

**REDESCRIPTION OF *LEPTOHYPHES EXIMIUS* EATON
AND DIAGNOSES OF THE GENERA
LEPTOHYPHES AND *TRICORYTHODES*
BASED ON THE STRUCTURE OF THE PTEROTHORAX
(EPHEMEROPTERA: TRICORYTHIDAE, LEPTOHYPHINAE)**

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Nymphs and eggs of the type species of the genus *Leptohyphes* — *L. eximius* Etn — are described for the first time. The structure of the imaginal and subimaginal pterothorax of *Leptohyphes* and *Tricorythodes* is described and used to distinguish these genera and to discuss their phylogenetic position.

INTRODUCTION

Originally the genus *Leptohyphes* Eaton, 1882 was monotypic, established for *L. eximius* Eaton, 1882, described from a single female imago (EATON, 1883-1888). Until recently, no other specimens of this species were known though, subsequently, more than 60 species were placed into the genus. The suggested new generic diagnoses were based on characters of male imagos and nymphs (but not female imagos!) (BURKS, 1953; TRAVER, 1958; ALLEN 1967; EDMUNDS et al., 1976) rather than on those of the type species. Consequently, these diagnoses are at least partly wrong; in particular some *Tricory-*

thodes nymphs were attributed to the genus *Leptohyphes* (KLUGE & NARANJO, 1990). The original generic diagnosis of *Leptohyphes*, based on the reduction of the paracercus (EATON, 1883-1888; KLUGE & NARANJO, 1990), is also found to be wrong.

Here redescriptions are given of the genera *Leptohyphes* (based on the type species) and *Tricorythodes* (based on 5 Cuban species).

LEPTOHYPHINAE EDMUNDS & TRAVER, 1954

NYMPH — The maxillae have the structure considered primitive for the infraorder Furcatergalia: 3 apical denticles well developed, 2 dentisetae (thickened bristles) in the dorso-medial row of bristles (Fig. 2c). Maxillar palp rudimentary (Fig. 2c). Submentum large, glossae and paraglossae shortened, paraglossae fused with mentum (Fig. 2d). Pronotum without concave collar on the fore margin, with more or less visible V-shaped suture (Fig. 1a). Wing pads fused over a large distance, but not completely (Fig. 1a). Femur with a more or less developed transversal row of bristles which is situated on the fore leg femur near the middle, and on the middle and hind femora near the base (Figs 2e-f, 8b). Tergaliae I and VII absent, tergaliae II operculate and completely covering tergaliae of the III-VI pairs. Each tergalia consists of an upper and a lower portion; the upper portion is an integral dorsal leaf, while the lower portion is divided into two leaves nearly up to its base, which may be named the lateral and the ventral leaf (Figs 1d-g, 9c-d). Sometimes the ventral leaf is reduced (Fig. 1h), sometimes the lateral leaf is also reduced.

IMAGO — Mesothorax strongly modified. Lateral portions of postnotum (lateropostnotum) strongly enlarged ventrally and nearly reaching furcasternum; they have a longitudinal and 2 dorsoventral sutures: the superior suture (dorsally from the longitudinal one) and the inferior suture (ventrally from the longitudinal one) (Figs 4c, 5d). Correspondingly, the muscle Tm2, which runs from the posterior scutal protuberance to the lateropostnotum, is strongly enlarged and has a dorsoventral position (Fig. 6a-c). The subalar-sternal muscles TSm3 (the direct wing depressors) are diminished (Fig. 6a-c), their ventral bases are widely separated but drawn together in front (Figs 4b, 5a-b).

