of *Coryphorus* improves this situation and allows us to establish the new family Coryphoridae for reasons discussed below.

Relationships

Coryphoridae NEW FAMILY is established for the monotypic genus *Coryphorus*. We establish Coryphoridae because of several autapomorphies which include the loss of cubital intercalaries in male and female adults, the reduced, desclerotized forceps located near the apex of a small distally produced male styliger plate, and the extreme reduction of labial palpal segments two and three in the nymph. The claw condition of the male imago is plesiomorphic. Members of the Leptohyphidae from North and Central America were recently divided into two subfamilies, Leptohyphinae and Tricorythodinae by Wiersema and McCafferty (2000). All species of both subfamilies of Leptohyphidae have similar foreclaws on male imagos.

The foreclaw character needs further explanation. Dissimilar foreclaws occur in imagos of all Ephemerelloidea except Leptohyphidae, all subimagos of the superfamily, and possibly some species of *Ephemerythus*. Although Gillies (1960) reported similar foreclaws for *Ephemerythus,* examined male imagos of *E. pictus* Gillies and *E. kiboensis* Gillies have dissimilar foreclaws. In all Leptohyphidae, male subimagos with dissimilar foreclaws molt to male imagos with similar foreclaws. Some confusion exists in the literature, as Traver (1959) reported dissimilar foreclaws for the holotype subimago of *Tricorythodes arequita* Traver, and Domínguez (1984) reported dissimilar foreclaws for the holotype subimago of *Haplohyphes baritu* Domínguez (erroneously listed as an imago in publication). Imagos of these species examined by the senior author have similar claws.

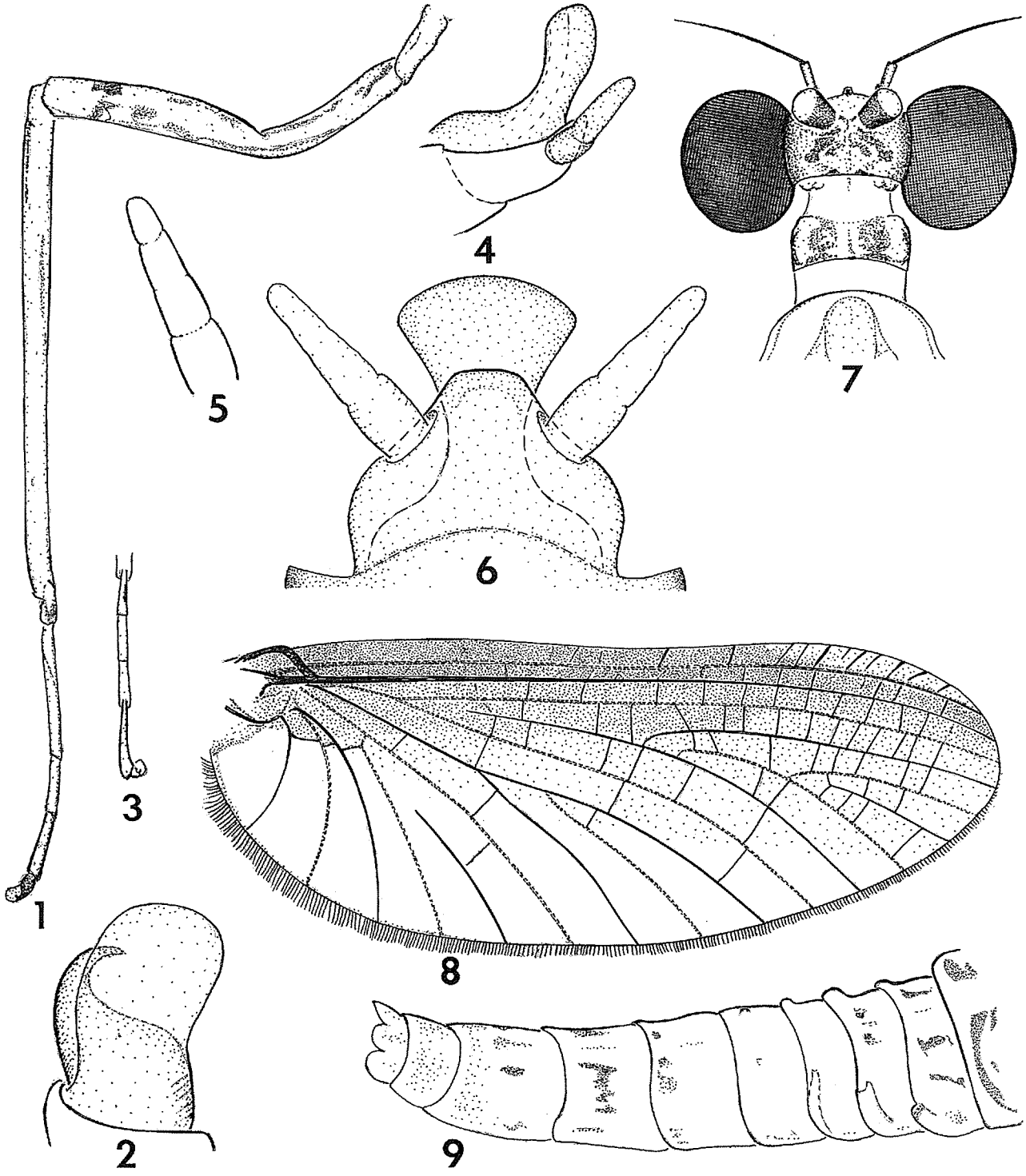
Apomorphic characters such as the fused penes and 2-segmented forceps are found throughout the superfamily, as are many plesiomorphic characters (for example 4-segmented tarsi). The undivided eyes are probably apomorphic as they are characteristic of most Leptohyphidae, Dicercomyzonidae, Ephemerythidae, and Tricorythidae. Nymphs of *Coryphorus* have a "gill basket" composed of dorsally expanded abdominal terga as do nymphs of *Machadorythus*, but this structure is composed of abdominal terga 3-6 in *Coryphorus* and terga 3-7 in *Machadorythus*, and the gill structure is different (Peters 1981, Elouard and Gillies 1989). This and other characters cited by Peters 1981 (elevated eyes and antennae, tubercles on the head) are presumed homoplasies for *Coryphorus* and *Machadorythus* as they reoccur in different forms in both genera (and in many families of Ephemeroptera). The fusion of the glossae and paraglossae is also considered to be independently evolved in *Coryphorus* and *Machadorythus* because of the different shape of the fused labium (Kluge 2000).

