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BRYOPHAGY IN THE AUCHENORRHYNCHA: SEASONAL HISTORY AND HABITS OF A MOSS SPECIALIST, *JAVESELLA OPACA* (BEAMER) (FULGOROIDEA: DELPHACIDAE)

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Abstract.—Specialization on mosses, previously unknown in the Fulgoroidea and apparently also for any auchenorrhynchan, is reported for the delphacid planthopper *Javesella opaca* (Beamer). New state records for this seldom-collected species are Alabama, Georgia, Massachusetts, New York, North Carolina, South Carolina, and Tennessee. Nymphs developed mainly on the gametophores of common hair-cap moss, *Polytrichum commune* Hedw. (Polytrichaceae), on granite flatrocks and in other communities, and once were found on another polytrichaceous moss, *Polytrichastrum alpinum* (Hedw.) G.L. Sm. At Boggs' Rock, a granite flatrock in northwestern South Carolina, late instars overwintered in mats of *Polytrichum commune,* and adults developed by mid- to late March. The only macropterous adults (n = 5) observed from June 1996 to July 1998 were found between 10 April and 2 May 1997; all other adults were brachypters. First instars of the season's first generation appeared from mid- to late May, with adults appearing from mid-June to early July. The first instars observed in August were those of an overwintering generation. Fluctuations in the numbers of planthoppers are discussed in relation to the condition of moss colonies (green vs. drought stressed) and weather (precipitation, temperature, and evaporation). In the laboratory, nymphs fed on thicker stems of the moss. The use of mosses is considered a derived host association in the evolution of the Delphacidae.

Key Words: Insecta, Delphacidae, moss feeding, *Polytrichum commune, Polytrichastrum alpinum,* granite outcrops

> The large gaps in our knowledge of the bryosystem, coupled with the ubiquity of mosses, leaves great scope for original research by bryofaunal ecologists.
>
> —I.M. Kinchin 1990

Studies on insect-plant interactions have emphasized vascular plants, the Tracheophyta, including seedless groups such as ferns, but especially the more economically important gymnosperms and angiosperms among the seed plants. Even though insects of nonvascular plants (Bryophyta) generally have been neglected by researchers (Gerson 1969, Lawrey 1987), the insect fauna associated with bryophytes evidently is not notably diverse when only those phytophages known to complete their development on these plants are considered. Among bryophytes, insects are found mainly on mosses—Bryophyta *sensu stricto*—rather than on hornworts and liverworts. Moss-inhabiting insects, which are recorded for most of the hemimetabolous and holometabolous orders (Gerson 1969), can be found on both aquatic and terrestrial mosses. In many cases, whether the species use

mosses for food or only for shelter is not known.

In the Homoptera, used in its traditional sense (the group is paraphyletic [e.g., von Dohlen and Moran 1995]), moss feeders include several sternorrhynchan groups: aphids, such as species of *Melaphis* Walsh, *Muscaphis* Börner, and *Myzodium* Börner (e.g., Patch 1938, Börner 1952, Müller 1973, Smith and Knowlton 1975, Richardson 1981, Moran 1989, Dolling 1991, Thomas and Lombard 1991), as well as certain ensign scales (Ortheziidae) (e.g., Kozár and Miller 1999, 2000) and mealybugs (Pseudococcidae) (Williams 1985). The use of mosses as true hosts by ortheziids is largely undocumented (Dolling 1991).

Bryophagy apparently has remained unknown in the Auchenorrhyncha (evidently also a paraphyletic taxon [e.g., Campbell et al. 1994, Sorensen et al. 1995, Hamilton 1996]). Dolling (1991) stated that all auchenorrhynchans feed on vascular plants. Herein bryophagy in the auchenorrhynchan superfamily Fulgoroidea is reported. I summarize data on the seasonality and habits of the delphacid planthopper *Javesella opaca* (Beamer) on common hair-cap moss, *Polytrichum commune* Hedw., and record nymphs and adults from the moss *Polytrichastrum alpinum* (Hedw.) G.L. Sm.; discuss fluctuations in the numbers of planthoppers relative to the condition of host colonies (green vs. brown and drought stressed) and weather conditions: precipitation, temperature, and evaporation; and suggest that mosses represent an evolutionarily derived host association in the Delphacidae. Seven new state records also are given for this seldom-collected species.

This contribution is dedicated to my friend and colleague, Craig A. Stoops, who called my attention to a delphacid he collected from moss when we were in the field in June of 1996. He helped make field collections and laboratory observations before he left Clemson University in January 1997.

