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Phylogeny of Limnephilidae and composition of the genus *Limnephilus* (Limnephilidae: Limnephilinae, Limnephilini)

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Abstract. A world revision of the family Limnephilidae (Trichoptera: Integripalpia) was undertaken as a necessary step to determine the position, structure, and phylogeny of the genus *Limnephilus* and family-group taxa for which it is nominotypical. The family Limnephilidae sensu lato and included taxa were analyzed with modern phylogenetic techniques. For the phylogenetic analysis, morphological characters of adults and immature stages were used, including traditionally used characters and some that have been poorly investigated or never studied. As a result of the analysis, new hypotheses of relationships are proposed among Plenitentoria taxa. For the first time, monophyly is inferred for the following taxa: superfamily Limnephiloidea, family Limnephilidae, subfamily Limnephilinae, tribe Limnephilini, and *Limnephilus sensu stricto*. Some other family-group taxa are distinguished based on high bootstrap support, unreversed synapomorphies, and/or topography, including a new family-group category for Trichoptera, "Branch," more inclusive than the family category and less inclusive than the superfamily category.

Key words: Trichoptera, Limnephilidae, *Limnephilus*, phylogeny.

Introduction

With nearly 900 species included in 99 genera, the "northern caddisfly," or "northern case-maker" family Limnephilidae (insect order Trichoptera, suborder Integripalpia, infraorder Plenitentoria) is the fourth largest family of Trichoptera (Morse, 2001, 2003). Highest species diversity and greatest population densities of limnephilids are in higher temperate latitudes of the northern hemisphere.

The family Limnephilidae until now has been considered complicated, and no divisions into subfamilies, tribes, and genera have been analyzed with modern phylogenetic techniques. The traditional elements of the Limnephilidae sensu lato were included in a single comprehensive classification of the world fauna in a landmark study by Schmid (1955). According to Schmid (1955) the family can be divided into four subfamilies: Dicosmoecinae Schmid, 1955; Drusinae Banks, 1916; Pseudostenophylacinae Schmid, 1955; and Limnephilinae Kolenati, 1848. The latter subfamily has been divided into four tribes: Chaetopterygini Hagen, 1858; Chilostigmini Schmid, 1955; Limnephilini Kolenati, 1848; and Stenophylacini Schmid, 1955. After recent phylogenetic analysis of "the former broad Limnephilidae," subfamily Neophylacinae and several genera allied to *Neothremma* were transferred from the Limnephilidae to the Uenoidae (Wiggins *et al.*, 1985; Vineyard and Wiggins, 1988). Further phylogenetic analysis of the Limnephiloidea led to erection of the families Apataniidae and Rossianidae and re-definition of the Goeridae (Gall and Wiggins, pers. communication). Through these modifications, the long-standing problem of Limnephilidae genera *Incertae Sedis* (Wiggins 1973, 1977) was resolved. However, even after this, the monophyly of the Limnephilidae has not been demonstrated. In a recent publication on Dicosmoecinae, Wiggins (2002) added much to our understanding of the phylogeny of this "Limnephilidae" lineage, but still did not provide evidence for monophyly of the family. Stuart and Currie (2001) used caddisfly larval behavioral data to support the monophyly of Integripalpia and each of 8 families except for the Limnephilidae.

Preliminary attempts to use modern DNA techniques with a small number of genera to infer relationships among limnephilids suggested that Limnephilidae may be monophyletic (Kjer *et al.*, 2001, 2002), and that some genera may be polyphyletic (Pauls *et al.*, 2005).

The present study was planned originally as a revision of the genus *Limnephilus*. However, in the process of the revisional work, it was realized that the problem of this genus is impossible to solve without resolving the family problem in general. Therefore, in our phylogenetic field of interest, we included other genera of Limnephilidae from all tribes and subfamilies, with special preference for nominotypical representatives. Since *Limnephilus* is the nominotypical genus of the family, it is a key to an understanding of "true limnephilids." Therefore, in order to answer a question, "What is *Limnephilus*?" we must first understand, "What are limnephilids?" "What is subfamily Limnephilinae?" "What is tribe Limnephilini?" and "What are the relationships among the limnephilid subfamilies, tribes, and genera?"

Methods

For phylogenetic analysis of higher-level relationships in the family Limnephilidae, as many limnephilid genera and species as possible were investigated to find synapomorphies for tribes and subfamilies. A total of 137 species from 98 integripalpian genera (86 of 99 limnephilid genera) were analyzed to reveal monophyly of Limnephilidae and discover higher-level phylogenetic relationships within the family Limnephilidae.

PAUP version 4.0b10 (Swofford, 1993) were used in the analysis, using the branch and bound analytical option.

Terminology for male and female genitalia is after Nielsen (1954, 1980). Some characters and metrics introduced in the phylogenetic analysis were described by Vshivkova (2006). An original metric "Gill Index" is described here for the first time.

