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SYSTEMATIC POSITIONS OF *ACENTRIA EPHEMERELLA* (DENIS & SCHIFFERMÜLLER), NYMPHULINAE, AND SCHOENOBIINAE BASED ON MORPHOLOGY OF IMMATURE STAGES (PYRALIDAE)

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ABSTRACT. *Acentria ephemerella* (Denis & Schiffermüller), the one known species of its genus, is sometimes placed in Schoenobiinae, but it lacks three important autapomorphies of that subfamily: larval prothoracic sac, exposed pupal mesothoracic coxae, and deep pitlike pupal mesothoracic spiracle. Apomorphies such as spinelike pupal frontal setae, lack of pupal mesothoracic spiracle, and reduced posterior pupal abdominal spiracles confirm that *Acentria* belongs in Nymphulinae. No larval or pupal characters were found to support *Acentria* as a separate family or subfamily (Acentropidae or Acentropinae). Several synapomorphies suggest Nymphulinae and Schoenobiinae are sister groups. They share long exarate pupal appendages and reduction of larval L2 seta on abdominal segments 1–8. The unisetose L group on abdominal segment 9 in other subfamilies of Crambiformes may be used as a synapomorphy to define a clade separate from Nymphulinae and Schoenobiinae in which the L group is bisetose on segment 9.

Additional key words: larva, pupa, cladogram, systematics.

Acentria ephemerella (Denis & Schiffermüller), formerly *Acentria* (=*Acentropus*) *nivea* (Olivier), has a long and varied systematic history (Speidel 1981, 1984). It was placed in Schoenobiinae because of a reduced proboscis, tubular CuP (1A) forewing vein, and lack of hindwing Cu pecten (hair fringe) (Hampson 1895, Forbes 1926, 1938). Other workers (Marion 1954, Roesler 1973, Leraut 1980, Goater 1986) thought *Acentria* should be in Acentropinae or Acentropidae largely because the adult lacks a praecinctorium. Nigmann (1908) and Speidel (1981) cited enlarged anterior abdominal pupal spiracles as an autapomorphy of Nymphulinae and thus considered *Acentria* to be in this subfamily because of its similar pupa. Larval chaetotaxy confirmed this view. Hasenfuss (1960) placed *Acentria* in Nymphulinae based on a bisetose L group on abdominal segment 9, and unusual arrangement of larval stemmatal (ocular) setae. Speidel (1984) suggested *Acentria ephemerella* is the correct name for *A. nivea* and recommended acceptance of Acentropinae instead of Nymphulinae as the valid subfamily name. The latter change, in agreement with Minet (1982), is not followed here because Nymphulinae has been stable and unambiguous in most checklists. Fletcher and Nye (1984) placed *Acentria* with Nymphulinae in their Pyraloidea catalogue. However, Yoshiyasu (1985) doubted the placement of *Acentria* with Nymphulinae because enlarged abdominal spiracles are also found in some aquatic Crambinae. The possibility remained that enlarged spiracles had arisen in certain species because of aquatic habits instead of common ancestry. Minet (1982, 1985) also considered *Acentria* to be a nymphuline, based on several apomorphies of the tympanum. As was traditional in the U.S., Munroe (1983) listed *Acentria* with Schoenobiinae. Batra (1977), Berg (1942), Buckingham and Ross (1981), Speidel (1981), and Yoshiyasu (1985) either illustrated stages of *A. ephemerella* or discussed its biology.

Only three workers have published Pyralidae cladograms (Fig. 1). Roesler (1973), relying mostly on adult morphology, recognized an Acentropidae-Crambidae complex. Yoshiyasu (1985) doubted the validity of Roesler's characters. He called attention to variability in the Nymphulinae radial vein and maxillary palpi, as well as to the presence of aquatic species in other subfamilies. More importantly, some key portions of Roesler's (1973) cladogram are defined by plesiomorphic features (lack of specialized scales in the male genitalia, for example). Kuznetzov and Stekolnikov (1979) considered Schoenobiinae and Nymphulinae to be unrelated, based almost exclusively on genital musculature. However, they studied very few species and paid only superficial attention to immature stages. Yoshiyasu (1985), considering characters of all stages, linked Schoenobiinae, Nymphulinae, and *Acentria* as sister groups but was unable to place this clade in an overall scheme. Instead, three clades were extended to a single point with dotted lines and a question mark at their bases (Fig. 1A). Thus, convincing evidence from adult (Minet 1982), larval (Hasenfuss 1960) and pupal (Nigmann 1908) morphology suggests *Acentria* belongs with Nymphulinae in spite of recent doubts (Yoshiyasu 1985, Goater 1986).

This paper examines apomorphic larval and pupal characters of *Acentria ephemerella* to provide additional evidence on the systematic position of *Acentria*. The relation of Nymphulinae to Schoenobiinae, and their taxonomic position within Crambiformes are also discussed.

