

Biosystematics of *Dannella* and Related Subgenera of *Ephemerella* (Ephemeroptera: Ephemerellidae)¹

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ABSTRACT

The subgenera *Attenella*, *Eurylophella*, *Dannella*, and *Timpanoga* of the genus *Ephemerella* form a monophyletic group of subgenera whose interrelationships are retraced phylogenetically. *Dannella* and the more highly derived *Timpanoga* form sister groups divergent from the highly derived *Eurylophella*, while *Attenella* is more ancestral in origin. *Ephemerella* (*Dannella*) *provonshai*

sp. n. shares an immediate common ancestor with *E. simplex*. The adult stage of *E. lita* is described for the first time, and keys and comparisons are given for the species of *Dannella*. Phylogenetic data substantiate the subgeneric classification of the last 18 years and permit certain biogeographic inferences.

Workers have long recognized various species-groups within the genus *Ephemerella* Walsh, which was comprehensively classified into subgenera by Edmunds (1959), at which time the subgenus *Dannella* was established. Thirteen subgenera are currently recognized in the genus (Allen 1971). *Dannella* was reviewed by Allen and Edmunds (1962) in their serial revision of *Ephemerella*.

Dannella is recognizable in the adult stage primarily by the relatively generalized condition of the male genitalia (Fig. 7 and 8). The larvae (Fig. 1) are distinguished by the absence of dorsal tubercles on the body, the nature of the abdominal gills, and the lack of tarsal claw denticulation (Fig. 16).

This study deals with the evolutionary biology of *Dannella* based on phyletic analysis of the subgenera of *Ephemerella* and the species of *Dannella*. The discovery of new species characters, a new species, and the previously unknown adult stage of another species have aided such interpretation and elucidated classification.

SUBGENERIC RELATIONSHIPS

Allen and Edmunds (1962) stated that the species of *Dannella* showed a relationship to other species of *Ephemerella* that possess gills on abdominal segments 4-7. Other than this general conclusion, relationships have been intimated only by historical interpretations of the makeup of "species-groups" of *Ephemerella* in North America (McDunnough 1930, Traver 1935, and Burks 1953).

The genus *Ephemerella* consists of species which, unlike other mayfly larvae, have lost the gills on abdominal segment 2. This evolutionary tendency is further developed within the genus in a group of species which have additionally lost the gills on abdominal segments 3 (a unique adaptation among mayflies). This group of *Ephemerella* species with gills on abdominal segments 4-7, comprises the subgenera *Dannella*, *Attenella* Edmunds (previously *Attenuatella*), *Timpanoga* Needham, and *Eurylophella* Tiensuu. These subgenera must have shared an immediate common ancestor (Fig. 2A), and there-

fore constitute the monophyletic group upon which this study will focus.

Phylogeny is deduced on the basis of external characters of the adults and larvae, and the common derivation (synapomorphy) or phenoclinal relationships of character states. Ancestors are hypothetical and conclusions are inferentially based.

This group of subgenera was most probably derived from a relatively generalized form of *Ephemerella*, which may be described in terms of the ancestral states of the characters of use in determining interrelationships. All of those character states are generally widespread throughout the genus and often the family and order; and further bases for their interpretation as ancestral should be apparent from following discussions of the subsequent origin of the various derived states among the subgenera treated. In the larval stage ancestrally, the body was not greatly flattened or widened but similar to Fig. 3, the maxillae possessed 3-segmented palpi and each had a medial cluster of setae opposite the base of the palpus as in Fig. 15, the tarsal claws were denticulate, filiform gills were present laterally or near laterally on abdominal segment 1 (similar to Fig. 3), imbricated, lamellate gills (similar to Fig. 3) were present on abdominal segments 3-7, the abdomen possessed paired dorsal tubercles (see Fig. 3, 4, and 6), and abdominal segments were more or less subequal in length (similar to Fig. 1). In the adult male genitalia, each 2nd segment of the forceps possessed a longitudinal row of small, nipple-like spines on its median margin (similar to Fig. 7, 8, 10, and 11), each 3rd segment of the forceps was no more than 3 times as long as wide (similar to Fig. 7-10), and the penes were laterally expanded apically (similar to Fig. 7-9 and 11).

The evolution of characters and origin of taxa in the lineage under consideration are outlined in Fig. 2-6. Hypothetical ancestors are given upper case letter designations and character state changes are given lower case letters to facilitate discussion. As the monophyletic group is defined, it came into existence with the origin of ancestor A, which, except for the loss of gills of abdominal segment 3 (a of Fig. 3-6), was ancestrally characteristic as above.