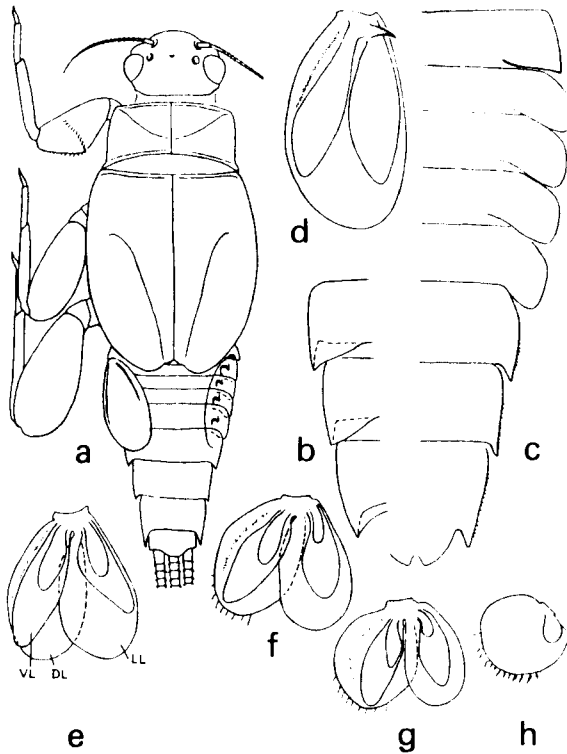


Fig. 1. *Leptohyphes eximius* Eaton, nymph: (a) dorsal view (right legs and right tergalia removed); — (b) left sides of abdominal segments VII-IX, dorsal view; — (c) left sides of abdominal segments II-VI, ventral view; — (d-h) tergalia of segments II-VI, ventral view. — [DL, LL, VL: resp. dorsal, lateral, and ventral leaves of tergalia]

Paracoxal suture running close to hind margin of episternum, so episternum seems to be integral (Figs 4c, 5d). Infrascutellum absent, scutellum with strongly convex ventral surface and strongly concave lateral surfaces (Fig. 7b). Fore wings with a row of setae on the hind margin; CuP arises from A_1 ; ICu arises from CuP, bifurcate. Metathorax strongly shortened; hind wings rudimentary or absent. Paracercus longer than cerci.

SUBMAGO — Cuticle colourless, without pigmented sclerotized fields on mesonotum (in contrast to Ephemerellidae and the majority of other families). Mesonotum covered by microtrichiae (minute bristles) as is shown in Figure 6d: the entire medioscutum, and the anterolateral parts of the sublateroscutum are covered by microtrichiae, while most of the sublateroscutum and the entire surface of the posterior scutal protuberance lack microtrichiae.

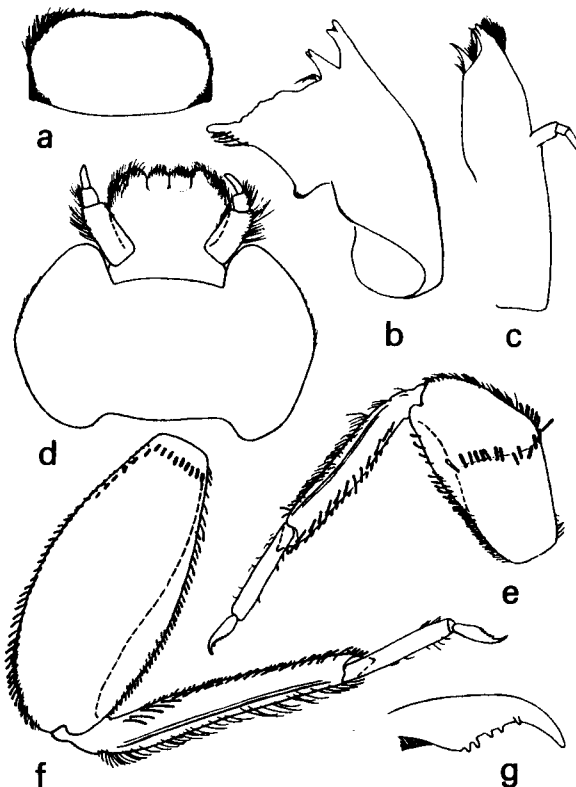


Fig. 2. *Leptohyphes eximius* Eaton, nymph: (a) labrum; — (b) right mandible; — (c) maxilla; — (d) labium; — (e) fore leg; — (f) hind leg; — (g) claw, dorsal view.

REMARKS — The position of the subimaginal microtrichiae is an important family and subfamily character, but has not been described so far. In contrast to Leptoxyphinae, the subimago of Dicercomyzinae has developed microtrichiae on the submedioscutum and nearly all of the sublateroscutum, but none on the medioscutum and the posterior scutal protuberances; subimagos of other Tricorythidae subfamilies were not examined. Subimagos of Ephemerellidae also have no microtrichiae on the medionotum, microtrichiae are developed only on the lateral parts of the sublateroscutum and sometimes also on the lateral parts of the anteroscutum. The Caenidae subimagos have all of the mesonotum covered with microtrichiae.