Materials and Methods

Study area.—Boggs' Rock (34°48.4′N, 82°41.6′W) in northwestern South Carolina was the main study site. It is 2.1 km north of Liberty, Pickens County, and lies just west of the intersection of U.S. highway 178 with state secondary road S-39-317 (Quarry Road). This granite-gneiss flatrock ranges in elevation from 262 to 293 m (Knox 1974). Several plant species endemic to granite flatrocks in the southeastern United States (e.g., McVaugh 1943, Shure 1999) are found at Boggs' Rock, but because permanent depression pools are absent (Knox 1974), flatrock endemics restricted to such pools also are lacking.

Host plants.—*Polytrichum commune* (Musci: Polytrichales: Polytrichaceae) is a dark green, robust, perennial moss of wide distribution in the New and Old Worlds except in tropical areas. Its leafy stems, rigid and erect (acrocarpic), are connected by an extensive system of subterranean rhizomes. Stems of this tall moss can reach a height of 45 cm (Crum 1976, Crum and Anderson 1981, Derda and Wyatt 1990). This dioecious moss reproduces asexually by vegetative branching and propagation from plant fragments, with some populations being maintained entirely by vegetative reproduction; it can also become established sexually from spores (Leslie 1975, Derda and Wyatt 1990, Wyatt and Derda 1997). Found on various acidic substrates in disturbed and natural communities, *P. commune* often is abundant on granite flatrocks. It is an important soil builder of the annual-perennial herb community of granite outcrops and a characteristic plant of that community. Its colonies or mats are persistent and often extensive (Burbanck and Phillips 1983, Derda and Wyatt 1990, Quarterman et al. 1993).

The moss variety on which the planthopper *J. opaca* was collected at Boggs' Rock and other rock outcrops is *P. commune* var. *perigoniale* (Michx.) Hampe. Plants of this variety are shorter and grow in denser tufts than those of the nominate variety (Crum

and Anderson 1981). Of the many varieties of *P. commune* that have been described, *perigoniale* has been the one most consistently recognized by authorities (Zouhair et al. 2000). *Polytrichum commune* var. *perigoniale*, however, is not genetically distinct from the nominate variety (Derda and Wyatt 1990). Overlapping in range with *P. commune* var. *commune*, *P. commune* var. *perigoniale* might represent only a "dry land phase" of a species that grows mainly in wet habitats (Crum and Anderson 1981). Derda (1998) considered *P. commune* var. *perigoniale* merely a phenotype of dry, exposed soils (cf. Zouhair et al. 2000).

In the southern Appalachians, *J. opaca* was found on *Polytrichum commune* var. *commune* and *Polytrichastrum alpinum*, a polytrichaceous moss that also has been placed in *Pogonatum* and *Polytrichum* (Smith 1971, Crum and Anderson 1981, Smith Merrill 1992). This coarse species, usually 4–16 cm high with erect stems, is Holarctic and particularly widespread at northern latitudes (Crum and Anderson 1981).

Field sampling.—After *J. opaca* was discovered at Boggs' Rock in June 1996, I surveyed other southeastern granite outcrops (flatrocks and monadnocks) for the presence of the delphacid on *Polytrichum* species. The seasonality of *J. opaca* was followed at Boggs' Rock, the study areas corresponding with granite outcrop divisions B and C in Knox's (1974) floristic study.

I (or C.A. Stoops) visited Boggs' Rock seven more times at irregular intervals in 1996 and collected planthoppers by placing a white enamel pan (28 × 40 cm) into a thick mat of the moss and using an axe handle to tap the overlying stems over the pan. Planthopper nymphs were field sorted by size and recorded as either early (I, II) or later (III–V) instars, and the sex of adults and the condition of the moss colonies were noted. The number of individuals of *J. opaca* observed was not standardized but generally was 10. Nearly all individuals were replaced on the moss, although voucher material of both nymphs and adults was collected and deposited in the Clemson University Arthropod Collection (CUAC); adults also were deposited in the collection of S.W. Wilson, Central Missouri State University, Warrensburg.

