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Reevaluation of the Phylogeny of the Ephemeroptera Infraorder Pannota (Furcatergalia), with Adjustments to Higher Classification

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ABSTRACT

Phylogeny of the cosmopolitan Ephemeroptera infraorder Pannota (Furcatergalia) is revised based on analysis of 46 characters from 34 Operational Taxonomic Units under the parsimony criterion of PAUP*, with *Rhoenanthus* Eaton (Scapphodonta: Potamanthidae) as an outgroup. Phylogenetic sequencing conventions were applied to the most parsimonious tree that was derived from this analysis. The resultant changes in classification include placing *Philolimnias* Hong, a monobasic genus from Eocene amber, into Philolimniidae, n. fam. Vietnamellidae is restricted to include only *Vietnamella* Tshernova, and *Austremerella* Riek is replaced in Austremerellidae, revalidation. *Teloganella* Ulmer is moved to Melanemerellidae (subfamily Teloganellinae, n. stat.). *Coryphorus* Peters is returned to Leptohyphidae (subfamily Coryphorinae, n. stat.).

The cosmopolitan mayfly (Ephemeroptera) infraorder Pannota of the suborder Furcatergalia includes approximately 600 species and nearly 60 genera, comprising about 20% of extant mayflies (McCafferty and Wang 2000, Brittain and Sartori 2003). McCafferty and Wang (2000) presented the first comprehensive treatment of Pannota and confirmed its division into two superfamilies, Caenoidea and Ephemerelloidea. Caenoidea contains two families, Caenidae and Neoephemeridae, and this classification has remained stable following the compelling evidence of Wang et al. (1997).

In contrast to the Caenoidea, several emendations to the Linnaean classification of ephemerelloid family groups (sensu ICZN 1999) have been proposed in recent years. These include contributions by Elouard and Oliarinony (1997), Oliarinony and Elouard (1997), McCafferty (2000), McCafferty and Wang (2000), Wiersema and McCafferty (2000), Hubbard (2002), Molineri et al. (2002), and Molineri and DomÌnguez (2003). Based on these studies, Ephemerelloidea could be divided maximally into eleven families (as listed by Sun et al. 2006): Coryphoridae, Dicercomyzidae, Ephemerellidae, Ephemerythidae, Leptohyphidae, Machadorythidae, Melanemerellidae, Teloganellidae, Teloganodidae, Tricorythidae, and Vietnamellidae (=Austremerellidae). Since the extensive study of McCafferty and Wang (2000), Molineri and DomÌnguez (2003) and Ogden and Whiting (2003, 2005) have presented hypotheses about the relationships of limited pannote taxa, and Kluge (2004) presented a nonranking classification system of Pannota. In order to maintain a consistent classification of mayflies within the Linnaean framework (McCafferty 1991, 2004), we found it prudent to reevaluate the phylogeny of Ephemerelloidea in light of recently available data (Oliarinony et al. 1998, McCafferty 2000, Oliarinony et al. 2000, McCafferty and

Benstead 2002, McCafferty et al. 2003, Jacobus and Sartori 2004, Molineri 2005, Jacobus and McCafferty, in press) and newly discovered characters.

In order to undertake the present study, we divided Pannota into operational taxonomic units (OTUs) that together represent all pannote family-group level taxa (senu ICZN 1999). All Ephemerelloidea genera are included as OTUs, except for one dubious fossil genus and many genera of the highly diverse Ephemerellinae (Ephemerellidae), Leptohyphinae, and Tricorythodinae (Leptohyphidae). Ephemerellinae is the subject of a nearly finished global revision (Jacobus and McCafferty, unpublished); for the purposes of this study, we utilize as representative OTUs the type genera of the subfamily's two tribes, Ephemerellini, s.s., and Hyrtanellini Allen. The South American fauna of Leptohyphidae is the subject of considerable revision and analysis at present (e.g., Molineri 2004, Molineri and Zuñiga 2004, Molinari 2005, Dias and Salles 2005, Dias et al. 2005, Ogden and Whiting 2005, Wiersema and McCafferty 2005, Baumgardner and Avila 2006, Dias and Salles 2006, Salles and Molineri 2006), and its supraspecific classification likely will be impacted, especially considering that the group has a Neotropical center of origin and is one of the most representative groups of mayflies in South America (McCafferty 1998, Salles and Molineri 2006). Therefore, we treat Leptohyphinae and Tricorythodinae (Wiersema and McCafferty 2000) each as a single OTU under the name of its respective type genus. The families and subfamilies of Caenoidea are represented by their type genera and are included to test the monophyly of Ephemerelloidea, in light of the similar characteristics of caenoids and many ephemerelloids, especially those included in the most historic and broad concept of Tricorythidae (McCafferty and Wang 2000).

