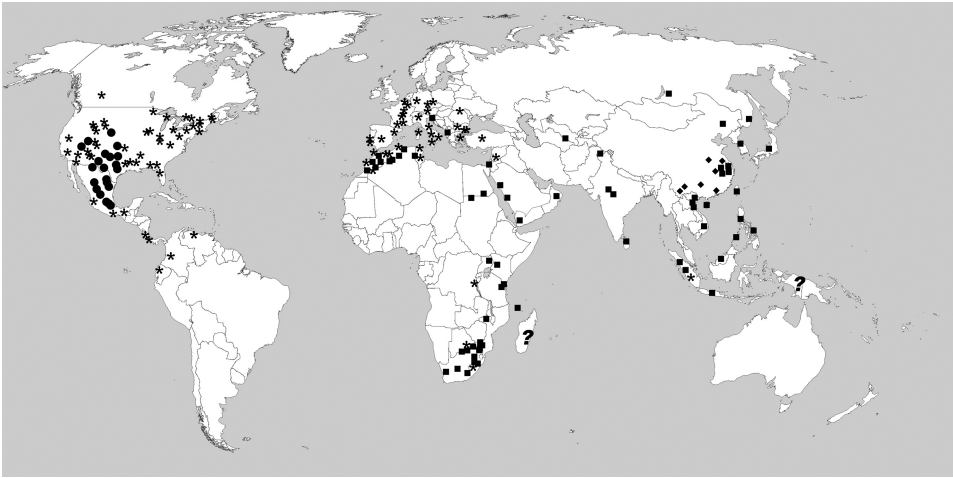


Figure 1. Distribution of *Choroterpes* and *Neochoroterpes*. Stars: *C. (Choroterpes)*; squares: *C. (Euthraulius)*; diamonds: *C. (Cryptopenella)*; circles: *Neochoroterpes*; question marks: subgenus undetermined (from O'Donnell and Jockusch 2008).

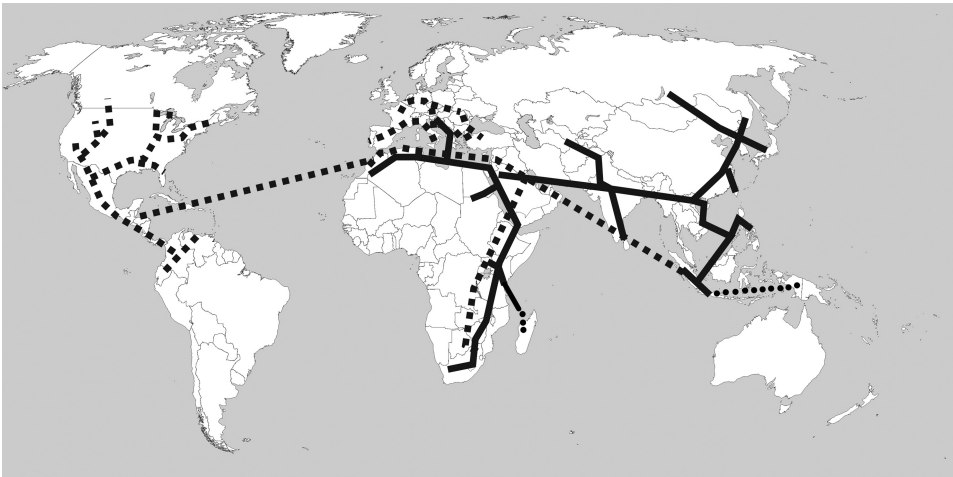


Figure 2. Tracks of *Choroterpes*. Square dotted lines: *C. (Choroterpes)*; solid lines: *C. (Euthraulius)*; round dotted lines: relationship undetermined.

During study of the material, a possible significant synapomorphy was found to be present in a number of pantropical genera as well as the *Choroterpes* complex. This character is the replacement of hair-like setae on the ventral side of the glossae with broad spatulate setae. Genera displaying this character are the *Choroterpes* complex (defined above) and *Askola* Peters, *Careospina* Peters & Alayo, *Choroterpides* Ulmer, *Fulletomimus* Demoulin, *Hagenulopsis* Ulmer, *Indialis* Peters & Edmunds, *Isca* Gillies, *Neohagenulus* Traver, *Thraulius* Eaton, and *Traverina* Peters.