Sampling at Boggs' Rock was conducted similarly in 1997 and 1998 but at more regular intervals than in 1996. I recorded the stage of the first 10 individuals of *J. opaca*—as early or late instars and adult males or females—found on the moss in Knox's (1974) outcrop division C, a colony of the host plant that became desiccated and brown without frequent rain. I also often recorded the stage of the first 10 individuals encountered in a supplemental sample from moss in a wetter area of the outcrop (Knox's division B). In 1997, after an initial collection in early January, I sampled weekly or biweekly from early March to late August; I also sampled in mid-September and early November. In 1998, samples were taken weekly (occasionally biweekly or every three weeks) from late February to late July when no more planthoppers were being collected, presumably because of drought conditions. After that, I sampled six more times from late August to late November in an attempt to collect *J. opaca*. Six additional attempts to collect the planthopper at Boggs' Rock were made from early April 1999 to late May 2002.

Fluctuations in planthopper numbers.—Data from the two nearest weather-recording stations were used to better interpret the numbers of planthoppers observed relative to the condition of moss colonies. The weather station at Pickens (34°53′N, 82°43′W) is about 10 km north of Boggs' Rock; the Clemson station (34°41′N, 82°49′W) is about 18 km southeast of the sample site.

Laboratory observations.—The work with *J. opaca* in the laboratory involved placing nymphs of several instars in plastic petri dishes or snap-cap vials that contained the gametophyte (1–5 stems) of common hair-cap moss. The feeding behavior of

nymphs, presence of exuviae, and number of days of observation were noted, but the duration of nymphal stadia was not determined.

Javesella opaca (Beamer)
(Fig. 1)

Javesella opaca was described in the genus *Delphacodes* Fieber from Connecticut by Beamer (1948), who selected as holotype a male collected at Willimantic on 8 August 1946. His type series also included adults taken from 3 August to 2 September 1946, at Storrs, Conn. (14 ♂, 8 ♀); Dingmans Ferry, Pa. (6 ♂, 5 ♀); and Mountain Lake, Va. (1 ♂). The only additional published record is that of Maw et al. (2000) from Quebec, Canada; this delphacid was listed as a provincial record without a specific locality and was recognized as belonging to the genus *Javesella* (as "*Javasella*") Fennah (Maw et al. 2000). According to K.G.A. Hamilton (personal communication, 2002), the Quebec record of *J. opaca* is based on a total of 13 males and 3 females from Covey Hill (5 June) and Laniel (5 June, 20–21 July). New state records, based on the present study (see Material examined), are Alabama, Georgia, Massachusetts, New York, North Carolina, South Carolina, and Tennessee.

The transfer of *opaca* to *Javesella* by Maw et al. (2000), made in a checklist without discussion of this nomenclatural change, is the appropriate generic placement (S.W. Wilson, personal communication, 1996). Mainly on the basis of genitalic characters, the polyphyletic genus *Delphacodes* should be restricted to about 10 Old World species (Asche 1985, Bartlett and Dietz 2000).

Seasonal history.—Late instars of *J. opaca* overwintered in mats of common haircap moss. In contrast to the yellow or yellow-brown nymphs found during spring and summer, the overwintered nymphs were darker and sometimes fuscous. The darker coloration, similar to that observed in certain other delphacids (e.g., Wilson and McPherson 1981), was observed at Boggs' Rock by early November in 1996 and 1997 (late instars collected in New York in mid-August and some early instars from Massachusetts in early September also were dark). Adults first were seen in 1997 during sampling on 16 March and were present on 29 March in 1998. In both years, males appeared first, but sex ratios usually became female biased within three weeks after adults began to appear. Overwintered fifth instars were last seen on 10 April in 1997 (2 in sample of 10) and 5 April in 1998 (1 of 20).

First instars of the season's new generation first were observed on 23 May in 1997 and 12 May in 1998. Adults of this generation, almost all males initially, first were seen in the 19 June sample in 1997 and the 22 June sample in 1998. Several late instars (7 of 20) of the new generation were still present in 1997 on 20 July. Early instars of a partial (overwintering) generation were found on 4 August 1997. In 1998, apparently because of drought conditions, no nymphs or adults could be collected after early July.

Nearly all the adults observed from June 1996 to July 1998 were brachypters. Only five macropters were seen during the study, all between 10 April and 2 May 1997; the three that were collected were females. Adults were not found after mid-August, with only nymphs observed from then until mid- to late March of the following year.

Fluctuations in planthopper numbers.—The numbers of *J. opaca* observed fluctuated widely during the period of study, depending mainly on the amount of precipitation at Boggs' Rock. Available moisture, in turn, affected the condition of the moss colonies inhabited by the planthopper.