The *Gill Index* (*GI*) is an original metric showing the number of gill clusters (or single filiament) on abdominal larval segments (Note: In the text below we will use "gill cluster" to mean two alternative conditions of abdominal gill appearance: as a cluster of filaments or as a single filament). A complete GI includes: 2 pairs of dorsal clusters + 2 pairs of ventral clusters + 2 pairs of lateral clusters = 6 pairs of clusters (GI=12 gill clusters). If all dorsal and ventral gill clusters are present, but lateral gill clusters are absent, GI = 8; if all dorsal and ventral gill clusters are present and posterolateral gill clusters are absent (i.e., among lateral gill clusters, only anterolateral gill clusters are present), GI = 10, and so on. The maximum number of gill clusters per abdominal segment is 12 (GI = 12). We consider GI complete when all dorsal and ventral gill clusters and at least one pair of lateral gill clusters are present, i.e., GI may be = 10, 12; GI *incomplete* - when lateral, or some dorsal (anterior or posterior) or some ventral (anterior or posterior) gill clusters are absent, i.e. GI < 10. GI is calculated based on whatever segment has the highest number of gill clusters and highest number of gill filaments in a cluster (usually abdominal segment II or III).

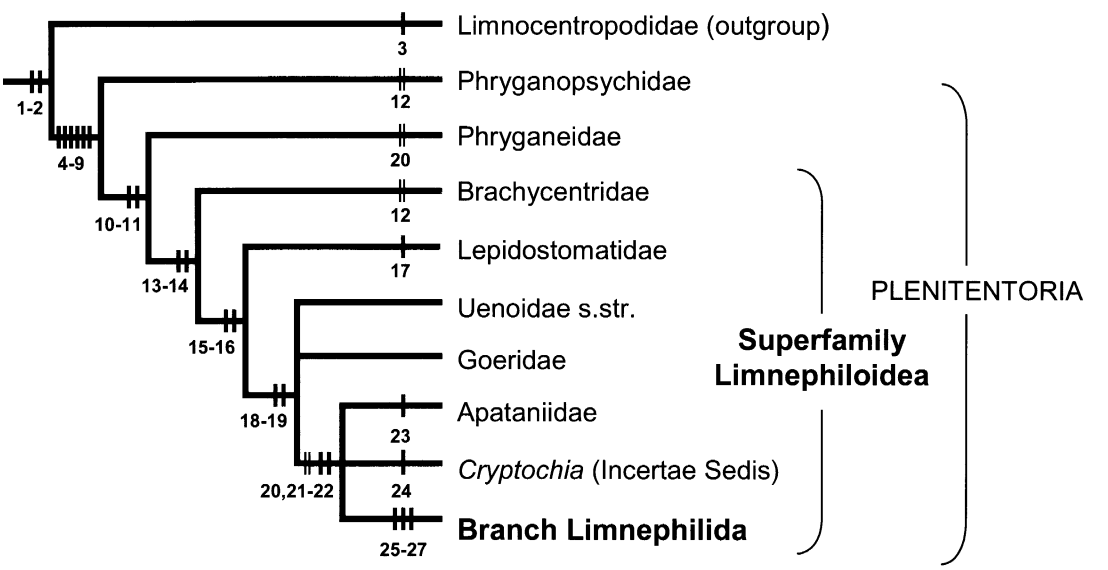

Figure 1. Higher phylogeny of Integripalpia and Plenitentoria.

Results of Phylogenetic Analysis

A strict consensus tree of 6659 trees was calculated with a heuristic search (Vshivkova, 2006). The tree was rooted using Phryganopsychidae [(*Phryganopsyche latipennis* (Banks)] as the outgroup family. Tree length = 1708. Consistency Index (CI) = 0.1148. Homoplasy Index (HI) = 0.8852. Retention Index (RI) = 0.6902. Rescaled consistency index (RC) = 0.0792. A bootstrap 50% majority-rule consensus tree was obtained with 400 bootstrap replicates.

Using results of these analyses, four cladograms were prepared (Figs. 1-4) based on inferred 91 synapomorphies (Table 1). As a result of this analysis, phylogenetic support for all of the nominotypical taxa: Limnephiloidea – Limnephilidae – Limnephilinae – Limnephilini – *Limnephilus* was obtained. Also, some other higher taxa are distinguished based on high bootstrap support, unreversed synapo-morphies, and/or topography.

Table 1. List of synapomorphies and codes.

(Abbreviations: 0 - plesiomorphic condition, 1 - apomorphic condition; A – adult, F – female, M – male, L – larva; GI – gill index).

