# Flesh Flies (Diptera: Sarcophagidae) Associated with North American Pitcher Plants (Sarraceniaceae), with Descriptions of Three New Species

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ABSTRACT The sarcophagid flies that breed in North American pitcher plants of the genus *Sarracenia* are taxonomically revised and described. The species are as follows: *Sarcophaga sarraceniae* Riley, 1874; *Fletcherimyia abdita* Pape 1990; *Fletcherimyia celarata* (Aldrich, 1916); *Fletcherimyia fletcheri* (Aldrich, 1916); *Fletcherimyia folkertsi* Dahlem & Naczi sp. nov.; *Fletcherimyia jonesi* (Aldrich, 1916); *Fletcherimyia oreophilae* Dahlem & Naczi sp. nov.; *Fletcherimyia papei* Dahlem & Naczi sp. nov.; and *Fletcherimyia rileyi* (Aldrich, 1916). Life history information is provided, including host associations between the flies and pitcher plant species. Misidentifications and dubious identifications of the male and female genitalia should allow identification of all the included species. A key is provided to sort male specimens whose genitalia have not been spread.

KEY WORDS Fletcherimyia, Sarcophagidae, Sarraceniaceae, pitcher plants, systematics

THE IMMATURE STACES OF several species of Diptera can be found living within the trapping leaves of the carnivorous North American pitcher plants, *Sarracenia* spp. This fauna includes the mosquito *Wyeomyia smithii* (Coquillett) (Culicidae), the midge *Metriocnemus knabi* Coquillett (Chironomidae), nine species of flesh flies (Sarcophagidae) (three of which are newly described in this publication), *Bradysia* mac*farlanei* (Jones) (Sciaridae), *Dohrniphora* cornuta (Bigot) (Phoridae), and an undescribed species of *Aphanotrigonum* Duda (Chloropidae) (Folkerts 1999). These flies, with the exception of the cosmopolitan *D.* cornuta, are intimately associated with the pitcher plants.

Sarcophagid flies have evolved to use the decaying insects within the North American Sarracenia pitchers as a larval food resource on at least two independent occasions. All eight members of the genus Fletcherimyia Townsend breed in Sarracenia L. as well as one species within the genus Sarcophaga Meigen: S. (Bercaeopsis) sarraceniae Riley. Two other separate invasions into a similar aquatic environment are seen with the sarcophagid species Sarcophaga (Pierretia) urceola (Shinonaga & Beaver) and Sarcophaga (Sarcosolomonia) papuensis (Shinonaga & Kurahashi), both of which breed in pitcher plants of the genus Nepenthes L. on the Malayan Peninsula and northern Australia, respectively (Beaver 1979, Shinonaga and Beaver 1979, Yeates et al. 1989, Pape 2004).

One additional species, Sarcophaga (Wohlfahrtiopsis) georgiana Dodge, has been reared on one instance from Sarracenia. This is the species mentioned by Aldrich (1916) as a variation of S. (W.) utilis Aldrich. A reference to Aldrich's citation is made by Yeates et al. (1989) when they mention Wohlfahrtiopsis utilis being collected from Sarracenia pitchers. Because the known range of this species extends into areas beyond the distribution of Sarracenia, indicating that its life cycle is not dependent upon pitcher plants, S. georgiana is not included in the following revisionary study. Other species in the subgenus Wohlfahrtiopsis are parasitoids, or perhaps scavengers, in adult scarabaeid beetles, and it is likely that this species also attacks Scarabaeidae (Dodge 1966). It is possible that the one rearing from a pitcher plant was the result of a previously parasitized beetle becoming caught in a pitcher, or trapped beetles might be especially susceptible to larviposition by the fly, as hypothesized by Dodge (1966). This species does occur in pitcher plant habitats, and we have collected this species resting on pitchers of Sarracenia leucophylla Rafinesque. We have not, however, obtained any evidence to suggest that S. georgiana is a true pitcher plant associate.

A variety of Sarcophagidae are found in pitcher plant habitats, and many of them spend time perching on the pitcher plants. Most of these are not intimately associated with the pitcher plants. On a collecting expedition to pitcher plant sites in Georgia, Florida, and Alabama during summer 2000, we collected large numbers of the common, dung-breeding species *Oxysarcodexia ventricosa* (Wulp) and *Ravinia derelicta* 

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Fig. 1. Male S. sarraceniae showing placement points of minutens for the spreading of the male genitalia.

(Walker) on pitcher plants. Smaller numbers of the following species also were collected on pitchers: *Blaesoxipha* (*Acanthodotheca*) masculina (Aldrich), *Helicobia rapax* (Walker), *Lepidodexia* (*Camptops*) unicolor (Aldrich), *Ravinia lherminieri* (Robineau-Desvoidy), *Sarcophaga* (*Bercaeopsis*) tarsata (Aldrich), and *Titanogrypa* (*Titanogrypa*) melampyga (Aldrich). This list is not meant to be an exhaustive account of sarcophagids that can be found in these unique habitats but to serve as an indication of the diversity of species that exist in conjunction with the true pitcher plant associates.

Life History. Adults of S. sarraceniae and Fletcher*imyia* spp. are found in pitcher plant habitats and are sometimes abundant (Rymal and Folkerts 1982; unpublished data). There is no evidence that the flies occur outside of these peculiar habitats (Sanjean 1957; unpublished data). Both males and females are usually found perching on the pitchers in the sun, but they often alight on the sides of the pitchers rather than on the very top. Collection records indicate that late May–early June and early to mid-August are good times to search for and collect adults. An unusual aspect of successfully collecting these flies is that they will often fly down, into the lower vegetation and leaf litter, rather than up, when a net is placed over them. Copulation occurs on, or in close association with, the pitcher plants in all these species (unpublished data). Adults occasionally become entrapped by the pitcher plants (Rymal and Folkerts 1982). There is some evidence to suggest that adult flies may play a role in the

pollination of *Sarracenia* pitcher plants (Jones 1908, 1935; Swales 1972; Krawchuk and Taylor 1999).

Sarcophagids are ovolarviparous. Through careful dissection, first instars can be collected from the abdomens of gravid females that have been pinned and dried. Forsyth and Robertson (1975) found that females of F. fletcheri (Aldrich) mature one clutch of larvae during their adult lives. They also noted that the clutch size varies between 8 and 14 in this species. The largest number of larvae dissected from any species of *Fletcherimyia* female examined by us was 36 from F. jonesi (Aldrich), but this number was significantly higher than the number of larvae found in other females of *F. jonesi*. The largest larvae were found in a female of the new species *F. oreophilae*, and only two were present. Females of *F. jonesi*, *F. oreophilae*, and *Fletcherimyia rileyi* (Aldrich) have been found with fully developed larvae when collected in copula, which raises the possibility that some species of Fletcherimyia may mature more than one clutch of larvae during their lives.

Several of the early reports of these flies' larvipostion behavior indicate that a female may deposit up to a dozen first instars into a single pitcher, as she disperses her offspring (Riley 1874a,b; Higley 1885). *F. fletcheri*, however, has been observed to larviposit single larvae into separate pitchers (Forsyth and Robertson 1975, Rango 1999a). The note by Fyles (1907) that females deposit eggs into the pitchers must refer to a mistaken observation of the larviposition event. Larvae are aggressive and cannibalistic (Riley 1874a,b; Mellichamp 1875, Higley 1885, Forsyth and Robertson 1975), and as a result usually only one mature larva is found within a single pitcher (Mellichamp 1875, Higley 1885, Fish 1976, Fish and Hall 1978, Rymal and Folkerts 1982, Farkas and Brust 1986, Nastase et al. 1991), although up to four mature larvae in a single pitcher have occasionally been found (Yanoviak and Folkerts 1991; unpublished data). High prey density may allow the development of more than one larva in a single pitcher (Rango 1999b).

The larvae of these species of pitcher plant associates are the only known aquatic representatives of the family Sarcophagidae (Johannsen 1935, Usinger 1956, Fish 1983, Dahlem 1991, Keiper et al. 2002). One of the most "aquatic" of these species is F. fletcheri, which lives in the open pitchers of Sarracenia purpurea L. (Fig. 7). The larvae of this species possess an unusually large and cuplike posterior spiracular pit (Johannsen 1935, Sanjean 1957), which allows them to float at the surface of the liquid within a pitcher. Larvae of F. fletcheri restrict their feeding to the water surface and only retreat deep into the pitcher when disturbed (Fish and Hall 1978, Bradshaw and Creelman 1984). The pitchers of S. rosea Naczi, Soper, Case and Case (Fig. 8) also show this open pitcher and pool-of-water design. The pitchers of other species of Sarracenia, however, are hooded (Figs. 2-8, 9), and the interior of the pitcher is merely moist, except for a few milliliters of fluid at the very base of the pitcher. A high rate of colonization of available pitchers has been noted in a variety of studies (Hubbard 1896. Wray and Brimley 1943, Forsyth and Robertson 1975, Rymal and Folkerts 1982, Hardwick and Giberson 1996, Rango 1999a). The larvae of S. sarraceniae have been shown to contain several enzymes that protect them from the digestive enzymes of the pitcher plants (Hepburn and Jones 1919).

Although it has been assumed that the larvae of these pitcher plant sarcophagids feed on the remains of insects captured by the plant, Bledzki and Ellison (1998) found that the rotifer *Habrotrocha rosa* Donner may serve as an important source of food for the larvae of *F. fletcheri* that inhabit pitchers of *S. purpurea*. Rotifers also have been found to inhabit the pitchers of *Sarracenia flava* L. (Baldwin and Menhinick 2000). Bacteria have been found to be an important part of the diet of the pitcher plant chironomid *M. knabi* (Cochran-Stafira and Von Ende 1998), but their role as a food resource to sarcophagid larvae has not been adequately investigated.

In addition to cannibalism, another source of larval mortality includes the closure of the pitchers of southern *Sarracenia* species because of feeding by larvae of the pitcher plant moths of the genus *Exyra* Grote (Lepidoptera: Noctuidae) (Folkerts and Folkerts 1996) (Fig. 10). This can lead to the starvation of already present larvae (Riley 1874b [*Exyra* as *Xanthoptera*], Jones 1935, Fish 1976). There may be a negative interaction between sarcophagid larvae and the larvae of *B. macfarlanei*, because these two pitcher plant associates are rarely found together in a pitcher (Folkerts 1999). The larvae also may be subject to predation by birds (Mellichamp 1875, Higley 1885) or even armadillos (Folkerts and Folkerts 1996).

The larvae leave the pitchers and pupariate in the soil or sphagnum moss in the vicinity of the pitchers (Higley 1885, Jones 1935). Some larvae actually pierce the pitcher to leave (Riley 1874a,b; Mellichamp 1875, Fyles 1907), but it is not clear whether this represents a species-specific behavior, or whether variation exists within a species in pitcher-leaving behavior. It is assumed that these flies overwinter (diapause) as puparia, as holds true for many other species of Sarcophagidae. Some evidence to support this idea is presented by Farkas and Brust (1986). Pupal mortality because of chalcidoid (?) parasitoids has been noted (Riley 1874b, Jones 1935), but such parasitoids have neither been adequately collected nor identified.

Nomenclatural History. Riley (1874a) described S. sarraceniae and provided descriptions of the larvae and puparium, in addition to the adult fly. No notation is given concerning holotype versus paratypes designation of specimens in this article, his only note being "Described from numerous specimens reared from Sarracenia variolaris and S. flava." Aldrich (1916) redescribed S. sarraceniae from a variety of newly collected and/or reared specimens and Riley's original series of specimens. Aldrich (1916) also provided descriptions of the new species Sarcophaga celarata, S. fletcheri, S. jonesi, and S. rileyi. He noted that these four species, plus S. sarraceniae and a variant form of S. utilis, had all been reared from pitchers of Sarracenia. He further noted that Riley's original type material was composed of specimens representing three species: S. sarraceniae, F. jonesi, and F. rileyi.

Townsend (1917) provided a key to describe a variety of new genera and listed the type species at the end of his key. He described both *Fletcherimyia*, with the type species as *S. fletcheri*, and *Peltopyga*, with the type species as *S. celarata*. No further information is given concerning other species that may be included in these two new genera. Townsend also described the new genus *Sarraceniomyia* with the type species as *S. sarraceniae*. Townsend (1938) further described the type species in this generic overview, but lists *Sarraceniomyia*, *Fletcherimyia*, and *Peltopyga* as monotypic genera. No mention is made of Aldrich's other species associated with *Sarracenia*.

Lopes (1946) redescribed *Fletcherimyia* and placed his new species *F. speciosa*, along with *Sarcophaga cessator* Aldrich and *F. fletcheri*, in this redefined genus. Roback (1954) redefined *Fletcherimyia* on the basis of the male genitalia, synonymized *Peltopyga* with *Fletcherimyia*, and included Aldrich's species *celarata*, *fletcheri*, *jonesi*, and *rileyi* within this genus. He also described the new subgenus *Speciosia* within the genus *Servaisia* and designated Lopes' *F. speciosa* as the type species of this monotypic subgenus, removing it from *Fletcherimyia*. He did not, however, mention the species *S. cessator*. Roback (1954) included *Sarraceniomyia* as a synonym of *Sarcophaga*.