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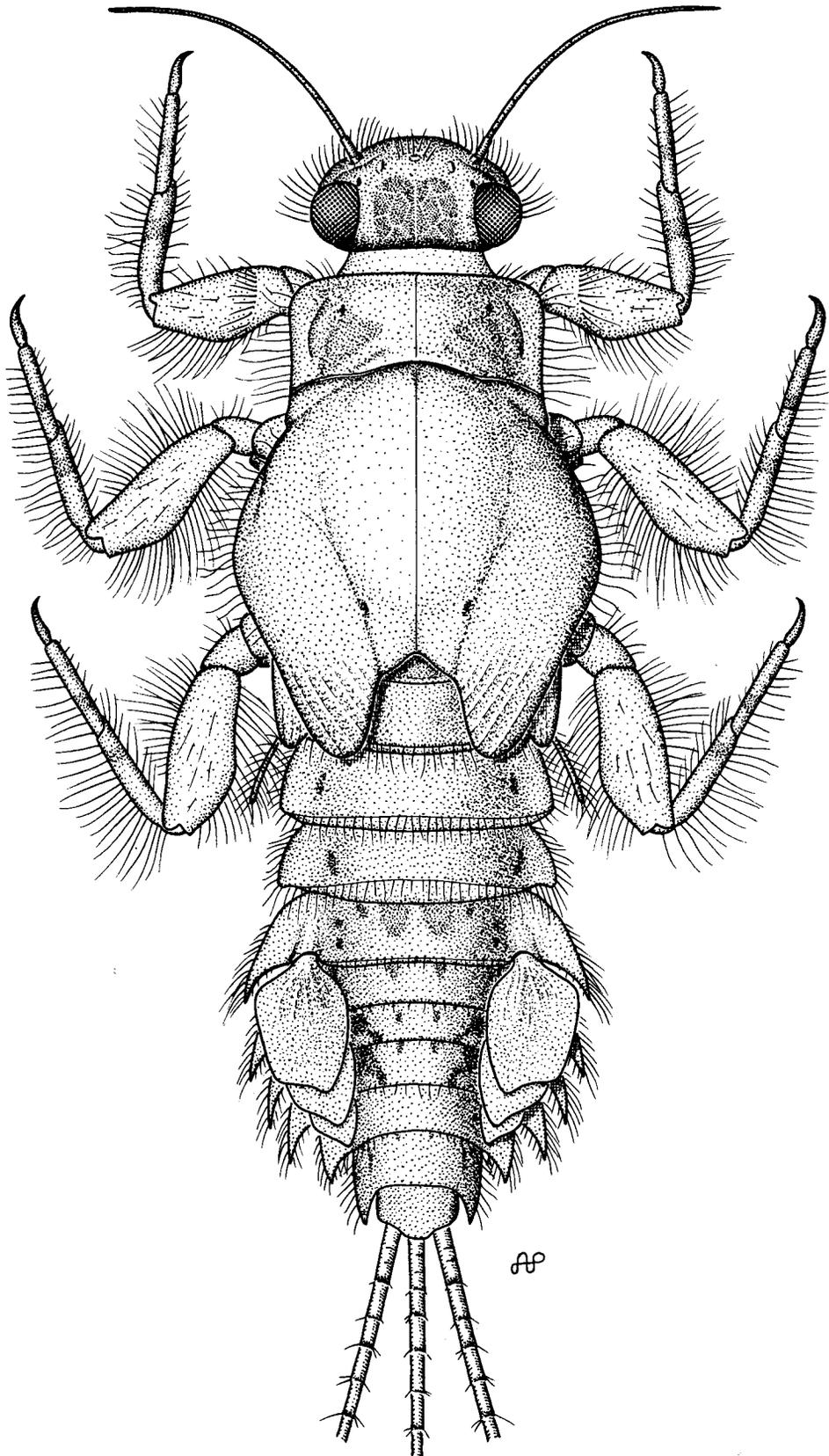


FIG. 1.—*Ephemerella (Dannella) provonshai* sp. n.