Genus *Coryphorus* Peters, 1981

(Figures 1-12)

Coryphorus Peters, 1981:207; Landa and Soldán 1985:104; Hubbard 1990:40; Peters and Peters 1993:45; McCafferty and Wang 2000:58.

Description. Imagos. Eyes of male undivided, greatly enlarged, separated on dorsum of head by width of an eye (Fig. 7); eyes of female small, lateral, separated on dorsum of head by a distance 3.7 times width of an eye. Lateral ocelli much larger than median ocellus. Membranes between head, prothorax, and mesothorax of male extended. Foreleg of male as in Fig. 1, with 3 apparent tarsal segments and possible small 4th segment fused at apex of tibia; foreclaw of male dissimilar, with hook and opposing pad (Fig. 3). Meso- and metathoracic tarsi of male and female 4-segmented, the 1st tarsal segment a little shorter than the 2nd, the 2nd and 3rd subequal and the 4th longer (Fig. 2). Forewing (male and female) as in Fig. 8 : Rs forked about 1/10th distance from base of wing; MA forked a little basal to mid wing, fork symmetrical; MP forked about 1/4 distance from base, MP_2 attached to MP_1 and CuA by cross veins; cubital area without intercalaries; Rs field with many cross veins, remainder of wing with few cross veins; posterior wing margin with setae. Hind wing absent. Male genitalia (Fig. 4-6): styliger plate produced distally, about as long as wide, with forceps located near apex (Fig. 6); forceps short, desclerotized, with remnant of basal segment visible and fusion line of third segment visible near apex in transmitted light (Fig. 5); penes fused, broad distally, about as long as forceps, with paired duct openings. Apex of 9th sternum of female broad, not extended posteriorly; 7th abdominal sternum broad, slightly produced distally. Three caudal filaments: broken off in male and female (a single cercus present in female subequal to length of body); terminal filament a little shorter than cerci in male subimago.



Figures 1-9. Male imago of *Coryphorus aquilus*. 1-3, legs: 1, foreleg; 2, foreclaw; 3, tarsi of metathoracic leg. 4-6, genitalia: 4, lateral; 5, detail of forceps; 6, ventral. 7, dorsal view of head and prothorax. 8, forewing (concave veins stippled). 9, abdominal terga 1-10.