Dodge (1956) noted that the genera most closely allied to his new genus *Idoneamima* are *Sarraceniomyja* and *Bercaeopsis*. Although Dodge did not pub-



Fig. 2–9. Host pitcher plants. (2) S. alata. (3) S. flava. (4) S. leucophylla. (5) S. minor. (6) S. oreophila. (7) S. purpurea. (8) S. rosea. (9) S. rubra subsp. wherryi. (10) S. flava showing damage to pitcher from a larva of *Exyra*.

lish separately on *Sarraceniomyia*, he did recognize it as a separate genus and specimens identified by him may carry this designation for the species *S. sarraceniae*.

Downes (1965) placed *Fletcherimyia*, with the species included by Roback, as a subgenus of *Blaesoxipha* 

Loew in his catalog of North American Sarcophagidae. He included *Speciosia* as a monotypic subgenus of *Blaesoxipha* and included *S. cessator* within the subgenus *Kellymyia* Townsend of the genus *Blaesoxipha*. He included *Sarraceniomyia* as a synonym of *Sar*- *cophaga*. Lopes (1969) raised *Speciosia*, with its single species *S. speciosa*, to full genus status. Lopes (1971) argued for full generic rank for *Fletcherimyia*.

Dodge (1966) described the variant form of *S. utilis*, noted by Aldrich (1916) to have been reared from *Sarracenia*, as the new species *Sarcophaga* (*Scarabaeophaga*) georgiana. As has been noted above, information presented by Dodge, and our unpublished data, lead us to the conclusion that this species is not a true inquiline of *Sarracenia*. This species is currently assigned to the subgenus *Wohlfahrtiopsis* Townsend of the genus *Sarcophaga*.

Rohdendorf (1971) described the new species *Fletcherimyia zayasi* from Cuba. He included this species in *Fletcherimyia* only provisionally and noted that it may belong to a different genus. Pape (1990) mentioned that *zayasi* was not a member of *Fletcherimyia* and should be placed within *Blaesoxipha*. Pape (1994) moved *zayasi* to the subgenus *Abapa* Dodge of the genus *Blaesoxipha*.

Shewell (1987) considered both *Fletcherimyia* and *Sarraceniomyia* as full genera within his key to the genera of Nearctic Sarcophagidae. He noted that *Sarraceniomyia* included only one Nearctic species (*S. sarraceniae*) and included four species within *Fletcherimyia*.

Pape (1990) redefined the genus *Fletcherimyia*, provided information on its nomenclatural history, and discussed its placement within the generic framework of the Sarcophagidae. He described the new species F. abdita and designated a paratype of F. rileyi as the holotype of this species. He also assigned Sarcophaga sarraceniae to the subgenus Liosarcophaga Enderlein of the genus Sarcophaga. Pape (1996), in his catalog of world Sarcophagidae, moved sarraceniae to the subgenus Bercaeopsis Townsend of the genus Sarcophaga and treated Sarraceniomuia and Idoneamima as synonyms of Bercaeopsis. Pape (1996) included five species within the genus Fletcherimyia: abdita, celarata, fletcheri, jonesi, and rileyi. We agree with the placement of Pape (1996) of the pitcher plant species of Sarcophagidae and add three new species to the genus *Fletcherimyia*.

Mistaken Identifications. The description of S. sarraceniae by Riley (1874a) represents one of the first North American species of Sarcophagidae described by an American author. It was described at a time before the usefulness of the male genitalia in species recognition was generally accepted. As such, the name was quickly applied to a wide variety of different sarcophagids possessing the general "Sarcophaga" body form. Osborn (1896) noted that "S. sarraceniae is probably the most common American species of Sarcophagidae." It is evident from identifications present in the literature that even Riley himself was unable to separate S. sarraceniae from other sarcophagid species. Coquillett (1892), in his discussion of the known habits of Sarcophagidae, mentioned that "In his Seventh Report on the Insects of Missouri (p. 181), Prof. Riley states that the larvae of Sarcophaga sarraceniae feed upon dead insects, and in his Ninth Report (p. 95) he states that they also feed upon the eggs of locusts." These records seem to represent errors in the identifications of the flies.

Howard (1900) listed *S. sarraceniae* as "a common, widespread and dangerous species" in his investigation of the insect fauna of human excrement. Howard (1902) provided the following information: "The common flesh-fly of Europe *Sarcophaga carnaria* does not seem to occur in this country but we have a closely allied species, *S. sarraceniae*, which has been reared from larvae found feeding upon dead insects in the pitchers of the common pitcher plants and which is often reared from dead insects and from excrement." The erroneous association of *S. sarraceniae* with dung and dead insects outside of pitcher plants is found in the literature as late as 1972 in Swan and Papp's discussion of this species.

Comstock (1879) and Riley (1885) reported on the rearing of *S. sarraceniae* from the cotton leafworm, *Alabama argillacea* (Hübner) (Lepidoptera: Noctuidae) (=*Aletia argillacea*). These rearing records are undoubtedly based on misidentifications, but this association does not persist in subsequent literature. Callan (1946) incorrectly noted *S. sarraceniae* as a synonym of *Sarcodexia sternodontis* (Townsend) [=*S. lambens* (Wiedemann)] when he reported on the rearing of *S. sternodontis* from the South American bollworm *Sacadodes pyralis* Dyar.

McGillivray and Houghton (1903) noted that *S. sarraceniae* was collected in the Adirondack Mountains of New York, but the identification is highly questionable because it represents the only described species of Sarcophagidae listed. Aldrich (1905) cited several early rearing records and also cited locality information from Johnson (Florida), Slosson (New Hampshire), M. and H. (New York), and Fyles (Quebec). Herms (1907) provided very interesting biological observations and experimentation dealing with larval development of a species (or several species?) of Sarcophagidae from organic debris on a Cedar Point beach in Ohio (at Lake Erie). It is obvious, however, that his observations do not refer to *S. sarraceniae*.

Morgan (1901) noted that S. sarraceniae was reared from Melanoplus differentialis (Thomas) (Orthoptera: Acrididae). Aldrich (1914) mentioned that S. sarraceniae had been reared from grasshoppers from Wellington, KS, and Washington, DC. Kelly (1914, 1915) provided information on S. sarraceniae larvipositing on adults and nymphs of the grasshopper *Chortophaga* viridifasciata (De Geer) and on the larger nymphs of M. differentialis and Melanoplus bivattatus Say (Orthoptera: Acrididae). There is also a note that Chalcis coloradensis Cresson was found as a parasitoid emerging from the puparia of S. sarraceniae that emerged as parasites of grasshoppers in 1900. The mistaken association of S. sarraceniae with grasshoppers continues to Thompson (1950), who listed S. sarraceniae as a parasite of C. viridifasciata.

Parker (1915) noted that *S. tuberosa sarraceniae* was bred from fish but was not found in excreta. Herms (1915) noted that "*S. sarraceniae* Riley is a typical flesh fly, has the appearance of an overgrown house fly ... The young are deposited on meat, or if extruded in the vicinity of meat not accessible to the fly, the larvae crawl to the food." In all likelihood, these observations do not refer to *S. sarraceniae*.

Aldrich (1915) mentioned a rearing by Mr. D. E. Fink in 1914 from a pupa of the green June beetle, *Cotinis nitida* (L.) (Coleoptera: Scarabaeidae) (=Al*lorhina nitida*). The rearing from *C. nitida* persists in the literature from this point to Davis and Luginbill (1921, 1922), Thompson (1943), and Roback (1954).

Aldrich (1916) corrected some of these identification problems with his description of the new species S. (*Liosarcophaga*) sarracenioides. He specifically noted that the information provided by Morgan (1901), Herms (1907), Banks (1912) (S. sarraceniae?), Kelly (1914, 1915), Howard (1902), Williston (1908), and his own papers (1905, 1914, 1915) refers to S. sarracenioides rather than S. sarraceniae.

Sleesman (1935) reportedly included the "blowfly" S. sarraceniae as a test animal in his experiments on the toxicity of lubricating oil emulsions to the eggs of the onion maggot and other flies. His use of eggs in his experiments indicates that he probably was using some species of Calliphoridae rather than a sarcophagid, let alone S. sarraceniae itself.

The strong possibility of mistaken identification of S. sarraceniae has important ramifications within the cytological work that has been done with the Sarcophagidae. Stevens (1908) provided information on chromosomes and meiosis of S. sarraceniae. No information is given concerning where his specimens came from, but his introduction seems to indicate that he was using this name as a catch-all for sarcophagids. Metz (1916) provided illustrations and information on the paired association of chromosomes in S. sarraceniae. Again, no information on where the study material came from or who identified it is provided. Information on S. sarraceniae chromosomes, and relationships with other sarcophagid species provided by Boyes (1953, 1963, 1967) and Boyes and Wilkes (1953) is based on the work of Stevens (1908) and Metz (1916). Boyes and Wilkes (1953) and Boyes (1963) mentioned that the chromosome complements differ between Stevens and Metz' papers. This indicates that the original authors were probably working with two very different species, perhaps neither of which represented S. sarraceniae.

#### Materials and Methods

This revision is based on an examination of >350 specimens, including the primary types of *F. abdita*, *F. celarata*, *F. fletcheri*, *F. jonesi*, and *F. rileyi*. The terminology follows that of McAlpine et al. (1981) for general morphology, Sinclair (2000) for terminology of the male terminalia, and Roback (1954) for details of the phallus.

The following acronyms for specimen depositories are included in the new species descriptions: CNC, Canadian National Collection of Insects; FSCA, Florida State Collection of Arthropods; GD, personal collection of G. A. Dahlem; GWF, personal collection of George W. Folkerts; NHMD, Natural History Museum of Denmark; RFCN, personal collection of R.F.C. Naczi; and USNM, United States National Museum of Natural History.

Larvae were reared in the following manner. Larvae collected in the field were removed from pitchers and placed in individual test tubes with distilled water and freshly killed insects. Honey bees and bumble bees served as the majority of food items. Test tubes were placed in plastic shoeboxes with sand in the bottom and a damp paper towel. Mature larvae crawled out of the tubes to pupariate in the sand. Puparia were transferred to individual rearing cups with dry sand in the bottom and a cotton ball-capped test tube with sugar water (for feeding of adult) extending from the side of the cup. Rearings were conducted at room temperature in the laboratory; no effort was made to monitor or modify temperature or humidity levels. Pupariation and emergence dates were recorded. We suspect that the pupal mortality we observed may have been because of insufficient humidity in the rearing containers.

Female associations were made possible by our collecting of mating pairs of the following species: *S. sarraceniae, F. abdita, F. fletcheri, F. jonesi, F. oreophilae,* and *F. rileyi.* The associations of males and females of *F. folkertsi* and *F. papei* were based on series of specimens collected by us from the same locality at the same time. Female identifications were based on examination of the genital sternites 6, 7, and 8. These sterna are often distorted in dried specimens and/or partially obscured by the abdominal terga, making dissection of female specimens necessary for species-level identifications.

We have provided a key for the sorting of unspread male specimens of *Fletcherimyia*. Although this key works well for the majority of specimens, direct examination of the phallus remains the preferred and most accurate means for identifying these species. No key is provided for the females. Females will generally have to be dissected to remove their sterna 6, 7, and 8 for identification. Once dissected, they can be compared with the provided figures of the female genitalia for identification.

The genitalia of all male sarcophagids should be spread when the fresh specimens are pinned, to allow examination of the phallus and other genitalic features (Fig. 1). This is easily accomplished by taking the fresh, pinned specimen and inserting the pin, at an acute angle, into a piece of flat Styrofoam, so that the specimen is resting on its side. Best results are obtained when specimens are allowed to sit for 10–24 h in a cool location before pinning. Insert one minuten on top of the fifth abdominal tergite, just before the genital capsule. Under the microscope, use forceps and another minuten to spread the genitalia by placing the minuten on the anterior surface of the cerci and gently pushing back until the cerci are parallel with the main pin. The phallus should extend down at this point and be clearly visible. Let the specimen dry for 2 to 3 d and then remove the minutens. The genitalia will remain spread for future examination. Alcohol preservation of adult specimens is not recommended, unless for DNA analysis or soft tissue studies, because the specimens often become distorted when pinned from alcohol and because it is often difficult, if not impossible, to spread the male genitalia. Alcohol specimens will usually need to be dissected to view the

male genitalia, resulting in a much higher time commitment to properly determine their identity. When comparing dried, spread specimens to the figures in this article, it should be noted that aedeagal structures (especially membranous structures) may look slightly different, because all of our genitalic figures are of aqueousmounted, cleared (in hot KOH solution), dissected specimens.

We performed an extensive literature search for the included species. Although we expect that we may have missed a few references to these species, we feel that the literature review, which accompanies each species, includes all major citations (as well as most minor citations). All references to the particular species are included, although some citations may be based on misidentifications (see information provided in the "Mistaken Identifications" section) and some may represent only a very brief mention of the species with no original information provided. References including significant information on pitcher plant sarcophagids are usually noted in the "Biology" section associated with a particular species, or elsewhere in this article.

### Sarcophaga (Bercaeopsis) sarraceniae Riley (Figs. 1, 12a,b, 14a,b, 23, 32, 41)

Note: some of the following references represent misidentifications. See previous section for more information.