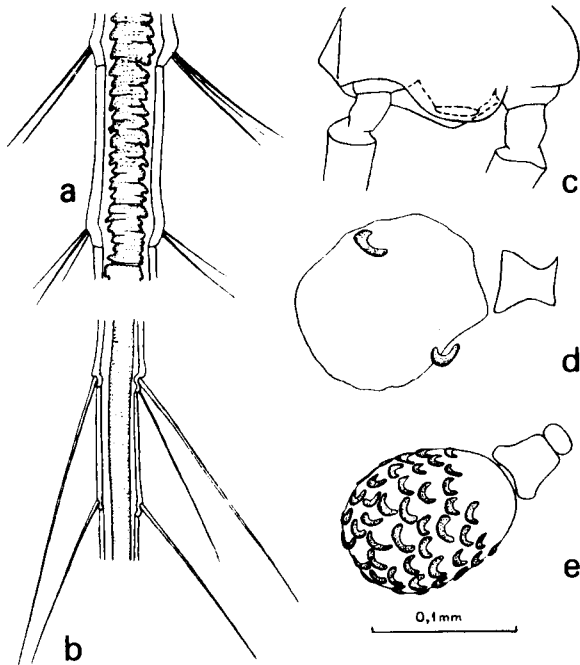


Fig. 3. *Leptohyphes eximius* Eaton (Figs a, c-e) and *Tricorythodes cubensis* Kluge & Naranjo (Fig. b): (a-b) median part of cercus of mature female nymph, inside which is visible subimaginal paracercus; — (c-d) *L. eximius* holotype: c: X abdominal segment, ventral view, - d: egg; — (e) *L. eximius* egg taken from mature nymph.

GENERIC ORGANISATION — Currently, 6 New World genera are included into the subfamily, viz. *Leptohyphes* Eaton, 1882, *Tricorythodes* Ulmer, 1920, *Leptohyphodes* Ulmer, 1920, *Tricorythopsis* Traver, 1958, *Haplohyphes* Allen, 1966, and *Cotopaxi* Mayo, 1968 (the last four contain 1-4 species and are poorly known). The African mono-typic genus *Tricorythafer* Lestage, 1942 is also placed into the Leptohyphinae, but its position is doubtful.

The diagnosis of the subfamily given above is based on the characters of *Leptohyphes* and *Tricorythodes*, for the other genera the structure of the imaginal and subimaginal thorax and nymphal tergaliae is unknown.

LEPTOHYPHES EATON, 1882

Type species: *L. eximius* Eaton, 1882

NYPH — Lower portion of tergaliae of segments III-V with additional ventral leaves (Figs 1e-g, 9c). Lower portion of tergalia of segment II with a ventral spine (Fig. 1d).

IMAGO — Mesonotum with distinct transverse mesonotal suture (Fig. 4a, c: MNS). Posterior scutal protuberances divergent posteriorly (Fig. 4a). On the lateropostnotum the superior dorsoventral suture reaches the longitudinal suture behind the point where the inferior dorsoventral suture reaches the longitudinal suture (Fig. 4c). Lateropostnotum separated from the coxal cavity by epimerum (Fig. 4c).

SUBIMAGO — Anteroscutum completely covered by microtrichiae.

F e m a l e — Metathoracic wing muscles Tm1 and TPm1 developed (Fig. 6c), hind wings absent.

M a l e — The males of the type species are unknown; to *Leptohyphes* were attributed male imagos with developed hind wings.

DISCUSSION — There are 66 species that were included into this genus, but at least some of them are incorrectly placed and must be transferred to *Tricorythodes*. The diagnosis given above is based only on the type species.

LEPTOHYPHES EXIMIUS EATON, 1882

Figures 1-2, 3a, c-e, 4, 6c

M a t e r i a l — 1 ♀ imago (holotype), Argentina, Cordova [No. 57, type 11230, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts,

U.S.A.]; 4 ♀ nymphs (1 mature, with developed cuticle of subimago and imago), Argentina, Tecuman prov., Rio Augustura, Tafi del Valle, 28-I-1969.

