

**CRITICAL COMMENTARY ON
THE GENUS *SIPHONISCA*
(EPHEMEROPTERA: SIPHLONURIDAE)^{1,2}**

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ABSTRACT: Data are presented that contravene certain unfounded statements that have been published regarding *Siphonisca aerodromia*, a siphonurid mayfly from extreme northeastern U.S.A. and eastern Canada. The species is shown to be locally common in restricted habitats within its geographic range. A large number of mayfly species in North America are known from fewer locale records and specimens. Paleontological data indicate that *Siphonisca* is not represented in the fossil record, the Holarctic family Siphonuridae *sensu stricto* is not represented prior to the Tertiary, and *S. aerodromia* should not be considered a living fossil. Cladistic data place *Siphonisca* as a sister group of the genus *Parameletus*. The presence of lateral abdominal flanges in the adults are independent adaptations in a number of distantly related mayfly lineages and are related to gill position and type in the larval stage. The presence of laterally expanded abdomens in some Paleozoic insects does not necessarily denote close relationships with particular lineages of extant mayflies. The fact that *Siphonisca* is monotypic is not unique among North American mayfly genera.

In an appendix to the 1908 Report of the State Entomologist of New York, James G. Needham described the northeastern Nearctic siphonurid mayfly *Siphonisca aerodromia*. The description of the new genus and species was initially drafted for a single female adult from Sacandaga Park, Johnstown, New York, collected by C. P. Alexander. However, based on additional material of both male and female adults also collected by Alexander on June 6, 1909, and also from Sacandaga Park, the male description was also included. The date ascribed to this species has often been 1908 (e.g., Traver 1935; Burian and Gibbs 1988, 1991; McCafferty 1996). The date of the species name should be 1909, as listed by Edmunds and Allen (1957) and Edmunds (1962) because the name was not published or available until 1909 and because the description was in part based on 1909 data. Incidentally, for the same reason, the name *Potamanthus inequalis* Needham, which appeared in the same appendix, should also be dated 1909, as has been historically recognized in the literature. With respect to this somewhat awkward chronology, Bae and McCafferty (1991), in their comprehensive revision of the family Potamanthidae, referenced the name *P. inequalis* under the synonymy of *Anthopotamus myops* as "*Potamanthus inequalis* 1909 Needham In: Needham 1908. . ."

The larval stage of *S. aerodromia* was originally described by Clemens (1915)

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from larvae collected by Alexander at the species' type locality. Alexander's collecting notes were included in the paper by Clemens. Various other works essentially reviewed data from the original materials of this species from Sacandaga Park up until the time that Magnin and Harper (1970), Fiance (1978), and Hutchinson (1989) reported it from parts of eastern Canada; Gibbs (1980) and Burian and Gibbs (1991) reported specimens from several localities in Maine; Gibbs and Mingo (1986) provided some life history and feeding data; Burian and Gibbs (1988) thoroughly redescribed the species; and Gibbs and Siebenmann (1996) most recently critically studied the biology of the species. In the latter paper, another record from New York was mentioned, but with no data associated with it. No other species of *Siphonisca* have been discovered, and the genus remains monotypic and restricted to northeastern North America.

Two primary conceptions associated with this relatively large sized and striking species seem to have preoccupied both researchers who have recently worked with the species and others who have written about it. The first is the presence of unusually large lateral flanges on the abdomen of the adults that are conspicuous in flight. The other is the continually repeated idea that *S. aerodromia* is one of the rarest mayflies. Both of these conceptions have now apparently been linked with an idea that *S. aerodromia* is unique among recent mayflies and is somehow a "living fossil" (Anonymous 1995). We argue herein that these conceptions are not valid. Abdominal flanges are found in a number of pisciform mayflies, including both siphonurids and non-siphonurids, but are more common outside North America (abdominal flanges are also independently evolved in pannota mayflies and others). *Siphonisca* appears to be very closely related to another more widespread genus of the family Siphonuridae. And, based on its abundance and studied populations recently found of the species, *S. aerodromia* should be considered locally common and is not rare compared to many other mayflies in North America.

DISCUSSION

Alexander (pers. comm. with GFE) stated of his 1909 collections of *S. aerodromia*, that "they were abundant and they kept high in the air where they were conspicuous by reason of the wide abdomen (lateral expansions of segments 5-9)." The noted insect morphologist G. C. Crampton was intrigued by the resemblance of the abdominal flanges to similar expansions on the thorax or abdomen of certain Paleozoic insects (Alexander, pers. comm.). This led to additional collecting trips to Sacandaga Park, where Alexander and, later, Crampton obtained more specimens (see Edmunds *et al.* 1976). Needham (1908) compared the abdomen of *S. aerodromia* to that of the New Zealand *Oniscigaster wakefieldi* McLachlan (Oniscigasteridae), one of the other species known at the time to have abdominal flanges. We know of no suggestion by Crampton

that the abdominal flanges of *Siphonisca* represented a retention of Paleozoic characteristics or a suggestion that *Siphonisca* was more primitive than other extant pisciform mayflies. Furthermore, *Siphonisca* was not compared with Paleozoic insects in Crampton's insect morphology notes (read by GFE in a course given at the University of Massachusetts by J. F. Hanson).

