

New Genus of Oligoneuriidae (Ephemeroptera) from South America

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ABSTRACT A new genus and two species, *Fittkauneuria carina* Pescador & Edmunds and *F. adusta* Pescador & Edmunds, from the highlands of Venezuela and Brazil, are described. The description of the genus is based on male imago, egg, and nymphs. *Fittkauneuria carina* is described from male imago and nymphs, whereas *F. adusta* is known only from nymphs. The male imago of *Fittkauneuria* is distinguished by the relatively numerous cross veins of the fore- and hind wings and lack of genital forceps; the nymph is distinguished by the epicranium which is strongly tapered anteriorly and has vestigial or weakly developed gill tufts. Preliminary cladistic analysis of the family Oligoneuriidae indicates that *Fittkauneuria* shares synapomorphies with the African genera *Elassoneuria* and *Oligoneuriopsis* and forms a monophyletic group.

KEY WORDS *Fittkauneuria*, mayflies, new genus

OLIGONEURIIDAE IS A unique group of mayflies. The nymphs are filter feeders of seston or interstitial organic particles, the adults generally have reduced wing venation, and the males forelegs are shorter than the mid- or hind legs. Because of their adaptation for swift flight, the oligoneuriids are perhaps the most highly evolved adult mayflies (McCafferty & Edmunds 1979). Except for the primitive genus *Chromarcys*, oligoneuriids have highly geminate convex and concave longitudinal pairs of veins and an expanded upturned cubital area of the forewings that firmly locks with the downturned costal margin of the hind wings during flight. The nymphs have radiated into three distinct ecological types: (1) strong swimmers found on rock, sand, or mud substrates; (2) agile burrowers found in loose sand; or (3) slow moving forms that cling tenaciously to rocks, snags, or trapped debris in the current. The family is essentially pantropical and believed to have evolved on the South America–Africa–Madagascar–India landmass (Edmunds 1972, 1975). The recently described extinct oligoneuriid genus *Colocrus* from Ceara Crato, Brazil, strongly supports this hypothesis, and the family appears to have evolved at the latest during the Lower Cretaceous Period (McCafferty 1990).

A recent interpretation of the higher classification of Ephemeroptera by McCafferty (1990, 1991) recognized three subfamilies of Oligoneuriidae (Chromarcyinae, Colocrinae, and Oligoneuriinae). This latest taxonomic definition of the family includes the following genera: *Chro-*

marcys (Chromarcyinae); *Colocrus* (Colocrinae); and *Elassoneuria*, *Oligoneuriopsis*, *Fittkauneuria* (proposed below), *Lachlania*, *Oligoneuria*, *Oligoneuriella*, *Spaniophlebia*, *Homooneuria*, and *Oligoneurisca* (Oligoneuriinae).

Nymphs and a male imago of Oligoneuriidae that were collected from the highlands of Brazil and Venezuela are morphologically distinct from currently known oligoneuriid genera and are described here as a new genus with two new species.