Character 1. (F) Prespermathecal diverticulum absent (0); present (1).
Character 2. (A) Haustellum without parallel grooves, or with grooves only apically (0); parallel grooves present on full length of haustellum (1).
Character 3. (L) Gill clusters absent or present at least dorsally and ventrally (0); gill clusters or their rudiments present only posterodorsally (1).
Character 4. (L) Abdominal gill clusters absent, or total number of gill clusters less than 10 (GI < 10) (0); gill clusters complete (GI = 10-12) (1).
Character 5. (A) Mandibles sclerotized (0); membranous (1).
Character 6. (L) Prosternal horn absent (0); prosternal horn present (1).
Character 7. (A) Tibial spurs with sensilla on surface (0); sensilla absent (1).
Character 8. (A) Mandibles hidden under labrum at rest (0); not hidden (1).
Character 9. (L) Lateral gill clusters absent (0); lateral gill clusters present (1).
Character 10. (A) Width of anterolateral areas (areas located laterad of frontoclypeus) less than 1/3 of frontoclypeus width) (0); wider than 1/3 of frontoclypeus width (1).
Character 11. (A) Dorsal branches of tentorium incomplete (0); complete (1).
Character 12. (A) Spinules on inner spur surface irregularly distributed (0); arranged in oblique rows (1).
Character 13. (A) Mandibles present as membranous lobes (0); reduced to short swellings or completely absent (1).
Character 14. (A) Labrum not separated into basilabrum and distilabrum, labral swelling/warts absent (0); distilabrum differentiated from basilabrum by transverse swelling/warts (1).
Character 15. (A) Tibial spurs each with 0-1 rim (0); with 2 rims (1).
Character 16. (A) Spur rim(s) comprised of teeth-like spinules forming comb(s) (0); spur rims comprised of flattened leaf-like spinules (1).
Character 17. (A) Spur outgrowths (sensilla and/or spinules) short (shorter than width of spur base) or medium (equal to width of spur base or slightly exceeding it) (0); noticeably longer (1).
Character 18. (L) Chloride epithelia absent (0); present (1).
Character 19. (F) Distal part of spermathecal duct prior to prespermathecal diverticulum branch unsclerotized (0); sclerotized ring present (1).
Character 20. (A) Falsicalcar (ae) absent or single at distal edge of each hind tibia near base of apical spurs (0); two falsicalcarae (1).
Character 21. (M) Two (apical) or three (2 apical, 1 preapical) foreleg spurs present (0); single apical foreleg spur present (1).
Character 22. (F) Posterior margin of sternite VIII without three-lobed structure ("vulvar scale") (0); with three-lobed structure (lateral lobes of which produced by external gonopods of sternites VIII or IX) (1).
Character 23. (F) Middle lobe of vulvar scale sclerotized, without wrinkles (0); membranous or semi-membranous and wrinkled (1).
Character 24. (M) Inferior appendages with long second segment situated in the middle portion of first segment (0); very long rod-like second segment situated to upper end of first segment (1).

Table 1. List of synapomorphies and codes, continued.

Character 25. (F) Spermathecal gland located closer to caudal end of spermatheca (0); closer to spermathecal vestibule base (1).
Character 26. (A) Internal intermediate surface (furrow) between spur rims covered with spinules from base to apex (0); furrow bare or covered with spinules only in basal area (1).
Character 27. (F) Spermathecal gland short (0); medium or very long (1).
Character 28-27. (F) Distal end of spermathecal vestibule without sclerotization or with dorsoventrally depressed sclerotized ring (0); with band-like, cap-like or funnel-like sclerotized ring (1).
Character 29. (M) Simple distiphallus not inserted into basiphallus (represented as whole structure "phallobase+phallotheca") (0); simple distiphallus (not divided into phallicata and endophallus) partially divided from basiphallus, or completely divided and inserted into basiphallus (1).
Character 30. (L) Posterior half of pronotum is narrower or equal to anterior half of pronotum in dorsal aspect (0); pronotum broadest at about midpoint in dorsal aspect (1).
Character 31. (M) Hind wing with short DC and Forks I and II stalked, pointed, or shallowly rooted (0); hind wing DC long, Forks I and Fork II always obviously rooted (specific "limnephilid pattern" forming anterior anastomoses) (1).
Character 32. (F) Protruding lobe of e.gon.VIII (middle lobe of "vulvar scale") sclerotized, or membranous and wrinkled (0); membranous and smooth (1).
Character 33. (M) Length of Fork III base on both wings shorter than, or subequal to DC width (0); longer than DC width (1).
Character 34. (M) Hind wing Fork V not closed apically (0); fused apically (1).
Character 35. (M) Both fore- and hind wings with *rs* and *m-cu* cross-veins straight (0); *m-cu* on fore wing and *rs* on both wings curved basad (1).
Character 36. (M) Parameres unarmed (0); armed (1).