Sarcophaga sarraceniae Riley, 1874a: 238-240, Fig. 11; type locality: South Carolina; male holotype (description). Riley 1874b: 209-214, Fig. 26 (biology). Riley 1875a: 180–181 (biology). Riley 1875b: XIII (biology). Mellichamp 1875: 117, 130–132 (biology). Comstock 1879: 205–206 (biology). Riley 1885: 101, 107–108 (biology). Higley 1885: 53–55 (biology, copy of original description). Coquillett 1892: 24 (biology). Hubbard 1896: 315 (biology). Osborn 1896:122 (biology). Austen 1896: 239 (biology). Howard 1900: 548, 565–566 (biology). Morgan 1901: 24–25. (biology). Howard 1902: 164–165, Fig. 92 (biology). McGillivray and Houghton 1903: 13 (distribution). Hine 1904: 92 (distribution). Jones 1904: 15 (biology). Aldrich 1905: 513 (distribution, rearing records). Fyles 1907: 111 (biology). Herms 1907: 48, 49, 50, 54–55, 60, 62, 63, 74, 76, 77 (biology). Jones 1908: 155, 156 (biology). Williston 1908: 348 (figure of adult). Banks 1912: 17 (larval description). Aldrich 1914: 444 (biology). Kelly 1914: 439, 441, 442 (biology). Parker 1914: 28 (distribution). Herms 1915: 238 (biology). Aldrich 1915: 242, 243, 244 (biology). Parker 1915: 247 (biology). Kelly 1915: 82 (biology). Kelly 1915: 82 (biology). Parker 1916: 440 (morphology). Hepburn and Jones 1919: 460-462 (physiology). Davis and Luginbill 1921: 20 (biology). Davis and Luginbill 1922: 164 (biology). Sleesman 1935: 453, 455–456 (biology). Bezzi 1926: 16 (biology). Hallock 1937: 262 (distribution). Brimley 1938: 371 (distribution). Hallock 1940b: 204, 212 (key). Hallock 1942: 225, Fig. 175 (distribution, male genitalia). Thompson 1943: 10 (biology). Callan 1946: 474 (biology, synonymy).



Fig. 11. Scanning electron micrograph of laterally extended surstyli of *F. oreophilae*.

Thompson 1950: 8 (biology). Boyes 1953: 574–575 (chromosomes). Boyes and Wilkes 1953: 127, 128 (chromosomes). Roback 1954: 45, 66, 68, 71, Figs. 171–173 (systematics, male genitalia). Usinger 1956: 482 (biology). Sanjean 1957: 6, 8 (review of larval descriptions). Downes 1965: 959 (catalog). Curran 1965: 402 (figure of adult). Boyes 1967: 375 (chromosomes). Swan and Papp 1972: 645, Fig. 1389 (biology). Rymal and Folkerts 1982: 135 (biology).



Figs. 12–13. Spermatheca (a) and accessory gland (b). (12) S. sarraceniae. (13) F. abdita.

Farkas and Brust 1986: 1307–1308 (distribution, biology). Juniper et al. 1989: 257 (biology). Folkerts 1999: 257, 262 (biology). Marshall et al. 1999: 394 (biology). Giberson and Hardwick 1999: 408 (biology).

- Sarcophaga sarraceneae (misspelling of sarraceniae); Lahille 1907: 76.
- Sarcophaga sarraciniae (misspelling of sarraceniae): Stevens 1908: 359, 363, Figs. 25–36 (chromosomes).
- Sarraceniomyia sarraceniae; Townsend 1917: 192, 195 (generic placement and key). Townsend 1938: 65 (redescription). Shewell 1987: 1168 (key). Yeates et al. 1989: 38 (biology). Yanoviak and Folkerts 1991: 80 (biology).
- Sarcophaga serraceniae (misspelling of sarraceniae); Mattos 1926: 83.
- Sarcophaga tuberosa sarraceniae (Riley): Parker 1914: 30, 36 (morphology). Parker 1915: 247 (biology). Metz 1916: 218, 234, Figs. 81–82 (chromosomes).
- Sarcophaga (Liosarcophaga) sarraceniae; Pape 1990: 47 (biology).
- Sarcophaga (Bercaeopsis) sarraceniae; Pape 1996: 304, 307 (catalog).

Male. Length 11-14 mm. Fronto-orbital plate, parafacial, and anterior margin of gena yellowish gray pruinose. Occiput, most of gena, and postgena gray pruinose. Ocellar triangle with pair of well developed, divergent, and proclinate setae, along with scattering of smaller setae. Inner vertical seta large and slightly reclinate. Upper orbital seta parallel to slightly divergent and reclinate. Postocellar setae parallel and slightly proclinate. Paravertical setae slightly convergent. Row of postocular setae alternating between longer and shorter setae, the most dorsal seta longest, with long set diminishing in size, especially after first three or four, lateral of vertex. Rows of frontal setae strongly divergent at level of pedicel, with two to three setae extending past pedicel. Line of three to five strong setae at ventral margin of parafacial near eye. Vibrissae strong, convergent, crossing at ca. threefourths of length. Yellowish white setae restricted to postgena.

Scutum with three dark vittae. Postpronotum with two anterior and one posterolateral seta. Chaetotaxy: acrostichals = 0 + 1 (prescutellar); dorsocentrals = 4(anterior two setae close to anterior margin) + 4(second seta weak); intra-alars = 1 + 2 (sometimes three); supra-alars = 2 + 3; postalars = 2. Notopleuron with four setae, anterior and third seta much weaker than second and posterior seta. Scutellum with one basal, one discal (weak), one subapical, and a weak pair of convergent apical setae. Katepisternum with three strong dorsal setae. Postalar wall setulate. Wing with row of dorsal setae on  $R_{4+5}$  from Rs to ca. onehalf to three-fourths distance to r-m crossvein.

Fore tibia with two to three anterodorsal setae at ca. one-third distance from base and one posteroventral seta at ca. two-thirds distance from base. Tarsal claws of fore leg reduced, without pointed claws and shorter in length than the tarsal claws of the mid and hind legs. Mid femur with a row of anterior, anteroventral, and posteroventral setae, posteroventral row with setae stout, but pointed along apical one-half; three to four strong posterior setae near apex. Mid tibia with one to three posterodorsal setae near base; anterior seta ca. one-third distance from base and an anteroventral, anterior and one to two posterior setae at ca. twothirds distance from base. Tarsal claws of mid leg with pointed tips. Hind femur with rows of anterodorsal, anterior, and anteroventral setae; row of long, thin posteroventral setae on apical one-third; one to three posterodorsal setae on apical one-third; posterior seta near apex. Hind tibia with row of anterior setae and villous row of long thin anteroventral and posteroventral setae; posterior seta ca. one-third distance from base; posterior seta ca. two-thirds distance from base; strong anterodorsal, posterodorsal, anteroventral, and posteroventral apical setae. Tarsal claws of hind leg with pointed tips.

Abdominal terga 1 + 2 with group of lateral marginal setae. Tergite 3 with one lateral marginal and zero to one (weak) median marginal. Tergite 4 with three lateral marginals and one strong median marginal. Tergite 5 with row of marginal setae; orangish in ground color along apical margin.

Syntergosternite 7+8 without marginal setae (Fig. 14a). Fifth sternum with long, slender posterior arms and open medial window. Scattered, thin setae on posterior arms to medial window area, without stout spines on inner surface (Fig. 23). Phallus with vesica projecting anteriorly and with distal pointed hook; harpes extends anteriorly, about as far as vesica, about midway between vesica and juxta; lateral filament thin and clearly visible between harpes and juxta; juxta extending anteriorly to approximately the same length as the vesica and harpes (Fig. 14a,b). Postgonite bilobed at apex. Pregonite tapering to point at apex. Surstylus triangular, with thin setae. Cercus elongate and separated from other cercus in apical one-fifth of length with several stout spines laterally on apical one-half and long thin setae concentrated on basal one-half; apical points divergent (Fig. 32).

Female. Length 10–12 mm. Differs from male as follows. Two proclinate orbital setae present. Dorsocentrals = 3 + 4; supra-alars = 1-2 (anterior weak or absent) + 3. Scutellum without apical setae. Fore tibia with three posterodorsal setae. Tarsal claws of fore leg with pointed tips. Mid femur without posteroventral row of setae; two strong posterior setae near apex. Mid tibia with two anterior setae ca. one-third distance from base. Hind femur with strong setae along posteroventral row; single posterior and posterodorsal seta near apex. Hind tibia without villous row of long thin anteroventral setae; with anterodorsal and posterodorsal seta ca. one-third distance from base; anterodorsal and posterodorsal seta ca. two-thirds distance from base; and two anteroventral setae. Abdominal tergite 4 with two to three lateral marginals, a median marginal, and a strong marginal seta approximately midway between lateral marginals and median marginal seta. Tergite 6 narrowly divided by membrane in middle; with about eight marginal setae on each side, evenly spaced and about equal in size. Sterna 6, 7, and 8 with strong, bristlelike setae



Figs. 14–18. Male genitalia (a) and phallus (b). (14) S. sarraceniae. (15) F. abdita. (16) F. celarata. (17) F. fletcheri. (18) F. folkertsi. H, harpes; J, juxta; LF, lateral filaments; V, vesica.

near posterior margin (Fig. 41). Sternum 9 unsclerotized, but with a pair of strong, bristlelike setae posteriorly (Fig. 41). Spermathecae darkly sclerotized and with conspicuous constrictions; spermathecal tube abruptly widening at ca. one-fifths of length from apex (Fig. 12a). Accessory glands membranous (Fig. 12b).

**Immature Stages.** The larva and puparium were described and illustrated by Riley (1874a,b).

Type Material. Lectotype male [USNM]. Labels on the lectotype specimen: (1) forceps [small piece of card with part of genitalia glued to it with the word written on it]; (2) 342.x [small piece of paper with leg glued on it, somewhat obscuring script]; (3) TD4692 [small pencil label, written by Townsend, refers to his dissection number]; (4) Type; No. 780; U.S.N.M. [red label]; (5) Sarcophaga; sarraceniae; [male sign] Holotype Riley, MS [on this label, the "[male sign] holotype" is added later in ink]; (6) S. sarraceniae; Riley; HOLOTYPE [this label is a later addition and is handwritten]. Locality given in Riley's paper seems to be South Carolina. Aldrich (1916) refers to the "holotype" with spread genitalia by Townsend. This is a lectotype designation by Aldrich, by inference of holotype.

Distribution. CANADA: British Columbia? (see Discussion below), Ontario; UNITED STATES: Alabama, Florida, Georgia, Mississippi, New York, North Carolina, South Carolina.

**Biology.** Riley (1874a) described S. *sarraceniae* from numerous specimens reared from S. *flava* (Fig. 3) and S. *minor* (=*variolaris*) (Fig. 5). This species seems to



Figs. 19-22. Male genitalia (a) and phallus (b). (19) F. jonesi. (20) F. oreophilae. (21) F. papei. (22) F. rileyi.

be a generalist in a variety of pitcher plant species (Rymal and Folkerts 1982). It has been reared from *S. flava* (Jones 1904, 1908; Aldrich 1916; personal records), *S. leucophylla* (Fig. 4) (Aldrich 1916; personal records), *S. minor* (Mellichamp 1875, Aldrich 1916), and *S. purpurea* (Fig. 7) (Higley 1885, Fyles 1907, Farkas and Brust 1986). It is the most common pitcher plant sarcophagid from sites in the southeastern United States (Yanoviak and Folkerts 1991; unpublished data).

Aldrich (1916) redescribed *S. sarraceniae* from some of Riley's original type series and additional specimens reared from pitcher plants. He also noted that earlier citations of *S. sarraceniae* as a scavenger or parasitoid of grasshoppers probably apply to the species *S. sarracenioides*.

We reared two males and one female *S. sarraceniae* from pitchers of *S. flava* and one male from a pitcher of *S. leucophylla*. Twenty-three specimens were reared from first instars obtained from a freshly killed gravid female from Colquitt County, Georgia. The larvae were easily reared, but there was a high amount of mortality during the pupal stage, with 15 of the 23 dying at this time. Six of the eight survivors progressed through the three instars and pupariated in 13 d. The other two took 22 and 28 d. An average of 19 d was spent as puparia in the specimens that we reared (13, 14, 14, 16, 16, 17, 19, 22, 24, 24, 24, and 24 d, respectively).

**Discussion.** Hine (1904) listed *S. sarraceniae* from Vancouver, British Columbia. Although this may be possible, because *S. purpurea*'s range extends into British Columbia, we consider this identification to be highly dubious, because no additional specimens or records have been noted from this area and because this citation dates from a time before male genitalia were extensively used for species identification. *S. sarraceniae* is probably the species referred to by



Figs. 23–31. Male fifth sternite. (23) S. sarraceniae. (24) F. abdita. (25) F. celarata. (26) F. fletcheri. (27) F. folkertsi. (28) F. jonesi. (29) F. oreophilae. (30) F. papei. (31) F. rileyi.

Lloyd (1942) as the "*Sarcophaga*" that produces large white maggots that feed upon the remains of insects in pitchers of *Sarracenia*. Jones (1920) refers to "sarcophagid flies" and "*Sarcophaga*" that inhabit a variety of different species of *Sarracenia*. Baldwin and Menhinick (2000) refer to "*Sarcophaga* flies" living in pitchers of *S. flava*. However, these notes by Jones, Lloyd, and Baldwin and Menhinick could refer to a variety of the sarcophagid associates of pitcher plants.

