

Evolution of Baetiscidae (Ephemeroptera): current state of knowledge of the family

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Recent discovery and description of fossil Baetiscidae has dramatically changed the biogeographical and evolutionary perspective of the family. Since the mid-eighteenth century until recently, the family has been known only from the Nearctic realm and all extant species of the family still remain geographically limited to this region. Here, we present the first parsimony algorithm generated cladistic analysis of the phylogeny of *Baetisca* based on external morphological characters of both larvae and adults. The results are compared with the previously published phylogeny of the genus and differences between the two studies are discussed. The southeastern United States is the centre of biodiversity of the genus where 11 of the 12 currently known nominal species have been reported. Biogeographical and evolutionary implications of the current geographic range of extant *Baetisca* and fossil species are discussed.

Keywords: *Baetisca*; Baetiscidae; Ephemeroptera; mayflies; zoogeography

Introduction

The Baetiscidae are some of the most distinctive and unusual looking mayflies. With their stout and spinous thoracic notal shield that covers the thorax and the first six abdominal segments (Figure 1), the larvae might well rival some of the most bizarre types of dinosaurs of the Mesozoic (Berner and Pescador 1988). In fact, when Walsh (1864) first discovered and described the larva, Hagen told Walsh that the larva was the most extraordinary animal he had seen and wondered whether it really belonged to the Insecta (Berner and Pescador 1980). The most comprehensive accounts of the family to date are the papers by Berner and Pescador (1980) and Pescador and Berner (1981). Berner and Pescador (1980) extensively reviewed the taxonomy, phylogeny, ecology, and life history of *Baetisca*, which at the time was the only known genus in the family Baetiscidae. This was subsequently followed with revised descriptions of the larvae and adults of the various species including their geographic distributions and phylogenetic relationships (Pescador and Berner 1981). The recent discovery and description of fossil specimens within the Baetiscidae has greatly altered the biogeographical perspective of the family.

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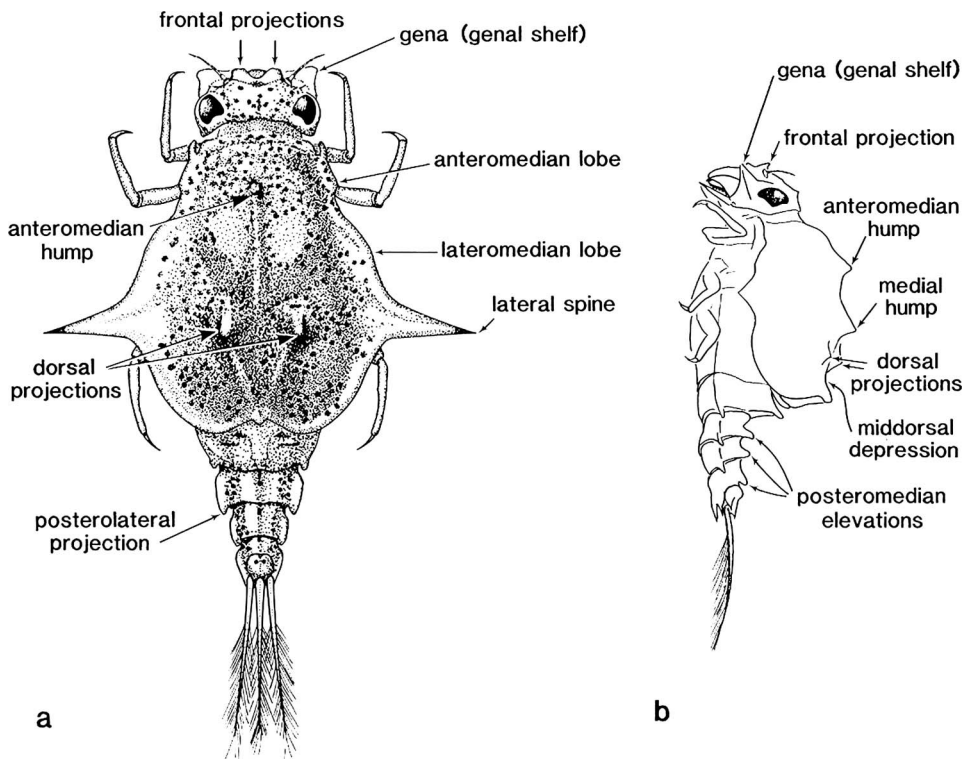


Figure 1. Schematic showing larval characters of *Baetisca* (adapted from Pescador and Berner 1981).