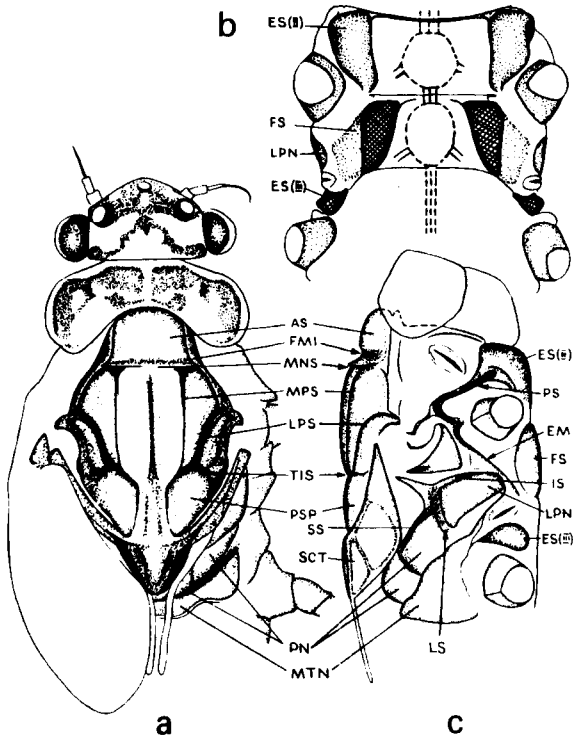


Fig. 4. *Leptohyphes eximius* Eaton, female subimago dissected from mature nymph: (a) head and thorax dorsally (right wing removed); — (b) pterothorax ventrally (oblique net-like hatching shows ventral bases of muscles TSm3(II) and TPm1(III), interrupted line shows position of mesothoracic and metathoracic nerve ganglia); — (c) thorax from the right side. — [AS: anteroscutum; — EM: epimerum; — ES(II): episternum of mesothorax; — ES(III): episternum of metathorax; — FMI: fore mesonotal transverse invagination; — FS: furcasternum; — IS: inferior dorsoventral suture of lateropostnotum; — LPN: lateropostnotum; — LPS: lateroparapsidal suture; — LS: longitudinal suture of lateropostnotum; — MNS: mesonotal suture; — MPS: medioparapsidal suture; — MTN: metanotum; — PN: postnotum; — PS: paracoxal suture; — PSF: posterior scutal protuberance; — SCT: scutellum; — SS: superior dorsoventral suture of lateropostnotum; — TIS: transverse interscutal suture]

NYMPH — Cuticle colourless. Head and pronotum with hypodermal patterns as in subimago (Fig. 4a). Mesonotum with longitudinal dark lines. Legs light, without patterns; one specimen has femora with small indistinct dark marks in the distal parts. Opercula (dorsal portion of tergalia II) light, with more or less developed dark patterns in the proximal half. Head, thorax and abdomen without spines or tubercles. Submentum nearly the same width at top and base. Maxillary palp relatively large. Fore femora widened near their middle, with transverse row of short obtuse bristles. Middle and hind femora oval. Tibiae of all legs three-edged, with longitudinal ridges on the inner, outer, and dorsal sides. Claws slightly curved, with small denticles on the inner side. Abdominal terga with long hairs and elongate flat squamae. Dorsal portion of tergalia II (opercula) nearly oval, with convex inner margin; lower portion consisting of two leaves, without additional leaves, with sclerotized basal spine. Tergaliae of pairs III-V with 1-2 additional ventral leaves on each of the two leaves of the lower portion; these additional leaves vary in number and form, they may be narrow and long (Fig. 1e-g) or roundish. Tergaliae of pair VI roundish, with a single ventral leaf.

FEMALE IMAGO — It is adequately described by EATON (1883-1888) except for one character: the median caudal filament (paracercus) is well developed, not shorter than the cerci (while according to Eaton's description it is abortive).