We included the Eocene fossil genus *Philolimnias* Hong in our analysis. The mouthparts described by Hong (1979) for this adult preserved in amber probably are misinterpretations of a crumpled nasal carina and frontal shelf that bear vestiges of projections that were present on the larva, such as found on adults of the extant genus *Vietnamella* Tshernova (Wang and McCafferty 1995). The monospecific Jurassic genus *Turfanerella* Demoulin (Ephemerellidae) was excluded from our analysis because no phylogenetically informative characters are apparent from the fossilized abdominal fragments that comprise the single known specimen (Ping 1935: Fig. 1; Demoulin 1954: Figs. 1–2). Edmunds (1972) suggested that *Turfanerella* might belong instead to Siphlonuridae (Ephemeroptera: Piscaforma), and McCafferty and Wang (2000) noted its dubious inclusion in Ephemerellidae.

PHYLOGENETIC ANALYSIS

We chose the genus *Rhoenanthus* Eaton as an outgroup for rooting trees and forming hypotheses about character state polarity. *Rhoenanthus* is hypothesized to be the most pleisiotypic genus of the family Potamanthidae, which is the most pleisiotypic family of Pannota's sister group, Scapphodonta (Bae and McCafferty 1991, McCafferty 2004).

We screened all available life stages from each of our OTUs for phylogenetically informative characters, with eggs being examined via Scanning Electron Microscopy at the Life Science Microscopy Facility, Purdue University. We excluded certain characters from consideration for analysis, including autapomorphies, ambiguous or highly variable morphometric data, and characters prone to convergence, such as coloration, internal anatomy, loss of palp on the maxilla, and the length of certain wing veins (e.g., Peters and Peters

1993, McCafferty and Wang 2000, McCafferty 2004).

We used MacClade (Maddison and Maddison 2005) to build a data matrix (Fig. 2) that includes 46 characters taken from the egg, larva, and adult stages. Character states are indicated by numerals. Missing or unknown data are indicated by a question mark (?). Inapplicable character states are indicated by a dash (–); these include, for example, character states that cannot be scored because the structure in question is not present (e.g., size and orientation of gills 2 for the genus *Ephemerella* Walsh, which has gills on only segments 3–7). Polymorphisms are indicated by an ampersand (&). Each character is to be considered of the "unordered" type (Swofford 2002, Maddison and Maddison 2005), unless otherwise indicated (o=ordered; i=irreversible). The characters are not weighted in any other way. We utilize the wing venation nomenclature employed by McCafferty and Wang (2000).

Eggs

1. Number of polar caps (0=0; 1=1; 2=2).
2. Scalelike attachment structures [Fig. 1] around base of polar cap (0=absent; 1=present).