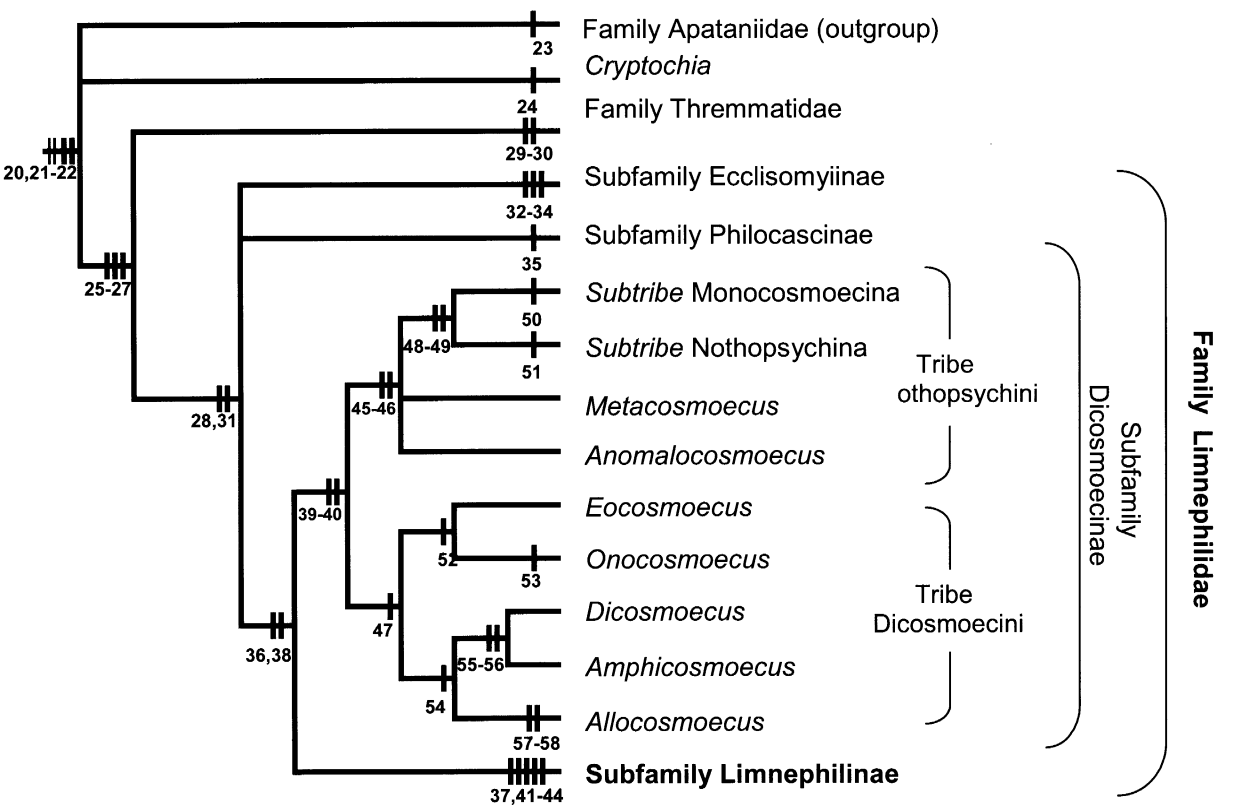

Figure 2. Phylogeny of Branch Limnephilida.

Table 1. List of synapomorphies and codes, continued.

Character 37. (M) Parameres armed with tiny spinules or hair-like outgrowths (0); parameres with various structures (spinules, bristle-like structures, teeth) (1).

Character 38. (M) Phallicata not differentiated as an anterior part of distiphallus (between parameres and endophallus) (0); differentiated as a separated tube-like area (membranous or sclerotized) (1).

Character 39. (A) Forewing posterior anastomosis (PA) consisting of 2 or 3 parts (0); PA consisting of one part (cross-vein *m-cu* only) ("dicosmoecine pattern") (1).

Character 40. (A) Forewing PA consisting of one part and *m-cu* directed apically (0); PA consisting of one part directed posterad (1).

Character 41. (F) External gonopods of sternite IX (e.gon.IX) not exposed or exposed as laterally compressed folds [= side lobes of "vulva scale" ("= portions of IXd) forming with middle lobe (= e.gon. VIII) "false vulva scale"] (0); e.gon. IX fully exposed, thick or very dorsoventrally depressed, and forming (with middle lobe) typical limnephilid "true vulvar scale" (1).

Character 42. (F) Middle lobe (e.gon. VIII) with dorsal portion tightly connected with inner genital structures which may be exposed externally, forming sclerotized projection appearing to be middle lobe ("false middle lobe") (0); middle lobe slightly or well-sclerotized dorsal (inner) surface separated from inner genital structures (1).

Character 43. (M) Phallocrypt with sclerotized strips situated ventrolaterally (0); dorsally, or dorsolaterally (1).

Character 44. (M) Tergum X developed, forming (with superior and intermediate appendages) subanal genitalic complex, with inner and outer branches of intermediate appendages protruding caudad (0); tergum X reduced, with outer branches of intermediate appendages spread ventrolaterally and differentiated into *lateral upper apices* and *ventral lower apices* (1).

Character 45. (F) External gonopods (e.gon IX) not exposed (0); external gonopods (e.gon IX) completely or partially exposed as laterally compressed folds along each side of middle lobe of vulva scale (1).