The objective of this paper is to update the current knowledge of the family in the context of the zoogeographical and evolutionary implications of both fossil and extant taxa.

Materials and methods

The geographic range of the genus *Baetisca* discussed herein was largely based on comprehensive locality records of the various species that were included in Pescador and Berner (1981). Subsequent locality data of the genus after the 1981 paper, including published records, specimens loaned from various public and private institutions, and personal collections were added for more updated coverage of the geographic range of the genus. Locality records were entered in a relational database and used to generate a GIS map of the geographic distribution of the various species of *Baetisca*.

For phylogenetic analysis, a data matrix was constructed for 10 species of *Baetisca* using 21 characters of both mature larvae and adults (Tables 1 and 2 and Figure 1). *Baetisca callosa* was excluded from the analysis for lack of mature specimens for study. The recent acquisition of numerous specimens of *Baetisca bernerii* and examination of this material has shown a lack of consistently reliable morphological characters of both larvae and adults to distinguish this species from *Baetisca carolina*, thus they are considered conspecific in the analysis.

Table 1. Character data matrix for the 11 species used in the cladistic analysis.

	Character states																				
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Prosopistoma variegatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Baetisca becki</i>	1	0	0	1	0	1	3	2	0	0	1	0	0	0	1	1	3	3	0	1	1
<i>Baetisca carolina</i>	2	1	0	0	0	1	2	1	0	0	1	0	0	0	1	0	1	3	0	1	1
<i>Baetisca columbiana</i>	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	1	?	?	?
<i>Baetisca escambiensis</i>	2	1	1	0	0	1	3	0	0	0	0	1	1	1	0	1	1	3	1	1	1
<i>Baetisca gibbera</i>	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0
<i>Baetisca lacustris</i>	1	0	0	1	0	1	2	2	0	0	1	0	0	0	1	1	2	2	0	0	0
<i>Baetisca laurentina</i>	1	0	0	1	1	1	2	2	0	1	0	0	0	0	1	1	1	2	0	0	0
<i>Baetisca obesa</i>	1	0	0	1	1	1	2	2	0	0	1	0	0	0	1	1	1	2	0	0	0
<i>Baetisca rogersi</i>	1	0	0	1	0	2	2	2	1	0	1	0	0	0	1	0	3	3	0	1	1
<i>Baetisca rubescens</i>	2	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	2	0	1	2

? = adult unknown.

As Prosopistomatidae are commonly considered as sister group of Baetiscidae (Ogden et al. 2009), the type species of the genus *Prosopistoma*, *P. variegatum*, was chosen as outgroup. The matrix was analysed using TNT (Goloboff, Farris and Nixon 2003) under implied weights with the most parsimonious tree obtained using implicit enumeration. Trees were redrawn with WinClada (Nixon 1999).

Results and discussion

Fossil Baetiscidae

Recent discovery of fossil Baetiscidae has dramatically changed the evolutionary perspective of the family. *Balticobaetisca velteni*, a new genus and species from Baltic Amber (Eocene), is the first fossil record of the Baetiscidae and the first Old World record for this family (Staniczek and Bechly 2002). The lack of both a mid-dorsal transverse and apical cleft in sternum IX of the female imago and a mid-dorsal transverse elevation in abdominal tergum VI according to Staniczek and Bechly (2002) are plesiomorphic characters separating this fossil genus from *Baetisca*. Moreover, that the fossil specimen is about 45 million years old, and lived in a zoogeographical region that has undergone catastrophic climatic changes since then, suggests beyond reasonable doubts that this taxon is indeed not congeneric with extant *Baetisca*.