Larvae

3. Labrum width (0=less than three times wider than long; 1=three or more times wider than long).
4. Glossae and paraglossae (0=no appreciable reduction or fusion; 1=reduced and partially fused; 2=fused fully).
5. Labial palp segment 3 (0=present and not reduced in size; 1=reduced in size; 2=absent).
6. Maxilla shape (0=robust; 1=dorsoventrally flattened).
7. Prominent row of setae on dorsal surface of maxilla (0=absent; 1=present).
8. Robust lateral bristle on mandible (0=absent; 1=present).
9. Spatulate setae on margin of prothorax (0=absent; 1=present).
10. Stout, spatulate setae on margins of coxal projections (0=absent; 1=present).
11. Forewing pads (0=slight or no basal fusion; 1=fused basally for over one-half their length) [i].
12. Posterior margins of abdominal terga (0=no processes; 1=single median process; 2=pair of processes).
13. Setae on outer margin of posterolateral projections [among those taxa with such projections] (0=short and usually spatulate; 1=elongate).
14. Orientation of abdominal gills (0=lateral; 1=dorsally recumbent).
15. Dorsal portion of abdominal gills (0=lanceolate; 1=lamellate).
16. Ventral portion of abdominal gills (0=lanceolate; 1=triangular; 2=bifurcate).
17. Gill 1 (0=present; 1=absent) [i].
18. Gill 2 (0=present; 1=absent) [i].
19. Gill 2 length (0=does not extend beyond posterior margin of segment 4; 1=extends well beyond posterior margin of segment 4).
20. Gill 2 shape (0=not quadrate; 1=quadrate).
21. Shape of dorsal portion gill 3 and subjacent gills (0=undivided; 1=bifurcate).
22. Gill 3 (0=present; 1=absent) [i].
23. Gill 4, if it is the anteriormost lamellate gill (0=extends not past segment 6; 1=extends well beyond posterior margin of segment 6 but not beyond most posterior gill; 2=extends beyond segment 6 and most posterior gill) [o].
24. Gill 5 (0=present; 1=absent) [i].
25. Gill 7 (0=present; 1=absent).
26. Caudal filaments with lateral, hairlike setae (0=absent; 1=present).
27. Median caudal filament (0=elongate; 1=reduced; 2=stublike).

Adults

28. Compound eye of male (0=dioptic; 1=holoptic).
29. Foreleg claws of male (0=one distally acute and one blunt distally; 1=both claws blunt).
30. Mesothoracic notum (0=relatively unmodified; 1=with sutural ommation; 2=with sutural ommation membraneous).
31. Forewing setal fringe (0=absent; 1=present).
32. Number of marginal intercalaries present in each interspace of forewing (0=0; 1=1; 2=2).
33. Forewing marginal intercalaries, if present (0=attached; 1=detached).
34. Forewing MP2 (0=extending to near base; 1=not extending to near base).
35. Forewing MP2 length relative to ICuA (0=at least as long; 1=shorter).
36. Forewing CuA (0=attached to R1 and not directed towards CuP; 1=detached from R1 and directed towards CuP).
37. Forewing ICuA (0=attached to a cubital vein; 1=long and not attached to any cubital vein).
38. Forewing ICuA (0= at least three attachments to CuA; 1= two attachments to CuA; 2=one attachment to CuA; 3=medially attached to CuP by discreet crossvein; 4=apparently directly attached to CuP) [o].
39. Forewing CuP (0=not curved inwards; 1=curved inwards).
40. Hindwing (0=present in both sexes; 1=present in male, absent in female; 2=absent in both sexes).
41. Hindwing size and venation, if present (0=not appreciably reduced; 1=reduced).
42. Length of male subgenital plate, relative to total length of genital forceps (0=much less than one-fourth; 1=approximately one-third; 2=more than one-half).
43. Penes auxillary processes (0=absent; 1=present with length less than one-half length of forceps; 2=present with length nearly subequal to length of the forceps; 3=present and much longer than forceps) [o].
44. Forceps segments number (1=1; 2=2; 3=3; 4=4).
45. Deep longitudinal groove on inner margin of forceps (0=absent; 1=present).
46. Forceps segment 1 length (0=at least as long as wide; 1=much less than width).