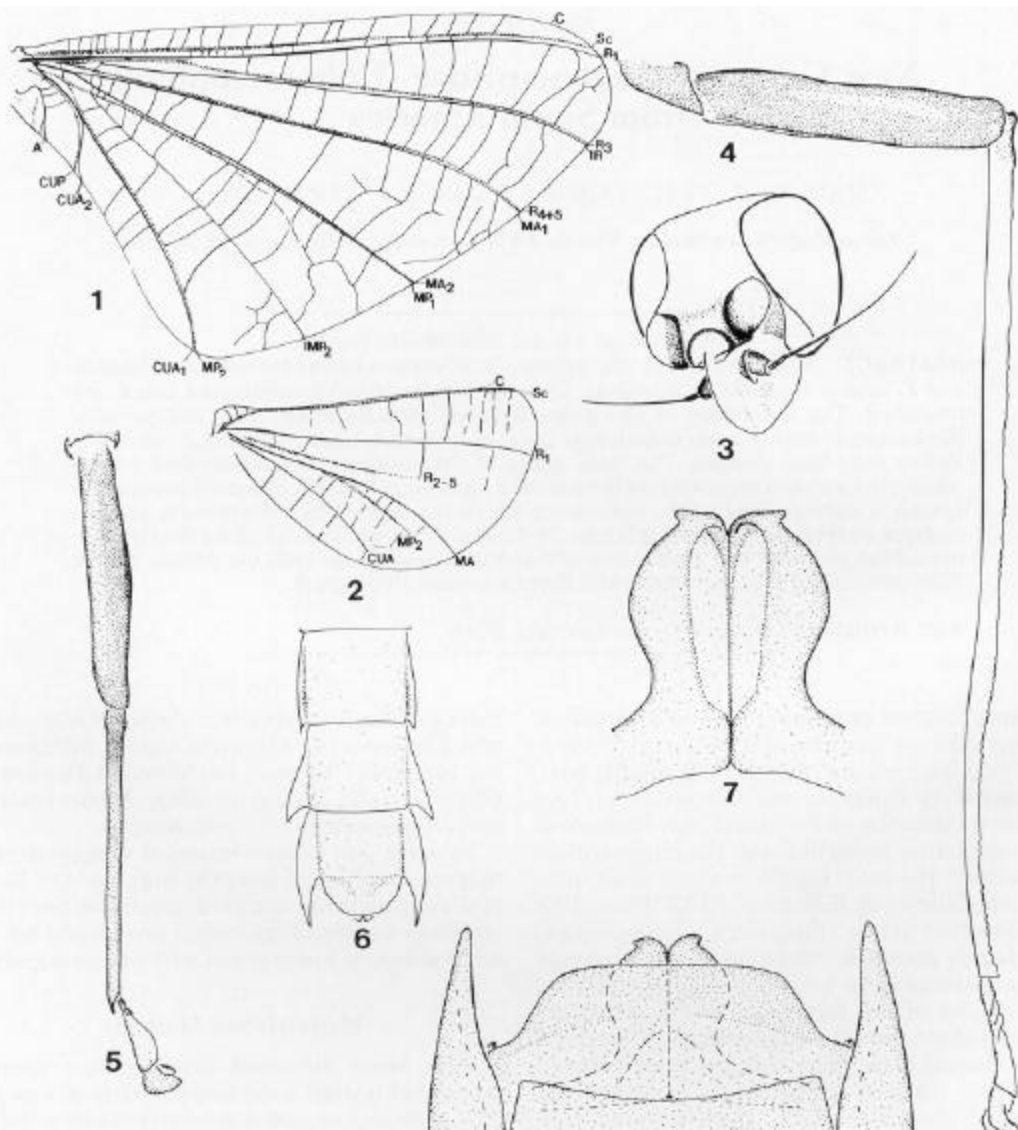
Materials and Methods

Eggs were extracted from mature nymphs whose subimagos were almost ready to emerge. The eggs and nymphal structures to be used for scanning electron microscopy were dehydrated through a graded series of 30, 50, 70, 90, 95, and 100% ethyl alcohol and then critical-point dried using CO₂. The specimens were mounted on Al stubs, sputter coated with gold palladium, and examined with a JEOL JSM-840 scanning electron microscope operated at 10 kv.

Measurements are given to the nearest 0.5 mm. Measurements of the segments of the adult male forelegs are expressed as a ratio of the length of the foretibiae, and the actual value is enclosed in parenthesis. The identification of wing veins is based on position and alternating convexity or concavity of longitudinal veins (Edmunds & Traver 1954).

Depositories of the material are as follows: Florida A&M University, Tallahassee (FAMU); Hydrobiologische Anstalt der Max-Planck-Gesellschaft, Plön, Germany (HAMPG); Instituto de Zoología Agrícola, Maracay, Venezuela

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Figs. 1-8. *Fittkauneuria carina*, ♂ imago. Forewing (1). Hind wing (2). Frontal view of head (3). Hind leg (4). foreleg (5). Abdominal sterna VII-X (6). Enlarged ventral view of penes (7). Ventral view of genitalia (8).

(IZAM); National Museum of Natural History, Washington, DC (NMNH); and University of Utah, Salt Lake City (UU).