More recently, a male imago of *Balticobaetisca* from Baltic Amber has been described as a second species, *B. stuttgartia*, which is distinguished from the female imago of *B. velteni* only by the distinctly more prominent costal projection of the hind wings (Godunko and Krzeminski 2009). Regardless of whether this male imago indeed represents a new species of *Balticobaetisca* or rather the male of *B. velteni*, its genitalia differ from the genitalia of all extant *Baetisca* in having separated penis lobes (plesiomorphic compared to the condition in *Baetisca*). Additionally, the first segment of the forceps medially is not only indented and with a median knob, but also with a distinct triangular projection on the inner margin (possibly apomorphic compared to *Baetisca*).

In a study of the Lower Cretaceous Crato Fossil Beds of Brazil, Staniczek (2007) described a new genus and species, *Protobaetisca bechlyi* (Figure 2), based on a larva. Its posteriorly extended mesonotum forms a carapace as is present in all Baetiscoidea,

Table 2. Characters and states used in the cladistic analysis.

Character	Character states	
<i>Larva</i>		
0. Frontal projection	(1) bilobed	(2) non-bilobed
1. Genae	(1) not produced into spines	
2. Compound eyes	(1) striped	
3. ♀ occipital tubercles	(1) present	
4. Lateral margins of mesonotal shield	(1) nearly parallel	
5. Lateromedian lobe of mesonotal shield	(1) weakly developed broadly rounded	(2) well-developed subtriangular
6. Lateral projections of mesonotal shield	(1) length subequal to shorter than width at base	(2) length 1.3–1.7x width at base
7. Dorsal projections of mesonotal shield	(1) present, low elevated, broadly rounded	(2) present, highly elevated, cone or peg shaped
8. Lateral margins of mesonotal shield	(1) finely denticulate	(2) coarsely serrate
9. Outlining/markings of ventral margin of mesonotal shield	(1) present	
10. Legs	(1) bicoloured	
11. Tarsal claws	(1) > 1/2 length of tarsi	
12. Lateral margins of abdomen	(1) glabrous or with few short hairs	
13. Posterolateral projections of abdominal segments VI–VIII	(1) weakly developed, apically blunt	(1) well-developed, apically sharp pointed

(continued)

Table 2. (Continued).

Character	Character states
14. Dorsoventral shape of larva	(1) distinctly convex
15. Length vs width of mesonotal shield	(1) length longer than width
16. Pattern of speckling/ markings on mesonotal shield	(1) reticulate
17. Apex of lateral projections of mesonotal shield	(2) finely checked or grainy (2) tapered to pointed, if sclerotised, only at tip
<i>Adult</i>	
18. Shape of penes	(1) subquadrangular
19. Forewings of imago	(1) basal 1/3-1/2 flushed with orange to reddish brown
20. Hind wings of imago	(1) basal 1/4-3/4 flushed with orange to reddish brown (2) almost entirely orange to reddish brown