METHODS

Morphological information on pyralid immature stages came from Passoa (1985), literature illustrations, and borrowed material. Unpub-

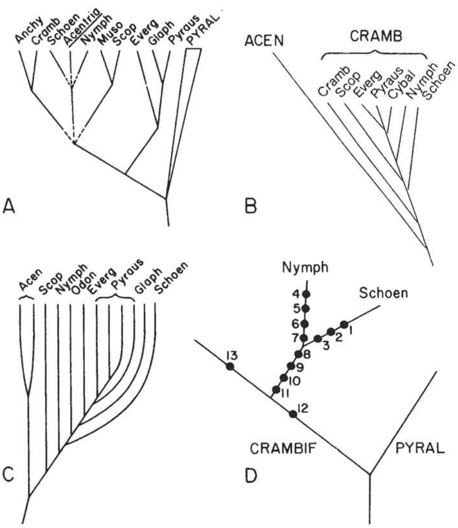


FIG. 1. Systematic position of *Acentria*, Nymphulinae, and Schoenobiinae after various authors. A, Yoshiyasu (1985). B, Roesler (1973). C, Kuznetsov & Stekolnikov (1979). D, Present study, with major apomorphies numbered as follows: 1—larva with prothoracic sac; 2—pupal mesothoracic spiracle pitlike; 3—pupal mesothoracic coxae exposed; 4—stemmatal setae in line with each other; 5—pupal frontal setae enlarged and spinelike; 6—pupal anterior abdominal spiracles enlarged and on conelike projections, posterior abdominal spiracles reduced; 7—pupal mesothoracic spiracle lost; 8—V1 lost on larval thorax; 9—L2 on larval abdominal segments reduced; 10—tegumen-vinculum plate developed, transtilla lost; 11—pupal appendages exarate with metathoracic legs exposed; 12—praecinctorium present; 13—larva with unisetose L group on A9. Abbreviations: ACEN—Acentropidae; Acen—Acentropinae; Anchy—Ancylolomiinae (Anchylolomiinae of Yoshiyasu 1985); CRAMB—Crambidae; Cramb—Crambinae; CRAMBIF—Crambiformes; Cybal—Cybalomiinae; Ever—Evergestinae; Glap—Glaphyriinae; Muso—Musotiminae; Nymph—Nymphulinae; Odon—Odontiinae; PYRAL—Pyraliformes; Pyraus—Pyraustinae; Schoen—Schoenobiinae; Scop—Scopariinae.

lished keys and a data matrix of larval characters by workers at the U.S. National Museum (C. Heinrich, H. Capps, and D. Weisman) ("USNM Tables") provided information on pyralid genera in that collection. Literature on Crambiformes immature stages included general works such as Fracker (1915), Mosher (1916), Peterson (1962), and Neunzig (1987) for the U.S., Hasenfuss (1960) for Europe, Nakamura (1981) for Asia, and Gerasimov (1947, 1949) for the U.S.S.R. Important articles on New World Nymphulinae immatures were selected from Munroe (1981, 1982). Yoshiyasu (1985) published a review on Japanese Nymphulinae and their systematic position. Schoenobiinae immatures were discussed by Passoa and Habeck (1987). Crawford (1961), Mauston (1970), and Tan (1984) provided descriptions of Crambini larvae and pupae. Agarwal and Chaudhry (1966), Passoa (1985), and Rothschild (1967) described Chilini immatures. Works on New World Pyraustinae included Allyson (1981, 1984), and Passoa (1985). Khot'ko and Molchanova (1975) studied Old World species. Some African pyralids were illustrated by Breniere (1979). Indian pyralids were described by Mathur and Singh (1963) and Mathur (1954, 1959).

Preserved larvae, and usually pupae, of the following species were examined:

Nymphulinae

Acentria ephemerella (Denis & Schiffermüller)
Nymphula depunctalis Guenée
N. fluctuosalis (Zeller)
Munroessa sp.
Synclita sp.
Parapoynx diminutalis Snellen
P. obscuralis (Grote)
Neargyractis slossonalis (Dyar)
Petrophila longipennis (Hampson)
P. bifascialis (Robinson)
P. avernalis (Grote)
P. jaliscalis (Schaus)
Usingeriessa onyxalis (Hampson)
Eoparargyractis sp.

Schoenobiinae

Rupela albinella (Cramer)
R. horridula Heinrich
R. leucatea (Zeller)
R. sp.
Scirpophaga (=*Schoenobius, Tryporyza*) *incertulas* (Walker)
S. excerptalis (Walker) (=*S. intacta* Snellen)
Donacaula sp.
D. maximella (Fernald)

This list represents 9 of 16 Nymphulinae genera and 3 of 5 Schoenobiinae genera in the U.S. (Munroe 1983). *Acentria* contains only one species, *A. ephemerella* (Speidel 1984). Larva and pupa terminology follows Stehr (1987) and Mosher (1916). Munroe (1972) and Minet (1982, 1983, 1985) were used to characterize adult subfamilies.

