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THE MAYFLY FAMILY BAETISCIDAE (EPHEMEROPTERA). PART I

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ABSTRACT

The history of the taxonomy and phylogeny of Baetisca, the single genus in the family Baetiscidae, is reviewed beginning with the description of Prosopistoma as a crustacean. The relationship of the Prosopistomatidae to the Baetiscidae is treated as well as the concurrence of the authors with Edmunds' conclusion that the two families are derived from a common ancestor but parallel evolution must explain some of their similarities. There is a summary of presently recognized species and characteristics by which nymphs are differentiated. A brief treatment of the ecology and life history of various species is included.

INTRODUCTION

If Latreille had had nymphal specimens of Baetisca in 1833, would he have been as puzzled by them as he was by Prosopistoma when he described these curious nymphs as a new genus of crustacean? Certainly, Baetisca nymphs are sufficiently different from other Ephemeroptera to cause one to conclude that he might have done so. The superficial similarities of the mesonotal shields and the gills were enough to lead early entomologists to the misconception that the two are very closely related. Only in recent years, through

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modern phylogenetic studies of all stages, has it been recognized that there are significant differences between them.

Say (1839) described a new species of Baetisca, which he called obesa, because of its short, robust body. Next, Walker (1853) characterized Baetis obesa both in Latin and English. Hagen (1861) also briefly redescribed the subimago following Say's earlier descriptions, and the species was recognized by Walsh (1862) as being a member of his new genus Baetisca after he secured male imagos. In 1863, he remarked (p. 178) "B. obesa Say, Walsh. Both genus and species new to me; very curious." Say's description was based on the subimago. Walsh (1864), after four years, successfully reared adults from the nymph and was then able to relate the two stages. He had sent a specimen of the nymph to Hagen, who wrote to Walsh "The larva No. 66 is the most extraordinary animal I have seen, so that I asked myself whether it really belonged to Insecta." After careful analysis he concluded that it was an insect assigned to the "Ephemerina." Even more surprising, he was able to relate the nymph to an adult Baetisca obesa which Walsh had sent to him earlier. Walsh (1864), with Hagen's confirmation in hand, gave an excellent description of the nymph and discussed his observations of its habitat and emergence.

Eaton (1871), in his A Monograph on the Ephemeridae, redescribed the genus and the single, known species, B. obesa in Latin. He illustrated the forewing (pl. II, Fig. 6) and the male genitalia (pl. V, Fig. 9), both rather poorly.

Provancher (1876) reported a species from Quebec as Cloe uni-color Hagen, but in 1877 decided that his specimens represented a new species, which he named Cloe rubescens, nov. sp. Subsequently, McDunnough (1921), after studying Provancher's male specimen, assigned it to Baetisca making rubescens the second species to be included in the genus.

Joly (1880) published a French translation of Walsh's (1864) description of Baetisca and added comments in footnotes. Here he compared features of Baetisca with those of Prosopistoma punctifrons (= P. foliacium Fourcroy) and P. variegatum Latrielle. Vayssière, (1882) in his very comprehensive paper on Ephemeroptera, reported that he saw analogies between Prosopistoma and Baetisca nymphs in their respiratory apparatus and he discussed their morphology at length as well as providing excellent illustrations. He concluded that Baetisca is to North America what Prosopistoma is to Europe and Madagascar.

Eaton (1885) described and illustrated both adult and nymphal stages of Baetisea. Subsequently, Needham (1905) reported that B. obesa had been taken in New York State and in Indiana and he included photographs of the nymph and subimaginal wings. Ulmer

(1920) merely listed the family Baetiscidae with only a single genus, Baetisea, included in it. The next reports of the genus were those of Clemens (1913, 1915) in his study of mayflies of the Georgian Bay area of Lake Huron.

Traver (1931) added two new species of Baetisca, carolina and the enigmatic callosa from North Carolina and West Virgina, respectively. Soon afterwards, McDunnough (1932) reported two additional species, B. laurentina and B. lacustris, from Canada, and also provided a key to the known nymphs. Traver again reported in 1932 on B. carolina in North Carolina and in 1937 she described B. thomsenae from that State. The latter species was synonymized with B. carolina by Berner (1955).