Utilizing the characters listed above, we conducted a heuristic search for best trees using the parsimony criterion of PAUP* under the default settings, except that multiple states were to be interpreted as polymorphisms (Swofford 2002). The heuristic search yielded one tree (Fig. 3) that was more parsimonious than any of the other rearrangements tried. This tree most notably differs from previous hypotheses about pannote phylogeny (e.g., McCafferty and Wang 2000, McCafferty and Benstead 2002) with regards to the branching sequence and composition of the basal ephemerelloid clades and the branching sequence of genera within Teloganodidae.

Numerals above each branch represent hypothesized character state changes; a numeral followed by a numeral in parentheses [n(x)] denotes a multistate character that changes to state "x", as indicated in the data matrix and list of characters. Reversals are indicated with a minus sign [-]. Polymorphism within an OTU is indicated by an asterisk [*].

HIGHER CLASSIFICATION

Our reclassification of taxa resulted from the application of phylogenetic sequencing conventions (Nelson 1972,1973) to our cladogram (Fig. 3). The genera *Austremerella* Riek, *Coryphorus* Peters, *Philolimnias* Hong, and *Teloganella*

Ulmer are assigned to families different from those in which they have been included most recently, given the restrictions imposed by a strict phylogenetic system of Linnaean classification (Hennig 1966, Wiley 1981). *Philolimnias* is placed into Philolimniidae, new family [Type Genus: *Philolimnias* Hong 1979: 336], and *Austremerella* is replaced in Austremerellidae, revalidation, due to their basal position relative to other ephemerelloid families. *Teloganella* is the sister group of *Melanemerella* Ulmer and thus is included in the family Melanemerellidae, subfamily Teloganellinae, new status. *Coryphorus* is included in the subfamily Coryphorinae, new status, of the Leptohyphidae, so that Dicercomyzidae can retain family status, as listed by Molineri et al. (2002) and followed by Sun et als. (2006). The linear classification of family groups given below reflects precisely the relationships indicated by our cladogram (Fig. 3).

Infraorder Pannota
Superfamily Caenoidea Spieth
- Family Neoephemeridae Needham, Traver and Hsu
- Family Caenidae Klapálek
  - Subfamily Caeninae, s.s.
  - Subfamily Madecocercinae McCafferty and Wang
  - Subfamily Brachycercinae Lestage

Superfamily Ephemerelloidea Demoulin
- Family Philolimniidae Jacobus and McCafferty, new family
- Family Vietnamellidae Allen
- Family Austremerellidae McCafferty and Wang, revalidation
- Family Ephemerellidae Klapálek
  - Subfamily Timpanoginae Allen
    - Tribe Attenellini McCafferty
    - Tribe Timpanogini, s.s.
    - Tribe Eurylophellini McCafferty
  - Subfamily Ephemerellinae, s.s.
    - Tribe Ephemerellini, s.s.
    - Tribe Hyrtanellini Allen
- Family Teloganodidae Allen
- Family Melanemerellidae Demoulin
  - Subfamily Melanemerellinae, s.s.
  - Subfamily Teloganellinae, McCafferty and Wang, new status
- Family Ephemerythidae Gillies
- Family Machadorythidae Edmunds, Allen and Peters
- Family Leptohyphidae Edmunds and Traver
  - Subfamily Coryphorinae Molineri, Peters and Zuñiga, new status
  - Subfamily Leptohyphinae, s.s.
  - Subfamily Tricorythodinae Wiersema and McCafferty
- Family Tricorythidae Lestage
  - Subfamily Tricorythinae, s.s.
  - Subfamily Ranorythinae Oliarinony and Elouard
  - Subfamily Madecassorythinae Elouard and Oliarinony
- Family Dicercomyzidae Edmunds and Traver

MATERIALS EXAMINED

We examined actual specimens of *Rhoenanthus* and all pannote genera included in our analysis, except for the fossil *Philolimnias*. In most cases, the specimens we examined bear our determination labels and may be located at the Albany Museum, Grahamstown, South Africa; Bernice P. Bishop Museum, Honolulu, Hawai'i, USA; Brigham Young University, Provo, Utah, USA; Canadian National Collection of Insects, Agriculture and AgriFood Canada, Ottawa, Ontario, Canada; Cornell University Insect Collection, Ithaca,