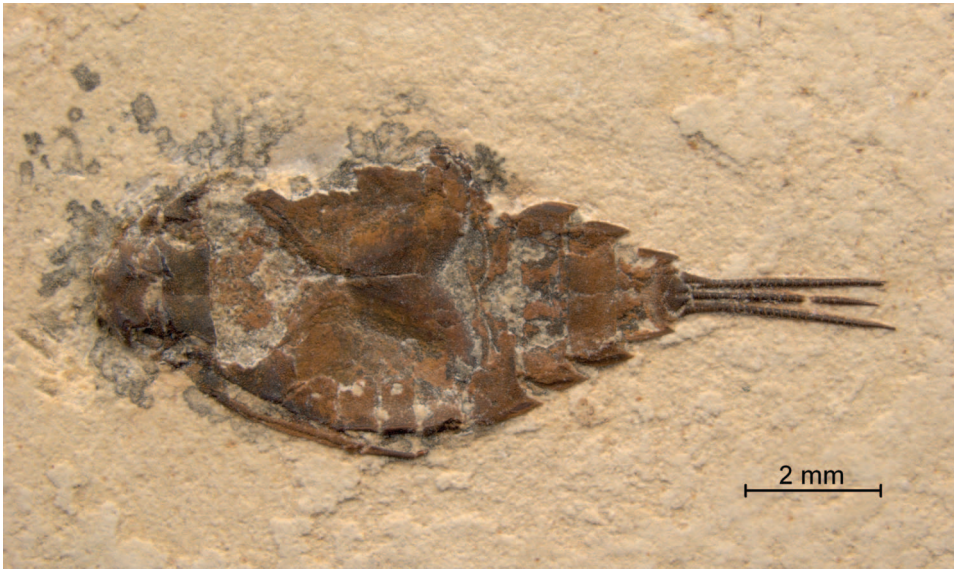


Figure 2. *Protobaetisca bechlyi*, larva.

and the prominent frontal head projections suggest the placement of this fossil specimen in the stem group of Baetiscidae. Jell and Duncan (1986) discussed a Lower Cretaceous specimen from Australia questionably identified as Siphonuridae, mentioning the similarities to Baetiscidae, but refrained from assigning it to the family. Nevertheless, the fossil appears to belong to either Baetiscidae or Baetiscoidea (Staniczek 2007). The presence of a prominent transverse subapical ridge on the carapace [Figure 1 in Jell and Duncan (1986)] suggests that the fossil specimen is more closely allied to the stemline of Baetiscidae than to the Prosopistomatidae. A fossil species *Cretomitarcys luzzii* from the Upper Cretaceous of New Jersey, originally described in †Cretomitarcyinae, a subfamily of Polymitarcyidae, by Sinitshenkova (2000) was recently assigned to Baetiscidae (Staniczek 2007), based upon the rounded hind wing with multiple intercalaries. The discovery of fossil specimens of Baetiscidae from the Neotropics, Nearctic, Palearctic and presumably Australasia vastly extends the palaeogeographic range of the family and certainly presents an interesting new concept of the probable evolution of the family.

Cladistic analysis

The cladistic analysis of 20 coded characters (Tables 1 and 2) resulted in a single most parsimonious tree with $L = 42$, $Ci = 71$ (Figure 3a). The original *Baetisca* phylogeny proposed by Pescador and Berner (1981) is presented for comparison (Figure 3b).

The most parsimonious tree shows two notable clades, the first consisting of *B. laurentina* and *B. obesa* united by the nearly parallel lateral margins of the mesonotal shield and the second consisting of *B. becki*, *B. rogersi*, *B. carolina*, *B. escambiensis* and *B. rubescens* which are united by colouration of fore and hind wings.

It is notable that *B. escambiensis* and *B. gibbera* are found in different clades in the current phylogeny compared to the previous phylogeny of Pescador and Berner