**Genus *Fittkauneuria* Pescador & Edmunds,
New Genus
(Figs. 1-29)**

Male Imago. Length: body 13.0 mm, forewing 13.0 mm. Eyes widely separated on meson of head by a length approximately equal maximum width of an eye. Epicranium produced to a prominent membranous ridge (Fig. 3). Antennae subequal in length with head, scape 5-6 times as

thick as pedicel and flagella. Thorax: width of pronotum ≈ 0.4 times length; a pair of long whitish membranous filaments attached underneath mesoscutellum and extended near posterior margin of abdominal segment I. Wings (Figs. 1 and 2): membrane of fore- and hind wings thickly covered with microtrichiae (wing membrane of subimago retained), particularly dense near and along margins; hind wings $\frac{1}{2}$ as long as forewings; maximal width of forewings ≈ 0.5 times maximal length; maximal width of hind wings slightly more than 0.5 times maximal length; fore- and hind wings with numerous cross veins (Fig. 2); cross veins of forewings evenly distrib-

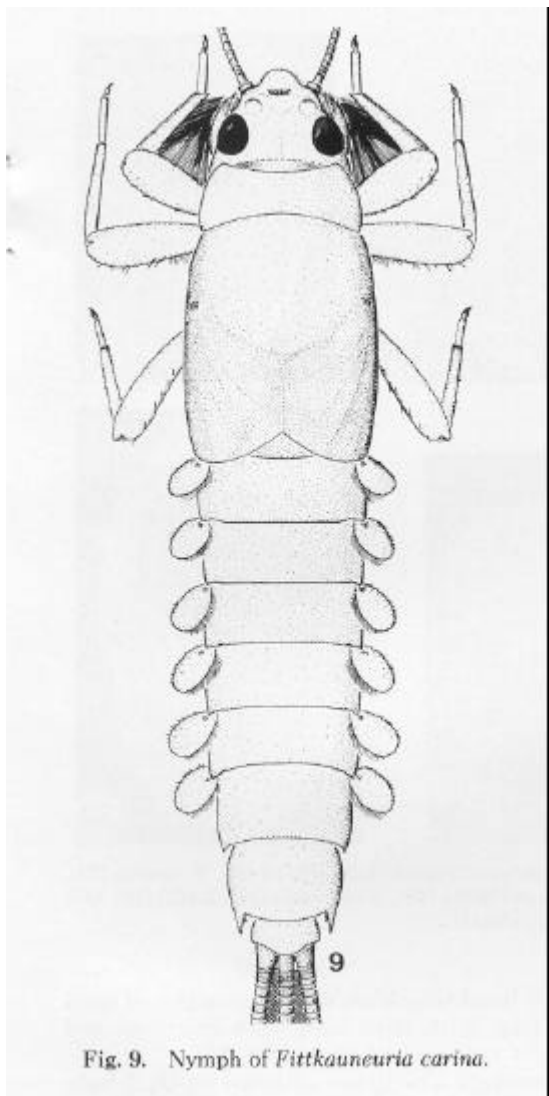
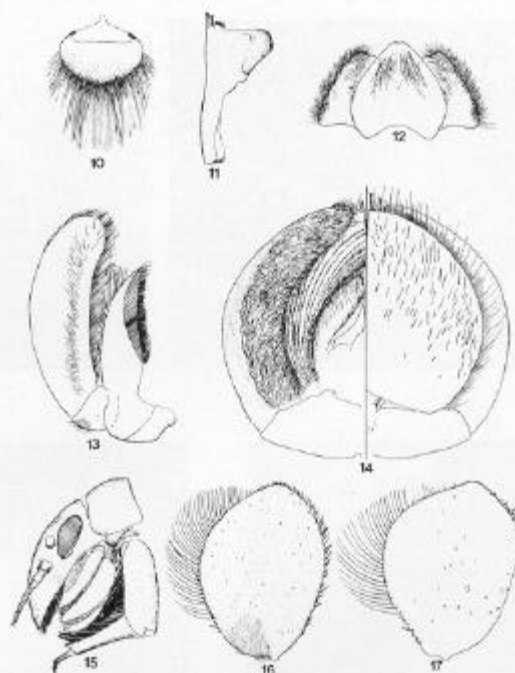


Fig. 9. Nymph of *Pittkauneuria carina*.