#### Genus Fletcherimyia Townsend

Fletcherimyia Townsend, 1917: 191. Type species: Sarcophaga fletcheri Aldrich, 1916, by original designation. Peltopyga Townsend 1917: 191. Type species: Sarcophaga celarata Aldrich, 1916, by original designation.

Male. Fronto-orbital plate, parafacial, and anterior margin of gena yellowish gray pruinose. Occiput, most of the gena and postgena gray pruinose. Ocellar triangle with pair of well developed, divergent, and proclinate setae, along with scattering of smaller setae. Inner vertical seta large and reclinate. Upper orbital seta reclinate and divergent. Postocellar setae parallel or convergent and often slightly proclinate. Paravertical setae parallel to convergent. Row of postocular setae alternating between longer and shorter setae, the most dorsal seta longest, with long set diminishing in size, especially after first three or four, lateral of vertex. Rows of frontal setae strongly divergent at level of pedicel, with one to two (usually two) setae extending past pedicel. Row of thin setae on parafacial extending from end of frontal setae to genal groove near eye. Vibrissae strong, convergent, crossing at ca.



**Figs. 32–40.** Male cerci. (32) S. sarraceniae. (33) F. abdita. (34) F. celarata. (35) F. fletcheri. (36) F. jonesi. (37) F. folkertsi. (38) F. oreophilae. (39) F. papei. (40) F. rileyi.



Figs. 41–50. Female genital sternites 6, 7, and 8. (41) S. sarraceniae. (42) F. abdita (morphological variation 1, most common). (43) F. abdita (morphological variation 2). (44) F. fletcheri. (45) F. folkertsi. (46) F. jonesi. (47) F. oreophilae. (48) F. papei. (49) F. rileyi. (50) F. celarata.

one-half of length. Yellowish white setae restricted to postgena.

Scutum with three dark vittae. Presutural acrostichals not differentiated; one weak prescutellar postsutural acrostichal present. Three postsutural supraalars, the middle seta more than  $2 \times$  length of anterior and posterior setae. Two postalar setae, the posterior seta  $\approx 2 \times$  the length of anterior seta. Postpronotum with anterior and two basal setae. Notopleuron with four setae, anterior and third seta much weaker than second and posterior seta. Scutellum with one basal, one discal (weak), one subapical, and with or without weak apical seta. Postalar wall setulate. Wing with row of dorsal setae on  ${\rm R}_{4\,+\,5}$  from Rs to ca. one-half to three-fourths distance to r-m crossvein.

Fore tibia with two to three anterodorsal setae at ca. one-third distance from base and one posteroventral seta at ca. two-thirds distance from base. Tarsal claws of fore leg reduced, without pointed claws and shorter in length than the tarsal claws of the mid and hind legs. Tarsal claws of mid leg without pointed apices. Mid femur with anterior row, anteroventral row; single posterior and posterodorsal setae near apex; and posteroventral row of setae, with stubby "comb" of setae along apical one-third. Mid tibia with differentiated anterodorsal seta and posterodorsal seta ca. one-third distance from base; with anterodorsal seta, anteroventral seta, posterior seta, and posterodorsal seta ca. two-thirds distance from base. Hind femur with anterodorsal row of setae, anterior row in basal one-half, anteroventral row, and single posterior seta near apex. Hind tibia with an anterodorsal and posterodorsal seta ca. one-third distance from base; with an anterior, anterodorsal, and posterodorsal seta ca. two-thirds distance from base.

Abdominal terga 1 + 2 with group of lateral marginal setae. Tergite 5 with row of marginal setae. Syntergosternite 7 + 8 with marginal bristles.

Female. Differs from male by the following characters: Head with well developed outer vertical seta and two proclinate orbital setae. Scutellum without apical setae. Mid femur with three to five anterior setae, two anteroventral setae, two posterodorsal setae, two to four posteroventral setae, and lacking row of stubby posteroventral setae near apex. Mid femur with small posterior "modified area" (reddish area bare of pruinosity). Mid tibia with two to five (usually two) anterodorsal setae, one anteroventral seta, two to four (usually two) posterodorsal setae and one posterior seta. Hind femur without distinct anteroventral row (usually two to four setae present), usually with a single posterior and posterodorsal seta present near apex, and two posteroventral setae. Hind tibia with two to five anterodorsal setae, one anteroventral seta, and two posterodorsal setae.

Sterna 6, 7, and 8 without strong, bristlelike setae. Accessory gland long and tubular, the distal two-thirds of length ribbonlike (Fig. 13b). Distinctly different from the usual *Sarcophaga*-like shape (Fig. 12b).

# Key to species (for use with unspread male specimens)

1. Three postsutural dorsocentrals; abdomen dis-
tinctly reddish or pale to base
1' Four postsutural dorsocentrals; abdomen mainly
gray with normal tessellation pattern 4
2. Surstyli, when viewed from the rear, distinctly
projecting laterally from the body (as in
Fig. 11); small body size, 6–9 mm <i>F. papei</i> n. sp.
2' Surstyli, when viewed from the rear, projecting
ventrally
3. Cerci curved inward so that the tips nearly touch
one another (Fig. 37) F. folkertsi n. sp.
3' Tips of cerci convergent, but widely separated
(Fig. 35) F. fletcheri (Aldrich)
4. Two katepisternal setae
4' Three katepisternal setae
5. Surstyli, when viewed from the rear, distinctly
projecting laterally from the body (Fig. 11);
cerci strongly curved inward (Fig. 38); apical
mesal projections of fifth sternite not distinctly
darker in pigmentation than the surrounding
cuticle (Fig. 29) F. oreophilae n. sp.
5'. Surstyli, when viewed from the rear, projecting

ventrally; cerci not strongly curved inward

(Fig. 36); apical mesal projections of fifth sternite darkly pigmented (Fig. 28) . . . . . . . .

- 6. Tips of cerci parallel (Fig. 34) . . . . . . . . . .
- 6'. Tips of cerci convergent (Fig. 33 and 40) . . 8
- 7'. Cerci shorter and thicker basally (Fig. 33) . . *F. abdita* Pape

# *Fletcherimyia abdita* Pape (Figs. 13a,b, 15a,b, 24, 33, 42–43)

*Fletcherimyia abdita* Pape, 1990: 48, Figs. 13 and 19, 24; type locality: Theodore, AL; male holotype (description). Pape 1996: 224 (catalog).

Male. Length 8–14 mm. Postpronotal lobe with one anterolateral seta and one posterolateral seta; one weak anteromedial seta present or absent. Chaetotaxy: dorsocentrals = 3-4+4 (anterior two weak); intraalars = 1+2 (anterior seta weak); supra-alars = 2 (anterior seta <one-half length of posterior seta) +3 (middle seta over  $2\times$  length of anterior and posterior seta). Katepisternum with two to three (usually three) dorsal setae. Abdominal tergite 3 with 0–1 lateral marginal and zero to one median marginal seta. Abdominal tergite 4 with 1–2 lateral marginal and one median marginal seta.

Fifth sternum with short posterior arms; posterior medial lobes broadly rounded and darkly sclerotized apically. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 24). Phallus with vesica rounded anteriorly and narrowing to a blunt point dorsally and with a spinelike process near middle; juxta more darkly sclerotized basally (Fig. 15a,b). Pregonite tapering to point at apex. Surstylus with oval lobe and one to two long, thin setae. Cercus elongate and separated from other cercus in apical one-half of length; with only the apical tips convergent (Fig. 33).

Female. Sternum 8 with deep, U-shaped, slightly irregular apical invagination along midline and with depressed lateral lobes (Figs. 42 and 43). This apical invagination is often asymmetrical. The posterior margin of sternum 7 usually has a slight indentation or notch at the midline. Spermathecae darkly sclerotized and without conspicuous lobes; spermathecal tube abruptly widening at ca. one-half of length from apex (Fig. 13a). Accessory glands membranous, long and thin, looking very flat in distal two-thirds (Fig. 13b).

**Diagnosis.** The phallus of the male is similar to that of *F. rileyi. F. abdita* can be separated from *F. rileyi* by the difference in the shape of the phallus, fifth sternite, and cerci. The deep U-shaped apical invagination of the sternum 8 separates the females from the similar *F. jonesi*, whose apical invagination is more V-shaped in appearance. The apical invagination is often asymmetrical and the base of the eighth sternite is more evenly expanded than that seen in *F. rileyi* females. The genital sterna most closely resemble that of *F. celarata*. Most females of *F. abdita* can be separated from *F. celarata* by the presence of a notch or slight indentation at the posterior midpoint of the seventh sternite. The male and female genitalia of this species tend to show more variation than other species within this genus.

**Type.** Holotype male [USNM]. Labels on holotype: (1) Theodore, Ala.; F.M. Jones; drummondi, VI-10; (2) Collection; J. M. Aldrich; (3) SARCOPHAGA; rileyi; Ald. Paratype. [yellow Aldrich paratype label]; (4) HOLOTYPE; Fletcherimyia [♂]; abdita; T. Pape det.

Distribution. UNITED STATES: Alabama, Florida, Georgia, Mississippi.

**Biology.** Pape (1990) described this species from four males from Theodore, AL, reared by F. M. Jones from pitchers of *S. leucophylla* (=*drummondi*) (two of these specimens were paratypes of *F. rileyi*); two males from Freeport, FL, reared from *S. leucophylla* (=*drummondi*); and five males from Biloxi, MS, reared by F. M. Jones from *S. alata* (=*sledgei*) (Fig. 2). Adults have been collected on *Sarracenia flava* (Fig. 3), *S. leucophylla* (Fig. 4), and *Sarracenia rubra wherryi* (Fig. 9) in Alabama and on *S. minor* (Fig. 5) in Georgia by R.F.C.N.

Dissections of female specimens for this revision yielded seven gravid females. These females contained 2, 7, 7, 8, 10, 13, and 18 first instars.

### Fletcherimyia celarata (Aldrich) (Figs. 16a,b, 25, 34, 50)

- Sarcophaga celarata Aldrich, 1916: 242–243, pl. 13, Fig. 115; type locality: Theodore, AL; male holotype (description). Brimley 1938: 370 (distribution). Usinger 1956: 482 (biology).
- Peltopyga celarata; Townsend, 1917: 191, 194, 195 (generic placement and key).
- Fletcherimyia celarata; Roback, 1954: 31, 40, 84, Figs. 375–376 (systematics, male genitalia). Yeates et al. 1989: 38 (biology). Pape 1990: 48, Figs. 14 and 21, 26 (male genitalia). Yanoviak and Folkerts 1991: 80 (biology). Pape 1996: 224 (catalog).
- Blaesoxipha (Fletcherimyia) celarata; Downes 1965: 945 (catalog, distribution).
- Blaesoxipha celarata; Rymal and Folkerts 1982: 134 (biology).
- Fletcherimyia celerata (misspelling of celarata); Folkerts 1999: 257, 262.

Male. Length 10 mm. Row of setae on parafacial thin but distinct and evenly spaced. Chaetotaxy: dorsocentrals = 4 (weak, strong, weak, strong) + 4 (anterior two weak); intra-alars = 2 (weak seta near suture line) + 2 (anterior seta weak); supra-alars = 2 (anterior seta <one-half length of posterior seta) + 3 (middle seta >2× length of anterior and posterior seta). Katepisternum with two to three (usually three) dorsal setae. Abdominal tergite 3 with one lateral marginal and one median marginal seta. Abdominal tergite 4 with 1–3 lateral marginals and one median marginal seta.

Fifth sternum with short posterior arms; anterior medial window small, medial lobes broadly rounded and with a small, darkly sclerotized areas near tip. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 25). Phallus with vesica separated into a large dorsal and ventral lobe, in lateral view, and with a spinelike process near base of dorsal lobe; juxta more darkly sclerotized basally (Fig. 16a,b). Pregonite tapering to point at apex. Surstylus nearly cylindrical with one to two long, thin setae. Cercus elongate and separated from other cercus in apical two-thirds of length; dorsal humps broadly rounded; the inner margins of the separated cerci nearly straight, with the tips not distinctly convergent (Fig. 34).

Female. Sternum 8 with deep, U-shaped, apical invagination that is sometimes slightly irregular along midline, and with depressed lateral lobes (Fig. 50). Posterior margin of sternum 7 without notch or indentation at midpoint.

**Diagnosis.** The shape of the phallus, with its large, forward-extending ventral lobe of the vesica, and the straight apical tips of the cerci, easily separate males of this species from all others. The female genitalia are most similar to that of *F. abdita*, but no midline indentation or notch is present on the posterior margin of sternum 7. The genital sterna are also similar to *F. jonesi* and *F. rileyi*. For characters useful to separate the female, see the diagnosis under *F. jonesi*.

Type. Holotype male [USNM]. Labels on holotype: (1) Theodore, Ala.; F. M. Jones; VI-9-16; (2) gen dr [red typewriter print]; (3) Type No.; 20555; U.S.N.M. [red label]; (4) Sarcophaga; celerata; Ald..

**Distribution.** UNITED STATES: Alabama, Florida, Mississippi, (North Carolina?), Texas.

**Biology.** Aldrich (1916) described *F. celarata* from seven males reared by F. M. Jones from cups of *S. leucophylla* (=*drummondi*) (Fig. 4), 4–22 June 1916, from Theodore, AL. Yanoviak and Folkerts (1991) found that *F. celarata* was the third most collected sarcophagid from various pitcher plant sites in coastal Mississippi, Alabama, and the Florida panhandle.