A small, rather curious article about *S. aerodromia* recently appeared in *Fly Fisherman Magazine* (Anonymous 1995). The article was accompanied by a photograph of a female adult mayfly taken in western Pennsylvania that was labeled as "An adult mayfly that may be a rare carnivorous Tomah mayfly." ["Tomah mayfly" is a vernacular name given to *S. aerodromia*, alluding to the stream in Maine where most published scientific studies of the mayfly have been conducted; but the photographed mayfly from Pennsylvania is most certainly not *Siphonisca*, based on its obvious non-siphonuroid wing venation.] We take exception to certain impressions conveyed by statements about *S. aerodromia* given in that article because the article will most certainly be seen by some entomologists, and erroneous or unfounded information regarding the species may be cited in the literature. Obviously, popular articles must be taken with "a grain of salt," because errors in fact can be common; however, this article is additionally vexing because an ephemeropterist is evidently the source of the information. We are particularly concerned with impressions of *S. aerodromia* that are conveyed with the statements: ". . . it's so rare—in effect a flying fossil dating from the Paleozoic Era – that it disappeared for 50 years and was considered extinct" and that it "has been called the rarest mayfly in the world." Moreover, the article indicated that in the Spring, 1995 issue of the *Maine Legacy*, the magazine of the Maine Nature Conservancy, the mayfly was cited as standing apart from other North America mayflies by not sharing its genus with any other.

From existing published records of *S. aerodromia* (see references above), it has become apparent that the species – while restricted somewhat geographically to the extreme northeastern United States and eastern Canada, and by habitat availability (stream backwaters and temporary floodplains) – is nonetheless locally common and often abundant where it occurs. Despite this, a recent scientific article continued to promulgate the misconception of rareness by using the phrase "the rare mayfly *Siphonisca aerodromia*" in its title (Gibbs and Siebenmann 1996). We estimate that at least 100 North American mayfly species, representative of most North American families, are presently known from fewer specimens and fewer locale records. In many of these cases, the "rarity" of such species is a collecting artifact. In other words, efficient sampling historically has not been possible because usual collecting techniques have not been amenable to capturing the species in their peculiar habitats or with respect to their peculiar life histories. A few examples of North American species that are not generally collected as larvae for these reasons include deep-

water riverine species such as the heptageniids *Acanthomola pubescens* Whiting and Lehmkuhl, *Anepeorus simplex* (Walsh), and *Raptoheptagenia cruentata* (Walsh); fast-swimming psammophilous species such as *Analetris eximia* Edmunds (Acanthametropodidae) and *Pseudiron centralis* McDunnough (Pseudironidae); very small species such as the baetids *Apobaetis indepressus* Day and *Paracloeodes minutus* (Daggy); certain clay-burrowing species such as *Pentagenin vittigera* (Walsh) (Ephemeridae) and *Tortopus primus* (McDunnough) (Polymitarcyidae); and early season emergers whose developed larvae are only available in late fall, winter and very early spring, such as the more northern temperate species of Metretopodidae.

Siphonisca aerodromia should not be considered a fossil any more than any other extant mayfly species. The oldest fossils that have been associated with the family Siphonuridae *sensu lato* date from the Jurassic (see discussion of McCafferty 1990). However, such data are based on the broadest historical concept ever given to that family (see McCafferty and Edmunds 1979, McCafferty 1990). The actual clade to which *Siphonisca* belongs is a much more restricted Holarctic grouping [Siphonuridae *sensu* McCafferty (1991) and Kluge *et al.* (1995)], and includes along with *Siphonisca*, the genera *Edmundsius* Day, *Parameletus* Bengtsson, *Siphonurus* Eaton, and provisionally *Siphuriscus* Ulmer (see McCafferty and Wang 1994a). Fossils that are possibly assignable to this particular clade include members of the genera *Aphelophlebodes* Pierce from the Miocene of California and *Baltameletus* Demoulin and *Siphonurus* from Eocene Baltic amber. Siphonuridae *sensu stricto* is not an archaic group and is comparable in age to most other extant mayfly families.

Neither *Siphonisca* and its close relatives (other Siphonuridae), nor any other extant group of mayflies are fossils "dating from the Paleozoic." Most extant families of mayflies (McCafferty 1991) are also represented by fossils from the Tertiary as is Siphonuridae, but only seven of them, not including Siphonuridae, apparently have representative fossils from the Mesozoic, and no extant families have representative fossils from the Paleozoic, although there are strictly fossil families of mayflies from that era (see Hubbard 1987, McCafferty 1990).