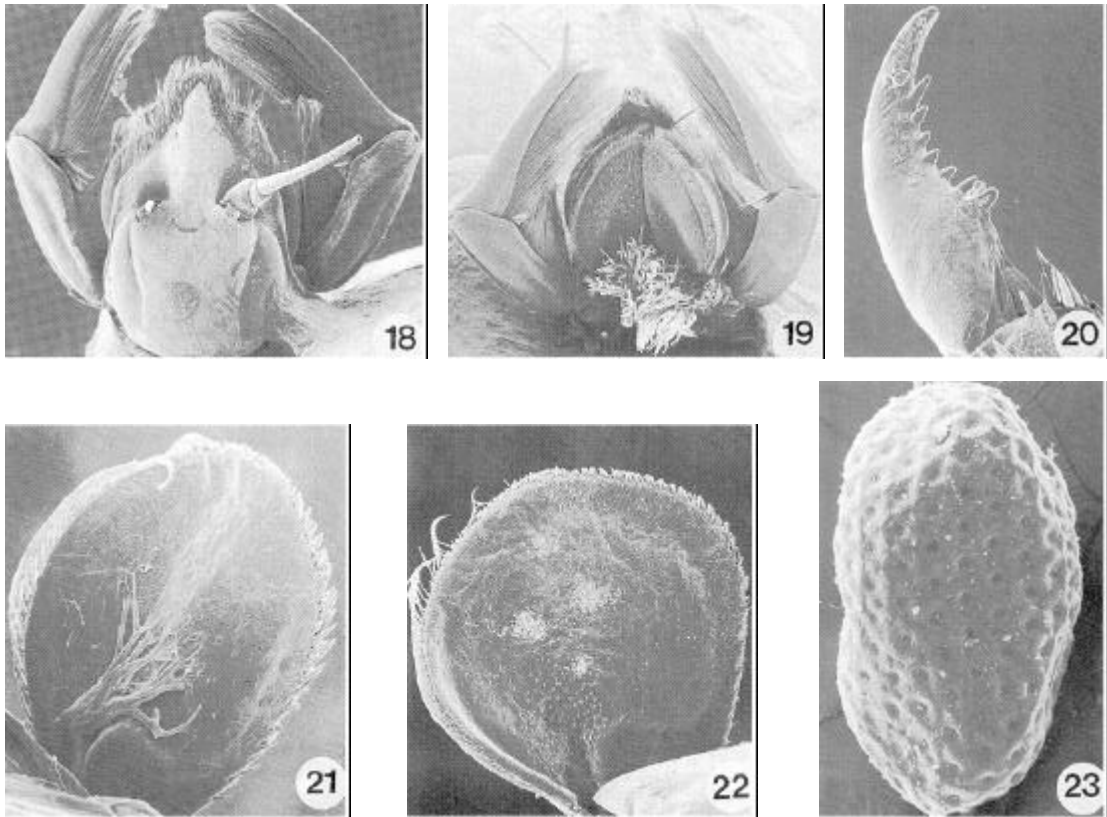


Figs. 10-17. Mouthparts, head, and abdominal gills of mature nymph: *Pittkauneuria carina* (10-16); *F. adusta* (17). Labrum (10). Left mandible (11). Hypopharynx (12). Right maxilla (13). Labium, dorsal [left], ventral [right] (14). Lateral view of head (15). Gill 4 (*F. carina*) (16). Gill 4 (*F. adusta*) (17).

Egg. Oblong, polar caps absent; chorion adorned with evenly spaced and relatively deep circular indentations (Fig. 23).

uted throughout entire wing (Fig. 1); vein IMP_2 of forewings developed and basally attached close to furcation of MP_1 and MP_2 (Fig. 1); MA of hind wings unforked (Fig. 2). Legs: ratios of segments in male forelegs, 0.7:1.00 (1.7 mm) : 0.04:0.04:0.20; forelegs ≈ 0.5 times length of meso- and metathoracic legs; foretarsi membranous, tarsal segments 1 and 2 slightly sclerotized, tarsal segment 3 enlarged, 4 times length of segment 2 (Fig. 5); meso- and metatibiae membranous, approximately 3 times length of femora; claws blunt (Fig. 4). Abdomen: posterolateral spines weakly developed on segments I-VII, flared and enlarged on segments VIII-IX (Fig. 6). Male genitalia: width of styliger plate approximately 3 times maximal length, apex truncate; genital forceps absent; penes short and bulbous with small slightly curved apical projection on each lobe (Figs. 7 and 8). Caudal filaments: terminal filament slightly shorter than cerci.