**Discussion.** Aldrich (1916) noted that he could not distinguish the females of *celarata* from *rileyi* and *jonesi* but also noted that four females in the same lot were probably *celarata*. These four females were found labeled as paratypes of *F. celarata* in USNM and one of these has been identified as *F. abdita*.

Brimley (1938) noted that *F. celarata* was collected in May in Havelock, NC. This is the only record of *celarata* from North Carolina. This species seems to be associated with *S. leucophylla*, which is not found in North Carolina. This leads us to conclude that this record is based on a misidentification.

A series of specimens from Warren, TX, was examined from the CNC, but no host information was given on the specimens' labels.

# Fletcherimyia fletcheri (Aldrich) (Figs. 17a,b, 26, 35, 44)

- Sarcophaga fletcheri Aldrich, 1916: 96–98, pl. 4, Fig. 38; type locality: Tuckerton, NJ; male holotype (description). Brimley 1938: 370 (distribution). Hallock 1937: 261 (biology, distribution). Hallock 1940a: 130, Figs. 59–61 (biology, male genitalia). Hallock 1940b: 204, 210, 213 (key). Hallock 1942: 219–220, Figs. 149–151 (distribution, male genitalia). Usinger 1956: 482 (biology). Sanjean 1957: 11, 17, 18, 20, 21, 33, 34, 35, 37, 38, 39, 40, 41, 60–61, Figs. 141–149 (biology, larval descriptions, key to larvae).
- Fletcherimyia fletcheri; Townsend 1917: 191, 193, 195 (generic placement and key). Roback 1954: 31, 40, 83, 84, Figs. 366–369 (systematics, male genitalia). Judd 1959: 175, 176, 177 (biology). Farkas and Brust 1986: 1307–1308 (distribution, biology). Fairchild et al. 1987: 648, 651 (biology). Shewell 1987: Fig. 31 (wing). Yeates et al. 1989: 38 (biology). Pape 1990: 47, Figs. 15 and 21, 27 (distribution, male genitalia). Pape 1996: 224 (catalog). Rango 1999b: 82–85 (biology). Folkerts 1999: 257, 262. Marshall, et al. 1999: 394. Buckley et al. 2003: 826 (biology). Krawchuk and Taylor 2003: 153, 154–158, 160 (biology). Buckley et al. 2004: 182 (biology). Butler et al. 2005: 7 (biology).
- Sarcophaga dux sarracenioides (?), nec Aldrich; Johannsen 1935: 38, Figs. 79–84 (second, third instar, and puparium). Sanjean 1957: 7 (review of larval descriptions).
- Sarcophaga (Fletcherimyia) fletcheri; Spencer and Buckell 1957 (distribution).
- Blaesoxipha (Fletcherimyia) fletcheri; Downes 1965: 945 (catalog, distribution).
- Blaesoxipha fletcheri; Swales 1969: 762 (biology). Swales 1972: 41, 45-46 (biology). Forsyth and Robertson 1975: 174-178 (biology). Fish and Hall 1978: 172, 173, 178, 179, 181 (biology). Beaver 1979: 13 (biology). Rymal and Folkerts 1982: 134-135 (biology). Larson and Colbo 1983: 661–662. Fish 1983: Fig. 25 (larva). Bradshaw and Creelman 1984: 294, 300-301 (biology). de la Rosa and Nastase 1987: 339 (biology). Borkent 1987: 267 (biology). Wood 1987: 190 (biology). Givnish 1989: 263 (biology). Juniper et al. 1989: 254, 256–257, 263 (biology). Nastase et al. 1991: 356 (biology). Heard 1994a: 494 (biology). Heard 1994b:1648, 1650 (biology). Hardwick and Giberson 1996: 1956, 1959-1962. Petersen et al. 1997: 63 (biology). Heard 1998: 80 (biology). Bledzki and Ellison 1998: 193, 195-198 (biology). Cochran-Stafira and Von Ende 1998: 882 (biology). Rango 1999a: 19, 20, 24, 27, 28 (biology). Giberson and Hardwick 1999: 404, 407, 408, 410, 414, 418.
- Blaseoxiphia fletcheri (misspelling of Blaesoxipha); Southwood 1976: 45 (biology).
- Fletcheromyia fletcheri (misspelling of Fletcherimyia); Krawchuk and Taylor 1999: 829-830 (biology).
- Fletcherimyia (Blaesoxipha) fletcheri; Hamilton and Duffield 2002: 191–192, 193, Table 1 (biology)

Male. Length 9–12 mm. Chaetotaxy: dorsocentrals = 4 (weak, strong, weak, strong) or three (weak, strong, strong) + 3; intra-alars = 1 + 2 (anterior seta weak); supra-alars = 1 + 3 (middle seta over  $2 \times$ length of anterior and posterior seta). Katepisternum with three dorsal setae, middle seta weak. Abdominal tergite 3 with one lateral marginal and one median marginal seta. Abdominal tergite 4 with one to two (usually two) lateral marginals and one median marginal seta.

Fifth sternum with very short posterior arms; anterior medial window small, medial lobes not strongly produced, with only a small, projection extending past distal margin. Scattered, thin setae on posterior arms and medial area (Fig. 26). Phallus with vesica nearly triangular with outer margin, in lateral view, nearly parallel with corpus, and with a spinelike process near base; juxta more darkly sclerotized basally (Fig. 17a,b). Pregonite tapering to point at apex. Surstylus only slightly lobed apically. Cercus elongate and separated from other cercus in apical three-fifths of length; dorsal humps broadly rounded and small; the inner margins of the separated cerci curve out then in at the apex, with the tips distinctly convergent (Fig. 35).

Female. Length 7–8 mm. Abdominal tergite 3 with or without lateral marginal and with a weak median marginal seta. Sternites 6 and 7 subequal in size and shape. Sternum 8 with a shallow and rounded apical invagination. Depressed lateral lobes of sternum 8 basal, not extending up lateral margin to apex (Fig. 44).

Immature Stages. Johannsen (1935) and Sanjean (1957) provided descriptions and figures of the instars. The figures in Sanjean are preferred to those of Johannsen, whose figures overemphasize the size of the posterior cavity. Johannsen's figures are reprinted in Usinger (1956). Johannsen (1935) also provided a description of the puparium.

**Diagnosis.** This is the most common species collected from northern pitcher plant localities associated with *S. purpurea*. The phallus is somewhat similar to that of *F. folkertsi*, but the shape of the fifth sternite and the cerci allows easy separation. The fifth sternite and cerci are similar in shape to those of *F. papei*, but the surstyli do not project laterally and the shape of the phallus is very different. The basally located, depressed lateral lobes, and the shape of the apical invagination of sternum 8, separate females of *F. fletcheri* from *F. folkertsi* and *F. papei*.

Type. Holotype male [USNM]. Labels on holotype: (1) Tuckerton, N. J.; F. M. Jones; purpurea VIII-20; (2) Type No. 20505; U.S.N.M. [red label]; (3) Sarcophaga; fletcheri Ald.; Type [pink label].

**Distribution.** CANADA: British Columbia, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Prince Edward Island; UNITED STATES: Maine, Michigan, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Vermont.

**Biology.** Aldrich (1916) described this species from eight male and 11 female specimens. He noted that most of these specimens were reared by F. M. Jones

from S. *minor* (Fig. 5), S. *rubra* (Fig. 9), and S. *purpurea* (Fig. 7), but several of these are misidentifications (see below).

Female *F. fletcheri* deposit one larva per pitcher (Forsyth and Robertson 1975, Rango 1999a) and normally select young pitchers that have recently opened (Forsyth and Robertson 1975, Fish and Hall 1978, Farkas and Brust 1986). Forsyth and Robertson (1975) noted that females of *F. fletcheri* mature only one clutch of larvae, but they did not provide information on how this determination was made. The total number of larvae present within an individual female is relatively small when compared with other species of Sarcophagidae, ranging from eight to 14 (Sanjean 1957, Forsyth and Robertson 1975, Farkas and Brust 1986; unpublished data).

In northern latitudes, peak larval density occurs in late July to early August (Judd 1959, Forsyth and Robertson 1975, Rango 1999a). Usually only one larva will mature within a pitcher (Hallock 1942, Forsyth and Robertson 1975, Farkas and Brust 1986). The larva is aggressive and cannibalistic. Forsyth and Robertson (1975) gave an excellent account of the aggressive behavior of the larval *F. fletcheri*. Although the larvae are aggressive predators of conspecific larvae, they do not show this same tendency to the other two dipterans, *W. smithii* and *M. knabi*, which are often found as coinhabitants of the pitchers (Fish and Hall 1978). High prey density may allow more than one larva to develop within a pitcher (Rango 1999b).

The larvae can be successfully reared in the laboratory in small containers of water provided with freshly killed insects (Hallock 1942, Forsyth and Robertson 1975, Farkas and Brust 1986). Although dead insects make up the bulk of food eaten by larvae of *F. fletcheri*, Bledzki and Ellison (1998) showed that the larvae also feed on the rotifer *H. rosa* occurring within the pitchers.

Swales (1972) noted that adults of *F. fletcheri* were found resting within the flowers when *S. purpurea* was in bloom. Because the bodies of the sarcophagids were dusted with pollen, she noted that they were probably pollinators. Krawchuk and Taylor (1999) observed adults of *F. fletcheri* using the flower heads of *S. purpurea* as overnight roosting sites. They found flies landing on the sepals of the flower shortly before dusk and then noted the flies moving into the flower head for the night. Several mating pairs were found within the flower heads, although most heads contained one or two single flies. Feeding behavior on pitcher plant pollen was only observed once. Adults of *F. fletcheri* continued to use the flower heads as roosting sites even after the plants lost petals and stamens.

Hardwick and Giberson (1996) looked at the effects of transplantation of *S. purpurea* on the insect inquilines. This study took place between 1991 and 1993 on Prince Edward Island. No transplant effect was noted on sarcophagid populations. By summer 1993, *F. fletcheri*'s abundance in all transplant bogs was similar to that in other bogs in the region.

Krawchuk and Taylor (2003) investigated the relationship between patch size and relative isolation of patches of *S. purpurea* and the density of *F. fletcheri*. Their research was undertaken in peatland habitats in western Newfoundland. Their research suggests that larger pitchers are preferable larviposition sites within pitcher plant patches. However, larvae of *F. fletcheri* were only detected in 5% of the leaf samples. A mark-recapture experiment found that *F. fletcheri* showed a mean movement distance of 34 m, with a maximum recorded distance of 184 m. They did not include a parameter of time with these distance measurements. The effective mobility of adult *F. fletcheri* may allow much more cross-peatland movement than seen with smaller dipteran inquilines.

**Discussion.** Examination of the allotype and other female paratypes has revealed that the rearing records associated with *S. rubra* are in error, because these specimens are actually members of our newly described species *F. papei*. We have not seen the paratype(s) associating *F. fletcheri* with *S. minor*, but we feel that this association is also based on a misidentification. *F. fletcheri* seems to be solely associated with the pitcher plant *S. purpurea*.

The description of immature stages and figures provided by Johannsen (1935) are mistakenly identified as "Sarcophaga dux sarracenioides (?)".

#### Fletcherimyia folkertsi n. sp. (Figs. 18a,b, 27, 36, 45)

Male. Length 9–12 mm. Chaetotaxy: dorsocentrals = 4 (weak, strong, weak, strong) + 3; intraalars = 1 + 2 (anterior seta weak); supra-alars = 2 (anterior seta <one-half length of posterior seta) + 3 (middle seta > $2\times$  length of anterior and posterior seta). Katepisternum with two dorsal setae. Abdominal tergite 3 with one to two lateral marginals and one median marginal seta. Abdominal tergite 4 with two lateral marginals and one median marginal seta.

Fifth sternum with thin posterior arms; anterior medial window large, medial lobes strongly produced, with broad apical projections. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 27). Phallus with vesica rounded anteriorly and narrowing to a long point dorsally and with a spinelike process near middle of anterior edge; juxta more darkly sclerotized basally (Fig. 18a,b). Pregonite tapering to point at apex. Surstylus broadly rounded at apex with one to two long, thin setae. Cercus elongate and separated from other cercus in apical one-half of length; dorsal humps distinctly projecting dorsally; the separated cerci tapering, with inner margins curved and with the tips distinctly convergent (Fig. 36).

Female. Length 8–10 mm. Sternum 8 as broad or slightly broader that sternites 6 and 7, with small and rounded apical invagination, and with depressed lateral lobes extending laterally from base to near apex (Fig. 45).

**Diagnosis.** Males and females most closely resemble *F. fletcheri* and *F. papei*.

See diagnosis under *F. fletcheri* for details of characters to use for separation.