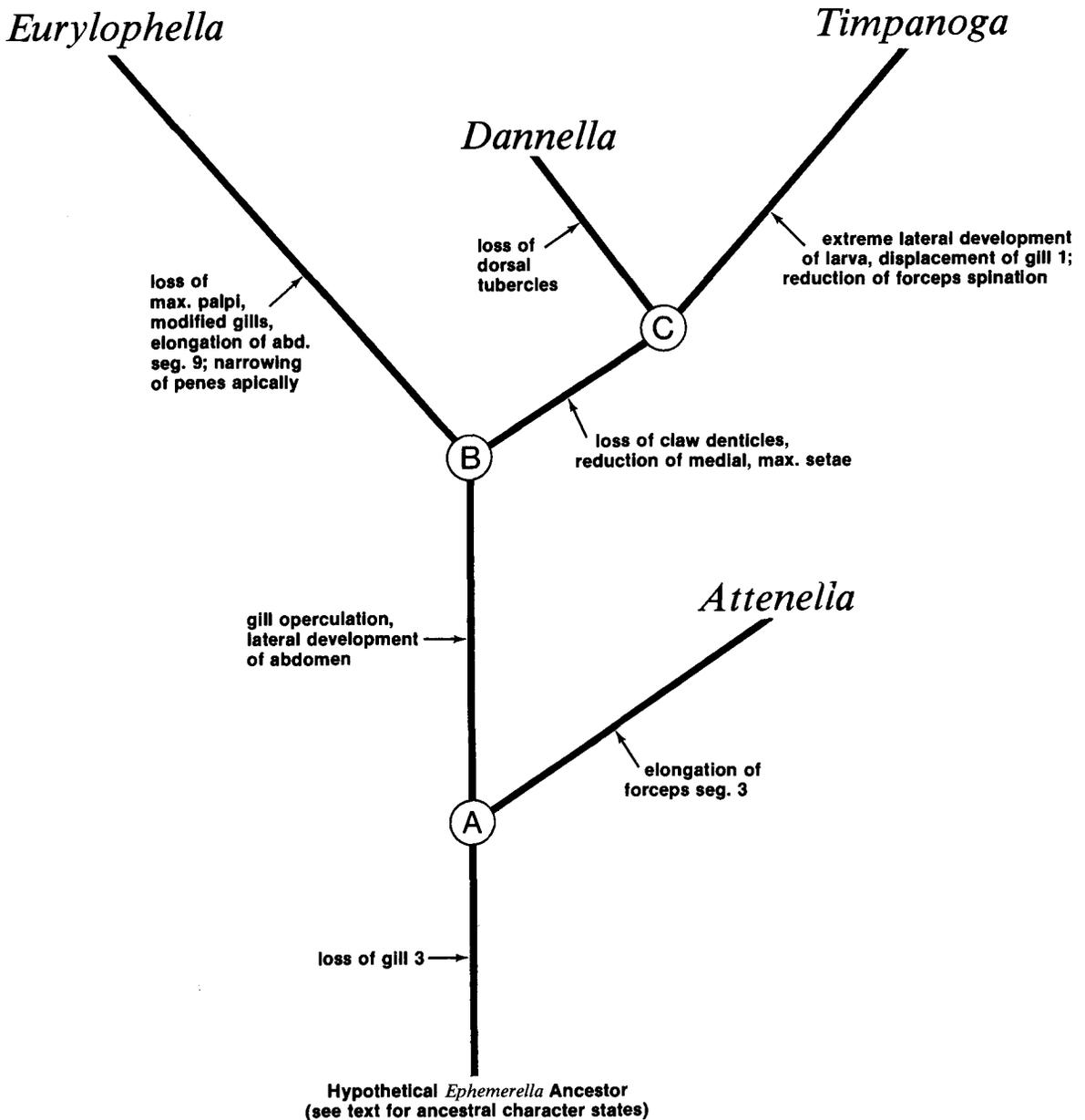


FIG. 2.—Phylogeny of the subgenera *Attenella*, *Eurylophella*, *Dannella*, and *Timpanoga*, and summary of major character state derivations.

Ancestor A gave rise to 2 lineages. In that leading to *Attenella*, the terminal segment of the adult male forceps became greatly elongated (Fig. 11) but, except for this uniquely derived character state and possibly the reduction of dorsal tubercles in the anterior abdominal segments (Fig. 3), *Attenella* represents a group retaining most of the ancestral character states. In terms of evolution of larval abdominal characters, its relatively ancestral position can be visualized in Fig. 3–6.

In the 2nd lineage to which Ancestor A gave rise, the gills on segment 4 became operculate (most

likely similar to Fig. 5) in that they more or less covered the other posterior gills (b of Fig. 4–6). Lateral processes of the larval abdomen also became more setaceous (Fig. 4–6) (as can be seen in *Dannella*, *Timpanoga*, and to various degrees in species of *Eurylophella*). Ancestor B, with the operculate condition, subsequently gave rise to 2 fundamentally distinct lineages.

In *Eurylophella*, representative of one lineage, new character states were derived as follows: in the larvae, abdominal segments 5–7 became relatively short compared to elongate segment 9 (Fig. 4c) and