EGGS — The surface is covered by horseshoe-shaped squamae. Lighted from above, these squamae have the same golden colour as the rest of the egg surface, but in transmitted light (on clarified slide) they seem to be dark brown on a light yellowish background. At one of the poles there is a small roundish cap situated on a long thick muff, which is narrowed towards the cap; inside this muff there is a tuft of fibrils.

DISCUSSION — The nymph can be associated with the imago on the basis of the structure of the imaginal thorax that was dissected from the mature nymph (Fig. 4a-c), egg structure, and the relatively long cerci of the female imago.

The eggs of the examined mature nymph are in good condition (Fig. 3e), but the eggs of the holotype are strongly glued together; only after boiling in water did it become possible to separate some of them. On the severely damaged egg of the holotype remainders of the squamae

and the muff of the polar cap (Fig. 3d) can be seen to have the same structure as on the eggs of the mature nymph.

The female imago of *L. eximius* has cerci as long as its fore wing, while female imagos of the examined species of *Tricorythodes* have cerci as long as 1/3 of their wing length; the mature female nymph of *L. eximius* has the subimaginal cerci strongly crumpled inside the nymphal cuticle (Fig. 3a), while the female nymphs of the examined species of *Tricorythodes* never have this (Fig. 3b), because the length of the adult cerci is the same as that of the nymphal ones.

According to Eaton's description of *L. eximius* and the genus *Leptohyphes*, its female imago has only 2 caudal filaments (EATON, 1883-1888, pp. 140, 314). Actually *L. eximius* has 3 caudal filaments and the median one is the longest. The specimen examined by Eaton was dry, its median caudal filament broken and the bases of the lateral caudal filaments were turned together, so it seemed that the median caudal filament was absent. After soaking the base of the broken median caudal filament becomes visible (Fig. 3c).

TRICORYTHODES ULMER, 1920

Type species: *Tricorythus explicatus* Eaton, 1892

Material examined — Nymphs, imagos, and subimagos reared from nymphs of 5 Cuban species, viz. *sierramaestrae* Kluge & Naranjo, 1990; *sacculobranchis* Kluge & Naranjo, 1990; *cupensis* Kluge & Naranjo, 1990; *montanus* Kluge & Naranjo, 1990 and *grallator* Kluge & Naranjo, 1990.

NYPH — Tergalae without additional leaves and spines on the lower portions.

IMAGO — Mesonotum without mesonotal suture (Fig. 5c-d). Posterior scutal protuberances drawn together posteriorly (Fig. 5c). On the lateropostnotum the superior and inferior dorsoventral sutures form a straight line that goes across the longitudinal suture (Fig. 5d). Lateropostnotum reaches coxal cavity, fused with epimerum (Fig. 5d).

SUBIMAGO — Anteroscutum covered by microtrichiae only in its lateral and hind parts (Fig. 6d).

F e m a l e — Metathoracic wing muscles absent (Fig. 6d) (hind wings also absent).

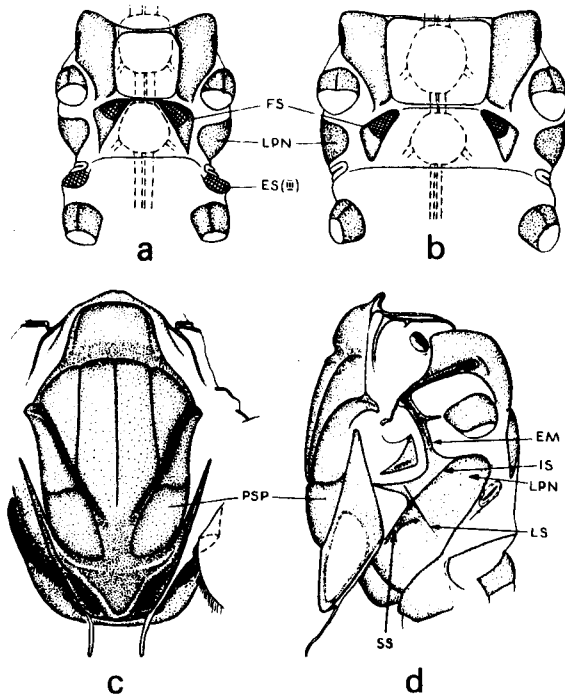


Fig. 5. *Tricorythodes cubensis* Kluge & Naranjo, pterothorax of imagos: (a) male; — (b-d) female [a-b: ventral view; — c: dorsal view; — d: lateral view. — Designations the same as in Fig. 4]

Male — Hind wings absent, but metathoracic wing muscle Tm1 and TPm1 developed (Fig. 6a). In imago both claws of fore leg similar and blunt, while in the subimago they are dissimilar, as on other legs of male and on all legs of female (KLUGE & NARANJO, 1990, figs 33-36). Forceps distinctly 3-segmented, the second segment with bulbous base, the third segment very small.