Type. Holotype male [FSCA]. Labels on holotype: (1) FLORIDA: Escambia; Co., Pensacola; 20-V-1993; R.F.C. Naczi; (2) HOLOTYPE; Fletcherimyia; folkertsi; Dahlem & Naczi [red label]. Allotype with same locality information [FSCA]. Total of 13 paratypes. Seven males with the same locality information as the holotype [USNM, CNC, NHMD, GWF, RFCN, (2) GD]. One male [GD]: Florida: Okaloosa Co.; S of Crestview; 29-IV-1991; R.F.C. Naczi. One female [GD]: Florida: Okaloosa Co.; 3 miles NW of Valparaiso; Elgin Air Force Base; 3-VIII-1994; R.F.C. Naczi. One female [GD]: Florida: Liberty Co.; ≈6 miles SW of Telogia; 1-VI-2000; Collectors: G.A. Dahlem; M.C. Earley; K.M. Flerlage; T.M. Foree; J.L. Gabbard; R.F.C. Naczi; P. Valentine; reared from Sarracenia rosea. One female [USNM]: Alabama: Geneva Co.;  $\approx$ 4 miles S of Hacoda; 3-VI-2000; Collectors: M.C. Earlev; K.M. Flerlage; T.M. Foree; J.L. Gabbard; R.F.C. Naczi; P. Valentine; reared from S. rosea. One male [GD] and one female [CNC]: Alabama: Mobile Co.; W of Citronelle; 22-V-1993; R.F.C. Naczi.

**Distribution.** UNITED STATES: Alabama, Florida. **Biology.** *F. folkertsi* seems to be associated solely with the pitcher plant *S. rosea* (Fig. 8). We have reared two females from pitchers of *S. rosea*. One specimen took 15 d to pass through the pupal stage and the other took 20 d.

**Etymology.** This species is named in honor of George W. Folkerts for his passion for American pitcher plants and the animals associated with them.

# Fletcherimyia jonesi (Aldrich) (Figs. 19a,b, 28, 37, 46)

- Sarcophaga jonesi Aldrich, 1916: 241–242, pl. 13, Fig. 114; type locality: Summerville, SC; male holotype (description). Hepburn and Jones 1919: 460 (biology). Brimley (1942): 27 (distribution). Wray 1967: 92 (distribution). Usinger 1956: 482 (biology).
- Fletcherimyia jonesi; Roback 1954: 31, 40, 84, Figs. 370–372 (systematics, male genitalia). Yeates et al. 1989: 38 (biology). Pape 1990: Figs. 16 and 22, 25 (male genitalia). Pape 1996: 224 (catalog). Folkerts 1999: 257, 262.
- Blaesoxipha (Fletcherimyia) jonesi; Downes 1965: 945 (catalog, distribution). Fish 1976: 201, 202 (biology).
- Blaesoxipha jonesi; Rymal and Folkerts 1982: 134 (biology).

Male. Length 10 mm. Row of setae along parafacial thin, evenly spaced and distinct. Chaetotaxy: dorso-centrals = 4 (anterior seta weak) + 4 (anterior two weak); intra-alars = 2 (weak seta near suture line) + 2 (anterior seta weak; supra-alars = 2 (anterior seta <one-half length of posterior seta) + 3 (middle seta  $>2\times$  length of anterior and posterior seta). Katepisternum with two dorsal setae. Abdominal tergite 3 usually without lateral marginal and median marginal setae. Abdominal tergite 4 with one lateral marginal and one median marginal setae.

Fifth sternum with distinct posterior arms; anterior medial window fairly large, medial lobes broadly rounded and darkly sclerotized near tip. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 28). Phallus with vesica separated into a dorsal and a protruding ventral lobe, in lateral view, and without a spinelike process near base of dorsal lobe; juxta more darkly sclerotized basally (Fig. 19a,b). Pregonite tapering to point at apex. Surstylus only slightly lobed apically with one to two long, thin setae. Cercus elongate and separated from other cercus in apical twothirds of length; dorsal humps broadly rounded; the inner margins of the separated cerci nearly parallel for a short distance at base, then divergent, with the tips not distinctly convergent (Fig. 37).

Female. Length 8–9 mm. Sternum 7 with little setation. Sternum 8 with deep V-shaped apical invagination and with lateral depressed lobes mainly basal (Fig. 46).

**Diagnosis.** The distinctive shape of the phallus will easily separate males of *F. jonesi* from the other species. The female's genitalia are similar to those of *F. abdita, F. celarata,* and *F. rileyi.* The female can be separated from *F. abdita* and *F. celarata* by the V-shaped, rather than U-shaped, apical invagination of sternum 8. It can be separated from *F. rileyi* by the thinner apical points and the lack of basal lateral expansion of sternum 8.

Type. Holotype male [USNM]. Labels on holotype:

- (1) Summerville, S.C.; F. M. Jones; minor, VII-18-15;
- (2) F. M. Jones; coll; (3) gen dr [red typewriter print];
  (4) Type No.; 20564; U.S.N.M. [red label]; Sarcophaga; jonesi; Ald.

**Distribution.** UNITED STATES: Alabama, Florida, Georgia, North Carolina, South Carolina.

**Biology.** Aldrich (1916) described *F. jonesi* from seven males from Summerville, SC, reared from *S. minor* and *S. flava* by F. M. Jones; three males that were part of the type series of *Sarcophaga sarraceniae* Riley; and one male from Tifton, GA.

*F. jonesi* has been associated with both *S. flava* (Fig. 3) (Aldrich 1916, Hepburn and Jones 1919) and *S. minor* (Fig. 5) (Aldrich 1916, Fish 1976).

Fish (1976) examined the relationship between the pitcher plant *S. minor* and *F. jonesi* at a site near Orange Heights in Alachua County, Florida, in mid-August 1974. Single larvae of *F. jonesi* were found in 64% of the pitchers examined, and all three larval stages were represented. *F. jonesi* does not damage the leaves in any way but it does consume substantial amounts of insect material captured by the plant.

Dissections of female specimens for this revision yielded six gravid females. These contained 2, 7, 12, 21, and 36 first instars. The 36 larvae obtained from one of these females represent the highest number of larvae observed in a gravid female of all the *Fletcherimyia* species.

We reared one female from a pitcher of *S. flava*. It passed through the pupal stage in 20 d.

# *Fletcherimyia oreophilae* n. sp. (Figs. 11, 20a,b, 29, 38, 47)

Male. Length 10–13 mm. Chaetotaxy: dorsocentrals = 4 (anterior seta weak) + 4; intra-alars = 2 (weak seta near suture line) + 2 (anterior seta weak); supra-alars = 1 + 3 (middle seta  $>2\times$  length of anterior and posterior seta). Katepisternum with two dorsal setae. Abdominal tergite 3 with zero to one lateral marginal and without median marginal seta. Abdominal tergite 4 with one lateral marginal and one median marginal seta.

Fifth sternum with short posterior arms; anterior medial window large, medial lobes broadly rounded. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 29). Phallus with vesica projecting to a large dorsal lobe, in lateral view, and with a spinelike process near apex; juxta more darkly sclerotized basally (Fig. 20a,b). Pregonite tapering to point at apex. Surstylus very broad with a scattering of thin setae, distinctly projecting laterally from the body (Fig. 11). Cercus elongate and separated from other cercus in apical two-thirds of length; dorsal humps strongly produced; the inner margins of the separated cerci are curved, with the tips distinctly convergent (Fig. 38).

Female. Length 11 mm. Sternum 8 rounded apically, without apical invagination (Fig. 47).

**Diagnosis.** Both the phallus of the male and the shape of sternum 8 of the female are very distinctive and easily separate this species from all others.

Type. Holotype male [FSCA]. Labels on holotype: (1) ALABAMA: Cherokee Co.; W of Jamestown; 31-V-1990; R.F.C. Naczi; (2) Collected; in-copuli; #6; (3) HOLOTYPE; Fletcherimyia; oreophilae; Dahlem & Naczi [red label]. Allotype [FSCA] collected in cop*ula* with the holotype, but on a separate pin. Total of 14 paratypes. One male with same locality information as holotype [USNM]. Two males [CNC, GD]: Alabama: Cherokee Co.; W of Jamestown; 7-V-1991; R.F.C. Naczi. Four males [(2) CNC, RFCN, GD]: Alabama: DeKalb Co.; SE of Fort Payne, "right site"; 7-V-1991; R.F.C. Naczi. One male [USNM]: Alabama: DeKalb Co.; SE of Fort Payne; 31-V-1990; R.F.C. Naczi. Five males [USNM, NHMD, (3) GD] and one female [GD]: Alabama: DeKalb Co.; SE of Fort Payne, "right site"; 5-VI-2000; on pitchers of Sarracenia oreophila; collectors: M.C. Earley; K.M. Flerlage; T.M. Foree; J.L. Gabbard; R.F.C. Naczi; P. Valentine.

Distribution. UNITED STATES: Alabama.

**Biology.** *F. oreophilae* seems to be solely associated with the pitcher plant *S. oreophila* (Fig. 6). This pitcher plant is currently federally listed as an endangered species.

Dissections of female specimens for this revision yielded one gravid female. This female contained two first instars. These larvae were exceptionally large, measuring  $\approx$ 7 mm in length.

Etymology. This species is named after its only known host plant, the endangered *S. oreophila*.

## Fletcherimyia papei n. sp. (Figs. 21a,b, 30, 39, 48)

Male. Length 6–9 mm. Chaetotaxy: dorsocentrals = 3 or four (anterior one or two weak) + 3; intra-alars = 1 + 2 (anterior seta weak); supra-alars = 1 + 3 (middle seta >2× length of anterior and posterior seta). Katepisternum with two dorsal setae. Abdominal tergite 3 with one lateral marginal and one median marginal seta. Abdominal tergite 4 with two lateral marginals and one median marginal seta.

Fifth sternum with thin posterior arms; anterior medial window large, medial lobes produced but without apical projections. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 30). Phallus with vesica rounded anteriorly and narrowing to a long point dorsally and with a spinelike process near bottom of anterior edge; juxta expanded anteriorly and more darkly sclerotized basally (Fig. 21a,b). Pregonite tapering to point at apex. Surstylus broadly rounded at apex with one to two long, thin setae, distinctly projecting laterally from the body. Cercus elongate and separated from other cercus in apical two-thirds of length; dorsal humps only slightly projecting dorsally; the separated cerci with the tips not distinctly convergent (Fig. 39).

**Female.** Length 6–9 mm. Sterna 6 and 7 subequal in size. Sternum 8 with shallow apical invagination and small lateral depressions located basally (Fig. 48).

**Diagnosis.** This is generally the smallest member of *Fletcherimyia*.

It most closely resembles *F. fletcheri* and *F. folkertsi*; see diagnosis under *F. fletcheri* for details of characters to use for separation.

Type. Holotype male [FSCA]. Labels on holotype: (1) ALABAMA: Washington Co.; 4.2 miles. S of Chatom, Route 17; 3-VIII-1994; R.F.C. Naczi; ex: Sarracenia rubra subsp. wherryi; (2) HOLOTYPE; Fletcher*imyia*; *papei*; Dahlem & Naczi [red label]. Allotype [FSCA]: Alabama: Washington Co.; 4.2 miles S of Chatom, Route 17; 2-VIII-1994; R.F.C. Naczi. Total of 14 paratypes. Six males with the same locality information as the holotype [USNM, CNC, NHMD, RFCN, (2) GD]. One female [GD]: Alabama: Washington Co.; 12.8 miles SSW of Chatom; 3-VIII-1994; R.F.C. Naczi. Six females [USNM]: Southern Pines, NC; F.M. Jones; *rubra*; collected on the following dates: VIII-4; VIII-24; VIII-25; VIII-25 (a paratype of S. fletcheri); VIII-26 (allotype of S. fletcheri); and VIII-31. One male [CNC]: Warren, TX; 7-I-1950; F. A. Cowan Collector.

**Distribution.** UNITED STATES: Alabama, North Carolina, Texas.

**Biology.** *F. papei* seems to be associated with the pitcher plant species *S. rubra* (including the subspecies *wherryi*) (Fig. 9). Rearing records of *F. fletcheri* from *S. rubra*, noted in Aldrich (1916), are the result of misidentified females of *F. papei*.

Dissections of female specimens for this revision yielded one gravid female, which contained 13 first instars. **Etymology.** This species is named in honor of Thomas Pape for his work on North American *Fletcherimyia* and his great accomplishments with the Sarcophagidae.

## Fletcherimyia rileyi (Aldrich) (Figs. 22a,b, 31, 40, 49)

- Sarcophaga rileyi Aldrich, 1916: 239–241, pl. 13, Fig. 113; type locality: Summerville, SC; male holotype (description). Hepburn and Jones 1919: 460 (biology). Brimley 1938: 371 (distribution). Usinger 1956: 482 (biology).
- Fletcherimyia rileyi; Roback 1954: 40, 84, Figs. 373–374 (systematics, male genitalia). Yeates et al. 1989: 38 (biology). Pape 1990: 48, Figs. 17 and 18, 23, 28 (paratypes, male genitalia). Pape 1996: 224 (catalog). Yanoviak and Folkerts 1991: 80 (biology). Folkerts 1999: 257, 262.
- Blaesoxipha (Fletcherimyia) rileyi; Downes 1965: 945 (distribution).
- Blaesoxipha rileyi; Rymal and Folkerts 1982: 134 (biology).

Male. Length 11–13 mm. Chaetotaxy: dorsocentrals = 4 + 4 (anterior two weak); intra-alars = 2 (weak seta near suture line) + 2 (anterior seta weak). Katepisternum with three dorsal setae, middle seta weak. Abdominal tergite 3 with one lateral marginal and without median marginal setae. Abdominal tergite 4 with one to two lateral marginals and one median marginal seta.