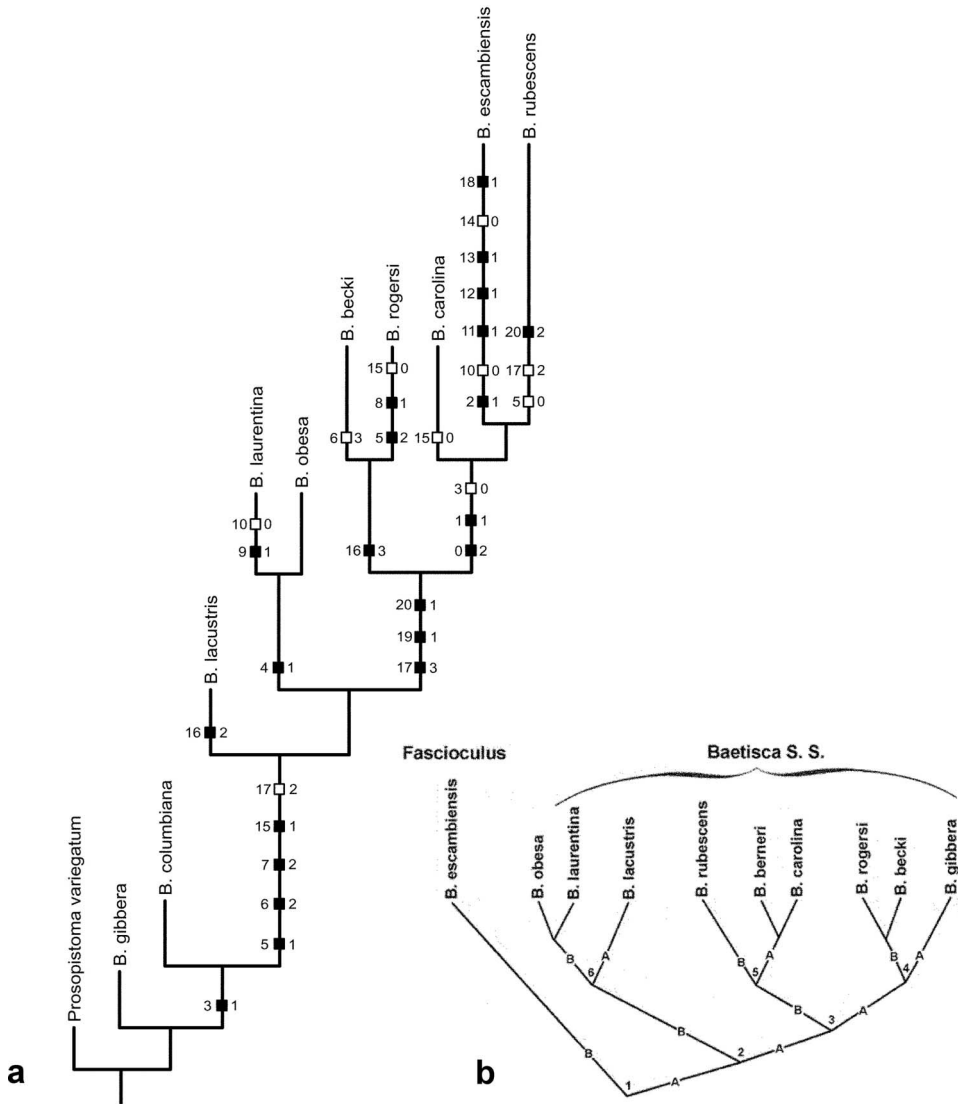


Figure 3. (a) Cladogram of the single most parsimonious tree resulting from the analysis. Synapomorphies are indicated in black and homoplasies in white. (b) The phylogeny of *Baetisca* presented by Pescador and Berner (1981).

(1981). *Baetisca escambiensis* which was previously thought to be sister to the remaining species of *Baetisca* is now shown to be a derived member of the clade ((*B. escambiensis* + *B. rubescens*) + *B. carolina*/*B. berneri*).

Zoogeography

The distribution pattern of fossil Baetiscidae appears to reflect a classic case of vicariance biogeography, where a previously continuous landmass was separated by geological events. Estimated sequences and times of tectonic events that separated this once continuous landmass have been well documented (Pielou 1979; Grimaldi

and Engel 2004) and the family is now recorded from four of the six continents from which mayflies are known. The family Baetiscidae now includes fossil records in the Neotropics (*Protobaetisca*), Nearctic (*Cretomitarcys*), Palearctic (*Balticobaetisca*) and presumably in Australasia.

The single extant genus *Baetisca* is currently limited to the Nearctic. The absence of extant Baetiscidae in areas where fossils have been recorded poses questions of possible events that may have led to extinction rather than lack of collection effort. The extinction of the Palearctic *Balticobaetisca* could well be related to the differential extinction of biota during the Pleistocene glaciations. In the face of advancing glaciers from the north, the east–west mountain ranges in much of the Palearctic were likely a barrier to migrations associated with the ice age, thus promoting greater extinction rates compared to the north–south ranges in the Nearctic which are believed to have provided more southern migration routes to biota (Stanley 1989 as discussed in McCafferty 1999). The Nearctic fossil genus *Cretomitarcys* was likely lost during glaciation events in North America. The extinction of *Protobaetisca* in the Neotropics may have been associated with the Cretaceous-Tertiary mass extinction, a phenomenon more widely known as the K-T boundary (Raup 1991; Grimaldi and Engel 2004). Cosmic events and subsequent increased volcanic activity have been theorised as the probable cause of the K-T boundary. Impacts of these events presumably caused catastrophic changes in and loss of habitats which led to mass extinction of diverse and unrelated lineages. This event appears to have had a major role in the extinction of many Mesozoic and Tertiary mayflies. The mayflies of the Tertiary account for a large part of the extant genera in the southern hemisphere (McCafferty 1999).