DISCUSSION — The structure of the imaginal thorax and the nymphal tergaliae of the type species, *T. explicatus*, has not been described. The generic diagnosis given above is based only on the five Cuban species, which belong to three different groups of species and are considered

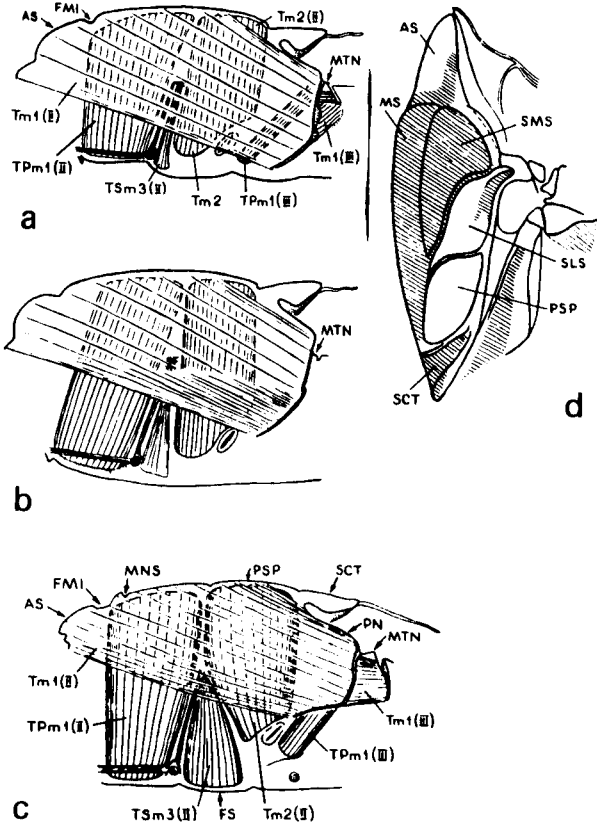


Fig. 6. Structure of pterothorax of Leptohyphinae [a-c: median section]: (a) *Tricorythodes cubensis* Kluge & Naranjo, male; — (b) same, female; — (c) *Leptohyphes eximius* Eaton, female; — (d) *T. grallator* Kluge & Naranjo, right half of mesonotal exuviae of subimago (oblique hatching shows surfaces covered with microtrichiae). — [MS: medioscutum; — SLS: sublateroscutum; — SMS: submedioscutum; — Tm1(II), Tm1(III): medial tergal muscle of meso- and metathorax; — Tm2(II): scuto-lateropostnotal muscle of mesothorax; — TPm1(II), TPm1(III): scuto-episternal muscles of meso- and metathorax; — TSm3(II): subalar-sternal muscle (direct wing depressor) of mesothorax. — Other designations as in Fig. 4]

to be congeneric with *T. explicatus* on the basis of the identical structure of the forceps which is unique for *Tricorythodes* and is not found in other mayfly genera. In addition to the above species there are 28 species formally placed in this genus. The structure of the forceps has been described for 17 of them (it is of the same type as in the type species), and the nymphal tergaliae are figured only for *T. atratus* (McD.) (BURKS, 1953, fig. 90A-B). The generic position of the other 11 species placed in *Tricorythodes* is not quite clear. In *Tricorythodes* must be placed some of those which are known only as nymphs and were formally placed in *Leptohyphes*.