Despite the wide variation in the numbers of planthoppers that could be beaten from *Polytrichum*, at least 10 individuals usually could be found on each sample date; few, however, were found in July of 1998. Precipitation that year was about 160 cm at Pickens and about 156 cm at Clem-

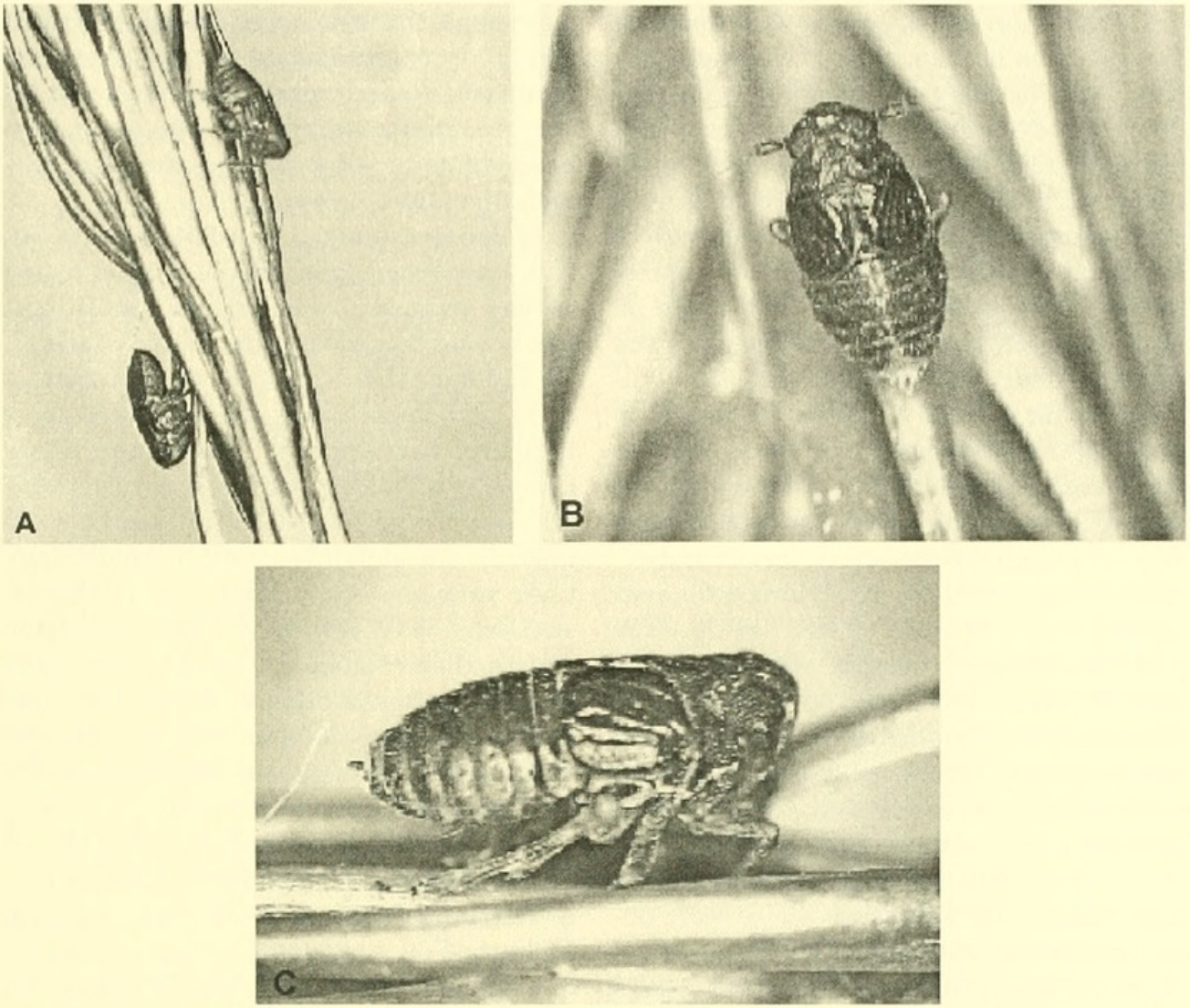

Fig. 1. *Javesella opaca*. (A) Females (brachypters) on leafy gametophyte of common hair-cap moss, *Polytrichum commune*; (B) dorsal and (C) lateral views of female.