CHARACTER POLARITY

Certain assumptions are necessary before a cladistic study of *Acentria*, Nymphulinae, and Schoenobiinae can proceed. Pyralidae is assumed monophyletic because of apomorphies in the tympanum (Minet 1982, 1983, 1985) and venation (Munroe 1972). All Pyralidae cladograms (Fig. 1) agree there are two lineages, Crambiformes (sometimes called Crambidae) and Pyraliformes (sometimes called Pyralidae in a restricted sense). Crambiformes, which include Nymphulinae, Schoenobiinae, and *Acentria,* are apomorphically defined, in part, by a praecinctorium in the tympanum (Minet 1982). Although tympanic morphology of Midiliformes and other pyralids differ, larval characters, as discussed further on, support Minet's (1982) placement of this taxon within Crambiformes. Pyraliformes, which include all remaining pyralid subfamilies, are the sister group to Crambiformes, and thus comprise the outgroup. Minet (1985) apomorphically defined Pyraliformes by a tympanic "paraspina" and sclerotized pinaculum rings around larval seta SD1. Speidel (1984) mentioned scale morphology, dimorphic labial palps, and reduction of proboscis, ocelli, and leg spurs as apomorphies of *Acentria*. A shortened, stout gnathos, and broad basal portion of the apophysis united *Acentria* and *Kasania* on a single clade.

Unless stated otherwise, Watrous and Wheeler's (1981) method of outgroup comparison was used to polarize characters. This method is especially appropriate when most characters have two states, and relatives are easily defined. In spite of criticisms (Farris 1982, Clark & Curran 1986), outgroup comparison appears to be the most reliable way to determine polarity (Donoghue & Cantino 1984). All morphological features relevant to the systematic positions of *Acentria*, Nymphulinae, and Schoenobiinae are mentioned below even if their polarity is somewhat uncertain. References under each morphological feature usually provide illustrations.

Larval Characters

Stemmatal (ocular) setae. Hinton (1946) considered S1 close to stemmata 3 and 4, S2 level with stemma 5, and S3 below all stemmata as the usual arrangement in Lepidoptera. This trend is also true in Pyralidae where all Pyraliformes and Crambiformes except Nymphulinae show this arrangement (Hasenfuss 1960, Yoshiyasu 1985). Two states occur in Crambiformes: setae in nonlinear arrangement or in line with each other. Since all Pyraliformes (the outgroup) have a nonlinear arrangement, this is considered plesiomorphic. The alternative state in Crambiformes, stemmatal setae in a line with each other, is apomorphic.

Mandible. Based on study of Pyralidae mandibles (Passoa 1985, Neunzig 1987, Peterson 1962), presence of a dentate ridge under the first scissorial tooth is an unusual modification. Inner teeth are sometimes present on the first molar ridge, especially in Pyraustinae (Peterson 1962, Passoa 1985), but in the latter case they do not form a ridge. Two character states occur in Crambiformes: ridge absent or present. Since all Pyraliformes lack a ridge (Passoa 1985), this is plesiomorphic. A dentate ridge, the alternative state, is apomorphic.

Thoracic V1 seta. Hinton (1946) stated V1 was present on all first and last instar Lepidoptera he examined. In Crambiformes, two character states occur: V1 absent (Yoshiyasu 1985) or present (Passoa 1985). Since V1 is present in Pyraliformes (Passoa 1985), this is plesiomorphic. Therefore, loss of this seta is considered apomorphic.

Rothschild (1967) speculated V1 may not be lost in *Tryporyza* (Schoenobiinae) but instead could have migrated to the coxae as in some Tineidae and Psychidae (Hinton 1946). The extreme reduction in body setal length of Nymphulinae and Schoenobiinae (setae may be difficult to see even under a compound microscope), coupled with lack of knowledge about coxal setae and their homologies, makes evaluation of Rothschild's hypothesis impossible at present. In any event, either case would be apomorphic as V1 is not found on the coxa in the outgroup (Pyraliformes).

Prothoracic membranous sac. The Schoenobiinae membranous sac is apparently a unique structure not homologous to other lepidopteran cervical glands (Passoa & Habeck 1987). In Crambiformes, two character states occur: prothoracic sac present or absent. All Pyraliformes lack a prothoracic sac (Passoa 1985). Therefore, presence of a membranous prothoracic sac is apomorphic.