The classic work by Needham, Traver, and Hsu (1935), The Biology of Mayflies, gave a comprehensive summary of the taxonomic knowledge of Baetisca. Neave (1934) described B. bajkovi from Manitoba and Spieth (1933, p. 359) concluded that "Baetisca seems a distinct entity in the phylogenetic arrangement of mayflies." He erected the superfamily Baetiscoidea to accommodate the family.

Baetisca rogersi was described from northwestern Florida by Berner (1940) and further details were added by him in 1950. He summarized the knowledge of the southeastern species of the genus in 1955 and described two new ones at that time, B. escambiensis and B. gibbera. Burks treated the Illinois species in 1953, and in 1962 the late Justin Leonard and his wife Fannie did the same for Michigan. Daggy (1945) reported that the genus occurs in Minnesota.

Following World War II, with the great upsurge of interest in aquatic insects, Baetisca was frequently encountered in stream studies and reports of its occurrence grew. In 1959, Berner summarized our knowledge of the genus to that date in tabular form. Until Edmunds' (1960) report no species was known positively to occur in western North America and in that paper he described Baetisca columbiana, a species not subsequently reported. Schneider and Berner (1963) described another Florida species, B. becki, from the northwestern part of the State. Later, Pescador and Peters (1971) described the imago of becki reared from the nymphal stage. The most recently described species, B. berneri, is that of Tarter and Kirchner (1978) from West Virginia. The latest treatment of Baetisca was given by Edmunds, Jensen, and Berner (1976) in their book on North and Central American mayflies.

PHYLOGENETIC RELATIONSHIPS OF THE BAETISCIDAE

Few papers have been published dealing with the relationships of Baetiscidae and Prosopistomatidae. In 1917, Lameere included

two subfamilies in his Prosopistomidae, Hexagenitinae, which is composed of the fossil genus *Hexagenites*, and Prosopistominae, divided into two tribes, the Baetiscini and Prosopistomini.

In a discussion of the systematic position of *Prosopistoma*, Gillies (1954) concluded that both *Baetisea* and *Prosopistoma* are derived from a common stock of great antiquity, but since then evolution and specialization have proceeded independently. His conclusion was based on the nymphs having many structural features in common, notably a mesonotal carapace, branchial chamber, and cephalization of the central nervous system, and the adults having the similarly unique arrangement of the cubital veins of the wings.

Fontaine (1958), studying the affinities of *Prosopistoma*, noted the nymphal similarities with *Baetisca*. She proposed two causes that might result in the similarities: (1) *Prosopistoma* and *Baetisca* possess true systematic affinities and come from the same ancestor and (2) *Prosopistoma* and *Baetisca* are two evolved genera—*Prosopistoma* having the higher degree of evolution (the mesonotal shield forming a true respiratory chamber, the labium completely encircled in its basilar portion, the nervous system with the thoracic and abdominal ganglia fused into a single mass). They are parallel evolutionary lines and are distinct from the remainder of the Ephemeroptera.

Fifty-two years after the appearance of his study of the morphology of immature Ephemeroptera, Vayssière published in 1934 an anatomical study of *Baetisca obesa* and *B. carolina*. He concluded that the internal anatomy of *Baetisca* is much like that of *Prosopistoma* and that his ideas put forward in 1882 about the relations of the two had now been authenticated.

Landa's (1969) investigation of the comparative anatomy of mayfly nymphs indicated that the Neoephemeridae showed close relationships to the Caenidae, Prosopistomatidae, and particularly to the Baetiscidae. In the Caenidae, he concluded that Brachycercus is more closely related to Baetisca than is Caenis. His phylogeny, based on the comparative anatomy of the tracheal system, Malpighian tubes, and the nerve band of nymphs and illustrated in a 1973 paper, represented the Neoephemeridae and the Baestiscidae as being related and the Caenidae related to the Prosopistomatidae. The four families are derived from a common stem.