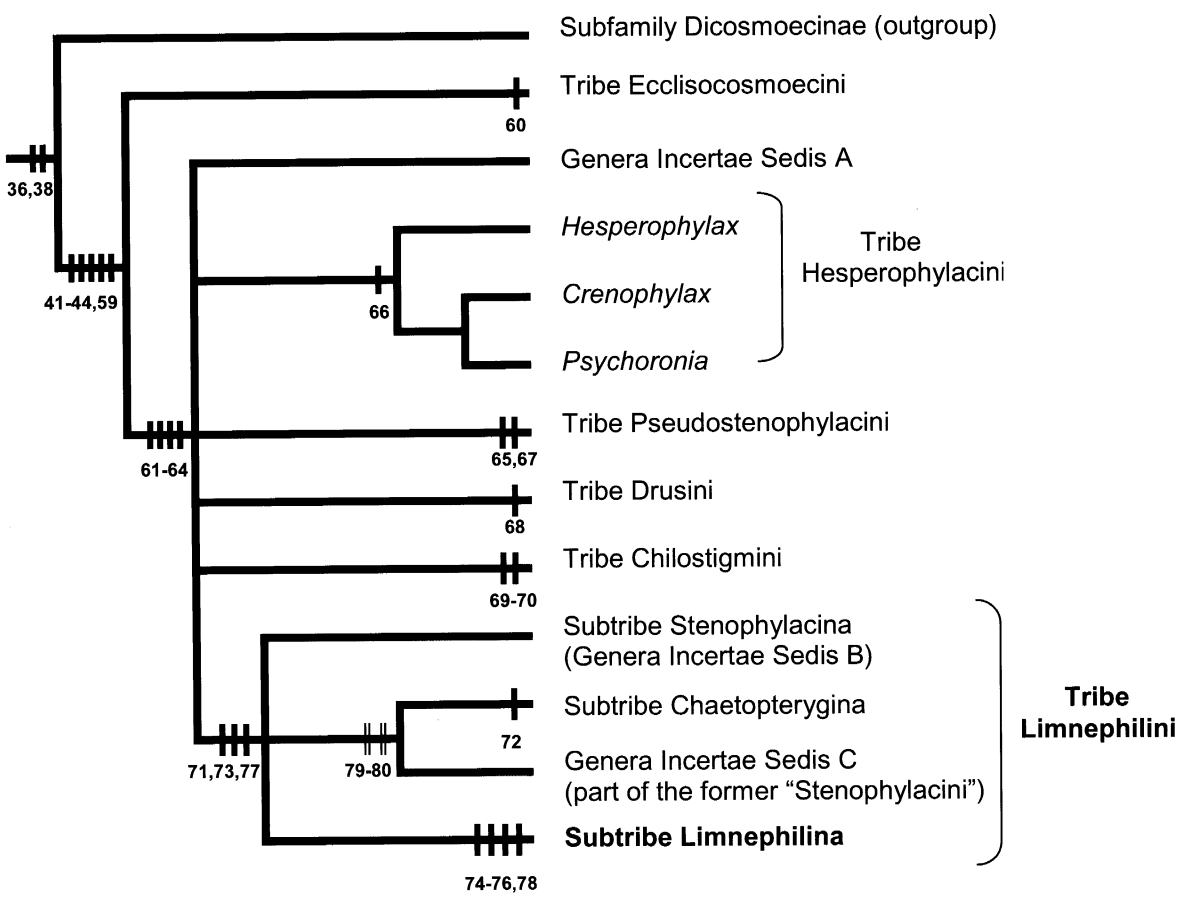

Figure 3. Phylogeny of the Subfamily Limnephilinae.

Table 1. List of synapomorphies and codes, continued.

Character 46. (L) Abdominal gill clusters consisting of less than 8 gills (0); abdominal gill clusters consisting of more than 8 filaments ("multi-gilled larvae") (1).
Character 47. (L) Tergal and sternal gill clusters each with greater or less than 4 filaments (0); 4 filaments in a cluster ("4-gilled larvae") (1).
Character 48. (F) Sternite VIII without narrow medial longitudinal membranous area (0); divided medially by narrow membranous area (1).
Character 49. (F) Apex of middle lobe of "vulva scale" (e.gon. VIII) oval (0); very short triangle (tightly fused with externally exposed inner genital parts forming "false middle lobe") (1).
Character 50. (F) Anterolateral portion of sternite VIII without incision (0); with incision (1).
Character 51. (F) Lateral lobes of "vulva scale" (e.gon. IX) not exposed or only partially exposed next to middle lobe of "vulva scale" (0); completely exposed (1).
Character 52. (M) Phallicata absent (0); present, membranous and very wrinkled (1).
Character 53. (M) Endothecal parameres separated from phallicata, apically with spinules or tiny setae (0); parameres fused with phallicata for some distance, membranous apically with few strong large spines arising from membranous area (1).
Character 54. (M) Phallicata membranous (0); phallicata slightly sclerotized and smooth (1).
Character 55. (M) Phallicata short (0); phallicata a long, narrow tube (1).
Character 56. (M) Endophallus short or not telescopic (0); endophallus long and telescopic (inserted into long tube-like phallicata in repose) (1).
Character 57. (M) Endophallus not flaring laterally, without erectile lateral lobes (0); flaring laterally at extremity and equipped with two erectile lateral lobes (1).
Character 58. (M) Parameres armed with short outgrowths (shorter or subequal to width of paramere) (0); stick-like parameres armed with setae-like outgrowths at least twice as long as width of parameres (1).
Character 59. (M) Inferior appendages clearly two-segmented, or partially fused, rarely one-segmented, subequal or larger than superior appendages (0); one-segmented, smaller than superior appendages (1).
Character 60. (F) Supragenital plate wide (usually more than half width of IX segment width) with prominent or parallel sides (0); supragenital plate bottle-shaped and concave at lower end (1).
Character 61. (M) Dorsum VIII not modified posteriorly (protruded or curved posteriorly) (0); dorsum VIII modified (protruded or curved posteriorly) (1).
Character 62. (M) Dorsum VIII without spines or pegs (0); dorsum VIII with spines or pegs (1).
Character 63. (F) Spermathecal vestibule apical sclerotization absent, ring-like, or band-like (0); funnel-like (1).
Character 64. (F) "Vulva scale" with broad common base (base of three-lobed structure wider than 1/3 width of sternite VIII) (0); vulva scale with narrow common base (base of three-lobed structure much less than 1/3 width of sternite VIII) (1).
Character 65. (M) Parameres stick-like, more or less straight or slightly curved dorsad or ventrad (0); parameres arbalest-like, curved laterad or mesad (1).
Character 66. (M) Parameres with long sclerotized shaft (3 times longer than its width), without broom-like burst of spines (0); shaft very short (subequal to its width), apically with broom-like burst of strongly sclerotized, recurved spines (1).
Character 67. (M) Parameres each with slightly or strongly sclerotized shaft (except base) (0); more than half of proximal shaft membranous (1).
Character 68. (M) Dorsum VIII posteriorly without pegs (1); covered with pegs possessing oval apices (1).
Character 69. (A) Forewing vestiture dense or moderately dense (0); sparse (1).
Character 70. (A) Stigmal calosity not developed or diffuse and forming whitish, thickened stigmal area (0); well-developed and sharply defined, yellowish (1).
Character 71. (F) Middle lobe of vulva scale not dorsoventrally depressed and not sclerotized dorsally (from inner surface) (0); dorsoventrally depressed and sclerotized both dorsally and ventrally (inner and outer surfaces) (1).
Character 72. (A) Forewing membrane without long, straight-erect setae, or straight erect setae on veins only, or straight erect setae shorter than anterior-posterior width of discoidal cell (0); long straight erect setae present both on veins and wing membrane, these setae subequal to or longer than width of discoidal cell (1).