son, figures that actually exceeded annual averages of 142 cm for Pickens (1952–2001) and 134 cm for Clemson (1930–2001). Looking only at total precipitation for 1998, however, is misleading; after substantial rains on 1 May (nearly 6 cm) and 8 May (>3.6 cm), rainfall was scant in the weeks preceding the planthopper's disappearance. At Pickens, precipitation for the last half of May was only 1.4 cm; rainfall for June totaled 13.6 cm, with nearly half of the total falling on the month's 20th day. After 20 June, only 0.3 cm of rain fell during the next 30 days, a period when daily maximum temperatures substantially exceeded normal highs. Temperatures were at least 32.2°C (90°F) from 21 June to 14 July, with nine consecutive days of 36.1–36.7°C (97–98°F). Evaporation at Clemson (data are unavailable for Pickens) exceeded rainfall by 15.2 cm for the 30 days following 20 June.

Only four adults and no nymphs were observed during regular sampling on 4 July 1998; seven adults were seen when a supplemental sample was taken on 6 July. No additional individuals were found during sampling on seven dates from 24 July to 29 November 1998. Two adult males were found in early April 1999, but *J. opaca* was not observed at Boggs' Rock in late March, mid-May, and mid-August 2000; in late March and early November 2001; or in late May 2002.

Habits.—*Javesella opaca* was found at Boggs' Rock in thick mats of common haircap moss in marginal areas of rock outcrops. Moss colonies harboring the planthopper grew beneath shrubs and small trees, particularly Chinese privet (*Ligustrum sinense* Lour.; Oleaceae) and eastern red-cedar (*Juniperus virginiana* L.; Cupressaceae). The delphacid was not found in more exposed colonies of the moss. Even when nymphs and adults were most numerous, they were difficult to detect on mats of *Polytrichum*; only occasionally were a few individuals observed on the surface of *P. commune* mats. The largest numbers of planthoppers—early instars only—were found on 8 June 1997. *Javesella opaca* had been difficult to find on 23 May 1997 when moss colonies were brown (a total of 9 individuals was observed in both the regular and supplemental samples), but on 8 June after recent rainfall, more than 30 first and second instars were found in each of three 1-pan samples from now green areas of moss. When nymphs were numerous, exuviae dislodged from moss also were observed during sampling.

In the southern Appalachians, *J. opaca* was found at an altitude of about 1,130 m on *Polytrichastrum alpinum* (Alleghany Co., NC). The moss was mostly obscured by various grasses. Populations of the planthopper also were found at about 1,685 m in mats of *Polytrichum commune* var. *commune* (Carter Co., TN).

When nymphs were placed in petri dishes or vials with sprigs of gametophyte from *Polytrichum commune*, they quickly (<5 min.) settled on the thicker stems and inserted their stylets. While feeding, nymphs (n = 10+) remained motionless, except for an occasional twitching of the legs, and typically stayed at one site for two hours or more. Only once was a clear drop of excretion or honeydew seen at the end of the anus. First instars were not reared to adulthood, but preliminary observations suggest that *J. opaca* could be easily reared on moss in the laboratory. Nymphs of various instars were maintained in a petri dish on the same sprigs of *P. commune* for 16 days and nymphal exuviae were observed. A first instar placed in a 4-dram vial with two moistened stems of moss molted once and was still alive after 27 days.

Material examined.—Adults from a locality are listed first, followed by a listing of any nymphs; when nymphs at Boggs' Rock were recorded in the field as early (I, II) and later (III–V) instars, the numbers of early and later instars are separated by a hyphen. An asterisk beside the word *nymph(s)* indicates that voucher material is housed in the CUAC. Collections were made by the author (no collector indicated), C.A. Stoops (C.A.S.), both of us (C.A.S. & A.G.W.), or W.K. Reeves (W.K.R.) from *Polytrichum commune*, except in Alleghany County, North Carolina, where the host was *Polytrichastrum alpinum* and in Pennsylvania where the host was identified as *Polytrichum* sp.