L2 seta on abdominal segments. Hinton (1946) remarked that L1 and L2 are macroscopic and frequently subequal in length throughout Lepidoptera. This is true for all Pyraliformes and Crambiformes except Schoenobiinae (Hasenfuss 1960) and Nymphulinae (Neunzig 1987, Yoshiyasu 1985). Therefore, when L1 and L2 are subequal in length, this is plesiomorphic. A very short, almost microscopic, abdominal L2 seta is apomorphic.

Thoracic L seta. Neunzig (1987) noted that all Pyraliformes have three setae in the L group of mesothorax and metathorax. In Crambiformes, two character states occur: L group bisetose (some Nymphulinae and Schoenobiinae) or L group trisetose (most Crambiformes). Therefore, loss of the thoracic L seta is considered apomorphic.

L2 on A9. All Pyraliformes have L1, L2, and L3 present on A9, whereas L2 is either present (Schoenobiinae and Nymphulinae) or absent (most Crambiformes) in other pyralid larvae (Neunzig 1987, Hasenfuss 1960). L1 is always present in Pyralidae while L3 is always absent in Crambiformes. Because outgroup comparison demands a character distribution in which a feature is present or absent in the group being studied, L2 is the only seta that can be polarized at present. Since L2 is present in the outgroup, the plesiomorphic state within Crambiformes occurs when L2 is present (bisetose condition). In contrast, the apomorphic state occurs when L2 is lost (unisetose condition).

Yoshiyasu (1985) also considered loss of L setae in Crambiformes to be apomorphic but he polarized both bisetose and unisetose conditions as apomorphies. Unfortunately, this idea cannot be confirmed by outgroup comparison until more information is available on the sister group of Pyralidae. If the unisetose condition is apomorphic, the bisetose condition may be part of a trend from trisetose (plesiomorphic state) to a unisetose L group on A9.

Extra pinacula. When present, pinacula are located only around setal bases in Pyraliformes and most other Lepidoptera (Hinton 1946, Passoa 1985). In Crambiformes, two character states occur. There may be extra pinacula (apparently lacking setae) on the thorax and abdomen of Crambinae, a few Pyraustinae, and Scopariinae (MacKay 1972, Passoa 1985) while extra pinacula are absent in Nymphulinae and Schoenobiinae. Therefore, development of secondary pinacula is considered apomorphic. When extra pinacula are lacking, this is plesiomorphic.

Pupal Characters

Frontal setae. Frontal setae are about as thick as other body setae in Pyraliformes (Passoa 1985). In Crambiformes, they are thin in all subfamilies except Nymphulinae (Passoa 1985) and several described Musotiminae (Nakamura 1977, for example). Therefore, thin setae are plesiomorphic while thick spinelike frontal setae are apomorphic.

Mesothoracic spiracle. Outgroup comparison is of limited value here since both clades have equal character distributions. In Pyraliformes, all subfamilies except Galleriinae and some Phycitinae have a mesothoracic spiracle (Passoa 1985). Among Crambiformes, all subfamilies except Nymphulinae have a mesothoracic spiracle. Loss of the mesothoracic spiracle is considered apomorphic by parsimony since three independent losses (Nymphulinae, Galleriinae, and some Phycitinae) is a more likely evolutionary scenario than independent gain of this spiracle many times in other pyralid subfamilies. Moreover, Mosher (1916) found a mesothoracic spiracle on nearly all other Lepidoptera studied. This supports the contention that a mesothoracic spiracle was probably present in ancestors of Pyralidae.

No Pyraliformes examined during this study have a deep pitlike mesothoracic spiracle. In Crambiformes, all subfamilies except Schoenobiinae lack a deep pit. Therefore, a pitlike mesothoracic spiracle is considered apomorphic while absence of a pitlike mesothoracic spiracle is plesiomorphic.

It should be noted that some Pyraustinae (for example, *Spoladea* and *Asciodes*) have pits adjacent to the mesothoracic spiracle while a few Epipaschiinae have the spiracle set in a shallow concavity. This should not be confused with the situation in Schoenobiinae where only a deep pit can be found and no trace of the spiracle is visible inside the pit.

Anterior abdominal spiracles on A1–3. All Pyraliformes lack enlarged anterior abdominal spiracles set on conelike projections (Passoa 1985). In Crambiformes, two character states exist. Nearly all species of Crambiformes except Nymphulinae (Speidel 1984) and *Thopeutis forbesellus* (Fernald) (Crambinae) lack enlarged anterior abdominal spiracles set on conelike projections. Therefore, lack of enlarged anterior abdominal spiracles is plesiomorphic while their presence on conelike projections is apomorphic. Speidel (1981) also considered enlarged anterior abdominal spiracles of Nymphulinae pupae to be apomorphic.

Posterior spiracles. All Pyraliformes examined during this study have anterior and posterior spiracles subequal in diameter. In Crambiformes, two character states exist. Most species, except Nymphulinae and a few Pyraustinae, have spiracles subequal in diameter throughout the abdomen. This is considered plesiomorphic. Reduced posterior spiracles are considered apomorphic.