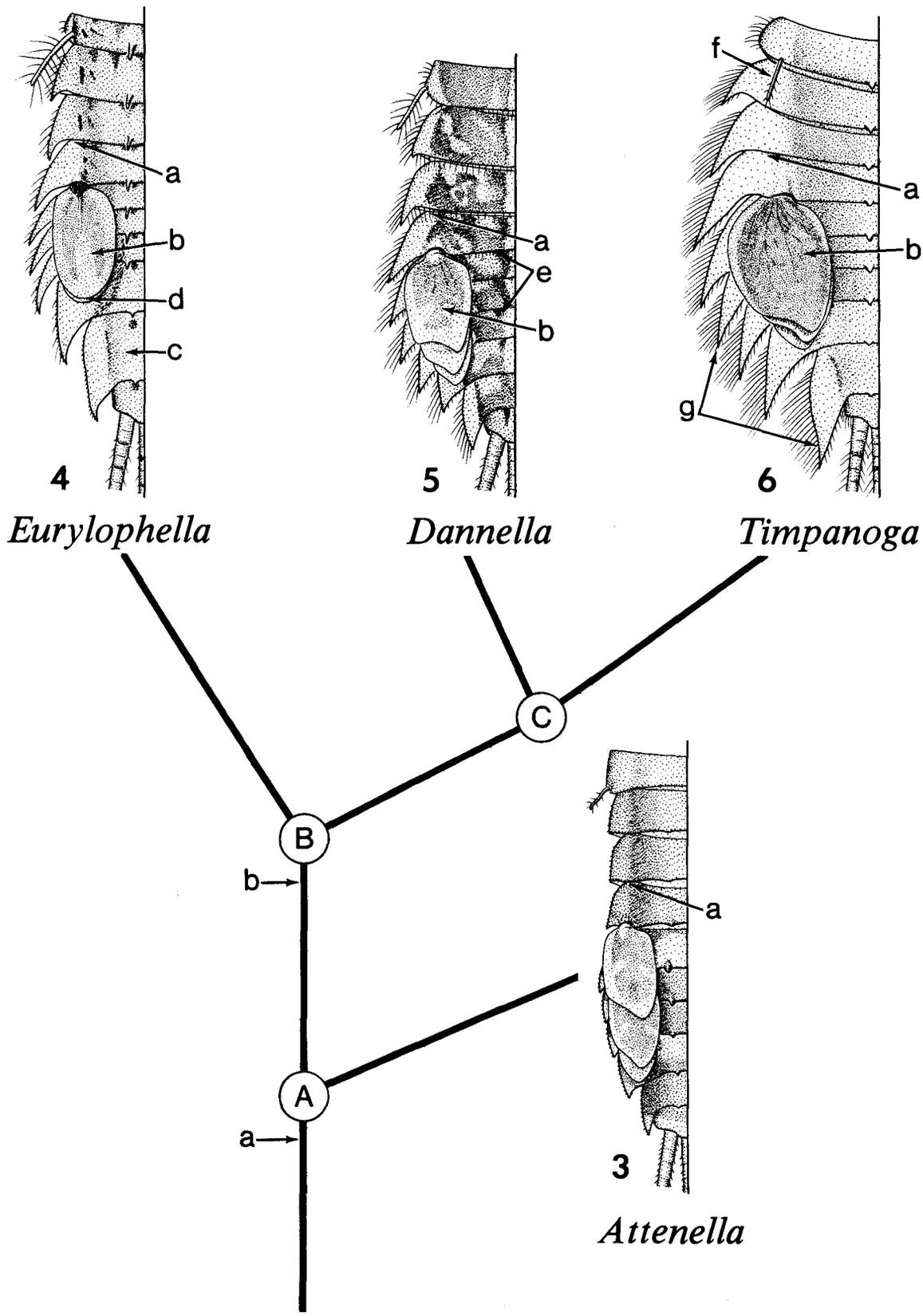


FIG. 3-6.—Evolution of subgeneric larval abdominal characters (see text for further explanation). 3. *E. margarita*, 4. *E. funeralis*. 5. *E. lita*. 6. *E. hecuba*.