Table 3 and Figure 4 show the current geographic distribution of *Baetisca* species. All species except for the enigmatic species *B. columbiana*, and the

Table 3. Taxa of Baetiscidae with known stages and distributions.

Baetiscidae	Stage	Distribution
† <i>Balticobaetisca velteni</i> Staniczek & Bechly, 2002	A	Baltic
† <i>Balticobaetisca stuttgartia</i> Godunko & Krzeminski, 2009	A	Baltic
† <i>Cretomitarcys luzzii</i> Sinitshenkova, 2000	A	USA: New Jersey
† <i>Protobaetisca bechlyi</i> Staniczek, 2007	L	Brazil: Crato Beds
<i>Baetisca becki</i> Schneider & Berner, 1963	L A	USA: SE
<i>B. bernerii</i> Tarter & Kirchner, 1978	L A	USA: SE, NE
<i>B. callosa</i> Traver, 1931	L	USA: SE
<i>B. carolina</i> Traver, 1931	L A	USA: SE, NE
<i>B. columbiana</i> Edmunds, 1960	L	USA: NW
<i>B. escambiensis</i> Berner, 1955	L A	USA: SE
<i>B. gibbera</i> Berner, 1953	L A	USA: SE
<i>B. lacustris</i> McDunnough, 1932	L A	USA: SE, NE CAN: NE, NW
<i>B. laurentina</i> McDunnough, 1932	L A	USA: SE, NE, NW CAN: NE, NW, FN
<i>B. obesa</i> (Say, 1839)	L A	USA: SE, NE CAN: NE, FN
<i>B. rogersi</i> Berner, 1940	L A	USA: SE
<i>B. rubescens</i> (Provancher, 1878)	L A	USA: SE, NE CAN: NE

L = larva, A = adult; SE = southeast, NE = northeast, NW = northwest, FN = far north.

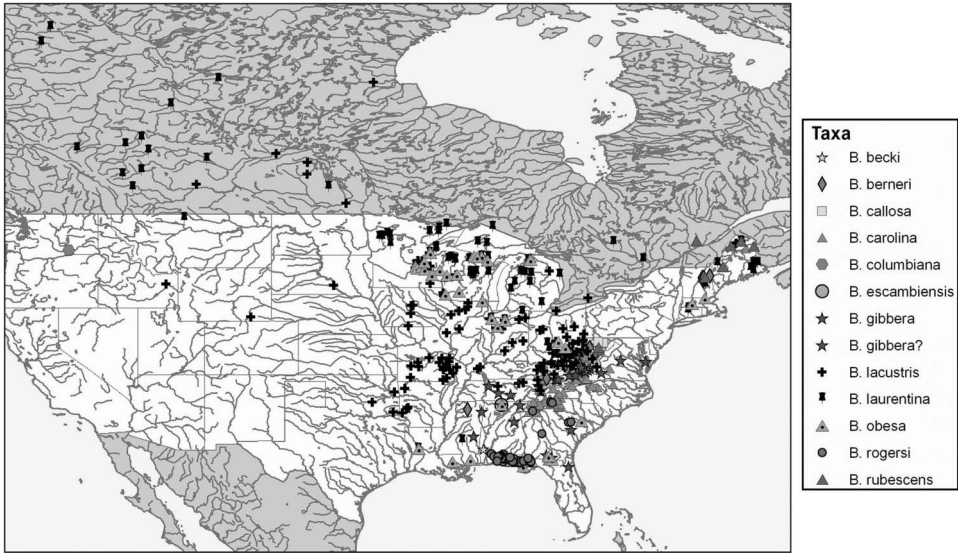


Figure 4. GIS map of the distribution of the 12 species of *Baetisca* in North America. Map prepared by Katherine Milla and the FAMU GIS lab, May 2008.