Demoulin (1956 and 1969) presents cogent arguments in support of his contention that the Baetiscidae are derived from the Oniscigasterinae and the Prosopistomatidae from the Ameletopsinae and that both families should be included in the superfamily Siphlonuroidea. He has given an interesting analysis of morphological evidence leading him to his conclusions; however, we remain in agreement with Edmunds' interpretation of the phylogeny of these

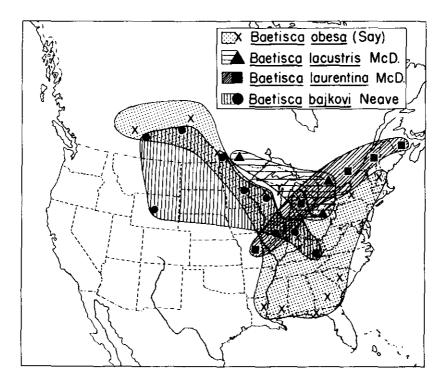


Figure 1. Presently known distribution of the species of Baetisca in North America.

two families.

In Edmunds' comprehensive study (1972) of the evolution of Ephemeroptera, a diagram of a probable phylogeny for the families and subfamilies was given. He discussed in detail his reasoning for the derivation as pictured and postulated that parallel evolution must explain some of the similarities existing between the Baetiscidae and Prosopistomatidae. Similar phylogenetic relationships were given by Koss (1973) and Rick (1973) using egg and nymphal characters respectively. Riek is somewhat more reserved, however, about the relationships of these two groups. He stated that although the Prosopistomatidae and Baetiscidae are referred to the same superfamily at present, the differences both in nymphs and adults are such that a more-detailed study may indicate that they are not as closely related as at present assumed. He pointed out that the Prosopistomatidae, in which the venation is very reduced, are the only Recent mayflies in which there is no evidence of a triadic branching of MA. The Baetiscidae, on the other hand, have the most generalized venation of all Recent species;

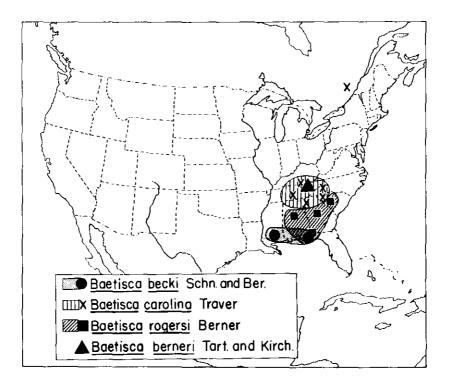


Figure 2. Presently known distribution of the species of *Baetisca* in North America.

the venation differs from that of the Lower Permian Misthodotidae mainly in the basal alignment of the veins. There is also a slight reduction in the anal field.

Edmunds et al. (1976) again diagrammatically represented the Baetiscidae and the Prosopistomatidae as being derived from a common ancestor, which are, in turn, related to the Neoephemeridae and the Caenidae. Our conception of phylogenetic relationships of the Baetiscidae are in accord with these. The presumed common origin of the Baetiscidae and the Prosopistomatidae are reflected in the assignment of the two families to the same superfamily, Prosopistomatoidea. McCafferty and Edmunds (1979), in proposing the suborders Schistonota and Pannota, have retained the superfamily Prosopistomatoidea for the Baetiscidae and Prosopistomatidae. We find no convincing data to contradict Edmunds' argument as to the kinship of these two families.

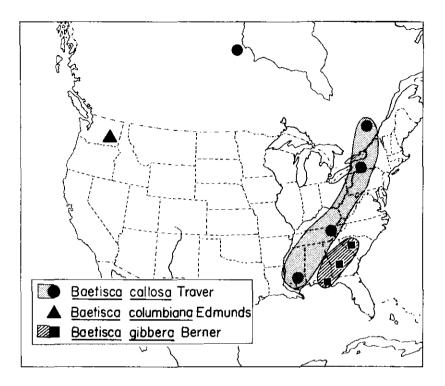


Figure 3. Presently known distribution of the species of *Baetisca* in North America.

TAXONOMY AND DISTRIBUTION

Presently, there are thirteen described species in the genus Baetisea, each of which will be treated in detail in Part II of our report on the family. The adults are most readily separated on the basis of wing pigmentation, with the male being the more distinctive sex. There is some likelihood that we shall be able to separate species of subimagos by differences in color pattern in the wings, but further study is necessary before we can determine the validity of this characteristic as a distinguishing one.

The various species of *Baetisea* are most easily characterized by nymphal differences and similarities. The structures we have employed for differentiation include the following:

Head: Shape and size of the frontal projections; shape and size of the genal projections; surface sculpturing.