New York, USA; Enns Entomology Museum, Columbia, Missouri, USA; Florida A&M University, Tallahassee, Florida, USA; Illinois Natural History Survey, Champaign, Illinois, USA; Iowa State University, Ames, Iowa, USA; Musée cantonal de zoologie, Lausanne, Switzerland; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA; The Natural History Museum, London, England, UK; Purdue University Entomological Research Collection, West Lafayette, Indiana, USA; Royal Ontario Museum, Toronto, Ontario, Canada; Snow Museum, University of Kansas, Lawrence, Kansas, USA; Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA. Some specimens from the Enns Entomology Museum and Iowa State University will be deposited in Thailand with the National Science Museum, Pathum Thani; and the Royal Forestry Department, Bangkok.

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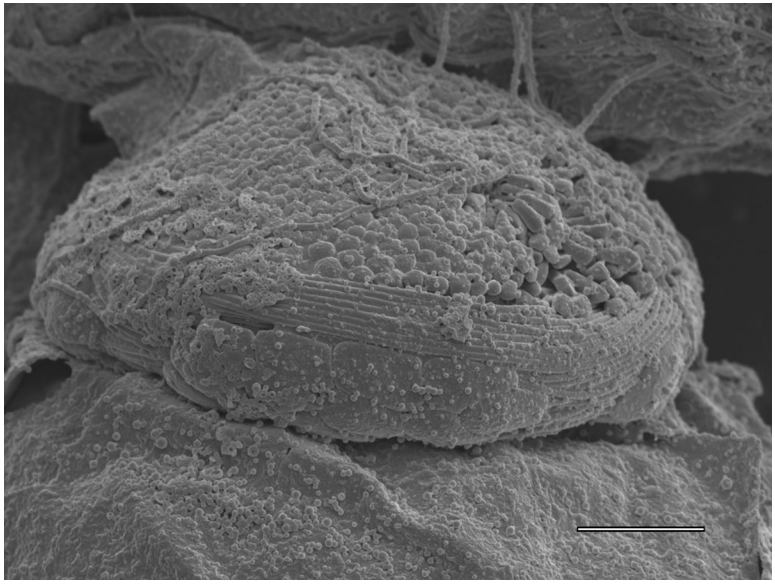

Fig. 1. *Teloganella* egg; scalelike attachment structures at base of polar cap (scalebar = 10 μm).