Results

The global distribution of the members of the *Choroterpes* complex is shown in Figure 1. The areas of greatest diversity of *Choroterpes s.s.* lie in western North America to Central America, the Mediterranean region, with outliers in eastern Africa, and South Asia (Table 1). *Choroterpes (Euthraulius)* is an Eastern Hemisphere group and *Choroterpes (Cryptopenella)* and *Neochoroterpes* are relatively restricted subgenera in China and the US–Mexico areas, respectively. Two generalised tracks (Figure 2) were found based on these distributions. *Choroterpes s.s.* has its main massing across the Atlantic along a Caribbean–Mediterranean track, while *C. (Euthraulius)* has local massings in South Africa and along the East Asian Pacific Rim. The position of the other genera with spatulate glossal setae are shown relative to the *Choroterpes* tracks in Figure 3.

Discussion

From the point of view of terrestrial biogeography, the overall pattern of the tracks for *Choroterpes s.l.* corresponds to a combination of the Tethys plus the ‘Great Rift System’ (Figure 4, Croizat 1958). Not surprisingly, marine paleobiogeographers have found the Tethys track a more useful explanation of dispersal than their terrestrial colleagues. At least one reconstruction of the prehistoric Tethys biogeographic unit (Westermann 2000) incorporates Croizat’s Rift track, which in turn suggests that current distributions of the *Choroterpes* complex are an ‘onshore analog’ of the Mesozoic Tethian marine biota (Figure 5).

Ecological data on *Choroterpes* complex mayflies is scanty for most species. The hypothesis of a Tethyan distribution suggests that the ancestors of *Choroterpes*, in contrast to many mayflies, originally favoured warm, lowland coastal streams. In fact, this is exactly the habitat in which two species recently described from Costa Rica occur (Ávila and Flowers 2006), and similar observations have been made for species in Spain (Puig and Gaiño 1996) and East Africa (Gillies 1957). In all three of these areas, *Choroterpes* has been found in temporary as well as in permanent streams. Without explicit data we can still surmise that the *C. (Euthraulius)* localities along the Arabian Peninsula, Israel, and eastern Mediterranean islands are also

Table 1. Numbers of species of the *Choroterpes* complex listed by geographic area.

Area	Taxon			
	<i>Choroterpes s.s.</i>	<i>C. Euthraulius</i>	<i>C. Cryptopenella</i>	<i>Neochoroterpes</i>
Eastern North America	1			
Western North America–Mexico	3			4
Central–South America	4			
Northern Europe	1			
Mediterranean	7	1		
Africa	3	6		
Northern Asia		1	3	
Southern Asia	1	7		

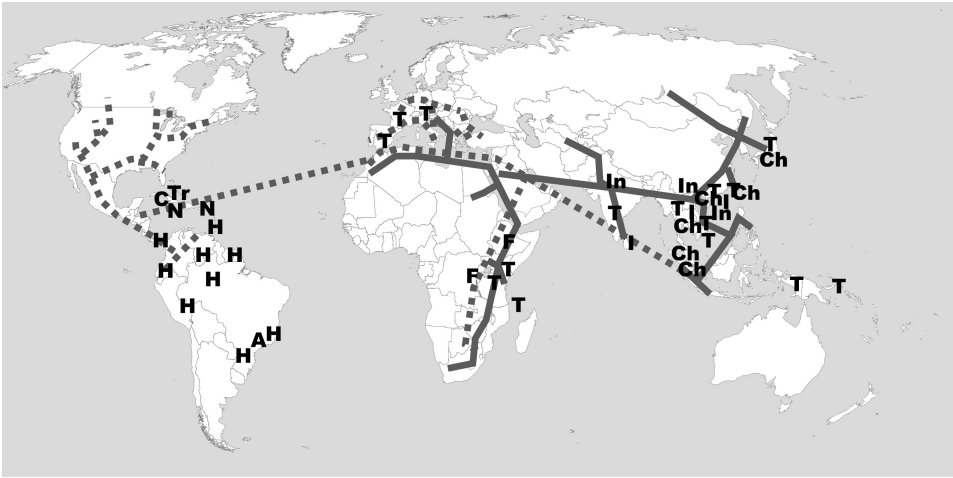


Figure 3. Map of *Choroterpes* complex tracks and distributions of other leptophlebiid genera with blade-like glossal setae. A, *Askola*; C, *Careospina*; Ch, *Choroterpides*; F, *Fullemimus*; H, *Hagenulopsis*; I, *Isca*; In, *Indialis*; N, *Neohagenulus*; T, *Thraulius*; Tr, *Traverina*.