Mature Nymph. Body length excluding caudal filaments, 13.0-18.0 mm. Head: epicranium prominently tapered anteriorly with thick marginal hairs and dense peg-like dorsal setae (Figs. 15 and 18); antennae 2 times length of head, attached near anterior base of eyes (Fig. 15). Mouthparts: labrum small, ovate with long dorsal and marginal hairs (Fig. 10); outer and inner incisors of mandibles subequal in width (Fig. 11), inner margin of inner incisor with prominent dentitious spines; prosthecae with several prominent spinous branches (Fig. 11); maxillary gills multibranching (Fig. 19); segment 1 of maxillary palpi ≈ 0.5 times length of segment 2; galealacinia of maxillae covered with long thick hairs, 2 prominent submarginal rows of long spines; labial palpi covered with thick hairs, segment 1 ≈ 0.3 times length of segment 2 (Fig. 13); superlingua of hypopharynx short, not extended beyond apex of lingua, margins with long hairs (Fig. 12); lingua broad, deltoid, with shallow midapical emargination (Fig. 12); labium as in Fig. 14; segment 1 of labial palpi ≈ 0.3 times length of segment 2; glossae small 1.8 times length of paraglossae, paraglossae with long pectinate hairs along margins (Fig. 28) and ventral setae (Fig.



Figs. 18–23. Scanning electron microphotographs of *Fittkauneuria* nymph and egg (18–21). *F. carina* (23). *F. adusta* (22). Dorsal view of head [20X] (18). Ventral view of head [20X] (19). Metatarsal claw [250X] (20). Gill 4, ventral view [120X] (21). Gill 4, ventral view [120X] (22). Egg [500X] (23).

14); Thorax: marginally glabrous (Fig. 9); width of pronotum ≈ 3 times length. Legs: foretarsi developed (Figs. 9 and 19); forecoxae and foretrochanters subequal in length; metatrochanters distinctly longer than metacoxae; tarsi ≈ 0.4 times length of tibiae; trailing edge of femora and tibiae with moderately long spines, dorsal surface with short stubby setae; leading edge of meso- and metatarsi with 2 rows of spines; tarsal claws hooked and denticulate, middle denticles smallest (Fig. 20). Abdomen: posterolateral spines on segments VIII–IX, trailing edge of posterolateral spines on segment IX with minute hairs (Fig. 9); terga with hairs, moderately long attenuated setae, and fringed setae (Figs. 24 and 25); sterna with moderately long attenuated setae (Fig. 26). Gills: gill 1 ventral, tufts multi-branched, lamellae absent; gills 2–7 dorsal (Fig. 9), lamellae plate-like with thick marginal spines and long hairs along trailing edge (Figs. 9, 16 and 17); dorsal surface of gill lamellae scaly with blade-like setae, and fringed setae; scales on lamellae apically terminated with fine hair (Fig. 27); gill with tufts (Fig. 21) or without tufts (Fig. 22). Terminal filament short, ≈ 0.5 times length of cerci, with long hairs throughout entire

length; basal two-thirds of inner margins of cerci with long hairs; cerci scaly with short hair and spicules near apex of joints (Fig. 29).

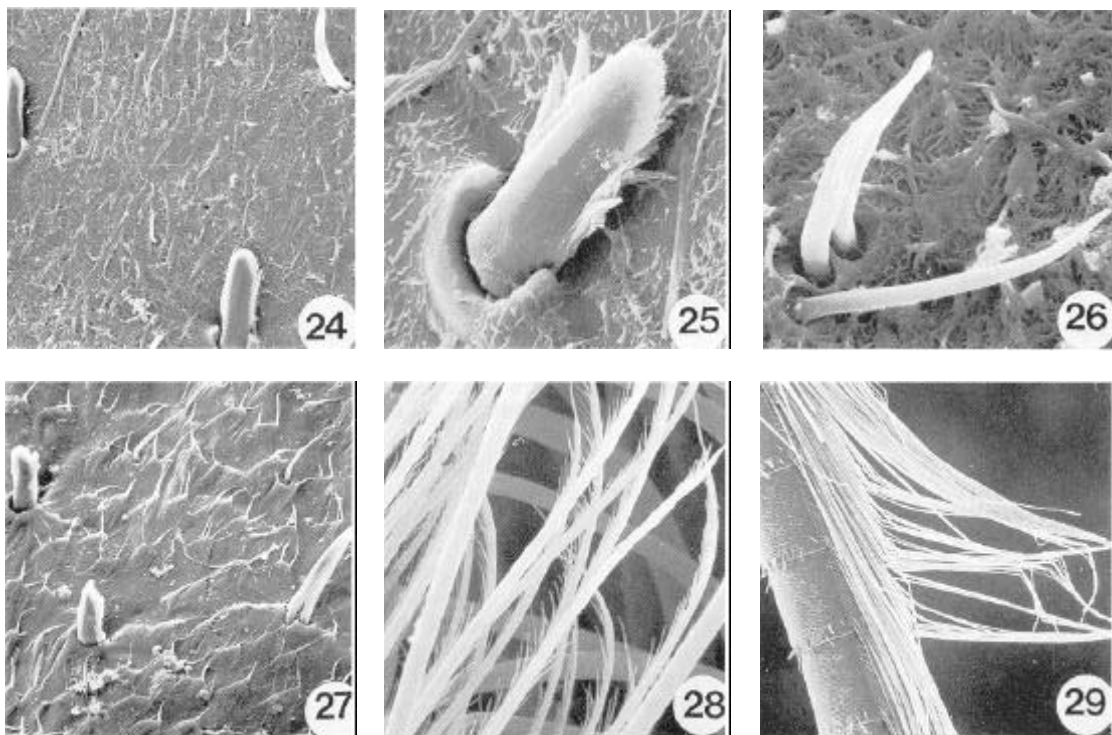
Etymology. The genus is named for Dr. Ernst-Josef Fittkau, Hydrobiologische Anstalt der Max-Planck-Gesellschaft, Plön, Germany, in honor of his significant contribution to the study of South American freshwater ecosystems and the first collection of the genus in 1965. Masculine.