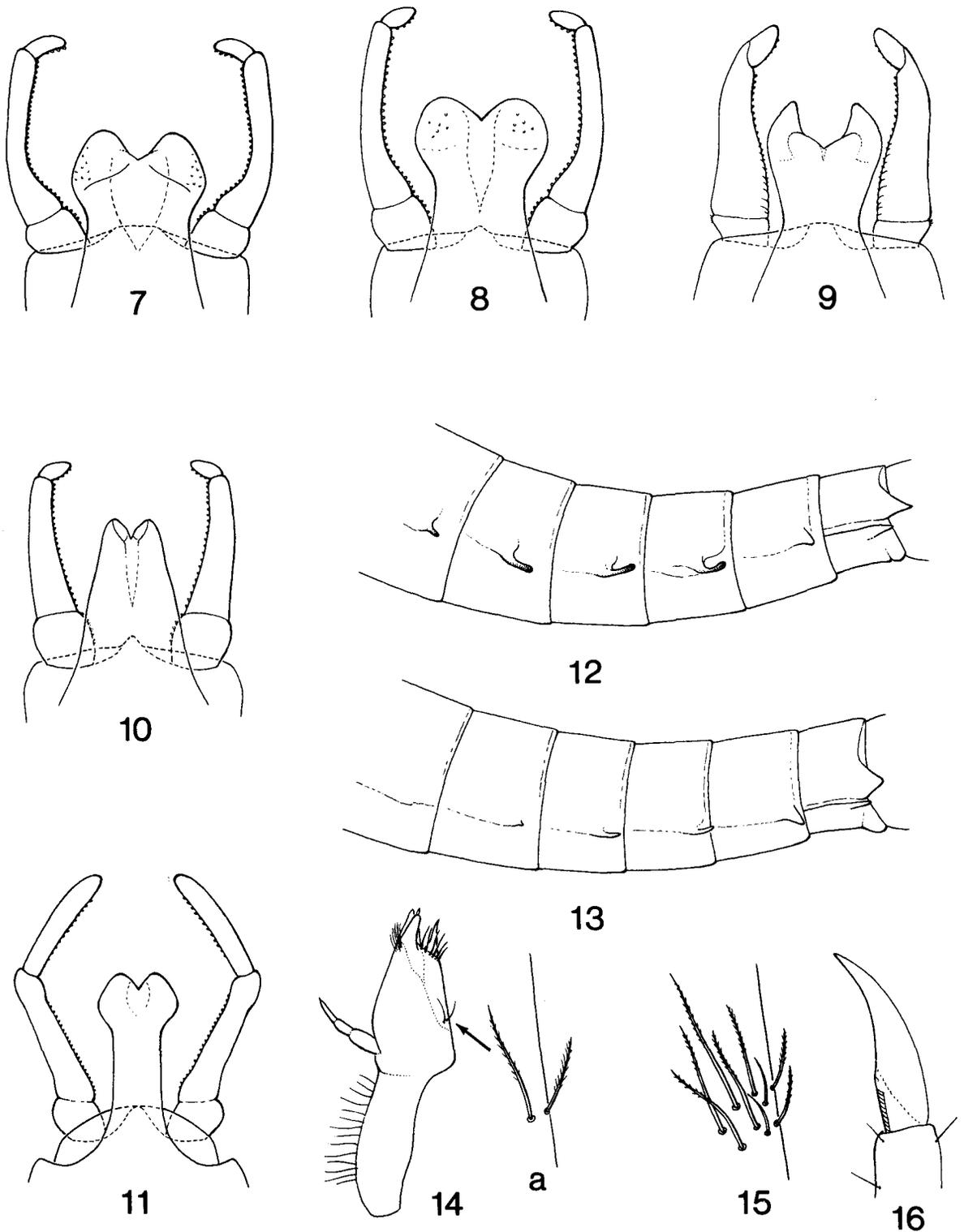


FIG. 7-16.—7-11. Male genitalia. 7. *E. (Dannella) lita*. 8. *E. (Dannella) simplex*. 9. *E. (Timpanoga) hecuba*. 10. *E. (Eurylophella) bicolor*. 11. *E. (Attenella) attenuata*. 12 and 13. Male abdominal segments 4-9, lateral view. 12. *E. (Dannella) lita*. 13. *E. (Dannella) simplex*. 14 and 15. Maxilla. 14. *E. (Dannella) provonshai*, a. Enlarged medial setae. 15. Maxillary medial setae of *E. (Eurylophella) funeralis*. 16. Larval tarsal claw of *E. (Dannella) provonshai*.

the maxillary palpi were lost; in the adult males, the penes were no longer expanded apically (Fig. 10). This lineage is also typified by relatively well developed gill operculation, and gills on abdominal segment 4 that are rounded to various degrees apically (Fig. 4d).

In the 2nd lineage to which Ancestor B gave rise, originated Ancestor C, whose larvae lost all denticles in the tarsal claws (Fig. 16), and had lost all but 2 of the medial maxillary setae (Fig. 14 and 14a). These changes represent 2 uniquely derived character states present in *Dannella* and *Timpanoga*. The gills in this lineage are emarginate apically (Fig. 1, 5, and 6, and see discussion of *Dannella* spp. below). It is doubtful, however, that this shape is derived, since at least some species of *Attenella* have similar apical margins (Fig. 3). Species data will further substantiate the relationship of *Dannella* and *Timpanoga*.

In the *Dannella* lineage from Ancestor C, all dorsal paired tubercles were lost in the larvae (Fig. 5e).

Timpanoga is represented by a single highly evolved species, *E. hecuba* (Eaton). In the larvae of this species, the filiform gills of abdominal segment 1 have become considerably displaced dorsally (hidden by the wing pads in mature larvae), and become posteriorly oriented (Fig. 6f). Eaton (1883-88), in describing this species from a larval exuvia, stated that gills on segment 1 were probably absent. Although these gills are present, subsequent workers (Traver 1935, Allen and Edmunds 1959, Edmunds et al. 1976) have not indicated their presence.

Also, in the *Timpanoga* lineage, the lateral processes of the larval abdomen became extremely developed (Fig. 6g), accompanied by the lateral expansion of the head and spinal extensions at extremities of the legs. The gills on segment 4 became more operculate than the more intermediate type found in *Dannella*. The adults lost the basal, medial spination of segment 2 of the forceps (Fig. 9), which apparently was replaced by a wrinkling of the integument in this area.