Fifth sternum with short posterior arms; anterior medial window large, medial lobes not strongly produced, with only a small, projection extending past distal margin. Scattered, thin setae on posterior arms and medial area, with a few longer, stout setae on posterior arms (Fig. 31). Phallus with vesica rounded anteriorly and narrowing to a blunt point dorsally and with a spinelike process near middle; juxta more darkly sclerotized basally (Fig. 22a,b). Pregonite tapering to point at apex. Surstylus broadly oval at apex with several long, thin setae. Cercus elongate and separated from other cercus in apical three-fourths of length; dorsal humps broadly rounded; the separated cerci fairly thin, with the tips distinctly convergent (Fig. 40).

Female. Length 7–13 mm (most 10–13 mm). Sternites 6 and 7 with fairly dense setation. Sternum 8 with deep, V-shaped apical invagination and with well developed lateral depressions extending apically to near tip (Fig. 49). The base of sternum 8 with distinct lateral extensions.

**Diagnosis.** The phallus is similar to that of *F. abdita* but the spinelike process near the middle of the vesica and the shape of the cerci will separate this species. The female genitalia are similar to those of *F. abdita*, *F. celarata*, and *F. jonesi*. For characters useful to separate the female, see the diagnosis under *F. jonesi*.

Type. Holotype male [USNM]. Labels on holotype: (1) Summerville, S.C.; F.M. Jones; minor, VIII-9-15;

(2) F. M. Jones; coll; (3) Type No.; 20554; U.S.N.M.
 [red label]; (4) Sarcophaga; rileyii Ald. [pink label].
 Distribution. UNITED STATES: Alabama, Florida,

Georgia, Mississippi, North Carolina, South Carolina.

**Biology.** Aldrich (1916) described this species from seven males and one female that were a part of the material described by Riley as *S. sarraceniae*, all specimens reared by F. M. Jones from pitchers of *S. minor* and *S. flava*; and two males [misidentified, see below] from Theodore, AL, reared by F.M. Jones from pitchers of *S. leucophylla* (=drummondi).

*F. rileyi* is associated with *S. flava* (Fig. 3) (Aldrich 1916, Hepburn and Jones 1919) and *S. minor* (Fig. 5) (Aldrich 1916). Yanoviak and Folkerts (1991) found that *F. rileyi* was the second most commonly collected sarcophagid from various pitcher plant sites in coastal Mississippi, Alabama, and the Florida panhandle.

We collected *F. rileyi* on pitchers of *S. flava* in Alabama and Florida. Two males and two females were reared from *S. flava*. The larvae pupariated 13 d after collection. The females emerged 17 and 21 d later, whereas the males emerged after 21 and 24 d.

Dissections of female specimens for this revision yielded two gravid females. These contained 31 and 32 first instars.

**Discussion.** The allotype female dissected and examined by us seems to be *F. rileyi*, although the specimen is smaller than most females of this species. The two male paratypes reared from *S. leucophylla* were discovered by Pape (1990) to be a different species, which he described as *F. abdita*.

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#### **References Cited**

- Aldrich, J. M. 1905. A catalogue of North American Diptera (or two-winged flies). Smithson. Misc. Collect. 46: 1–680.
- Aldrich, J. M. 1914. Description of Sarcophaga kellyi, pp. 443–445 + pl. XL. In E.O.G. Kelly, A new sarcophagid parasite of grasshoppers. J. Agric. Res. 2: 435–446.
- Aldrich, J. M. 1915. The economic relations of the Sarcophagidae. J. Econ. Entomol. 8: 246.
- Aldrich, J. M. 1916. Sarcophaga and allies in North America. Entomological Society of America, Thomas Say Foundation, Vol. 1, La Fayette, IN.
- Austen, E. E. 1896. Necrophagous Diptera attracted by the odour of flowers. Ann. Mag. Nat. Hist. 18: 237–240.
- Baldwin, A. S., and E. F. Menhinick. 2000. A record of desiccated rotifers in a single trap of the yellow pitcher plant *Sarracenia flava* with notes on their distribution and rehydration rates. J. Elisha Mitchell Sci. Soc. 116: 69–74.

- Banks, N. 1912. The structure of certain dipterous larvae with particular reference to those in human foods. U.S. Dep. Agric. Bur. Entomol. Tech. Bull. 22: 1–44.
- Beaver, R. A. 1979. Biological studies of the fauna of pitcher plants [*Nepenthes*] in west Malaysia. Ann. Soc. Entomol. Fr. 15: 3–17.
- Bezzi, M. 1926. Le "stupide mosche." Riv. Sci. Nat. "Natura". 17: 1–19.
- Bledzki, L. A., and A. M. Ellison. 1998. Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution of the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae). Hydrobiologia 385: 193–200.
- Borkent, A. 1987. Insects associated with pitcher plant Sarracenia purpurea L., pp. 267. In J. D. Lafontaine, S. Allyson, V. M. Behan-Pelletier, A. Borkent, J. M. Campbell, K.G.A. Hamilton, J.E.H. Martin, and L. Masner [eds.], The insects, spiders and mites of Cape Breton Highlands National Park. Biosystematics Research Centre, Report No. 1.
- Boyes, J. W. 1953. Somatic chromosomes of higher Diptera. II. Differentiation of sarcophagid species. Can. J. Zool. 31: 561–576.
- Boyes, J. W. 1963. Somatic chromosomes of higher Diptera. VII. Sarcophagid species in relation to their taxonomy. Can. J. Zool. 41: 1191–1204.
- Boyes, J. W. 1967. The cytology of muscoid flies, pp. 371– 384. In J. W. Wright and R. Pal [eds.], Genetics of insect vectors of disease. Elsevier, Amsterdam, The Netherlands.
- Boyes, J. W., and A. Wilkes. 1953. Somatic chromosomes of higher Diptera. I. Differentiation of tachinid parasites. Can. J. Zool. 31: 125–165 + 2 pls.
- Bradshaw, W. E., and R. A. Creelman. 1984. Mutualism between the carnivorous purple pitcher plant and its inhabitants. Am. Midl. Nat. 112: 294–304.
- Brimley, C. S. 1938. The insects of North Carolina. Being a list of the insects of North Carolina and their close relatives. North Carolina Dep. Agric., Div. Entomol., Raleigh, NC.
- Brimley, C. S. 1942. Supplement to insects of North Carolina. North Carolina Dep. Agric., Raleigh, NC.
- Buckley, H. L., J. H. Burns, J. M. Kneitel, E. L. Walters, P. Munguia, and T. E. Miller. 2004. Small-scale patterns in community structure of *Sarracenia purpurea* inquilines. Community Ecol. 5: 181–188.
- Buckley, H. L., T. E. Miller, A. M. Ellison, and N. J. Gotelli. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. Ecol. Lett. 6: 825–829.
- Butler, J. L., D. Z. Atwater, and A. M. Ellison. 2005. Redspotted newts: an unusual nutrient source for northern pitcher plants. Northeast. Nat. 12: 1–10.
- Callan, E. M. 1946. A note on Sarcophaga lambens (Wied.), a parasite of the South American bollworm, Sacadodes pyralis Dyar. Rev. Entomol. 17: 474–475.
- Cochran-Stafira, D. L., and C. N. Von Ende. 1998. Integrating bacteria into food webs: studies with Sarracenia purpurea inquilines. Ecology 79: 880–898.
- Comstock, J. H. 1879. Dipterous parasites, pp. 203–211. In Report upon cotton insects. U.S. Dep. Agric., Div. Entomol., Washington, DC.
- Coquillett, D. W. 1892. The dipterous parasite of Melanoplus devastator in California. Insect Life 5: 22–24.
- Curran, C. H. 1965. The families and genera of North American Diptera, 2nd revised ed. Henry Tripp. Woodhaven, New York.

- Dahlem, G. A. 1991. Sarcophagidae (Oestroidea), pp. 871– 873. In F. W. Stehr [ed.], Immature insects, vol. 2. Kendall/Hunt Publishing Co., Dubuque, IA
- Davis, J. J., and P. Luginbill. 1921. The green June beetle or fig eater. North Carolina Agric. Exp. Sta. Bull. 242: 1–35.
- Davis, J. J., and P. Luginbill. 1922. The green June beetle or fig eater. Rev. Appl. Entomol. Ser. A 10: 164–165.
- de la Rosa, C. L., and A. J. Natase. 1987. Larvae of *Metriconemus* cf. *fuscipes*, *Limnophyes* sp., *Pentaneurini* (Diptera: Chironomidae) and *Culicoides* (Diptera: Ceratopogonidae) from pitcher plants, *Sarracenia purpurea*. J. Kans. Entomol. Soc. 60: 339–341.
- Dodge, H. R. 1956. A new sarcophagid genus with descriptions of fifteen new species (Diptera). Ann. Entomol. Soc. Am. 49: 242–263.
- Dodge, H. R. 1966. Sarcophaga utilis Aldrich and allies (Diptera, Sarcophagidae). Entomol. News 77: 85–97.
- Downes, W. L., Jr. 1965. Family Sarcophagidae, pp. 933– 961. In A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson [eds.], A catalog of the Diptera of America north of Mexico. Agriculture Handbook No. 276. Agricultural Research Service, USDA, Washington, DC.
- Fairchild, W. L., D. C. Eidt, and C.A.A. Weaver. 1987. Effects of fenitrothion insecticide on inhabitants of the leaves of the pitcher plant, *Sarracenia purpurea* L. Can. Entomol. 119: 647–652.
- Farkas, M. J., and R. A. Brust. 1986. Pitcher-plant sarcophagids from Manitoba and Ontario. Can. Entomol. 118: 1307–1308.
- Fish, D. 1976. Insect-plant relationships of the insectivorous pitcher plant Sarracenia minor. Fla. Entomol. 59: 199–203.
- Fish, D. 1983. Phytotelmata: flora and fauna, pp. 1–27. In J. H. Frank and L. P. Lounibos [eds.], Phytotelmata: terrestrial plants as hosts for aquatic insect communities. Plexus Publishing, Inc., Medford, NJ.
- Fish, D., and D. W. Hall. 1978. Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant, *Sarracenia purpurea*. Am. Midl. Nat. 99: 172–183.
- Folkerts, D. 1999. Pitcher plant wetlands of the southeastern United States. Arthropod associates. Chapter 11, pp. 247–275. In D. P. Batzer, R. B. Rader, and S. A. Wissinger [eds.], Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.
- Folkerts, D. R., and G. W. Folkerts. 1996. Aids for field identification of pitcher plant moths of the genus *Exyra* (Lepidoptera: Noctuidae). Entomol. News 107: 128–136.
- Folkerts, G. W. 1982. The Gulf Coast pitcher plant bogs. Am. Sci. 70: 260–267.
- Forsyth, A. B., and R. J. Robertson. 1975. K reproductive strategy and larval behavior of the pitcher plant sarcophagid fly, *Blaesoxipha fletcheri*. Can. J. Zool. 53: 174–179.
- Fyles, T. W. 1907. Two-winged flies. Ann. Rep. Entomol. Soc. Ont. 38: 102–111.
- Giberson, D., and M. L. Hardwick. 1999. Pitcher plants (Sarracenia purpurea) in eastern Canadian peatlands. Ecology and conservation of the invertebrate inquilines. Chapter 18, pp. 401–422. In D. P. Batzer, R. B. Rader, and S. A. Wissinger [eds.], Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.
- Givnish, T. J. 1989. Ecology and evolution of carnivorous plants, pp. 243–290. In W. G. Abrahamson [ed.], Plantanimal interactions. McGraw-Hill, New York.
- Hallock, H. C. 1937. A list of the Sarcophagidae of New York (Diptera). Entomol. News 48: 258–262.