Table 1. List of synapomorphies and codes, continued.

Character 73. (M) Sclerotized strengthening strips of phallocrypt present dorsally and well-developed (0); reduced or vestigial (1).
Character 74. (M) Sclerotized dorsal strengthening strips of phallocrypt reduced (0); vestigial (1).
Character 75. (F) Ventral portions of segment IX (IXc-d) located laterally to vulva scale (0); located above vulva scale and supragenital plate (1).
Character 76. (M) Superior appendages subequal to or smaller than inferior appendages (0); superior appendages (usually remarkably) larger than inferior appendages ("claspers type") (1).
Character 77. (M) Superior appendages uniformly sclerotized (0); often with apical or mesal, heavily sclerotized areas, teeth, or spine-like projections (1).
Character 78. (L) Larval gill clusters each with 0-2 or more than 3 filaments (0); 3 filaments in each gill cluster ("three-gilled larvae") (1).
Character 79. (M) Fore femur normal (0); raptorial (1).
Character 80. (M) Fore femur grasping structure ("femur-tibial brush") absent (0); present (1).
Character 81. (F) Lateral vulva scale lobes not triangular (0); triangular (1).
Character 82. (M) Parameres pointed or branched at apex (0); parameres strongly widened at apex (spatula-like in lateral view) and bearing spines along margin (1).
Character 83. (M) First tarsal segment longer than or subequal to second (0); shorter than second (1).