Mesothoracic and metathoracic coxae. All Pyraliformes and all Crambiformes except Schoenobiinae have hidden mesothoracic and metathoracic coxae. Thus, exposed mesothoracic and metathoracic coxae are apomorphic while hidden coxae are plesiomorphic. Davis (1986) noted that only the forecoxa is exposed in higher Lepidoptera, and thus he considered exposed mesothoracic coxae to be apomorphic.

Metathoracic legs. All Pyraliformes have obtect appendages; the metathoracic legs, if not hidden, have only their tips exposed. This is also true of most Crambiformes, except Nymphulinae and Schoenobiinae which have exarate appendages with metathoracic legs clearly exposed. Fully exposed metathoracic legs and exarate appendages are considered apomorphic while partially hidden metathoracic legs are plesiomorphic.

Adult Characters

Proboscis. Most pyralids have the proboscis well developed and scaled but some Crambiformes (Schoenobiinae) and Pyraliformes (Peoriinae) lack a proboscis (Munroe 1972). This character distribution (present or absent in each clade) limits the usefulness of outgroup comparison. Instead, a reduced proboscis is considered apomorphic by parsimony since two independent reductions are more likely than many acquisitions.

Forewing CuP. Forewing CuP is another difficult character to polarize by outgroup comparison since it may be either a fold or a tubular remnant in each clade of Pyralidae (E. G. Munroe pers. comm.). Perhaps a fully developed vein was gradually lost until only a tubular remnant remained at the distal end of the forewing. This reduction of CuP continued so only a fold now marks its former position. Since Common (1970) noted a trend in higher Lepidoptera where anal and radial veins are gradually lost in advanced forms, reduction of CuP to a fold is tentatively called apomorphic. Further studies on Pyraloidea ancestors would help polarize this character, but dugeoneids, which Minet (1982) believed could be the sister group of the Pyralidae, have CuP developed.

Another possibility, independent reacquisition of CuP in Schoenobiinae, some Nymphulinae and some Pyraliformes, is equally parsimonious with the reduction of CuP in most Crambiformes, most Pyraliformes, and some Nymphulinae. CuP reduced to a fold would be plesiomorphic while gain of a tubular remnant would be apomorphic. This polarization of CuP is especially attractive if morphological studies show the sister group of Pyralidae is not Dugeoneidae (dugeoneids have CuP developed).

Praecinctorium. The praecinctorium is either present (Crambiformes) or absent (Pyraliformes) in Pyralidae. Dugeoneidae, a tentative sister group of Pyralidae, lacks a praecinctorium. Thus, presence of a praecinctorium is apomorphic whereas its absence is plesiomorphic.

Acentria probably lost the praecinctorium secondarily because it may be vestigially present in the tympanum (Minet 1985). Given presence of a praecinctorium as a groundplan apomorphy of Crambiformes, absence or extreme reduction of praecinctorium must be an apomorphic reversal.

Tegumen-vinculum plate. All Pyraliformes lack the t-v plate (Yoshiyasu 1985). This is also true for all Crambiformes except Nymphulinae and Schoenobiinae (Yoshiyasu 1985). Therefore, presence of the t-v plate is considered apomorphic.

Cu hindwing pecten. Munroe (1972) noted that cubital pecten occurs in both Crambiformes and Pyraliformes, and this limits outgroup comparison as a method of analysis. However, parsimony would indicate that several independent gains of cubital pecten are more likely than numerous losses. This suggests that presence of pecten is apomorphic while its absence is plesiomorphic. Roesler (1973) also considered presence of pecten to be apomorphic.