- Hallock, H. C. 1940a. The Sarcophaginae and their relatives in New York, Part I. J. N Y Entomol. Soc. 48: 127–153.
- Hallock, H. C. 1940b. The Sarcophaginae and their relatives in New York. II. J. N Y Entomol. Soc. 48: 201–230.
- Hallock, H. C. 1942. The Sarcophaginae and their relatives in New York. II. J. N Y Entomol. Soc. 50: 215–241.
- Hamilton, R.I.V., and R. M. Duffield. 2002. Novel observations of midge and mosquito larval population dynamics in leaves of the northern pitcher plant, *Sarracenia purpurea* L. Hydrobiologia 482: 191–196.
- Hardwick, M. L., and D. J. Giberson. 1996. Aquatic insect populations in transplanted and natural populations of the purple pitcher plant, *Sarracenia purpurea*, on Prince Edward Island, Canada. Can. J. Zool. 74: 1956–1963.
- Heard, S. B. 1994a. Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*). Evol. Ecol. 8: 493–502.
- Heard, S. B. 1994b. Pitcher-plant midges and mosquitoes: a processing chain commensalisms. Ecology 75: 1647–1660.
- Heard, S. B. 1998. Capture rates of invertebrate prey by the pitcher plant, *Sarracenia purpurea* L. Am. Midl. Nat. 139: 79–89.
- Hepburn, J. S., and Jones, F. M. 1919. Occurrence of antiproteases in the larvae of the Sarcophaga associates of Sarracenia flava. Control Bot. Lab. Univ. Penn. 4: 460– 463.
- Herms, W. B. 1907. An ecological and experimental study of Sarcophagidae with relation to lake beach debris. J. Exp. Zool. 4: 45–83.
- Herms, W. B. 1915. Medical and Veterinary Entomology. The MacMillan Co., New York.
- Higley, W. K. 1885. The Northern Pitcher-plant or the Sidesaddle Flower, Sarracenia purpurea, L. Bull. Chicago Acad. Sci. 1: 41–55.
- Hine, J. S. 1904. The Diptera of British Columbia. Can. Entomol. 36: 85–92.
- Howard, L. O. 1900. Contribution to the study of the insect fauna of human excrement. [With especial reference to the spread of typhoid fever by flies.] Proc. Wash. Acad. Sci. 2: 541–604.
- Howard, L. O. 1902. The insect book. Doubleday, Page & Co., New York.
- Hubbard, H. G. 1896. Some insects which brave the dangers of the pitcher-plant. Proc. Entomol. Soc. Wash. 3: 314– 316.
- Johannsen, O. A. 1935. Aquatic Diptera. Part II. Orthorrhapha-Brachycera and Cyclorrhapha. Mem. Cornell Univ. Agric. Exp. Stn. No. 177.
- Jones, F. M. 1904. Pitcher-plant insects. Entomol. News 15: 14–17.
- Jones, F. M. 1908. Pitcher-plant insects. III. Entomol. News 19: 150–156.
- Jones, F. M. 1920. Another pitcher-plant insect. (Diptera, Sciarinae). Entomol. News 31: 91–94.
- Jones, F. M. 1935. Pitcherplants and their insect associates, pp. 25–34. In M. V. Walcott [ed.], Illustrations of North American pitcherplants. Smithsonian Institution, Washington, DC.
- Judd, W. W. 1959. Studies of the Byron Bog in southwestern Ontario. X. Inquilines and victims of the pitcher-plant, *Sarracenia purpurea* L. Can. Entomol. 91: 171–180.
- Juniper, B. E., R. J. Robins, and D. M. Joel. 1989. The carnivorous plants. Academic, San Diego, CA.
- Keiper, J. B., W. E. Walton, and B. A. Foote. 2002. Biology and ecology of higher Diptera from freshwater wetlands. Annu. Rev. Entomol. 47: 207–232.
- Kelly, E.O.G. 1914. A new sarcophagid parasite of grasshoppers. J. Agric. Res. 2: 435–445 + pl. XL.

- Kelly, E.O.G. 1915. A new sarcophagid parasite of grasshoppers. Rev. Appl. Entomol. Ser. A 3: 81–82.
- Krawchuk, M. A., and P. D. Taylor. 1999. Roosting behaviour by *Fletcheromyia fletcheri* (Diptera: Sarcophagidae) in *Sarracenia purpurea* (Sarraceniacea). Can. Entomol. 131: 829–830.
- Krawchuk, M. A., and P. D. Taylor. 2003. Changing importance of habitat structure across multiple spatial scales for three species of insects. Oikos 103: 153–161.
- Lahille, F. 1907. La langosta y sus moscas parasitarias. An. Minist. Agric. Sec. Zootecn. Bact. Vet. Zool. 3: 1–136.
- Larson, D. J., and M. H. Colbo. 1983. The aquatic insects: biogeographic considerations, pp. 593–677. In G. R. South [ed.], Biogeography and ecology of the island of Newfoundland. Junk Publishing, The Hague, The Netherlands.
- Lloyd, F. E. 1942. The carnivorous plants. The Ronald Press Company, New York.
- Lopes, H. S. 1946. Sarcophagidae do México, capturados pelo professor A. Dampf. (Diptera). Mem. Inst. Oswaldo Cruz 44: 119–146.
- Lopes, H. S. 1969. Family Sarcophagidae. A catalogue of the Diptera of the Americas south of the United States. Departmento de Zoologia, Secretaria da Agricultura, São Paulo. No. 103.
- Lopes, H. S. 1971. Notes on *Tephromyiini* with description of a new species of *Mantidophaga* Townsend (Diptera, Sarcophagidae). Rev. Bras. Biol. 31: 3–13.
- Marshall, S. A., A. T. Finnamore, and D C A. Blades. 1999. Canadian peatlands. Diversity and habitat specialization of the arthropod fauna. Chapter 17, pp. 383–400. *In* D. P. Batzer, R. B. Rader, and S. A. Wissinger [eds.], Invertebrates in freshwater wetlands of North America: ecology and management. Wiley, New York.
- Mattos, W. B. 1926. As Sarcophagas de S. Paulo, 2nd ed., Sao Paulo, Brazil.
- McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood [eds.]. 1981. Manual of Nearctic Diptera. Volume 1. Biosystematics Research Institute Research Monograph No. 27.
- McGillivray, A. D., and C. O. Houghton. 1903. A list of insects taken in the Adirondack Mountains, New York. II. Entomol. News 14: 12–13.
- Mellichamp, J. H. 1875. Notes on Sarracenia variolaris, pp. 113–133. Proc. Am. Assoc. Adv. Sci. Part II. Sect. B.
- Metz, C. W. 1916. Chromosome studies on the Diptera II. The paired association of chromosomes in the Diptera, and its significance. J. Exp. Zool. 21: 213–280.
- Morgan, H. A. 1901. The differential grasshopper in the Mississippi delta – other common species. U.S. Dep. Agric., Div. Entomol. Bull. No. 30: 7–33.
- Nastase, A. J., C. de la Rosa, and S. J. Newell. 1991. A comparison of three methods for collecting dipteran insect larvae which inhabit the northern pitcher plant (*Sarracenia purpurea*). Am. Midl. Nat. 125: 356–359.
- Osborn, H. 1896. Insects affecting domestic animals: an account of the species of importance in North America, with mention of related forms occurring on other animals. U.S. Dep. Agric. Bull. No. 5: 1–302.
- Pape, T. 1990. Revisionary notes on American Sarcophaginae (Diptera: Sarcophagidae). Tijd. Entomol. 133: 43–74.
- Pape, T. 1994. The world *Blaesoxipha* Loew, 1861 (Diptera: Sarcophagidae). Entomol. Scand. Suppl. No. 45.
- Pape, T. 1996. Catalogue of the Sarcophagidae of the World (Insecta: Diptera). Memoirs on Entomology, International. Volume 8. Associated Publishers, Gainesville, FL.
- Pape, T. 2004. Family Sarcophagidae (Insecta: Diptera), pp. 849–851. In C. M. Yule and Y. H. Sen [eds.], Fresh-

water Invertebrates of the Malaysian Region. Monash University, Acad. of Sciences Malaysia. Kuala Lumpur, Malaysia.

- Parker, R. R. 1914. Sarcophagidae of New England: males of the genera *Ravinia* and *Boettcheria*. Proc. Boston Soc. Nat. Hist. 35: 1–77
- Parker, R. R. 1915. [Additional comments related to paper by J.M. Aldrich]. J. Econ. Entomol. 8: 246–247.
- Parker, R. R. 1916. Sarcophagidae of New England: genus Sarcophaga. J. Econ. Entomol. 9: 438-441.
- Petersen, R. L., L. Hanley, E. Walsh, H. Hunt, and R. M. Duffield. 1997. Occurrence of the rotifer, *Habro-trocha* cf. rosa Donner, in the purple pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae) along the eastern seaboard of North America. Hydrobiologia 354: 63–66.
- Rango, J. J. 1999a. Summer phenology of aquatic insect communities inhabiting the leaves of the northern pitcher plant, *Sarracenia purpurea* L. Northeast. Nat. 6: 19–30.
- Rango, J. J. 1999b. Resource dependent larviposition behavior of a pitcher plant flesh fly, *Fletcherimyia fletcheri* (Aldrich) (Diptera: Sarcophagidae). J. N Y Entomol. Soc. 107: 82–86.
- Riley, C. V. 1874a. Descriptions and natural history of two insects which brave the dangers of *Sarracenia variolaris*. Trans. Acad. Sci. St. Louis 3: 235–240.
- Riley, C. V. 1874b. On the insects more particularly associated with Sarracenia variolaris (spotted trumpet-leaf). Can. Entomol. 6: 207–214.
- Riley, C. V. 1875a. Seventh annual report on the noxious, beneficial, and other insects of the State of Missouri. Jefferson City.
- Riley, C. V. 1875b. 2° Note sur le Sarcophaga sarraceniae (Extrait par M. Lichtenstein). Ann. Soc. Entomol. Fr. 5: XII-XIII.
- Riley, C. V. 1885. Fourth report of the United States entomological commission, being a revised edition of Bulletin No. 3, and the final report on the cotton worm, together with a chapter on the boll worm. Washington, DC.
- Roback, S. S. 1954. The evolution and taxonomy of the Sarcophaginae. Ill. Biol. Monogr. 23: i-v, 1–181.
- Rohdendorf, B. B. 1971. On the Sarcophagidae from Cuba. Časopis Moravského Musea 55: 89–114.
- Rymal, D. E., and G. W. Folkerts. 1982. Insects associated with pitcher plants (Sarracenia: Sarraceniaceae), and their relationship to pitcher plant conservation: a review. J. Ala. Acad. Sci. 53: 131–151.
- Sanjean, J. 1957. Taxonomic studies of Sarcophaga larvae of New York, with notes on the adults. Mem. Cornell Univ. Agric. Exp. Sta. No. 349.
- Shewell, G. E. 1987. Sarcophagidae, pp. 1159–1186. In J. F. McAlpine, B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood [eds.], Manual of Nearctic Diptera. Volume 2. Biosystematic Research Institute Research Monograph 28: i-vi, 675–1332.
- Shinonaga, S., and R. A. Beaver. 1979. Pierretia urceola: a new species of sarcophagid fly found living in Nepenthes pitcher plants in West Malaysia. Ann. Soc. Entomol. Fr. 15: 37–40.
- Sinclair, B. J. 2000. Morphology and terminology of Diptera male terminalia, pp. 53–74. *In* L. Papp and B. Darvas [eds.], Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance). Volume 1. General and applied Dipterology. Science Herald, Budapest, Hungary.

- Sleesman, J. P. 1935. Ovicidal tests on certain dipterous eggs with especial reference to the onion maggot, *Hylemyia* antiqua Meig. J. Econ. Entomol. 28: 453–457.
- Southwood, T.R.E. 1976. Bionomic strategies and population parameters, pp. 26–48. In R. E. May [ed.], Theoretical ecology, principles and applications. Blackwell Scientific Publications, W.B. Saunders Co., Philadelphia, PA, and Toronto, Canada.
- Spencer, G. J., and E. R. Buckell. 1957. On the acridiophagous Sarcophagidae of British Columbia with records of all others taken in the province. Proc. Entomol. Soc. Br. Columbia 54: 29–36.
- Stevens, N. M. 1908. A study of the germ cells of certain Diptera, with reference to the heterochromosomes and the phenomena of synapsis. J. Exp. Zool. 5: 359–374.
- Swales, D. E. 1969. Sarracenia purpurea L. as host and carnivore at Lac Carre, Terrebonne Co., Quebec. Le Naturaliste Canadien 96: 759–763.
- Swales, D. E. 1972. Sarracenia purpurea L. as host and carnivore at Lac Carre, Terrebonne Co., Quebec. Part II. Le Naturaliste Canadien 99: 41–47.
- Swan, L. A., and C. S. Papp. 1972. The common insects of North America. Harper & Row., New York.
- Thompson, W. R. 1943. A catalogue of the parasites and predators of insect pests. Section 1. Parasite host catalogue. Part 1. Parasites of the Arachnida and Coleoptera. The Imperial Parasite Service, Belleville, Ontario, Canada.
- Thompson, W. R. 1950. A catalogue of the parasites and predators of insect pests. Section 1. Parasite Host Catalogue. Part 11. Parasites of the Neuroptera, Odonata, Orthoptera, Psocoptera, Siphonaptera and Thysanoptera. The Commonwealth Bureau of Biological Control, Ottawa, Ontario, Canada.
- Townsend, C.H.T. 1917. Genera of the dipterous tribe Sarcophagini. Proc. Biol. Soc. Wash. 30: 189–197.
- Townsend, C.H.T. 1938. Manual of myiology. Part VI. Muscoid generic diagnoses and data. Stephanostomatini to Moriniini. Itaquaquecetuba, São Paulo, Brazil.
- Usinger, R. L. 1956. Aquatic insects of California. University of California Press, Berkeley.
- Williston, S. W. 1908. Manual of North American Diptera, 3rd ed. James T. Hathaway, New Haven, CT.
- Wood, D. M. 1987. Order Diptera, pp. 129–194. In J. D. La fontaine, S. Allyson, V. M. Behan-Pelletier, A. Borkent, J. M. Campbell, K G.A. Hamilton, J.E.H. Martin, and L. Masner [eds.], The insects, spiders and mites of Cape Breton Highlands National Park. Biosystematics Research Centre, Report No. 1.
- Wray, D. L. 1967. Insects of North Carolina. Third supplement. North Carolina Dep. Agric. Raleigh, NC.
- Wray, D. L., and C. S. Brimley. 1943. The insect inquilines and victims of pitcher plants in North Carolina. Ann. Entomol. Soc. Am. 36: 128–137.
- Yanoviak, S. P., and G. W. Folkerts. 1991. Sarcophagid flies associated with pitcher plants (*Sarracenia* sp.) in the Central Gulf region. J. Ala. Acad. Sci. 62: 80.
- Yeates, D. K., H. S. Lopes, and G. B. Monteith. 1989. A commensal sarcophagid (Diptera: Sarcophagidae) in *Nepenthes mirabilis* (Nepenthaceae) pitchers in Australia. Aust. Entomol. Mag. 16: 33–39.

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