	1 10 20 30
Rhoenanthus	2 0 1 0 0 0 0 0 0 0 0 0 0 – 0 0 0 0 0 0 0 0 0 – 0 0 1 0 1 ? 0
Attenella	1 0 0 0 1 0 0 0 0 0 1 2 0 1 1 2 0 1 – – 0 1 0 0 0 1 0 0 1 0
Austremerella	1 0 0 0 1 0 0 0 0 0 1 2 0 1 1 2 1 0 0 0 0 0 – 0 0 1 0 0 ? 0
Brachycercus	1 0 0 0 2 0 0 0 0 0 1 0 1 1 1 1 0 0 1 1 0 0 – 0 1 0 0 1 ? 2
Caenis	& 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 1 0 0 1 1 0 0 – 0 1 0 0 1 1 2
Coryphorus	1 ? 0 2 1 0 0 0 0 ? 1 1 – 1 1 2 1 0 1 1 0 0 – 0 1 0 1 1 0 0
Dannella	2 0 0 0 1 0 0 0 0 0 0 1 0 1 1 1 2 0 1 – – 0 1 1 0 0 1 0 0 0 0
Dentatella	0 – 0 0 1 0 0 0 0 0 0 1 2 1 1 1 2 0 1 – – 0 1 2 0 0 1 0 0 0 0
Dicercomyzon	? ? 1 1 1 1 0 1 0 0 1 0 0 1 0 1 1 0 1 0 0 0 – 0 1 0 2 1 0 0
Ephemerella	1 0 0 0 1 0 0 0 0 0 0 1 2 0 1 1 2 1 1 – – 0 0 – 0 0 1 0 0 & 0
Ephemerellina	? ? 1 0 1 0 0 0 0 1 1 1 0 1 1 2 1 0 1 0 0 0 – 0 1 1 0 0 0 0
Ephemerythus	1 0 0 1 1 0 0 0 0 0 0 1 0 0 1 1 2 1 0 1 0 0 0 – 0 1 1 0 1 1 0
Eurylophella	0 – 0 0 1 0 0 0 0 0 0 1 2 1 1 1 2 0 1 – – 0 1 2 0 0 1 0 0 0 0
Hyrtanella	1 0 0 & 1 0 0 0 0 0 0 1 & 0 1 1 2 1 1 – – 0 0 – 0 0 1 0 0 0 0
Leptohyphes	& ? 0 & 1 0 0 0 0 0 0 1 0 & 1 1 2 1 0 1 0 0 0 – 0 1 0 0 & 1 0
Lestagella	? ? 0 1 1 0 0 0 1 1 1 0 1 1 1 2 0 0 1 0 0 0 – 1 1 1 0 0 0 0
Limnokijara	? ? ? 1 1 0 0 0 0 0 0 1 0 0 1 1 2 1 0 1 0 0 0 – 0 1 1 0 1 0 0
Lithogloea	0 ? 0 0 1 0 0 0 0 0 1 1 1 1 1 1 2 0 0 1 0 0 0 – 0 1 ? 0 0 0 0
Macafertiella	1 0 1 1 1 0 0 1 1 1 1 1 & 1 1 2 1 0 1 0 1 0 – 0 1 0 2 ? ? ?
Machadorythus	1 0 0 2 1 0 0 0 0 0 0 1 0 1 1 1 2 1 0 1 0 0 0 – 0 1 0 0 1 0 0
Madecassorythus	1 0 0 2 1 1 1 0 ? ? 1 0 0 1 1 2 1 0 0 0 0 0 – 0 1 0 1 1 0 0
Madecocercus	? 0 0 0 0 0 0 0 0 0 0 1 0 1 1 1 1 0 0 1 1 0 0 – 0 1 1 0 1 ? 2
Manohyphella	? ? 0 0 1 0 0 0 1 1 1 1 1 1 1 1 2 0 0 1 0 0 0 – 0 1 0 0 0 ? 0

	30 40 46
Rhoenanthus	0 0 1 0 0 0 0 0 0 0 0 0 0 0 3 0 0
Attenella	0 0 1 1 1 0 1 0 1 1 0 0 0 0 3 0 1
Austremerella	0 0 1 1 1 0 1 0 0 1 0 0 ? ? ? ? ?
Brachycercus	2 1 0 – 0 0 0 1 – 0 2 – 0 0 1 1 –
Caenis	2 1 0 – 0 0 0 1 – 0 2 – 0 0 1 0 –
Coryphorus	0 1 0 – 1 1 1 – – 1 2 – 0 0 2 0 0
Dannella	0 0 1 1 1 0 1 0 0 1 0 0 0 0 3 0 1
Dentatella	0 0 1 1 1 0 1 0 1 1 0 0 0 0 3 0 1
Dicercomyzon	0 1 0 – 1 0 1 0 4 1 2 – 0 1 2 0 0
Ephemerella	0 0 1 1 1 0 1 0 1 1 0 0 0 0 3 0 1
Ephemerellina	0 0 1 1 1 0 1 0 2 1 0 0 0 0 3 0 0
Ephemerythus	0 0 2 1 1 0 1 0 4 1 1 1 1 0 2 0 0
Eurylophella	0 0 1 1 1 0 1 0 1 1 0 0 0 0 3 0 1
Hyrtanella	0 0 1 1 1 0 1 0 2 1 0 & 0 0 3 0 1
Leptohyphes	0 1 0 – 1 1 1 0 3 1 & 1 0 0 2 0 0
Lestagella	0 0 1 1 1 0 1 0 2 1 0 0 0 0 3 0 0
Limnokijara	0 0 2 1 1 0 1 0 4 1 0 1 1 0 2 0 0
Lithogloea	0 0 1 1 1 0 1 0 2 1 0 0 0 0 3 0 0
Macafertiella	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
Machadorythus	0 0 0 – 1 0 1 0 4 1 2 – 0 0 2 0 0
Madecassorythus	0 1 0 – 1 0 1 0 4 1 2 – 0 3 2 0 0
Madecocercus	2 1 0 – 0 0 0 1 – 0 2 – 0 0 1 1 –
Manohyphella	0 0 1 1 1 0 1 0 2 1 0 0 0 0 3 0 0