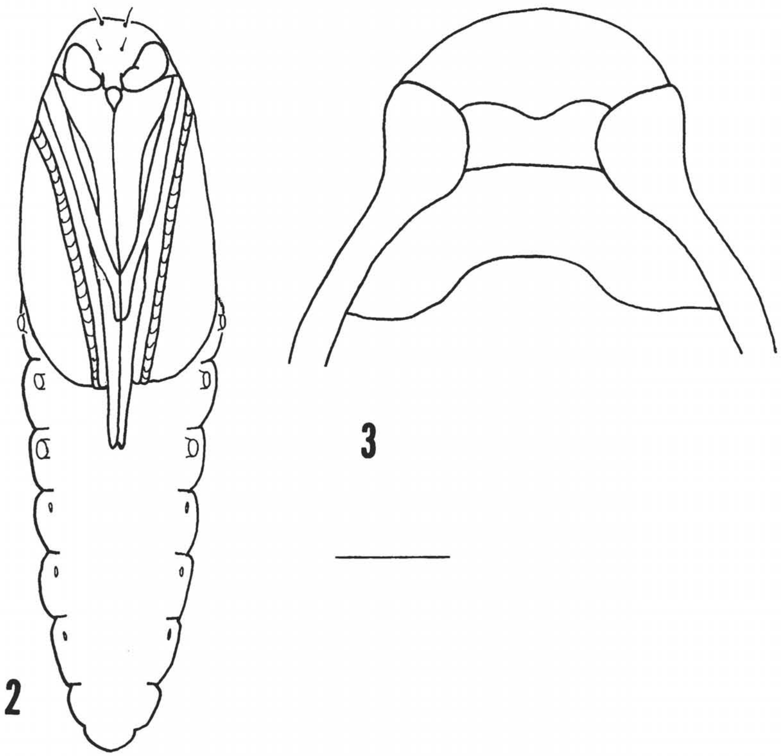
BIOLOGY

Aquatic habitat. Nearly all Pyraliformes are terrestrial, and do not form cases entirely of leaf fragments. This is true of all Crambiformes except Nymphulinae. When restricted to exclude Musotiminae, Nymphulinae include species which are always aquatic and frequently form cases. Thus, aquatic habit is apomorphic while terrestrial living is plesiomorphic. Speidel (1981) also considered aquatic living to be apomorphic.

TAXONOMIC AFFINITIES OF *ACENTRIA*

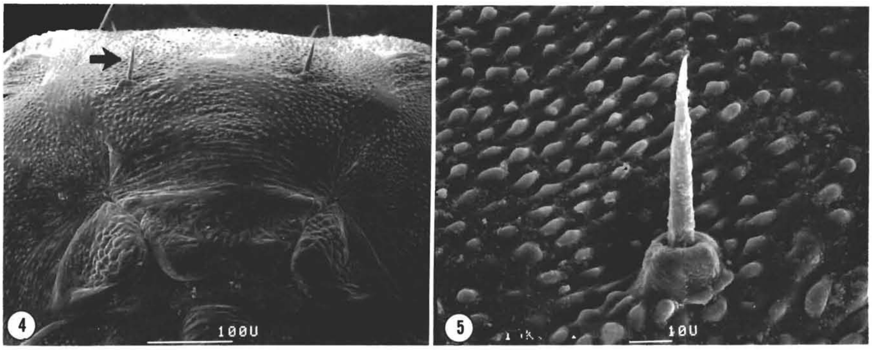
The above characters and their polarities provide additional information on the systematic position of *Acentria ephemerella*. Schoenobiinae larvae are apomorphically defined by a membranous prothoracic sac (Hasenfuss 1960, Passoa & Habeck 1987), which is absent from *Acentria* (Yoshiyasu 1985). *Acentria* also lacks the pitlike mesothoracic spiracle and exposed mesothoracic coxae (Figs. 2, 3) that apomorphically define Schoenobiinae pupae (Passoa & Habeck 1987). Therefore, immature stages of *Acentria* demonstrate the genus is misplaced in Schoenobiinae. Hampson (1895) and Forbes (1938) claimed affinity between *A. ephemerella* and Schoenobiinae because of a reduced proboscis, tubular forewing CuP, and absence of hindwing cubital pecten. Lack of cubital pecten is plesiomorphic; thus absence of this feature does not indicate relation (individuals sharing symplesiomorphies may not be relatives). The tubular forewing CuP may be apomorphic, but this character is found in both Nymphulinae and Schoenobiinae (Munroe 1972), and thus does not clarify the systematic position of *Acentria*. The single apomorphic adult character that *Acentria* and Schoenobiinae have in common, a reduced proboscis, perhaps arose through convergence since both taxa are associated with a similar (moisture-rich) aquatic environment. Although a reduced proboscis is usually considered characteristic of Schoenobiinae (Forbes 1938), some Nymphulinae also have the proboscis reduced (Yoshiyasu 1985), so a species with reduced mouthparts could be a member of either subfamily. Adult morphology, like that of immatures, provides little evidence that *Acentria* belongs in Schoenobiinae.

As mentioned earlier, there may be strong selection for enlargement of anterior abdominal spiracles in pupae of aquatic pyralids. These spiracles were considered autapomorphic for Nymphulinae (Speidel 1984), but they also occur in some aquatic Crambinae of Asia (Yoshiyasu 1985), *Thopeutis forbesellus* (Fernald) of the United States, and a few terrestrial Pyraustinae genera such as *Lygropia*, *Microthyris*, *Spoladea*, and *Marasmia* (Passoa 1985). Nevertheless, other pupal apomorphies indicate *Acentria* is related to Nymphulinae. Enlarged spinelike frontal setae are found on most Nymphulinae pupae (Yoshiyasu 1985), and are apomorphic for this subfamily. *Acentria* has these enlarged setae (Figs.