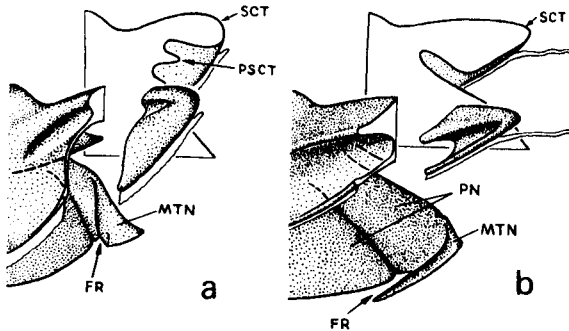


Fig. 7. Section of scutellum of imagos of Ephemerelloidea: (a) *Ephemerella aurivillii* (Bengtsson); — (b) *Tricorythodes cubensis* Kluge & Naranjo. — [PH: phragma between meso- and metathorax; — MTN: metanotum; — PN: postnotum; — ISCT: infrascutellum; — SCT: scutellum]

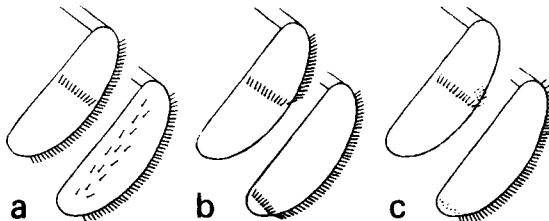


Fig. 8. Schemes of position of bristles on fore femur (upper figs) and middle or hind femurs (lower figs) of Ephemerelloidea: (a) selected species of *Ephemerella* s.l.; (b) Leptohyphinae, Ephemerythinae, Dicercomyzinae, Teloganodinae; — (c) *Tricorythus*.

PHYLOGENY

In the Leptohiphinae, the *Leptohyphes* is more primitive than the genus *Tricorythodes* and may be ancestral to it. The imago of *Leptohyphes* preserves the sharp transverse mesonotal suture, which is well developed in the ancestral Ephemerelloidea, while in *Tricorythodes* this suture is reduced. Mesothorax structure and wing musculature of *Leptohyphes* are not so strongly modified as in *Tricorythodes*. Metathorax and hind wing musculature of *Leptohyphes* are not so strongly reduced as those of *Tricorythodes*. The nymphal tergalia of *Leptohyphes* preserve the appendages of the lower portion (Fig. 9c) that are typical of Ephemerelloidea (Fig. 9a-b, e), while in *Tricorythodes* these appendages are completely reduced (Fig. 9d).

The Leptohiphinae share some characters (that seem to be synapomorphic) not only with other Tricorythidae subfamilies, but also with

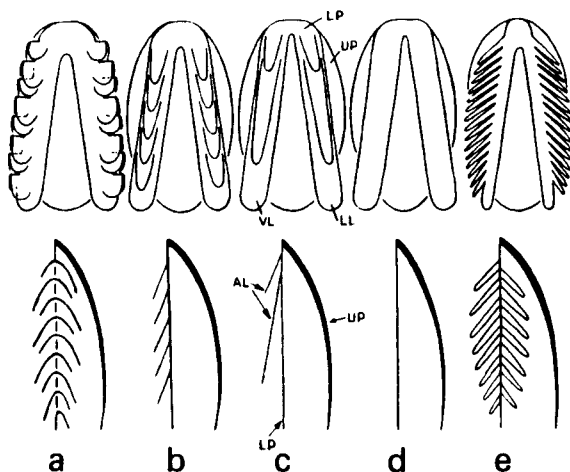


Fig. 9. Schemes of tergalia of Ephemerelloidea: (a) *Ephemerella* s.l.; — (b) selected species of *Eurylophella*; — (c) *Leptohyphes*; — (d) *Tricorythodes*; — (e) *Tricorythus*, *Ephemerythus*, *Teloganodes*. — [AL: additional leaves; — LL: lateral leaf; — LP: lower portion; — UP: upper portion; — VL: ventral leaf. — Upper row: ventral view, - lower row: lateral view]

Ephemerellidae and Caenidae. These synapomorphies (or seeming synapomorphies), however, do not allow to reconstruct the phylogeny. Some of these synapomorphies (groups C, D, E, listed below) suggest the evolutionary sequence, Ephemerellidae - *Leptohyphes* - *Tricorythodes* - Caenidae. But other apomorphies (group A) show that the superfamily Ephemerelloidea (which includes Ephemerellidae and Tricorythidae s. l.) is a sister group to the superfamily Caenoidea and cannot be ancestral to it. At the same time, Caenidae are related to Neophemeridae, which are related to Ephemeroidea, and this contradicts the idea that Caenidae would be related to Tricorythidae s. l.