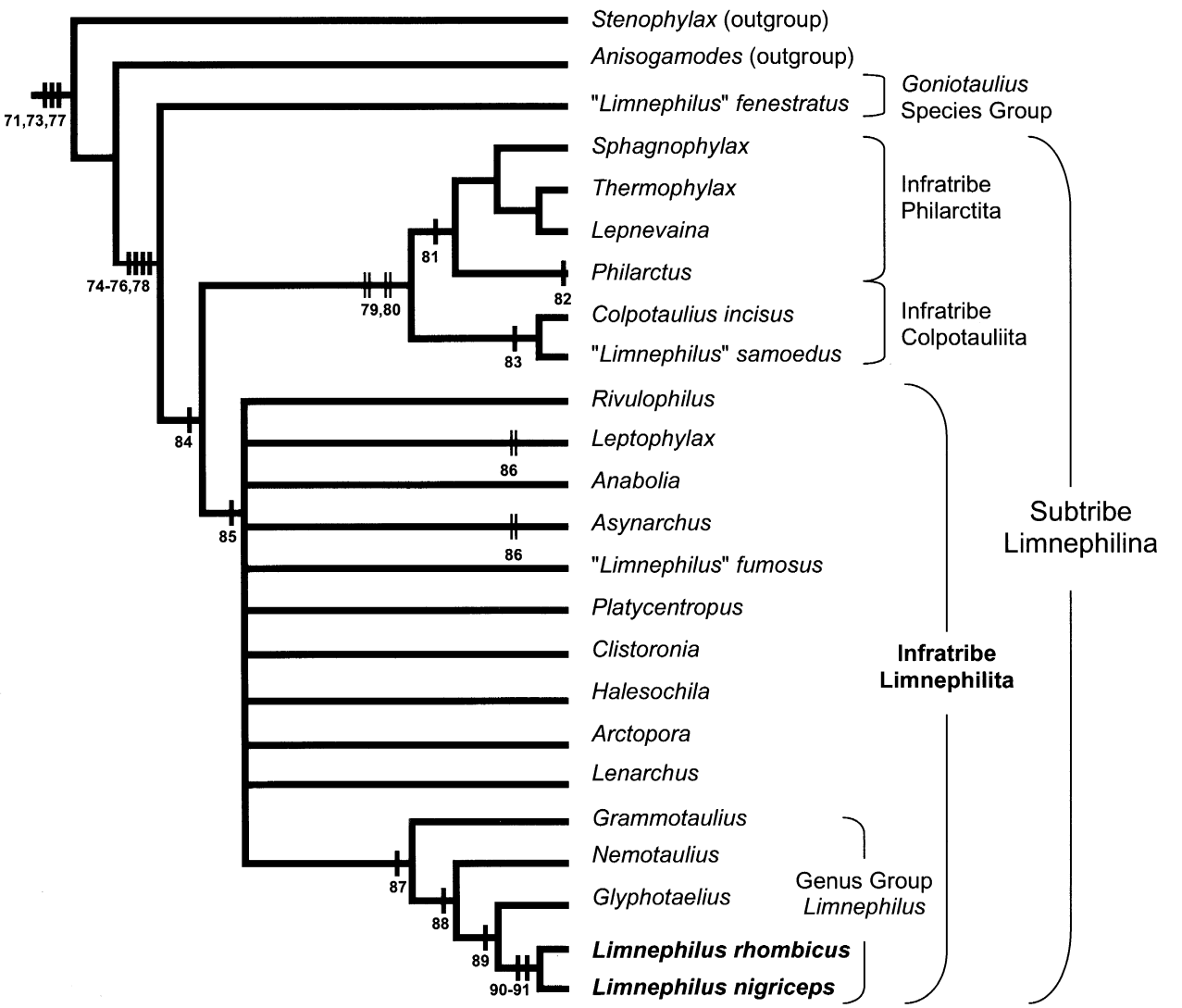

Figure 4. Phylogeny of the Subtribe Limnephilina.

Table 1. List of synapomorphies and codes, continued.

Character 84. (M) Phallicata and endophallus not separated by membranous theca (0); endophallus separated from phallicata by theca dorsally or circumferentially (1).
Character 85. (M) Parameres pointed stick-like (0); very branched or finger-like apically (1).
Character 86. (M) Phallicata not wrinkled, or wrinkled only from one side (dorsally or ventrally) (0); wrinkled overall (1).
Character 87. (M) Endophallus ventrally unsclerotized, or sclerotized overall, or with ventral sclerotized keel (0); endophallus ventrally with sclerotized flat plate (1).
Character 88. (L) Head and pronotum without "limnephilid" color pattern (0); with typical "limnephilid" color pattern (black triangle-like figure on head dorsum and darkened transverse band on anterior part of pronotum) (1).
Character 89 (L). Darkened anterior transverse band of pronotum narrow (0); transverse band of pronotum wide, occupied anterior third of pronotum (1).
Character 90. (F) IXc appendages not finger-like, fused with segment IXa-c (0); IXc appendages appearing as long finger-like processes separated from segment IXa-c by sutures (1).
Character 91. (M) Hind wing without androconial setae on R2 (0); with such setae on subapical portion of R2 (1).

Conclusions

Based on our phylogenetic analysis, several main conclusions concerning limnephilids are proposed:

1. Family Uenoidae is polyphyletic and subfamilies Uenoinae (*Farula*, *Neothremma*, *Sericostriata*, and *Uenoa*) and Thremmatinae (*Neophylax*, *Oligophlebodes*, and *Thremma*) should be considered as different taxa and elevated to family level. The family Thremmatidae (n.stat) and family Limnephilidae are united in a new family-group category "Branch Limnephilida" based on synapomorphies # 25-27 (Fig. 1).
2. New monotypical subfamiles Ecclisomyiinae (*Ecclisomyia*) and Philocascinae (*Philocasca*) are proposed based on synapomorphies # 32-34 and # 35, respectively. Genus *Philocasca* is removed from Limnephilinae because its phallocrypt sclerotized strips are situated ventrolaterally (unlike true limnephilids) as in all dicosmoecines and other outgroup families.
3. Two new tribes are proposed in subfamily Dicosmoecinae: a tribe Dicosmoecini (*Amphicosmoecus*, *Allocosmoecus*, *Dicosmoecus*, *Eocosmoecus*, and *Onocosmoecus*), and a tribe Nothopsychini; in a tribe Notopsychini two new subtribes are proposed: a subtribe Monocosmoecina (*Archeophylax*, *Austrocosmoecus*, *Monocosmoecus*, *Platycosmoecus*, and *Verger*) and a subtribe Nothopsychina (*Nothopsyche*, *Ironoquia*, and *Evanophanes*) based on inferred synapomorphies (see Fig. 2).
4. Subfamily Limnephilinae is supported by synapomorphies # 37, 41-44 (Fig. 2).
5. Genus *Ecclisocosmoecus* is moved to subfamily Limnephilinae and a new monotypical tribe is proposed Ecclisocosmoecini based on a synapomorphy # 60 (Fig. 3).
6. Three genera *Hesperopylax*, *Crenophylax*, and *Psychoronia* are grouped into a new tribe Hesperophylacini based on synapomorphy # 66.
7. The former subfamilies Pseudostenophylacinae and Drusinae are reduced to tribe category and supported by some inferred synapomorphies (see Fig. 3).
8. Tribe Limnephilini (n.stat.) is supported by synapomorphies # 71, 73, and 77 and includes a) a new subtribe Stenophylacina (some unresolved genera of a group "Genera Incertae Sedis B"); b) a subtribe Chaetopterygina (a group of genera belonging to the former tribe Chaetopterigini) supported by synapomorphy # 72, and c) a subtribe Limnephilina supported by synapomorphies # 74-76, and 78 including most genera belonging to the former tribe Limnephilini.
9. Subtribe Limnephilina is represented by two obvious clades: a clade *Philarctus* Genus Group (synapomorphy # 81), and *Colpotaulius* Genus Group (synapomorphy # 83) which is characterized by reversal characters 79-80 which are also noticed for a clade "Subtribe Chaetopterygina + Group of Genera Incertae Sedis C"), and a clade of "true limnephilid" genera characterized by synapomorphy # 85.
10. A nominotypical clade "*Limnephilus* Genus Group" is supported by synapomorphy # 87.
11. The species of the genus *Limnephilus* sensu stricto are characterized by synapomorphies 90-91.