FIGS. 2, 3. **2,** Ventral view of *Acentria ephemerella* pupa. Scale line = 0.8 mm. **3,** Dorsal view of *Acentria ephemerella* pupal antenna and thorax. Scale line = 0.25 mm.

4, 5) which indicates a close relation to Nymphulinae. In addition, very few pyralid subfamilies (Galleriinae, Nymphulinae, and some Phycitinae) lack a mesothoracic spiracle (Passoa 1985). Among Crambiformes, only Nymphulinae show this loss. *Acentria* has no mesothoracic spiracle (Fig. 3) and, as is typical for Nymphulinae, has enlarged anterior abdominal spiracles set on conelike projections (Fig. 2). This spiracular arrangement, when combined with much reduced posterior spiracles, is autapomorphic for Nymphulinae. *Thopeutis forbesellus* (Crambinae) has anterior abdominal spiracles set on weak conelike projections, but the abdominal spiracles are all equal in diameter. Some Pyraustinae have enlarged anterior abdominal spiracles (Passoa 1985), but unlike Nymphulinae, lack conelike projections and have posterior spiracles at least half the diameter of anterior ones. These examples show, as Yoshiyasu (1985) suspected, that convergence has produced enlarged spiracles and conelike projections in other Crambiformes.



FIGS. 4, 5. **4**, Micrograph of *Acentria ephemerella* labrum, pillifers, frons, and vertex. Arrow points to spinelike frontal seta. Scale line = 100 microns. **5**, Micrograph of *Acentria ephemerella* spinelike frontal seta. Scale line = 10 microns.

However, it still remains possible to define Nymphulinae pupae easily by their frontal setae and other spiracular modifications.

Besides the aquatic habit (Nigmann 1908) and stemmatal setal arrangement (Hasenfuss 1960), another larval apomorphy may help resolve the systematic position of *Acentria ephemerella*. Many Nymphulini have a dentate ridge on the mandible (Yoshiyasu 1985, "semicircular arrangement" of Lange 1956) which also occurs in *Acentria* (Yoshiyasu 1985). This contrasts with Argyractini larvae which have the mandible more elongated, flattened, and usually without the dentate ridge (Lange 1956). Other characters (Lange 1956, Speidel 1984) such as diet of submerged plants, prothoracic shield chaetotaxy, ability to make cases of leaf fragments, lack of gills on body, lack of palmate setae on labrum, and three enlarged pupal spiracles would indicate *A. ephemerella* lacks apomorphies of Argyractini and belongs in Nymphulini as defined by Lange (1956). Speidel (1984) did not use mandibles, pupal spiracles, or labral setae in his Nymphulinae cladogram. Since the tribal classification proposed by North American workers can be difficult to apply to certain Asiatic genera, for example *Nymphicula* (Yoshiyasu 1980), these features merit further attention.

In summary, *Acentria* is misplaced in Schoenobiinae because immature stages radically differ. In spite of some morphological specializations, there seems little reason to consider this genus separate from Nymphulinae. Placement of *Acentria* in its own family or subfamily was based, in part, on lack of a praecinctorium which is unusual among Crambiformes. Minet (1985), while studying the tympanum, found a possible praecinctorium vestige, and thus placed *Acentria* in Nymphulinae. No characters in immature stages were found to exclude *Acentria* from Nymphulinae as a separate taxon, although crochet arrangement is somewhat unusual. Since differences between the tympanum of *Acentria* and other nymphulines may not be as great as previously thought, and several additional larval and pupal apomorphies confirm its relation to Nymphulinae and exclude it from known Schoenobiinae, there seems little doubt that transfer of *Acentria* to Nymphulinae by Hasenfuss (1960) was correct.

It is worth noting that *Neoschoenobia decoloralis* Hampson, another disputed taxon placed in Nymphulinae (Inoue 1982, cited by Yoshiyasu 1985) and Schoenobiinae (Lewvanich 1981), might be a member of Schoenobiinae because it has exposed pupal coxae and lacks enlarged pupal spiracles and stemmatal setae in a straight line. Since illustrations by Yoshiyasu (1985) do not show a mesothoracic spiracle or a larval prothoracic sac, it seems wise to retain this species in Nymphulinae, although preserved specimens should be examined for these features.

RELATION BETWEEN NYMPHULINAE AND SCHOENOBIINAE

Historically, the systematic position of Schoenobiinae has been debated. Börner (cited by Munroe 1958) thought Crambinae and Schoenobiinae were close relatives. Roesler (1973) considered them unrelated based on maxillary palpi and cubital pecten. Kuznetsov and Stekolnikov (1979) included Crambinae, Schoenobiinae, and Nymphulinae as the most primitive members of their Crambidae.