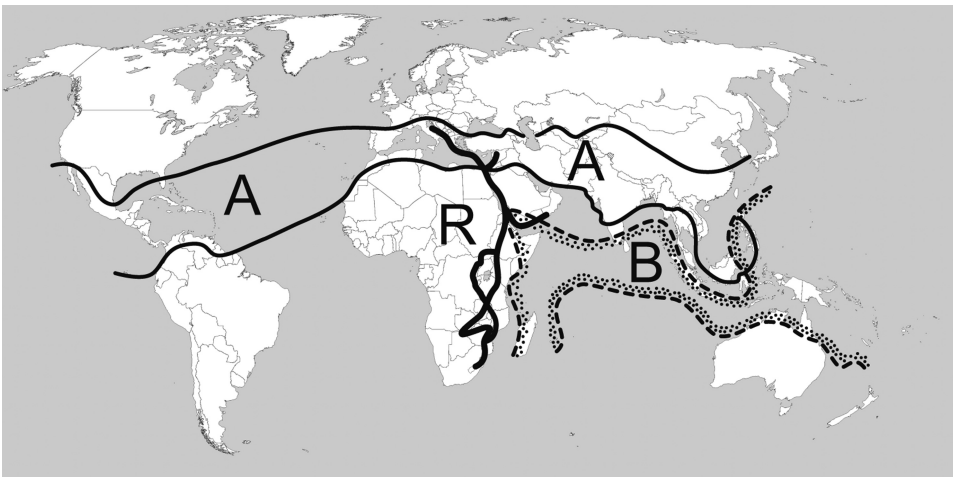


Figure 4. Map showing Tethys Geosyncline ("A"), Great Rift System ("R"), and the "Western Pacific" ("B") (modified after Croizat 1958).

likely not to be year-round streams. Granting that *Choroterpes* has also been found in permanent streams, it is not unreasonable to hypothesize that abundance in lowland streams near the coast and tolerance for temporary streams is sufficiently widespread that it could have been a characteristic of the ancestors of this complex.

A piece of evidence supporting this hypothesis, as well as a Tethian origin for this group of mayflies, is the pattern of current distributions. With only a single exception (*Choroterpes* (*s.s.*) *basalis* (Banks)), all living *Choroterpes* are found along either current continental margins, or margins of past epicontinental seas or plate margins

of the Mesozoic era. A hypothetical distribution is shown in Figure 6, where current distributions of the *Choroterpes* complex are ‘backcast’ on a mid-Jurassic reconstruction of the Tethys Sea. One point of interest is that during the initial stages of splitting, western Pangaea mayflies could have easily moved along the