In regard to the larval abdomen, *E. hecuba* individuals range from possessing well developed paired dorsal tubercles to having a relatively smooth dorsal surface. This intraspecific reduction and loss of tubercles parallels the derived state in *Dannella* and is evidently a common, independent variation within other subgenera of *Ephemerella* as well.

If present distributions of known species (Allen and Edmunds 1959, 1961, 1962, 1963a) of this essentially Nearctic group of subgenera are superimposed on this phylogeny, some inferences may be drawn concerning geographic dispersal. The hypothetical ancestor of this group of subgenera was most likely North American. *Attenella* consists of species which are eastern, western, or questionably amphinorth America in the case of one species, and *E. (Timpanoga) hecuba* is exclusively western. In *Eurylophella*, ca. half of the species are exclusively eastern in distribution and one species is western. *E. (Eurylophella) karelica* Tiensuu, known from northern and

east central Europe, most likely represents an invasion and subsequent isolation in the Palearctic. Only in *Dannella* and several species of *Eurylophella* do ranges extend into the central United States and these generally involve species which are also found in the east. Therefore, Ancestors A, B, and C were probably eastern or trans-North American. In any case, present distributions in central regions appear to be due to relatively recent dispersals and of eastern Nearctic origin. The single record of a species of *Eurylophella* from Madagascar was probably based on a mislabeled specimen (Allen and Edmunds 1963b), and Edmunds (pers. comm.) has indicated that this record should be disregarded since he has not found *Eurylophella* or any faunal elements suggesting its presence in Madagascar.

The phylogeny of this group clearly substantiates and further defines the subgeneric classification proposed by Edmunds (1959), and as such provides a basis for species placement within the group. Each of the 4 related subgenera appears to be monophyletic and distinguishable on the basis of derived character states. Although *Timpanoga* is very closely related to *Dannella*, it is sufficiently distinct to be given subgeneric status.

SPECIES OF DANNELLA

Allen and Edmunds (1962) included 2 nominal species in the subgenus *Dannella*: *E. simplex* McDunnough 1925, known from both the adult and larval stages, and *E. lita* Burks 1949, known from the larval stage only. A new species was collected in 1974 from the Ozark Mountains of Arkansas by the author, Mr. L. Dersch, and Mr. A. V. Provonsha, for whom this species is named. In addition, the previously unknown adults of *E. lita* were reared from larvae taken in northern Indiana in 1974.

Ephemerella provonshai n. sp.

Larva.—Length: body 6; caudal filaments 4 mm. General color uniformly very light brown, abdominal maculation very slight. Maxillary palpi 3-segmented (Fig. 14). Anterior margin of pronotum slightly emarginate (Fig. 1). Abdomen (Fig. 1 and 18): segment 2 without posterolateral processes; segment 3 with small, rounded posterolateral processes; posterolateral processes of segments 6-8 in flat plane of body with little upcurvature; posterolateral process of segment 9 posteriorly directed, and when measured along medial margin, much shorter than mid-tergal length of segment 9. Setae of cerci sparse.

Holotype.—Arkansas: Johnson Co., Mullberry Riv., 1 mi. west of Oark, Ozark Natl. For., VI-2-1974, W. P. McCafferty, L. Dersch, A. V. Provonsha, in collection of Purdue University, West Lafayette, Indiana (some parts slide-mounted).

Ephemerella lita

Adult Male (In alcohol).—Length: body 8; forewing 7 mm. General color brown. Head dark brown; dorsal portion of compound eyes pale, ventral portion black. Thorax dark brown, legs tan, wings hyaline,

veins pale, costal and subcostal regions of forewings opaque. Abdominal tergites brown with dark brown lateral maculations on segments 1-9 and submedian pair of short dark brown stripes on segments 3-10; segments 4-7 with small, dark, finger-like lateral vestiges of larval posterolateral processes (Fig. 12); tergite 9 with well developed, acute posterolateral processes (Fig. 12); sternites light brown, infuscated with brown posteriorly and laterally in anterior seg-

ments, becoming completely infuscated in sternite 9; genitalia as in Fig. 7. Caudal filaments tan, without long setae.

Material Examined.—15 males reared from larvae; Indiana: LaGrange Co., Pigeon Cr. at 1100 E., VI-10-1974. L. Dersch, D. Tyler, in collection of Purdue University, West Lafayette, Indiana.