Larval and pupal features indicate Crambinae and Schoenobiinae are not closely related phenetically or cladistically. Crambinae larvae have a unisetose L group on A9, and well developed extra pinacula on both thorax and abdomen (Passoa 1985, Tan 1984). Schoenobiinae larvae, in contrast, frequently have a bisetose L group on A9 and no pinacula (Passoa & Habeck 1987). Pupal structure is also radically different. Crambinae pupae either have a well developed cremaster (Crambini) or processes on the head or body (Chilini). Metathoracic legs are not exposed or are barely visible. Schoenobiinae pupae, in contrast, always have exposed metathoracic legs, and never have a cremaster or appendages on the head or body. In fact, it is difficult to find any synapomorphies in immature stages to link these two groups.

Immature stages do support the hypothesis of Passoa (1985) and Yoshiyasu (1985) that Schoenobiinae and Nymphulinae are related. Bollman (1955) and Allyson (1976) distinguished Schoenobiinae by their reduced L2 seta, but minute L setae are common on many Nymphulinae (Yoshiyasu 1985, Neunzig 1987). Additional apomorphies to unite Schoenobiinae and Nymphulinae include fully exposed metathoracic legs and exarate appendages. Other synapomorphies listed by Yoshiyasu (1985) are V1 lost on the larval thorax, and absence of transtilla with development of the t-v plate in male genitalia. One exception is *Rupela albinella* (Passoa & Habeck 1987) which has V1 present, but this may merely represent a reversion to the primitive state. All other known species in both subfamilies lack V1, so loss of this seta is probably a groundplan apomorphy. Finally, several characters merit further investigation as synapomorphies of the Nymphulinae–Schoenobiinae clade. These are mesothoracic pupal spiracle (does the pit in Schoenobiinae contain a spiracle, or is the pit the spiracle itself); absence of pupal cremaster (unknown polarity); L setae of thorax bisetose (apomorphic but its distribution within the clade needs study); loss of pinacula (unknown polarity); and CuP tubular at margin (unknown polarity). In addition, a bisetose L group on A9 was thought characteristic of only Nymphulinae (Yoshiyasu 1985, Hasenfuss 1960, Bollman 1955) but this condition is also found in several Schoenobiinae genera (Passoa & Habeck 1987). Some illustrations show a unisetose L group on A9 in Schoenobiinae (Hasenfuss 1960) but these probably represent cases where L2 was overlooked. Chaetotaxy of Schoenobiinae larvae is difficult to study without slide mounts of larval skin. Further study may also show the bisetose L group on A9 is a synapomorphy of the two subfamilies.

RELATIONS OF NYMPHULINAE–SCHOENOBIINAE CLADE IN CRAMBIFORMES

Relation of the Nymphulinae–Schoenobiinae clade to other subfamilies has been unclear. Yoshiyasu (1985) defined a clade uniting all Crambiformes, except Pyraustinae and its relatives, by a reduced transtilla. However, certain exceptions to this generalization limit its use as a synapomorphy. Yoshiyashu (1985) characterized Pyraustinae and Glaphyriinae by their well developed transtilla, but E. G. Munroe (pers. comm.) stated that the transtilla varies widely in these groups. One alternative to a clade defined by transtilla morphology, with far fewer exceptions, involves L setae on A9. The Nymphulinae–Schoenobiinae clade is separated from remaining Crambiformes by the number of L setae on A9. Other Crambiformes subfamilies, without exception, have a unisetose L group on A9 (loss of seta L2 is an apomorphy), which defines them as a monophyletic group. This seta is present (bisetose condition) in nearly all Nymphulinae (restricted sense) and Schoenobiinae larvae. Although the above phylogeny accepts some parallel evolution with the presence of a unisetose L group in a single Nymphulinae species (Yoshiyasu 1985) and in published figures of some Schoenobiinae (if these figures are correct), this represents only a very small number of species. Parallel evolution appears to be normal in the evolution of both Macrolepidoptera (Michener 1949) and Microlepidoptera (Kristensen 1984), so perhaps pyralids have also followed this trend. It seems unrealistic to expect a group with thousands of species to be defined by a single trait without parallelisms, so choice of a clade based on the L setae may represent the case with minimum homoplasy. Use of the unisetose L group on A9 as a synapomorphy supports Minet's (1982) contention that Midiliformes belong in Crambiformes since a *Midila* larva in the U.S. National Museum has a unisetose L group on A9. Moreover, separation of Musotiminae from Nymphulinae is supported by the fact that *Musotima* has a unisetose L group on A9 (Nakamura 1977) unlike the bisetose L group of other Nymphulinae (Hasenfuss 1960).

In conclusion, this study calls attention to the role of immature insects on Pyralidae classification and phylogeny. Modifications of pupae are especially diverse and in need of study. Future studies will probably use more larval and pupal characters, especially if the sister group of Pyralidae can be confirmed.

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