ALABAMA: Cherokee Co., Rt. 35, SE of Fort Payne, 31 Aug. 1996, 2 adults (sex undetermined), 10 Apr. 1997 (1 ♂, 9 ♀); Jackson Co., sandstone outcrop, Rt. 117, 0.3 km NW of jct. Rt. 71, Flat Rock, 10 Apr. 1997 (3 ♂, 4 ♀; 1 fifth instar). GEORGIA: Columbia Co., Heggie's Rock, E of Appling, 5 Apr. 1997 (4 ♂, 11 ♀), 26 Mar. 2002 (1 ♂; 1 fifth instar); Gwinnett Co., No Business Creek granitic outcrop, 2.6 km SSE of Snellville, 7 July 1996 (1 ♂), 26 Mar. 2002 (1 ♂, 4 ♀; 2 fifth instars). MASSACHUSETTS: Montague Sand Plains, 3.5 km N of Montague, 5 Sept. 2002 (1 ♂, 1 ♀; early instars). NEW YORK: Sullivan Co., Rt. 42, Forestburg, 3 Sept. 2002 (8 first through third instars); Ulster Co., Sam's Point Dwarf Pine Ridge Preserve, NE of Cragsmoor, 13 Aug. 2000 (12 ♂, 10 ♀; nymphs). NORTH CAROLINA: Alleghany Co., ca. 7 km ENE of Laurel Springs, 16 June 2002 (4 ♂, 1 ♀; late instars); Swain Co., Great Smoky Mountains National Park, nr. Ravens Fork, 8 Jan. 2001, W.K.R. (late instars). PENNSYLVANIA: Potter Co., NE of Keating Summit, 18 May 1997,

C.A.S. (3 late instars). SOUTH CAROLINA: Pickens Co., Boggs' Rock, 2.1 km N of Liberty, 16–17 June 1996, C.A.S. & A.G.W. (adults, sex undetermined; 25+ nymphs); 22 June 1996, C.A.S. (adults; nymphs*: 1–2); 6 July 1996, C.A.S. & A.G.W. (7 ♂, 10 ♀; nymphs*:0–11); 20 July 1996, C.A.S. (adults; nymphs*:0–4); 18 Aug. 1996 (5 adults, sex undetermined; nymphs:11–4); 29 Sept. 1996, C.A.S. & A.G.W. (nymphs:3–7); 13 Oct. 1996, C.A.S. & A.G.W. (nymphs:10–0); 9 Nov. 1996, C.A.S. & A.G.W. (nymphs:10–0); 4 Jan. 1997 (nymphs*:0–19); 7 Mar. 1997 (nymphs*: 0–11); 16 Mar. 1997, C.A.S. & A.G.W. (2 ♂; nymphs: 0–10); 21 Mar. 1997 (3 adults, sex undetermined; nymphs: 0–7); 4 Apr. 1997 (4 ♂, 4 ♀; nymphs*:0–2); 10 Apr. 1997 (3 ♂, 5 ♀; nymphs: 0–2); 18 Apr. 1997 (4 ♂, 6 ♀); 25 Apr. 1997 (3 ♂, 7 ♀); 2 May 1997 (3 ♂, 7 ♀); 10 May 1997 (3 ♂, 6 ♀; nymph:0–1); 23 May 1997 (2 ♂, 4 ♀; nymphs:2–0); 8 June 1997 (nymphs*:7–4); 19 June 1997 (3 ♂, 2 ♀; nymphs*:0–9); 29 June 1997 (2 ♂, 4 ♀; nymphs*:1–3); 5 July 1997 (3 ♂; nymphs*: 2–5); 13 July 1997 (11 ♂, 3 ♀; nymphs*: 2–4); 20 July 1997 (10 ♂, 3 ♀; nymphs*: 2–5); 4 Aug. 1997 (6 ♂, 2 ♀; nymphs*:11–1); 17 Aug. 1997 (nymphs*:8–1); 14 Sept. 1997 (nymphs*:2–0); 2 Nov. 1997 (nymphs: first through third instars): 28 Feb. 1998 (nymphs*:0–6); 15 Mar. 1998 (nymphs:0–10); 22 Mar. 1998 (nymphs:0–10); 29 Mar. 1998 (3 ♂; nymphs:0–7); 5 Apr. 1998 (7 ♂, 3 ♀); 12 Apr. 1998 (5 ♂, 5 ♀); 24 Apr. 1998 (1 ♂, 9 ♀); 5 May 1998 (1 ♂, 2 ♀); 12 May 1998 (2 ♀; nymphs:8–0); 18 May 1998 (nymphs:10–0); 27 May 1998 (1 ♀; nymphs:9–0); 6 June 1998 (nymphs:8–12); 22 June 1998 (12 ♂, 1 ♀; nymphs:1–6); 4 July 1998 (3 ♂, 1 ♀); 6 July 1998 (6 ♂, 1 ♀); 4 Apr. 1999 (2 ♂); York Co., granite flatrock, Clover, 20 Apr. 1997 (3 ♀; 1 fifth instar). TENNESSEE: Carter Co., Carver's Gap, Roan Mountain, 27 October 2002 (late instars).