geographically widespread *B. lacustris*, only occur east of the Continental Divide. The distributional pattern of the genus presents some interesting possibilities. Lehmkuhl (1972) speculated that all of the northern range of the most widely distributed species, *B. lacustris* and *B. laurentina*, including the entire Hudson Bay System, was glaciated 10–12 thousand years ago and they were pushed to the ice-free areas of the South. As the ice receded, these two species, and perhaps *B. obesa*, moved northward from parental populations via the Mississippi River drainage. The occurrence of disjunct populations of aquatic insect species, notably weak flyers like the mayflies and stoneflies, in the Saskatchewan drainage and Mississippi drainage in spite of the present day barrier that exists between the drainages could be explained by glacial river patterns (Lehmkuhl 1972, 1980; Pielou 1991). The Saskatchewan drainage once curved south and flowed into the Mississippi River system, and at that time aquatic insects including mayflies and stoneflies presumably entered the Saskatchewan drainage. Subsequently, the Saskatchewan drainage turned north to Hudson Bay isolating its aquatic insect population from that of the Mississippi drainage. Except for the widely spread *Baetisca obesa*, which occurs both east and west of the Mississippi drainage, the rest of the species of the genus are found primarily east of the drainage. For a more detailed discussion on the distribution of the genus see Pescador and Berner (1981).

The southeast region is the centre of diversity of *Baetisca*: 11 of the 12 known species occur there. The region includes some of the most evolutionarily significant areas on the continent and exhibits the greatest known diversity of several important groups of aquatic fauna including mayflies (Isphording and Fitzpatrick 1992). Climate and lack of glaciation appear to have had a major impact on the high diversity of the aquatic fauna in the region (Adams and Hackney 1992). Compared to the other regions of the continental United States, the subtropical climate of the southeast is conducive to both the life history and distribution patterns of

many aquatic insects. It has been well documented that many areas of the southeast served as refugia for organisms including aquatic insects that migrated from the north during glaciation (Pielou 1991). Being confined to streams and rivers, several of these organisms, notably mayflies and stoneflies, have limited mobility and poor dispersal abilities. Hence, northward movement at the end of glaciation was limited and these organisms either remained and adapted to the changing climate in the region or became extinct. It is reasonable to suppose that through time speciation occurred which contributed to the present diversity of the aquatic fauna in the region.

Conclusions

Based on fossil records the Baetiscidae are apparently of Pangaeian origin and thus originated at least 200 million years ago and their ancient distribution is presumably associated with vicariant events. The cladistic analysis yielded a new hypothesis regarding the evolutionary relationships of the 10 species of *Baetisca* included in the analysis. The extant genus *Baetisca* appears to be of boreal origin and their current distribution appears to be a result of glaciation events. The southeastern United States is the centre of diversity for *Baetisca*.

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References

- Adams, S.M., and Hackney, C.T. (1992), 'Ecological processes in southeastern United States aquatic ecosystems', in *Biodiversity of the southern United States aquatic communities*, eds. C.T. Hackney, S.M. Adams and W.H. Martin, New York: John Wiley & Sons, pp. 3–65.
- Berner, L., and Pescador, M.L. (1980), 'The mayfly family Baetiscidae (Ephemeroptera). Part I', in *Advances in Ephemeroptera Biology*, eds. J.F. Flannagan and K.E. Marshall, New York: Plenum Press, pp. 511–524.
- Berner, L., and Pescador, M.L. (1988), *The Mayflies of Florida* (rev. ed.), Gainesville, FL: University Presses of Florida.
- Godunko, R.J., and Krzeminski, W. (2009), 'New fossil findings of the mayfly genera *Balticobaetisca* Staniczek & Bechly, 2002 (Ephemeroptera: Baetiscidae) and *Borinquena* Traver, 1938 (Leptophlebiidae: Atalophlebiinae)', in *International Perspectives in Mayfly and Stonefly Research. Proceedings of the 12th International Conference on Ephemeroptera and the 16th International Symposium on Plecoptera, Stuttgart 2008*, ed. A.H. Staniczek, *Aquatic Insects*, 31 (Suppl. 1), 125–136.
- Goloboff, P.A., Farris, J.S., and Nixon, K.C. (2003), T.N.T.: Tree Analysis Using New Technology. Willi Hennig Society Edition, Version 1.1, February 2008.
- Grimaldi, D. (2005), *Evolution of the Insects*, New York, New York: Cambridge University Press.