(A) SYNAPOMORPHIES OF EPHEMERELLIDAE s. l. (incl. Ephemerellinae, Teloganodinae) + TRICORYTHIDAE s. l. (incl. Tricorythinae, Leptohyphinae, Ephemerythinae, Dicercomyzinae and Machadorythinae):

- (1) Tergaliae (Fig. 9a-e) consist of upper and lower portions, the lower portion is bifurcate or bilamelled, each of the two lobes with a row of appendages. Sometimes these appendages or some of the lobes may be secondarily reduced or fused; only in Dicercomyzinae are all tergaliae single-lamelled.
- (2) Nymphal pronotum without concave collar (in contrast to Caenidae, Neophemeridae, Potamanthidae, and Euthyplociidae), with V-shaped suture (sometimes slightly visible) (Fig. 1a).
- (3) Paraglossae fused with mentum (Fig. 2d).

(B) SYNAPOMORPHIES OF LEPTOHYPHINAE (*Leptohyphes* + *Tricorythodes*):

- (1) Two lobes of the lower portion of tergaliae deeply divided, nearly independent (Figs 1d-g, 9c, d).
- (2) Tergaliae of pair II operculate, tergaliae of pairs I and VII completely reduced (Fig. 1a).
- (3) Submentum enlarged (Fig. 2d).
- (4) Specific position of microtrichiae on mesonotum of subimago (Fig. 6d). [Since the subimagos of other Tricorythidae subfamilies have not been examined, it is unclear whether this is a peculiarity of Leptohyphinae, or a common feature of all Tricorythidae.]

- (C) SYNAPOMORPHIES OF TRICORYTHIDAE (incl. Tricorythinae, Leptohyphinae) + CAENIDAE:
- (1) Transverse interscutal suture present on mesonotum (Figs 4a, c, 5c-d, 6d; PROVONSHA, 1990, fig. 57 tis).
 - (2) Paracoxal suture close to hind margin of episternum of mesothorax (Figs 4c, 5d).
 - (3) Specific form of scutellum and absence of infrascutellum (Fig. 9d). The same in Ephemerythinae.
 - (4) Median invagination of mesothoracic furcasternum more or less wide, but narrowed anteriorly (Figs 4b, 5a-b).
 - (5) Presence of setae on hind margin of wing of imago (Fig. 5c).
 - (6) CuP arises from A₁ having lost its connection with the base of CuA; ICu bifurcate, basally connected with CuP (the same in all other Tricorythidae s. l.: Ephemerythinae, Dicercomyzinae, Machadorythinae).
 - (7) Thickened caudal filaments of male nymph (KLUGE & NARANJO, 1990, fig. 16), [seen in *Tricorythus*, *Tricorythodes* and Caenidae; male nymphs of *Leptohyphes* are not examined].
- (D) SYNAPOMORPHIES OF TRICORYTHODES + CAENIDAE:
- (1) On mesothorax lateropostnotum very strongly enlarged, reaching coxal cavity, and fused with epimerum in the same manner (Fig. 5d).
 - (2) Subalar-sternal muscles (TSm3) of mesothorax more or less reduced (Fig. 6a-b).
 - (3) Reduction of mesonotal suture (Fig. 5c-d); the same in *Tricorythus*.
 - (4) Posterior mesoscutal protuberances drawn together posteriorly (Fig. 5c).
 - (5) In female metathoracic wing muscles Tm1 and TPm1 completely reduced (Fig. 6a-b).
- (E) OUTAPOMORPHIES OF CAENIDAE IN THE THORAX STRUCTURE OF IMAGO:
- (1) Absence of the fore mesonotal transverse invagination (cf. Fig. 4a, c).
 - (2) Presence of medionotal membrane on mesonotum (PROVONSHA, 1990, fig. 57).

- (3) Subalar-sternal muscles (TSm3) of mesothorax reduced completely.
- (4) Metathoracic wing muscles Tm1 completely reduced not only in female, but also in male.
- (5) In male two halves of phragma between meso- and metathorax secondarily fused.

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