Discussion

When *J. opaca* was first collected from mats of *Polytrichum* in June of 1996, its presence on moss was considered incidental. I was unaware of any moss-feeding fulgoroids, a group in which adults of many species, including delphacids, can be found on plants that do not support nymphal development (e.g., DuBose 1960, Wilson et al. 1994). Because seeds of various angiosperms accumulate, germinate, and survive in mats of mosses (McVaugh 1943), even the planthopper nymphs collected from moss might have been associated with vascular plants, such as grasses or sedges, that were growing within the *Polytrichum* colonies. Delphacids develop mainly on monocots, especially grasses and sedges (Wilson et al. 1994). *Javesella kilmani* (Van Duzee) and *J. stali* (Metcalf) are associated with an aberrant host, the vascular cryptogam (sphenophyte) horsetails, *Equisetum* spp. (Equisetaceae) (Strickland 1940, Ossiannilsson 1978).

A consistent collection of nymphs and adults of the delphacid from *P. commune* at Boggs' Rock and elsewhere, coupled with observations of its moss-feeding behavior in the laboratory, soon indicated that *J. opaca* was a true bryophage. It can be regarded as a bryophilous species or a bryobiont (*sensu* Gerson 1982)—that is, an animal associated exclusively with bryophytes. As such, *J. opaca* becomes the first known bryophagous fulgoroid and apparently also the first auchenorrhynchan known to develop on mosses. Somewhat similarly, the first known bryophagous species of the largest family of Heteroptera, the Miridae, only recently was discovered (Yasunaga 2000; see also Wheeler 2001).

My collection of *J. opaca* in North Carolina on *Polytrichastrum alpinum* might shed light on how Beamer (1948) was able to collect 22 adults of this planthopper at a locality in Connecticut and 11 adults in Pennsylvania without associating the species with mosses. When I collected the first

specimens of *J. opaca* in North Carolina while sweeping grasses, I was unaware of the polytrichaceous moss growing under the grasses. Beamer probably would not have looked for delphacids in extensive mats of *Polytrichum commune* because no auchenorrhynchans were then known from mosses. He more likely would have swept the planthopper from the erect stems of *Polytrichastrum alpinum* (or another moss of similar growth habit) that grew beneath grasses, plants that are common hosts of Delphacidae. Delphacids should be more readily swept from a moss such as *Polytrichastrum alpinum* that grows in loose tufts than from one such as *Polytrichum commune* that has a more densely tufted (cespitose) growth habit. Even if Beamer had noticed the mosses while he swept grasses, he likely would not have associated the planthopper with a nonvascular plant.

The Delphacidae appear not to have diversified on mosses. Except for *J. opaca,* all other delphacids for which nymphal hosts are known develop on vascular plants. Fulgoroids and other homopterans that feed on plants other than angiosperms or on fungi likely are derived from angiosperm feeders (e.g., Wilson et al. 1994; see also Hamilton 1990). Even though *J. opaca* belongs to an "advanced" lineage (Stenocraninae-Plesiodelphacinae-Delphacinae) of the Delphacidae and belongs to the most morphologically advanced tribe of the most advanced delphacid subfamily (see Asche 1985, 1990; Emeljanov 1995), moss feeding by this planthopper might represent an ancient or relictual host relationship for the family. More likely, however, is that in the Delphacidae the use of mosses reflects a one-time host shift and an evolutionarily derived host association.

Bryophagy in the Delphacidae, a phloem-feeding group (e.g., O'Brien and Wilson 1985, Denno et al. 1987, Wilson et al. 1994, Watanabe and Kitagawa 2000), might have been predicted for polytrichaceous mosses. Although mosses are considered nonvascular plants (Buck and Goffinet 2000), the long-distance conducting systems of certain members of the Polytrichaceae are similar in structure and function to those of simple vascular plants (Tansley and Chick 1901, Thomas et al. 1988). Water moves in elements called hydroids; photosynthate, principally sucrose, moves in leptoids that are similar to sieve elements in the phloem of higher plants. Among mosses that have been studied, the conducting cells of *Polytrichum commune, Polytrichastrum alpinum,* and certain other polytrichaceous species are the most structurally complex (Collins and Oechel 1974, Behnke 1975, Scheirer 1980, Reinhart and Thomas 1981, Richardson 1981, Thomas et al. 1990).