Type Species. *Fittkauneuria carina* n. sp.

Species Included. *Fittkauneuria carina* n. sp. and *F. adusta* n. sp.

Distribution. Highlands of southeastern Venezuela and adjoining Brazil.

Discussion. *Fittkauneuria* can be distinguished from the other genera of Oligoneuriidae by the following combination of characters. In the male imago (1) membranous epicranium is produced to a prominent median ridge (Fig. 3); (2) fore- and hind wings have numerous cross veins (Figs. 1 and 2); (3) vein IMP_2 of the forewings is basally attached close to furcation of veins MP_1 and MP_2 (Fig. 1); (4) forelegs are ≈ 0.5 times length of meso- and metathoracic legs; (5) meso- and metatibiae are membranous and 3



Figs. 24–29. Scanning electron microphotographs of *F. carina* nymph. Abdominal tergal setae [1100X] (24). Enlarged abdominal tergal setae [4000X] (25). Abdominal sternal setae [3,500X] (26). Dorsal setae of gill lamella [1100X] (27). Marginal hairs of paraglossae [2700X] (28). Abdominal cercus [140X] (29).

times longer than the femora; (6) genital forceps are absent; and (7) penes are short and bulbous (Figs. 7 and 8). In the egg (1) polar caps are absent; and (2) chorion has relatively deep and circular indentations (Fig. 23). In the nymph (1) epicranium is prominently and uniquely tapered anteriorly, with thick marginal hairs (Figs. 15 and 18); (2) antennae are twice the length of head, and attached near the anterior base of eyes (Figs. 15 and 18); (3) leading edge of meso- and metatarsi have two rows of spines; (4) tarsal claws are developed and denticulate (Fig. 20); (5) gill lamellae 2–7 are broad and plate-like (Figs. 16 and 17); (6) prominent posterolateral spines occur on abdominal segments VIII and IX (Fig. 9); and (7) terminal filament is ≈ 0.5 times the length of cerci.

Preliminary cladistic analysis of the family Oligoneuriidae based on the external morphological characters of the adults and nymph indicates that *Fittkauneuria* shares synapomorphies with the African genera *Elassoneuria* and *Oligoneuropsis* and the three form a monophyletic group (M.L.P., unpublished data). The synapomorphies include the nymphs having the abdominal gill 1 attached underneath the segment and without lamella and the nymphal metatrochanters being distinctly longer than the metacoxae.

Fittkauneuria, however, can be distinguished from its African sister group by any one of the following characters. In the male imago (1) fore- and hind wings have several cross veins (Figs. 1 and 2); (2) vein IMP_2 of forewings is attached basally close to furcation of veins MP_1 and MP_2 (Figs. 1 and 2); (3) genital forceps are absent with the penes short and bulbous (Figs. 7 and 8). The eggs have a chorion that is sculptured with evenly-spaced, circular indentations (Fig. 23). In the nymph (1) the epicranium is strongly tapered anteriorly and has thick dorsal setae and marginal hairs, (Fig. 15 and 18) which alone is diagnostic; (2) leading edge of meso- and metatarsi have two rows of spines; (3) posterolateral projections occur on abdominal segments VIII and IX (Fig. 9); and (4) forecoxae and foretrochanters are subequal in length.