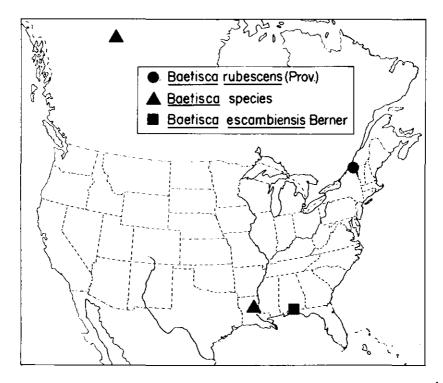


Figure 4. Presently known distribution of the species of Baetisca in North America.

Thorax: Lateral and dorsal projections of the mesothoracic shield; sculpturing and mottling pattern dorsally and ventrally.

Abdomen: Postero-median elevations and postero-lateral spines; mottling pattern

Based on our preliminary data, other nymphal characters that show considerable taxonomic value for species identification include: Head - marginal setation; eyes with or without stripes. Thorax - ratio between maximum length and width (including lateral projections) of mesonotal shield; legs, form and shape of femoral setae, setation of tibiae, and color pattern. Abdomen - form and shape of tergal setae and color pattern of caudal filaments.

The species, using nymphal morphology alone, fall roughly into four major groups as shown below. As the nymphal stage of *B. rubescens* is unknown, we have not listed it.

GROUP

A B C D

B. bajkovi B. becki B. callosa B. escambiensis
B. lacustris B. berneri B. columbiana
B. laurentina B. carolina B. gibbera

B. obesa B. rogersi

The various species are distributed widely over most of the eastern part of North America and into the Great Plains and north-westward to the Northwest Territories of Canada (Wiens $et\ al.\ 1975$). No species has yet been reported from the southwestern United States but one, B. columbiana, was described from the State of Washington. A single, dubious report of a California collection of Baetisea obesa was given by Eaton (1885) but there has been no further substantiation of the occurrence of the genus in this area (Day 1956). We have, therefore, concluded that Eaton's record was in error. Specific distributions of the species will be given in Part II but in general the known species, other than B. obesa, have rather restricted ranges. Some of this restriction reflects inadequate collecting rather than localization of the species (Figs. 1 - 4).

ECOLOGY AND LIFE HISTORY

There are only few detailed studies of the ecology and life histories of any species of Baetisca. Lehmkuhl (1972) reported on his study of the biology of B. bajkovi in Saskatchewan. Here, nymphs hatched in late summer, spent the winter under ice, and adults emerged in June and July of the following year. Pescador and Peters (1974) provided a detailed report of the life history and ecology of the southeastern B. rogersi in Florida. They concluded that eggs were dormant during the hot summer months, nymphs appeared in September and continued to be present through June of the following year. Emergence of adults began in April and continued to early July with only a single generation each year. The most recent life history study is that of Chaffee and Tarter (1979); working with B. bajkovi in West Virginia, they found it to be univoltine with greatest growth occurring from July to August. Subimagos emerged during May.

Most species of Baetisca are strictly rheophilic, except for B. lacustris and B. obesa. The nymphs of B. lacustris were described as lake dwellers while B. obesa can live in both running waters and ponds. Traver (1931) described the nymphal habitats of B. carolina and B. callosa and stated that the carolina nymphs were mostly collected from streams with their beds composed of loose gravel and sand near the quiet edge. Quoting Needham's account of his collecting of callosa nymphs in Johnny Cake Run near Mt. Storm,

West Virginia, Traver stated that they were found in a stream only a few inches deep with water flowing among the small stones and gravel. Traver also described the habits of nymphs, subimagos and imagos of *B. carolina*.

A paper by Berner (1955) on the Southeastern species of Baetisca gave accounts of the nymphal habitats of B. escambiensis, B. gibbera and B. obesa and included brief notes on the nymphal habits of escambiensis and obesa. Berner observed that escambiensis nymphs were collected most abundantly from river sandbars where an admixture of clay in the sand prevailed, the water current was relatively slow, and algal growth over the bottom was minimal. nymphs of gibbera were taken, from rather swiftly flowing streams, clinging to the underside of logs anchored at the bank or in areas where there was a thin overlaying layer of small pebbles. Compared to Walsh's observation of obesa nymphs in which he noted that they frequent rapidly-running rivers and attached themselves in repose to the undersurfaces of submerged stones, Berner observed a totally different sort of habitat of the species. He found the nymphs to occur almost invariably in very slow to almost stagnant water where they may be very common in moss which is attached to submerged trunks of trees, or other vegetation. Recently Pescador collected several nymphs of obesa from residual pools in flooded areas adjacent to the Chipola River in northwestern Florida.