The species of *Dannella* may be distinguished most easily by use of the following key, and additional

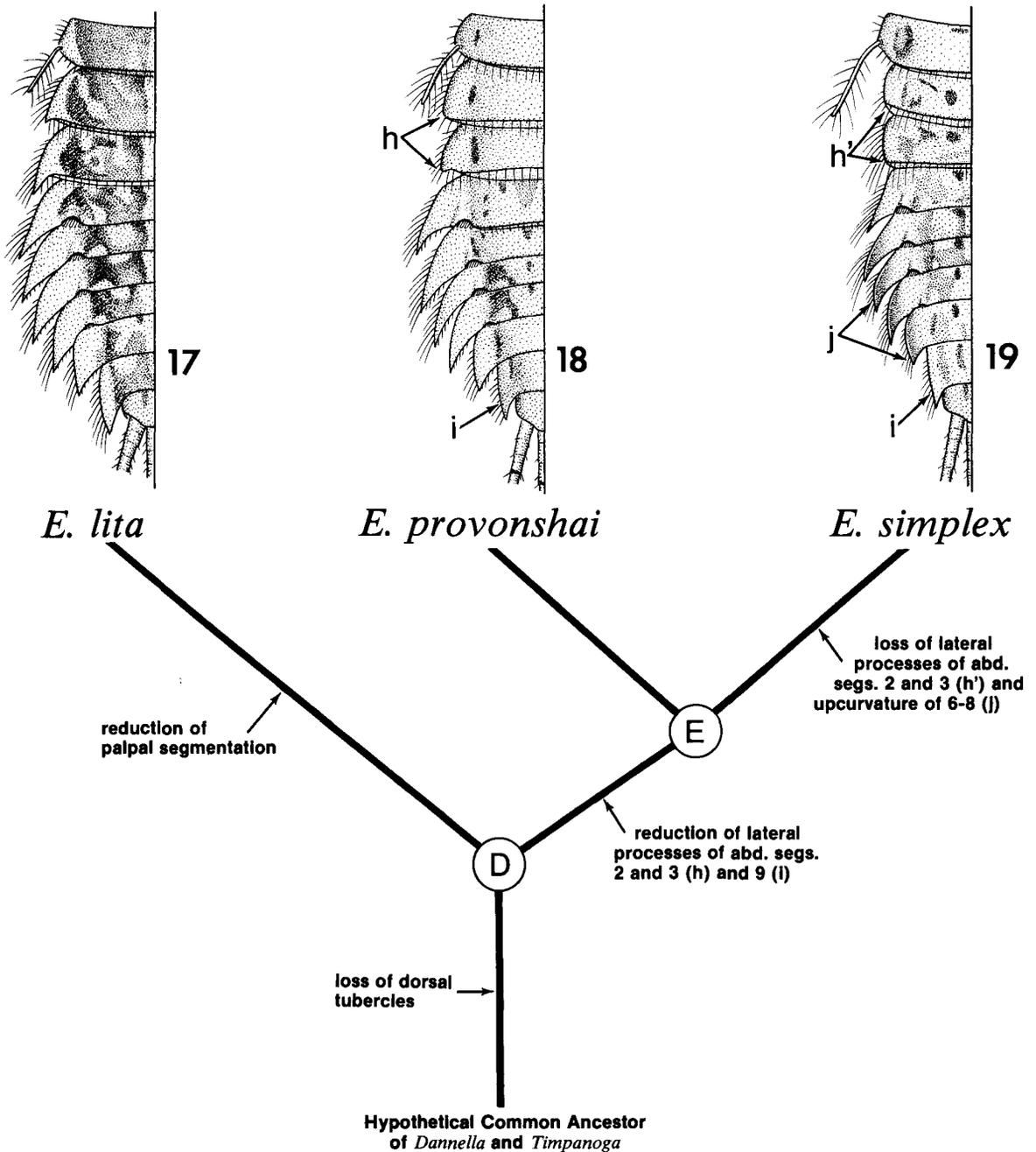


FIG. 17-19.—Phylogeny of *Dannella* spp. and evolution of larval abdominal characters (see text for further explanation). 17. *E. lita*. 18. *E. provonshai*. 19. *E. simplex*.

clarification of the species will become apparent in the discussion of specific relationships.

LARVAE

1. Posterolateral processes of abdominal segment 3 well developed and acute (Fig. 17); posterolateral processes of abdominal segment 9 (measured along medial margins) at least as long as mid-dorsal length of segment 9, with medial margins distinctly divergent from lateral margins of segment 10 as in Fig. 17 *lita*
Posterolateral processes of abdominal segment 3 not as above (Fig. 1, 18 and 19); posterolateral processes of abdominal segment 9 not so long as mid-dorsal length of segment 10, with medial margins nearly paralleling lateral margins of segment 10 (Fig. 1, 18 and 19) 2
2. Abdominal segment 3 with small, blunt posterolateral processes (Fig. 1); posterolateral processes of segment 6-8 only slightly upcurved (Fig. 1 and 18) *provonshai*
Abdominal segment 3 with no posterolateral processes (Fig. 19); posterolateral processes of segments 6-8 upcurved dorsally (Fig. 19) with apices nearly reaching mid-dorsal height of abdomen *simplex*