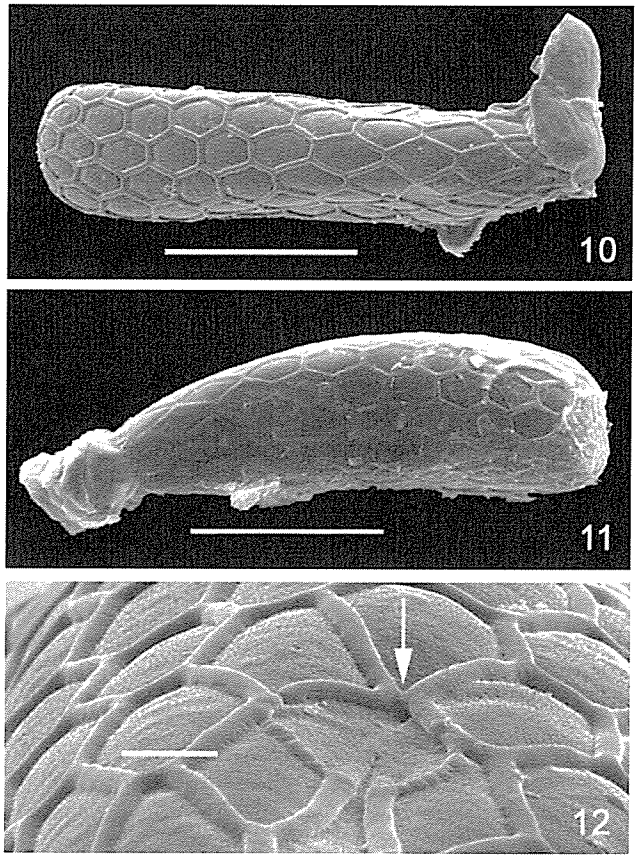
Egg. Length 240-310 μm; width 80-100 μm; with small, basal polar cap. Chorion as in Fig. 10-12; micropyle under chorionic ridge near base of egg.

Discussion. The longitudinal suture of the laterotergum is straight as described by Kluge (1992) for *Tricorythodes cubensis* Kluge and Naranjo, the posterior notal protuberances are slightly divergent posteriorly, and the medioparapsidal and lateroparapsidal sutures do not meet anterior to the transverse interscutal suture. The ventral nerve cord is visible in the male subimago as one ganglion in the mesothorax and 6 ganglia in abdominal sterna 1-5, but in the male imago these ganglia are fused in sterna 1-5 into a single undefined nerve band without visible connectives (nerve cord not visible in female).

Both forefemora of the male are curved (Fig. 1), apparently to fit around the enlarged eyes. In the male subimago, the forefemora are straight. Because only one male imago is available, we do not know if this character occurs in other specimens. For the same reason, we cannot be sure if the structure at the apex of the foretibia (Fig. 1) represents a modification of the tibia or partial fusion of a tarsal segment.

Imagos of *Coryphorus* can be distinguished from all genera of the Ephemerelloidea by the following combination of characters: 1) absence of intercalaries in the cubital field of forewing (Fig. 8); 2) setae present on posterior margin of forewing (Fig. 8); 3) male with large, fused, distally broadened penes and short desclerotized forceps (Fig. 4-6); 4) styliger plate of male produced distally, about as long as wide (Fig. 6); 5) ninth sternum of female broad, not extended; 6) eyes of male undivided, separated, greatly enlarged (Fig. 7). *Coryphorus* is distinguished from Neotropical Leptohyphidae by the same characters (except for wing setae and undivided male eyes) and by the dissimilar foreclaws of the male imago.

Within the Neotropics, *Leptohyphodes inanis* (Pictet), originally described from two specimens, is reported to have large eyes nearly meeting on the meson of head (Ulmer 1921) so the character "large eyes" is frequently used in keys to imagos (for example Traver 1958, Domínguez et al. 1992). *Coryphorus* is easily distinguished from *Leptohyphodes* by the lateral position of the large eyes in *Coryphorus* and other characters given above; also, the eyes of *Leptohyphodes* are divided into dorsal and ventral portions and those of *Coryphorus* are not.



Figures 10-12. Egg of *Coryphorus aquilus*. 10-11, lateral views (scale bar 100 μm); 12, detail of micropyle (scale bar 10 μm).