From the present phylogenetic analysis we infer that, from 197 species currently included in *Limnephilus*, only 57 are recognized as *Limnephilus sensu stricto*. Other species, such as "*Limnephilus*" *fenestratus*, "*Limnephilus*" *samoedus*, "*Limne-*

philus" *fumosus* should be removed from the genus and classified in other genera of the tribe Limnephilini or in other tribes. An appropriate placement of each of such "pseudo-*Limnephilus*" species is suggested as a result of the analysis, but confident classification awaits detailed study of their respective morphotaxa.

Table 2. Classification of Limnephiloidea based on analyzed taxa.

Infraorder Plenitentoria Weaver, 1983
- Superfamily Limnephiloidea Kolenati, 1848
  - Family Brachycentridae Ulmer, 1903
  - Family Lepidostomatidae Ulmer, 1903
  - Family Uenoidae Iwata, 1927
  - Family Goeridae Ulmer, 1903
  - Family Apataniidae Wallengren, 1886
  - Genus *Cryptochia* Family Incertae Sedis
  - [Family Rossianidae Gall, 1996]
  - Branch Limnephilida Kolenati, 1848
    - Family Thremmatidae Martynov, 1935
    - Family Limnephilidae Kolenati, 1848
      - Subfamily Ecclisomyiinae Vshivkova, Morse, and Ruiter, n. subfam.
        - Type genus *Ecclisomyia* Banks, 1907
      - Subfamily Philocascinae Vshivkova, Morse, and Ruiter, n. subfam.
        - Type genus *Philocasca* Ross, 1941
      - Subfamily Dicosmoecinae Schmid, 1955
        - Tribe Nothopsychini Vshivkova, Morse, and Ruiter, n. trib.
          - Type genus *Nothopsyche* Banks, 1906
          - Subtribe Monocosmoecina Vshivkova, Morse, and Ruiter, n. subtrib.
            - Type genus *Monocosmoecus* Ulmer, 1906
          - Subtribe Nothopsychina Vshivkova, Morse, and Ruiter, n. subtrib.
            - Type genus *Nothopsyche* Banks, 1906
            - Genus *Metacosmoecus* Subtribe Incertae Sedis
            - Genus *Anomalocosmoecus* Subtribe Incertae Sedis
        - Tribe Dicosmoecini Schmid, 1955
          - Genus *Eocosmoecus*
          - Genus *Onocosmoecus*
          - Genus *Dicosmoecus*
          - Genus *Amphicosmoecus*
          - Genus *Allocosmoecus*
      - Subfamily Limnephilinae Kolenati, 1848
        - Genera Tribe Incertae Sedis A
        - Tribe Hesperophylacini Vshivkova, Morse, and Ruiter, n. trib.
          - Type genus *Hesperophylax* Banks, 1916
        - Tribe Pseudostenophylacini Schmid, 1955, n. stat.
        - Tribe Drusini Banks, 1916, n. stat.
        - Tribe Chilostigmini Vshivkova, Morse, and Ruiter, n. trib.
        - Tribe Limnephilini Kolenati, 1848
          - Subtribe Stenophylacina Schmid, 1955, n. stat. (Genus Group B, including *Goniotaulius* Species Group)
          - Subtribe Chaetopterygina Vshivkova, Morse, and Ruiter, n. subtrib.
            - Type genus *Chaetopteryx* Stephens, 1829
          - Genera Subtribe Incertae Sedis C
          - Subtribe Limnephilina Kolenati, 1848
            - Infratribe Philarctita Vshivkova, Morse, and Ruiter, n. infratrib.
              - Type genus *Philarctus* McLachlan, 1880
              - Genus *Sphagnophylax*
              - Genus *Thermophylax*

Table 2. Classification of Limnephiloidea based on analyzed taxa, continued.

Genus *Lepnevaina*
Genus *Philarctus*
Infratribe Colpotauliita Vshivkova, Morse, and Ruiter, n. infratrib.
Type genus *Colpotaulius* Kolenati, 1848
Genus *Colpotaulius*
Species Group "*Limnephilus*" *samoedus* Genus Incertae Sedis
Infratribe Limnephilita Kolenati, 1848
Genus *Rivulophilus* Incertae Sedis
Genus *Leptophylax* Incertae Sedis
Genus *Anabolia* Incertae Sedis
Genus *Asynarchus* Incertae Sedis
Species Group "*Limnephilus*" *fumosus* Genus Incertae Sedis
Genus *Platycentropus* Incertae Sedis
Genus *Clistoronia* Incertae Sedis
Genus *Halesochila* Incertae Sedis
Genus *Arctopora* Incertae Sedis
Genus *Lenarchus* Incertae Sedis
Genus Group *Limnephilus*
Genus *Grammotaulius*
Genus *Nemotaulius*
Genus *Glyphotaelius*
Genus *Limnephilus*
Species Group *Limnephilus rhombicus*
Species Group *Limnephilus nigriceps*

* The brackets "[ ]" indicate that the family probably belongs in the Limnephiloidea, but specimens were not examined to include the family in this study.

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