Although the nymphs and male imago upon which the genus is established were not associated by rearing, there is no question that both life stages represent the same species. The nymphs and male imago have a similar abdominal color pattern, and posterolateral projections occur on abdominal segments VIII–IX. In addition, both life stages were collected from the same general locality and were the only Oligoneuriidae present.

*Fittkauneuria carina*Pescador & Edmunds, New Species
(Figs. 1–16, 18–21, and 23–29)

Male Imago (in alcohol). Length: body 13.0 mm, forewing 12.0 mm. Head: dull yellow, faintly washed with brown near base of eyes and sublateral margins of epicranium; vertex slightly elevated posteriorly and overlapping anterior margin of pronotum. Antennae dark brown. Eyes black. Ocelli pale white, black at base. Thorax: pronotum dark brown with median longitudinal ridges; meso- and metanota brown, dark brown on sublateral and posterior margin of mesoscutellum; mesonotal parapsidal furrows pale yellow, midtransversely connected by a narrow pale yellow band, forming a prominent H-shaped figure on mesonotum. Sterna brownish yellow, slightly darker along margins. Wings: membrane of fore- and hind wings pale grayish brown; longitudinal and cross veins light brown. Legs: prothoracic legs dark brown, except segment 3 of tarsi whitish; meso- and metathoracic legs dark brown except tibiae and tarsi pale yellow. Abdomen: terga brown, slightly darker sublaterally; terga with pair of small pale yellow submedian spots, and midlongitudinal pale yellow line; sterna brown. Genitalia: styliiger plate light brown; penes pale yellow, shape as in Figs. 7 and 8. Caudal filaments whitish with minute hairs.

Mature Nymph (in alcohol). Length: body 13.0–18.0 mm; caudal filaments 10.0–15.0 mm. Head: yellow with small irregular brown markings between ocelli and eyes. Ocelli pale white, dark brown at base. Eyes black. Antennae yellow, progressively paler distally, scape and pedicel faintly washed with brown. Thorax: nota pale yellow, faintly washed with brown near posterolateral corner of pronotum and base of wing pads; sterna whitish. Legs: pale yellow, leading edge of femora faintly washed with brown. Abdomen: terga brown with a longitudinal pale yellow median line, pair of inconspicuous pale yellow submedian spots; sterna yellowish and faintly washed with brown. Gills: width of gill lamellae 2 less than 0.7 times length; gill lamellae 3–7 oval, width less than 0.5 times length (Fig. 16); gills 2–6 with tufts (Fig. 21), vestigial on gill 7; length of postoral spines on segment 9 less than 0.3 maximal width of segment. Caudal filaments pale yellow.

Etymology. Carina L., meaning ridge

Type Material. HOLOTYPE: Male imago (in alcohol), VENEZUELA: T.F.A. Camp IV, 0° 58' N, 65° 57' W Cerro de la Niblina, 750 m, 15–18 March 1984, O.S. Flint, Jr. (NMNH). PARATYPES: 1 mature nymph (NMNH), VENEZUELA: T.F.A. Camp V, 0° 49' N, 66° N' W Cerro de la Niblina 1,250 m 23–24 March 1984, O.S. Flint, Jr.; 2 fairly mature nymphs (NMNH), 2 fairly mature nymphs (FAMU), 2 fairly mature nymphs

(IZAM), VENEZUELA: T.F.A. Camp XI, 0° 52' N, 65° 50' W, Cerro de la Niblina, 26–28 February 1985, P.J. & P.M. Spangler & R.A. Faitoute; 3 fairly mature nymphs (NMNH), 2 fairly mature nymphs (UU), 2 fairly mature nymphs (HAMPG), VENEZUELA: Amazonas; Dept. Río Negro, small forest stream nr. summit of Unturan Range, 1,000 m, 1° 33' N, 65° 12' W, 11 February 1989, pH 4.4, 20°C, D. A. Polhemus.

Discussion. The nymph of *F. carina* can be distinguished from the nymph of *F. adusta* by the following characters: (1) tufts on abdominal gills 2–6 (Fig. 21), (2) abdominal gill lamellae 2–7 oval (Fig. 16), (3) length of posterolateral spines on abdominal segment IX less than one-third the maximal width of the segment, and (4) brown markings of head not extensive and confined between ocelli and eyes.