Coryphorus aquilus Peters
(Figures 1-12)

Coryphorus aquilus Peters, 1981:211.

Description. Male imago (in alcohol). Body length (head to apex of tergum 10) 5.5 mm; forewing 5.3 mm; [caudal filaments broken and missing]. Total width of eyes and head 1.85 mm; head pale yellowish-brown, with dark brown marks on meson of head between eyes (Fig. 7); eyes black; base of lateral ocelli black, antennae hyaline (Fig. 7). Prothorax pale yellowish-brown, with darker brown marks dorsally as in Fig. 7; mesothorax light brown, darker dorsally, with blackish-brown mark between posterior scutal protuberances and a pair of lateral blackish marks on mesoscutum near base of wing. Longitudinal and cross veins of forewings deep gray, except apically hyaline in vein MP_2 and veins of cubital and anal area; forewing membrane dark gray basally and in cells C and Sc, faded in stigmatic area, lighter gray in radial cells, and pale gray

fading to hyaline in posterior half of wing (Fig. 8). Legs: measurements (in mm) of femur, tibia, tarsus: leg I -- 0.96, 1.44, 0.67; leg II -- 0.96, 0.80, 0.53; leg III -- 1.12, 0.83, 0.48; coxae and trochanters of all legs pale yellowish-brown; femora whitish with heavy blackish marks near apex and with smaller blackish streaks dorsally as in Fig. 1 (also as in Peters 1981, Fig. 29-31, legs of nymph); all tibiae whitish with a fine blackish streaks at base and middle, and prothoracic tibiae with yellowish-brown apex (possible fused 1st tarsal segment); tarsi and claws pale with hooked portion of claws brownish and with blackish mark on basal segment of tarsi of meso- and metathoracic legs. Abdominal terga (Fig. 9) whitish, terga 1-3 and 6-8 with submedian blackish-brown marks dorsally, marks small on terga 3, 6-8; terga 4-5 without marks; posterior portion of tergum 8, 9 and middle of tergum 10 washed with reddish-brown; no visible spiracular marks but lateral margins of terga lightly washed with gray; sterna whitish, sterna with small narrow median grayish line posteriorly, sterna 5-8 reddish-brown at lateral margins. Bases of cerci and terminal filament hyaline.

Male subimago. Body length 5.1 mm; forewing 5.3 mm; cerci 3.0 mm, terminal filament 2.5 mm. Characters of male imago, except forelegs short, head and thorax paler, marks of abdomen less extensive and distinct and small blackish sublateral marks on tergum 9; sterna 2-9 with small paired anterosubmedian pale gray marks. Cerci showing developing imaginal cerci under exuviae, cerci hyaline at base and apex with median 2/3 dark gray; terminal filament similar but pale gray.

Female imago (in alcohol). Body length 3.7 mm (body somewhat shrunken); wing 6.4 mm, cercus 3.0 mm [other caudal filaments broken and missing]. Coloration of head and thorax as in male imago. Legs: measurements (in mm) of femur, tibia, tarsus: leg I broken and missing; leg II -- 1.12, 0.72, 0.43; leg III -- 1.20, 0.96, 0.56; marks on femora of all legs heavier and more extensive than in male, tibiae as in male , no marks on tarsi. Wing coloration as in male except gray color of membrane reduced; basal third of cells C and Sc dark gray, membrane at base of other longitudinal veins gray, color faded apically and posteriorly. Abdominal terga whitish washed with black, marks more extensive than in male but abdominal segments compressed so details not visible; abdominal sterna completely washed with gray, with darker posteromedian mark on sterna 1-9; sterna 2-8 blackish-brown laterally. Cercus hyaline.

Egg (in alcohol). Yellowish-brown. All eggs were in a single clump with eggs extruded along the long axis and joined laterally.

Nymph. Described in Peters 1981.

Material. Colombia: Dpto. Amazonas, Leticia, 93 m elevation, stream at Km 11 on road to Tarapaca, E. Domínguez, M. C. Zuñiga de Cardoso & C. Molineri, at light 1800-2000 h on 28-I-1999 (imagos and egg). Collectors and data same except: stream at Km 15 on road to Tarapaca, at light 0400-0600, 10-II-1999 (male subimago). Deposited in Museo de Entomologia de la Universidad del Valle, Cali, Colombia.

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