The moss-feeding mirid described as a new species by Yasunaga (2000) belongs to a group of heteropterans that are mainly cell-content feeders on mesophyll rather than vascular-tissue feeders (Wheeler 2001). The mirid would not necessarily need to feed on a moss with a conducting system similar in structure to that of vascular plants. *Javesella opaca,* however, as a presumed phloem feeder, is likely restricted to polytrichaceous mosses with well-developed conducting cells. It might be more host restricted than are many other bryophagous insects (Gerson 1982, Lawrey 1987). In fact, most delphacids (74%) are recorded from a single plant genus (Wilson et al. 1994).

Javesella opaca might feed on gametophores of common hair-cap moss in a manner similar to that of the aphid *Myzodium modestum* Hottes on the same moss species (Thomas and Lombard 1991). The planthopper, however, does not feed in aggregations as does the aphid and might not alter the translocation of sugars in internal conducting tissues of the moss, as Thomas and Lombard (1991) demonstrated for the aphid. Occasional production of honeydew droplets by the sucrose-feeding *M. modestum* (Thomas and Lombard 1991) agrees with my observations on *J. opaca,* which presumably also feeds on photosynthate of common hair-cap moss.

Javesella opaca has been collected mainly on thick mats of *Polytrichum commune* in both natural and disturbed communities. This planthopper might also be found on *Polytrichastrum ohioense* (Ren. & Card.) G.L. Sm. In fact, Knox (1974) recorded *Polytrichastrum ohioense* as the only polytrichaceous moss at Boggs' Rock, but his voucher material actually is *Polytrichum commune* (L.E. Anderson, personal communication, 2002). Both polytrichaceous species can be found on granite outcrops (e.g., Oosting and Anderson 1939, McVaugh 1943), but *Polytrichum commune* is a characteristic plant of granite flatrocks and apparently is the dominant hair-cap moss in granite outcrop communities in Georgia and elsewhere in the southeastern states (e.g., Burbanck and Phillips 1983, Quarterman et al. 1993, Murdy and Carter 2000).

Given the persistence of *Polytrichum* colonies and the stability of granite flatrock communities, the observed low incidence (<3%) of macroptery might have been expected for *J. opaca* because dispersal might not be critical to the continuity of a planthopper population that lives in such a relatively stable or permanent habitat (e.g., Wagner and Liebherr 1992). From June 1996 to July 1998, the delphacid typically was observed at Boggs' Rock in small numbers when rainfall was scant and its host was metabolically inactive, but it could be collected in greater numbers from still green colonies of the moss in wetter areas of the flatrock. The more consistent availability of moisture in these wetter colonies apparently allowed egg hatch to continue, which sometimes led to asynchrony in the development of hopper populations in desiccated compared to greener host patches.

In 1998, a year of above-average precipitation, the delphacid was not found after early July. Apparently the low and uneven distribution of rainfall in late spring and early summer, combined with consecutive days of unusually high temperatures and evaporation, severely reduced the densities of *J. opaca* in the two sample areas at Boggs' Rock. Adults and nymphs were no longer seen, even in the usual wetter moss colonies, which had become desiccated. Although temperatures within green mats of *P. commune* generally are lower than those at the surface, desiccated mats are marked by internal temperatures higher than those of the ambient air (Leslie 1975). Other groups of arthropods, such as collembolans and mites, were scarce in 1998 when moss colonies were brown and dry. In contrast to the planthopper, collembolans and mites reappeared in numbers following abundant rainfall. That only two adults of *J. opaca* have been collected at Boggs' Rock since July 1998, even when moss was lush, suggests that its populations were substantially reduced during periods of low rainfall in the summer of 1998 rather than being found deeper in moss and, therefore, perhaps more difficult to dislodge from desiccated colonies of the host.

In the southern Appalachians, mats of *Polytrichum commune* in high-elevation mesic communities, such as grassy balds, would be constantly moist and should be considered an even more permanent habitat than the periodically dry mats of the moss in granite outcrops. The degree of brachyptery in *J. opaca* might be studied in populations occupying both permanent and less stable habitats. That this planthopper primarily ingests sucrose translocated in moss leptoids, as apparently is the case in several other moss-feeding hemipterans, requires verification. Also needed are surveys for additional moss species that might serve as hosts and studies of basic life-history parameters such as fecundity, longevity, and duration of the immature stages (eggs were not found in the present study), as well as observations on mating and oviposition behavior. In addition, the studies on nutritional ecology that Lawrey (1987) suggested be conducted on moss-feeding arthropods in general are appropriate to the research needs for *J. opaca*.

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