ADULTS

1. Posterolateral processes of abdominal segment 9 acute (Fig. 12); abdominal segments 4-7 with well defined, lateral, finger-like vestiges of larval posterolateral processes as in Fig. 12..... *lita*
Posterolateral processes of abdominal segment 9 not acute apically (Fig. 13); lateral finger-like vestiges of larval posterolateral processes of abdomen only slightly developed on segments 5-7 as in Fig. 13. *simplex*

The maxillary palpi of *E. provonshai* (Fig. 14) resemble those of *E. lita* in being 3-segmented, and differ from *E. simplex* where segmentation lines are weakened considerably. The degree of weakening differs among specimens of *E. simplex* examined, however. Terminal palpal setae are difficult to see and are not always so distinctive as shown in Allen and Edmunds (1962) among the species. The degree of operculation and shape of gills 4-7 are similar in the 3 species. In the whole-larva figure of *E. simplex* in Allen and Edmunds (1962) and the partial refigure in Edmunds et al. (1976), the gills appear oval, and evidently the artist mistook the oval pigmented area of gill 4 for the outline of the gill. The gills of all *E. simplex* examined are similar to those of Fig. 1 and 5. In addition, the posterolateral processes of segments 6-8 are subequally developed in the larvae of the 3 species, but in *E. simplex* they are more upcurved and therefore the abdomen appears less developed in earlier published figures. Comparison of adult penes (Figs. 7 and 8) may also aid in differentiating *E. lita* and *E. simplex*, however, these structures are evidently somewhat variable, at least in *E. simplex*.

SPECIES RELATIONSHIPS

The phylogeny of the species of *Dannella* is de-

picted in Fig. 17-19. The evolution of characters and phylogeny of the subgenera provide a presumptive basis for determining ancestral and derived character states among these species. Within *Dannella* there has been an evolutionary trend toward reduction of the posterolateral processes of the abdomen. As discussed previously, *Dannella* (Ancestor D of Fig. 17-19) had lost the paired dorsal abdominal tubercles in the larval stage (Fig. 5e). *E. lita* has retained most of the ancestral character states of this ancestor.

Ancestor D also gave rise to the common ancestor, E, of *E. provonshai* and *E. simplex*. The reduction of the posterolateral processes of abdominal segment 9 (i of Fig. 18 and 19) is common between the larvae of the latter species and must have been present in Ancestor E. Posterolateral processes of abdominal segments 2 and 3 were considerably reduced in Ancestor E and this condition has been retained in *E. provonshai* (Fig. 18h). In *E. simplex*, the posterolateral processes of segments 2 and 3 were entirely lost (Fig. 19h'), and thus the evolution of this character was completed. A phenocline regarding the development of the posterolateral processes of segments 2 and 3 can be seen in going from the state in *E. lita* (and Ancestor D) to that of *E. provonshai* (and Ancestor E), and finally that of *E. simplex*. The phenocline may be further pronounced at the ancestral end if Ancestor C (Fig. 2) is considered to be similar to *E. hecuba* (Fig. 6) in regards to this character. An additional adaptation which apparently goes hand in hand with the general trend of process reduction is seen in the upcurvature of processes 6-8 (Fig. 19j) in the relatively highly derived *E. simplex*.

An evolutionary trend in these species now becomes apparent in the transition of the length of the filiform gills of segment 1 (Fig. 17-19). Also, it is interesting that the bifurcation of the penes of the newly discovered adult of the relatively ancestral *E. lita* is relatively most similar to that of *E. hecuba* (Fig. 7 and 9) and thus, perhaps least changed from Ancestor D (Fig. 2).

E. simplex is widely distributed throughout eastern and north-central North America. *E. lita* has been taken in Pa., N.C., Ind., and Ill. In Ind., at least, it is far more common than *E. simplex*. On the basis of the phylogeny of these species, it appears most likely that the species which gave rise to the sister species, *E. provonshai* and *E. simplex* (Ancestor E of Fig. 17-19), was primarily Appalachian in distribution but ranged into the Ozark Plateau, possibly via the Illinois Ozarks or Cincinnati Arch. It is also likely that subsequent geographic isolation of the Ozark population instigated the speciation process. The fact that *E. provonshai* is consistently more ancestral than *E. simplex* in all relative characters studied, may correspond to *E. provonshai's* apparent isolation in a somewhat disjunct biogeographic area of North America, where it has remained little changed. On the other hand, although *E. provonshai* is the only species of *Ephemerella* known exclusively from the Ozark area, several Eastern species through-

out the genus extend into this region at the southwestern limits of their ranges. A remotely possible record of an unidentified species of *Dannella* in Colorado was reported by Ward (1975).

Ecological and biological information on these species, when known, should expand phyletic interpretations and allow a more in-depth analysis of historical biogeography.

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