The holotype was collected by light trap (blacklight) beside a river in Camp IV, in Cerro Niblina. The river was about 15–20 m wide and ≈60–90 cm deep. The water was darkly stained but clear and cold, and the substrates consisted of bedrock, boulders, and sand (O.S. Flint, Jr., personal communication). The nymphs collected from Camp V in Cerro Niblina were found in a small stream (30–40 cm in width and 7–10 cm in depth) in dense jungle. The substrates ranged from sand to boulders, and stream flow was from tumbles, pools, and runs (O. S. Flint, Jr., personal communication). The specimens were collected near the summit of the Unturan range from a small stream seeping along sandstone and then flowing down a rocky chute with numerous shallow sloping falls and rock-edged pools. The water was reddish amber (the color of claret wine). The stream was heavily shaded, and the surrounding rocks thoroughly covered with moss. At 970 m the stream encounters the granite of Precambrian Guiana Shield (D. A. Polhemus, personal communication).

*Fittkauneuria adusta*Pescador & Edmunds, New Species
(Figs. 17 and 22)

Mature Nymph (in alcohol). Length: body 14.0–18.0 mm; caudal filaments 10.0–14.0 mm. Head: yellow with extensive brown markings between eyes and extending between bases of antennae. Ocelli whitish, basally ringed with dark brown. Eyes black. Antennal flagella light brown, progressively paler distally, scape and pedicel dark brown. Thorax: nota brownish, mottled with dark brown; sterna pale yellow. Legs: brownish yellow, femora with basal and subapical dark brown bands. Abdomen: terga and sterna dark brown; each with pair of pale yellow submedian spots. Gills: gill tufts vestigial (Fig. 22); width of gill lamellae 2 more than 0.5 times length; gill lamellae 3–7 ovate, (Figs. 17 and 22); length of posterolateral spines of segment 9 ≈0.4

times maximal width of segment. Caudal filaments light brown.

Etymology. *adusta* L., meaning brown.

Type Material. HOLOTYPE: Mature nymph (in alcohol), VENEZUELA: La Escalera, 108 km, S. Río Cuyuni, 11–12 Feb. 1976 C. M. and O. S. Flint, Jr. (NMNH). PARATYPES, VENEZUELA: 5 mature nymphs (NMNH), 2 mature nymphs (IZAM) same data as holotype; 1 fairly mature nymph (HAMPG), BRAZIL: Amazonas State, mountain stream II, nr. Rio Marauia, 3 day trip above S. Antonio Mission, NW Taparuaquara, 26/27-I-1965. E. J. Fittkau.

Discussion. The nymph of *F. adusta* can be distinguished from the nymph of *F. carina* by any of the following characters: (1) gill tufts are vestigial (Fig. 22); (2) gill lamellae are ovate (Figs. 17 and 22); (3) length of posterolateral spines of abdominal segment 9 is ≈ 0.4 times the maximal width of its segment; and (4) brown markings of head are extensive, covering the vertex extending anteriorly between bases of antennae.

The holotype was collected in a cascading stretch of Río Cuyuni about 5 m wide and 15 inches to 30 cm deep. The water was clear and cold, and the substrates consisted of rubble, boulders, and bedrock (O. S. Flint, Jr., personal communication).

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References Cited

- Edmunds, G. F., Jr. 1972. Biogeography and evolution of Ephemeroptera. *Annu. Rev. Entomol.* 17: 21–42.
1975. Phylogenetic biogeography of mayflies. *Ann. Mo. Bot. Gard.* 62: 241–263.
- Edmunds, G. F., Jr. & J. R. Traver. 1954. An outline of a reclassification of the Ephemeroptera. *Proc. Entomol. Soc. Wash.* 56: 236–240.
- McCafferty, W. P. 1990. Chapter 2: Ephemeroptera, pp. 20–50. In D. A. Grimaldi [ed.], *Insects from the Santana formation, Lower Cretaceous of Brazil*. *Bull. Am. Mus. Nat. Hist.* 195.
1991. Toward a phylogenetic classification of Ephemeroptera (Insecta): A commentary on systematics. *Ann. Entomol. Soc. Am.* 84: 343–360.
- McCafferty, W. P. & G. F. Edmunds, Jr. 1976. The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Am.* 72: 5–12.

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