Fig. 2. Data matrix.

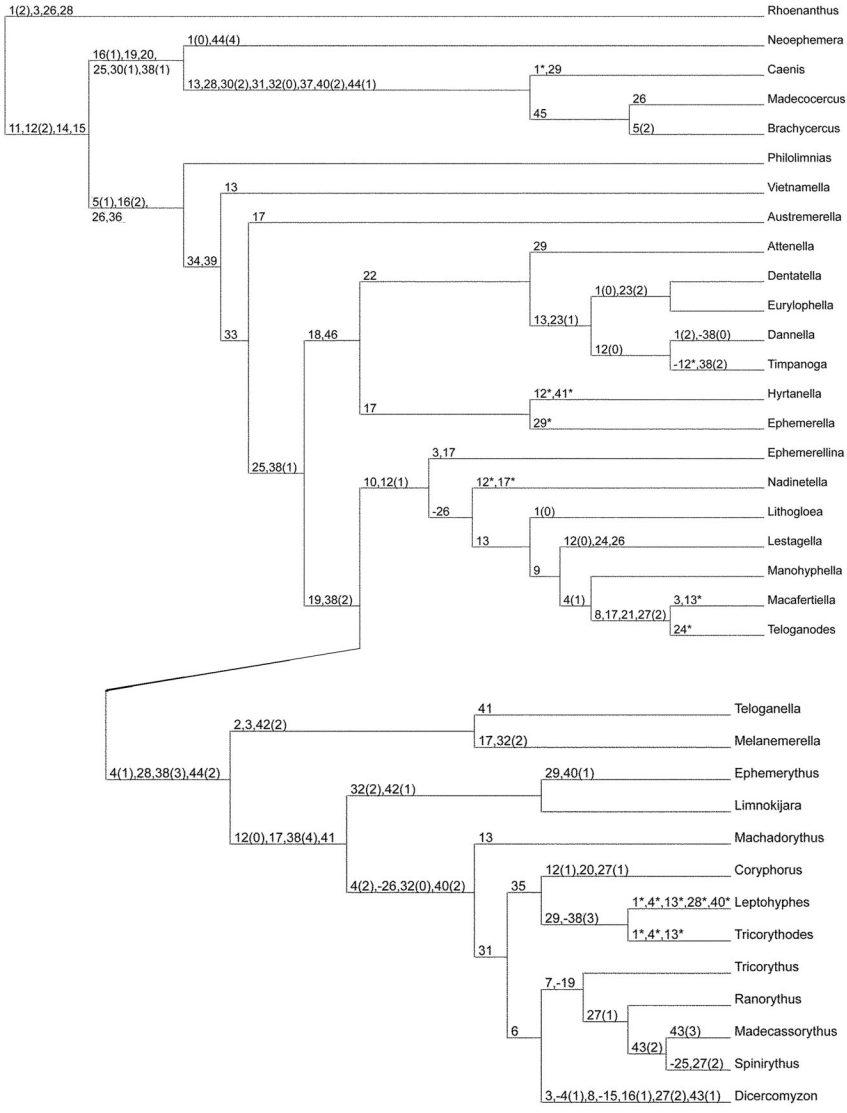

Fig. 3. Cladogram of Pannota.