Although cladistic analyses of all lineages of pisciform mayflies have not yet been performed satisfactorily to reach comprehensive conclusions regarding the entire group, all siphonuroid genera have been studied independently by both of us, and we have reached the same conclusion regarding the phylogenetic position of *Siphonisca*. *Siphonisca* apparently is the sister genus of *Parameletus*. Illustrative of this hypothesized relationship are the very similar apomorphic male genitalia and short hindtarsi shared by adults of the two genera. Of further possible consequence in this regard, *Parameletus* larvae in Utah are found in flooded *Carex* (Edmunds 1957), very similarly to that which has been reported for *Siphonisca* in Maine by Gibbs (1980). Like *Siphonisca*,

Parameletus has been a genus with species that are often difficult to find and collect.

It is evident that *Siphonisca*'s erroneous relationship with the Paleozoic has been associated with the observation that certain Paleozoic insects possessed somewhat similar laterally expanded abdomens. A number of extant mayflies have a larval abdomen that is variously expanded laterally. In every instance where this occurs, the abdominal gill lamellae originate dorsally rather than laterally on the abdomen and tend to overlay the lateral abdominal flanges. This feature is typical of the entire subgroup of mayflies known as pannoté mayflies (McCafferty and Edmunds 1979). In genera with highly developed flanges, e.g., those of the *Timpanoga* complex of the family Ephemerellidae (McCafferty and Wang 1994b), the larval flanges remain evident in the adults. In the non-pannoté and non-pisciform burrowing mayfly subfamily Palingeniinae of the family Ephemeridae, flanged larval abdomens are also carried over into the adults. Besides *Siphonisca*, other examples of this phenomenon among the pisciform mayflies include the genera *Oniscigaster* McLachlan and *Siphonella* Needham and Murphy (family Oniscigastridae) from the Southern Hemisphere. Given the wide variety of mayflies from disparate Ephemeroptera lineages demonstrating broad lateral flanges and the fact that it is apparently related to larval gill adaptation, we can not assume from such data, alone, any common derivations. This includes deducing a primordial relationship of *Siphonisca* with Paleozoic forms having similar modifications.

We do not know if the adult abdominal flanges are entirely non-adaptive vestiges of the larval structures or whether there may be some advantage (e. g., aerodynamic) accrued to the adult by their retained presence that explains their nearly full retention in such mayflies as *Siphonisca*. Only very slight lateral expansions are found in larvae of other Siphonuridae (with no appreciable adult vestiges of such). Abdominal flange development in *Siphonisca* and the loss of the fork of the MP vein in the hindwings of *Parameletus* are autapomorphies that allow us to continue to regard the two lineages as separate genera.

The claim that *S. aerodromia* disappeared for 50 years is not correct. It is true that 55 years occurred between the time Clemens (1915) discussed the species and the next publication reporting records of the species (Magnin and Harper 1970). However, the species was collected in New York up until the 1930's, when the type locality was altered due to the construction of the Sacandaga Reservoir. Fiance (1978) reported material that had been collected in 1952 in Canada. Lapses in records are most logically explained by the fact that there were few if any ephemeropterists collecting the habitats of *S. aerodromia* in the Northeast between the time when Alexander and Crampton were collecting the type locality in New York and the time when intensive local research was begun more recently in Maine by Gibbs and her students.

Finally, *S. aerodromia* does not stand alone among the North American mayflies in being monotypic. At the current time, 10 other North American

genera in various families are known from only one species (see McCafferty 1996). All of these can be considered just as unique in this respect as *Siphonisca*. Certainly, *S. aerodromia* is a striking species from its size and some details of its morphology. Many other mayflies in North America, however, are equally extraordinary, and others from around the world possess more highly unusual morphological attributes.

Local fascination with a particular species of aquatic insects can have very positive effects because it often leads to productive biological studies. The recent studies of *Siphonisca* are just one case in point. Some examples of other species that are fascinating in their own respect and that have received concentrated local attention in North America have included the behningiid *Dolania americana* Edmunds and Traver in Florida (e.g., Peters and Peters 1977, Peters *et al.* 1987), the polymitarcyid *Ephoron album* (Say) in Utah (e.g., Edmunds *et al.* 1956), and the heptageniid *Stenacron interpunctatum* (Say) in Indiana (e.g., McCafferty and Huff 1978, McCafferty and Pereira 1984, McShaffrey and McCafferty 1986). The only possible down side to such concentrated attention is that in interpreting and popularizing such data for general readership, distortions and exaggerations of information can and do occur to affect a degree of sensationalism, as has obviously been the case with *Siphonisca*. Our intent here has been simply to set the record straight.

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