The nymphs of *B. rogersi* usually inhabit gravel beds in sand bottom creeks (Berner 1940, 1950). Pescador and Peters (1974) observed that mature *rogersi* nymphs were typical members of a lithophilous association, living in the exposed, stony substratum section of the stream. Younger nymphs in the fourth through seventh instar live only in areas with a thick growth of filamentous algae and filamentous moss. Nymphs approaching emergence moved to quiet shallow sections of the stream, presumably to search for objects or places to leave the stream and emerge. Pescador and Peters also comprehensively discussed the habits of nymphs, subimagos and imagos of the species.

Nymphs of *B. becki* were observed by Schneider and Berner (1963) to occur in a swiftly flowing, clear, shallow, sand-bottomed stream under six to ten inches of water. Pescador and Peters (1971) collected *becki* nymphs from swifter, deeper water with more shifting, cleaner sand than nymphs of *rogersi* living in the same river. In a study of mayflies of Illinois, Burks (1953) observed that the nymphs of *B. bajkovi* developed in fairly rapid creeks and moderate-sized rivers. The early instar nymphs occur in the swift current, while the late instar nymphs migrate to the comparatively still eddies along the banks. Lehmkuhl (1972) stated that while nymphs of *B. bajkovi* are frequently collected in silty areas, their normal microhabitat appears to be solid substrate.

Except for McDunnough's (1932) brief comments on collecting numerous nymphal skins of *B. lacustris* found along the shores of Lake Erie and a mature nymph found in a pool, no other published accounts of the nymphal habitat of this species are known.

Leonard and Leonard (1962) briefly described the habitat of *B. laurentina* nymphs. The nymphs seem to prefer medium-sized to large rivers, where they partially submerge themselves in the flocculent surface layer of silt beds in quiet areas near the bank. In Wisconsin, Hilsenhoff (1975) found the nymphs of *Baetisea* in sandy streams where they inhabit sand and silt near the banks.

Nymphs of the recently described *B. berneri* seemed to prefer slow to medium water speeds with depths ranging from 15 to 46 cm, and a substrate mixture of sand, gravel, and small stones (Tarter and Kirchner 1978).

RESUME

Les auteurs examinent l'histoire de la taxonomie et de la phylogénie de la Baetisca, l'unique genre de la famille des baetiscidés, en décrivant d'abord le Prosopistoma en tant que crustacé. Ils traitent de la parenté qui existe entre la famille des prosopistomatidés et celle des baetiscidés et se déclarent d'accord avec la conclusion d'Edmund a l'effet que les deux familles descendent d'un ancêtre commun et que les similitudes sont sans doute dues au fait que leur évolution s'est effectuée parallèlement. L'ouvrage contient un précis des espèces présentement connues et des traits qui différencient les larves. Il contient également un aperçu de l'écologie et du cycle de vie des diverses espèces.

ZUSSAMENFASSUNG

Die Taxonomie und Phylogenie von Baetisca, der einzigen Gattung der Familie Baetiscidae, wird im geschichtlichen Überblick dargestellt, beginnend mit der Beschreibung der Nymphe von Prosopistoma als Krebstierchen. Es wird sowohl die verwandtschaftliche Beziehung der Prosopistomatiden zu den Baetisciden behandelt, als auch die Übereinstimmung der Autoren mit Edmunds' Schlußfolgerung, daß die beiden Familien auf eine gemeinsame Ahnenform zurückzuführen sind. Einige ihrer Ähnlichkeiten müssen jedoch durch parallele Evolution erklärt werden. Daran schließt sich eine Übersicht der zur Zeit anerkannten Arten und Charakteristiken, nach denen die Nymphen unterschieden werden. Auch eine kurze Behandlung der Ökologie und Lebensgeschichte verschiedener Arten ist beigefügt.

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