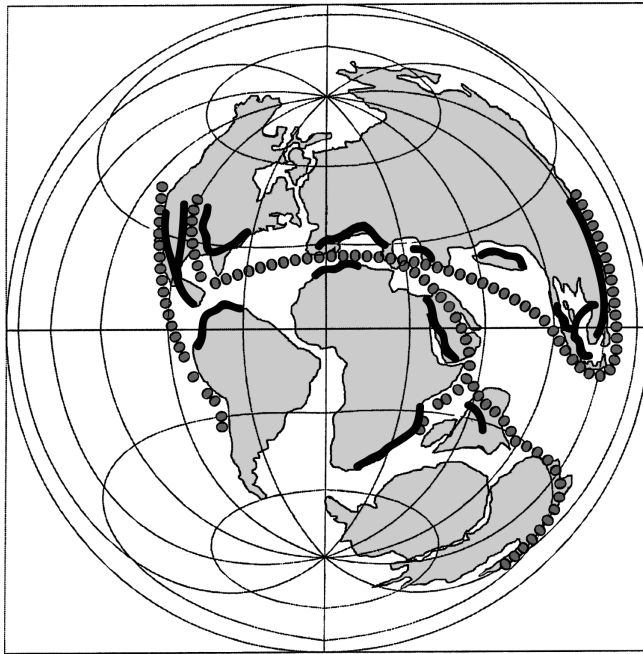
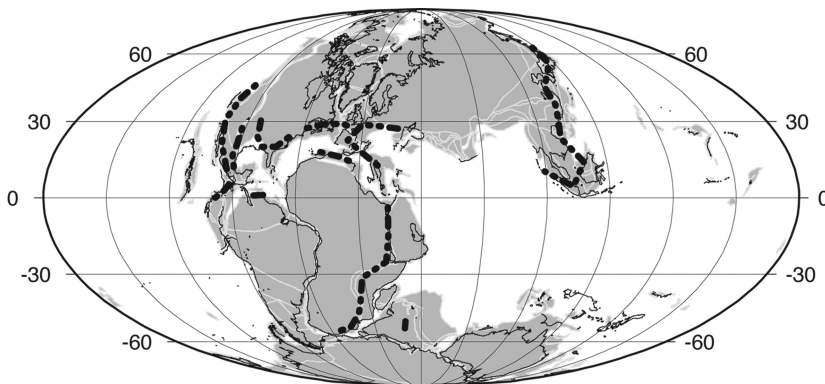


Figure 5. Map of Mid-Cretaceous Era world showing marine biogeographic units. Grey dots: Mediterranean-Caucasian (= Tethyan) biogeographic unit; heavy black lines: backcast of present day distributions of the *Choroterpes* complex (modified after Westermann 2000).



150 Ma Reconstruction

Figure 6. Current distribution of *Choroterpes* complex mapped on a map of the world in the Mid-Jurassic. Map was obtained through the Ocean Drilling Stratigraphic Network (2008).

Tethys shores to proto-North, Central or South America via the ‘Hispanic Corridor’ (Rais, Louis-Schmid, Bernasconi and Weissert 2007) (or in the opposite direction). The Hispanic Corridor was a long, narrow sea, not unlike the Mediterranean today. After the Mesozoic, ancestors of present day *Choroerpes* would have had to survive geologic uplifting and global climate cooling, which can account for the inland and high latitude populations and species found today.

A curious gap in the distribution of the *Choroerpes* complex is its absence from the Caribbean islands. In theory, these islands should be rich in suitable habitats (warm streams at low altitudes) for *Choroerpes* or its allies. However, when distributions of all the genera having spatulate glossal setae are considered (Figure 3), three (*Traverina*, *Cariospina*, *Neohagenulus*) are Caribbean endemics. Except for *Hagenulopsis*, widely distributed in the Caribbean and South America and *Askola* (Brazil), the examined genera with spatulate glossal seta are also distributed along the Tethys track. Future cladistic analysis will no doubt help determine if this group of genera is monophyletic.

Croizat (1958) presented a radical revision of traditional biogeography, proposing that ocean basins were the basic units of biogeography. Although these ‘radical realms’ found some resonance with some biogeographers (Grehan 2001, and see Williams and Ebach 2008 for a review), it is somewhat difficult to think of a terrestrial animal as belonging to an ‘oceanic’ realm. Terrestrial biogeographers have not hypothesised ‘Tethyan distributions’ with the same diligence as they have Gondwanian or Laurasian ancestries. However, in the case of freshwater organisms, Tethyan distributions can be discerned even when not labelled as such. In Bănărescu’s (1990) monumental review of freshwater biogeography, *Spelaeomysis* (Crustacea) freshwater Neritidae (Mollusca), Goeridae (Trichoptera) and some Blephariceridae (Diptera) all have distributions similar to *Choroerpes s.l.* In the case of the *Choroerpes* complex, the Tethys Sea has probably had a greater effect on its current distribution than any of the continental landmasses it presently inhabits.

In this study, it is proposed that the *Choroerpes* complex (and its probable sister clade, composed of genera with blade-like glossal setae) had their origins during the Mesozoic Era along the shores of the Tethys Sea, and exploited the shorelines of warm, productive, geologically active epicontinental seas to attain their present worldwide range. This period of Earth history resulted in extraordinary evolutionary creativity (Vermeji 2004), especially in the marine realm. For proto-*Choroerpes*, life on the beach would have had similar effects.

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