- Ishphording, W.C., and Fitzpatrick, J.J. Jr. (1992), 'Geologic and evolutionary history of drainage systems in the southeastern United States', in *Biodiversity of the Southeastern United States Aquatic Communities*, eds. C.T. Hackney, S.M. Adams and W.H. Martin, New York: John Wiley and Sons, pp. 19–56.
- Jell, P.L., and Duncan, P.M. (1986), 'Invertebrates, mainly insects, from the freshwater Lower Cretaceous, Koonwara Fossil Bed (Korumburra Group), South Gippsland', *Memoirs Association of Australasian Paleontologists*, 3, 111–205.
- Lehmkuhl, D.M. (1972), '*Baetisca* (Ephemeroptera: Baetiscidae) from the western interior of Canada with notes on the life cycle', *Canadian Journal of Zoologists*, 50, 1015–1017.
- Lehmkuhl, D.M. (1980), 'Temporal and spatial changes in the Canadian insect fauna: patterns and explanation of prairies', *The Canadian Entomologist*, 112, 1145–1159.
- McCafferty, W.P. (1999), 'Biodiversity and Biogeography: Examples from Global Studies of Ephemeroptera', in *Proceedings of the Symposium on Nature Conservation and Entomology in the 21st Century*, Chonan, Korea: Entomological Society of Korea.
- Nixon, K.C. WinClada ver. 1.00.08, 1999–2002.
- Ogden, T.H., Gattolliat, J.L., Sartori, M., Staniczek, A.H., Soldán, T., and Whiting, M.F. (2009), 'Towards a new paradigm in mayfly phylogeny (Ephemeroptera): combined analysis of morphological and molecular data', *Systematic Entomology*, 34, 616–634.
- Pescador, M.L., and Berner, L. (1981), 'The mayfly family Baetiscidae (Ephemeroptera). Part II. Biosystematics of the genus *Baetisca*', *Transactions of the American Entomological Society*, 107, 163–228.
- Pielou, E.C. (1979), *Biogeography*, New York: John Wiley and Sons.
- Pielou, E.C. (1991), *After the Ice Age, the Return of Life to Glaciated North America*, Chicago: The University of Chicago Press.
- Raup, D.M. (1991), *Extinction Bad Genes or Bad Luck*, New York: W.W. Norton.
- Sinitshenkova, N.D. (2000), 'New Jersey amber mayflies: the first North American Mesozoic member of the order (Insecta: Ephemeroptera)', in *Studies in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed. D. Grimaldi, Leiden: Backhuys Publishers, pp. 111–125.
- Stanley, S.M. (1989), *Earth and Life Through Time* (2nd ed.), New York: Freeman.
- Staniczek, A.H. (2007), 'Ephemeroptera: mayflies', in *The Crato Fossil Beds of Brazil: Window into an Ancient World*, eds. D.M. Martill, G. Bechly and R.F. Loveridge, Cambridge: Cambridge University Press, pp. 163–184.
- Staniczek, A.H., and Bechly, G. (2002), 'First fossil record of the mayfly family Baetiscidae from the Baltic amber (Insecta: Ephemeroptera)', *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)*, 322, 1–11.
- Walsh, B.D. (1864), 'On the pupa of the ephemerinus genus *Baetisca* Walsh', *Proceedings of the Entomological Society of Philadelphia*, 3, 200–206.