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A REVISION OF THE CAENIDAE WITH OCELLAR TUBERCLES IN THE NYMPHAL STAGE (EPHEMEROPTERA)

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Abstract: This study is a revision of the Caenidae, the nymphs of which possess occillar tu, bercles on the head, and is based mainly on nymphs. Three new genera, Cercobrachys (Holarctic. Oriental, Neotropic), Insulibrachys (Neotropic, Cuba) and Caenoculis (Oriental) are established. Fifteen new species are described: Brachycercus arcticus, B. berneri, B. edmundsi, B. floridicola B. kabyliensis, B. nasutus, B. pini, B. tuberculatus, Insulibrachys needhami, Cercobrachys etowah. C. colombianus, C. peruanicus, C. petersorum, C. serpentis, Caenoculis bishopi, C. dangi, and C. nhahoensis. The nymphs of B. flavus and B. prudens are described for the first time. The distribution, phylogeny and relationships of these genera are discussed.

The caenids possessing ocellar tubercles on the head represent a morphologically well defined group within the family. Although the genus Brachycercus was established more than 100 years ago (ARVY, 1980) no critical taxonomic treatment of this taxon has been published since then. Moreover, there has been considerable confusion concerning the proper status of the generic names Brachycercus, Caenis and Eurycaenis (cf. Campion, 1923; Berner, 1950; Jacob, 1974). Except for the widespread European species Brachycercus harrisella, the biology, life cycles, and adult habits of others are insufficiently known. EDMUNDS et al. (1976) state that "the identification of species is difficult, and the adults should be named with caution; the nymphs probably cannot be identified with the existing keys«. The only attempts to key some species have been made by NEEDHAM et al. (1935), BERNER (1950) for 5 Nearctic species, and by TSHERNOVA (1952) for 4 Far East Palearctic species. Because of specialized nymphal habits and often night activity of crepuscular adults, adequate collections of Brachycercus are not available from most parts of the world to contemplate species revision. Since the adults have few distinguishing characters, revisional studies must be based mainly on nymphs.

Recently I had an opportunity to study specimens of the genus Brachycercus in the

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collections of Florida A & M University, the University of Utah, and the University of Florida which included many undescribed and unnamed species and several genera of caenids with ocellar tubercles. While undoubtedly more species of these genera are yet to be found and described, the present study does provide a basic taxonomical treatment and summary of known distributional and ecological data.

Acknowledgements

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In listing the source of specimens, I have used the following abbreviations: CU - Cornell University, FAMU - Florida A & M University (Dr. Peters), FSCA - Florida State Collection of Arthropods (Dr. Berner), UU - University of Utah (Dr. Edmunds), IE - Institute of Entomology, Czechoslovak Academy of Sciences (T. Soldán).

SYSTEMATICS

Keys to the genera of the Caenidae with ocellar tubercles

Mature nymphs

- 2 (1) Both maxillary and labial palps 2-segmented (Figs 38—45); femora narrow, at most twice as wide as than tibiae (Figs 125—129), fore coxae widely separated; abdominal spines on segments II—VII, II—VIII, III—VI, III—VII or III—VIII (Figs 131—166).
- 4 (3) Pedicel at least 1.5—2.0 times longer than scape (Figs 9—12, 16), anterior margin of mesosternum flat, without bristles; spines on segment VI posterolateral, not bent medially (Figs 131—156); legs with bristles shorter than tibiae (Figs 121—123).

Adults

- 1 (2) Pedicel only slightly longer than scape or equal in length (Fig. 171); abdominal spines on segment VI considerably bent dorsally; eggs spindle-shaped, 4—6 times longer than broad (Fig. 250), chorion with 4—6 rounded and broad costae (Fig. 251) Cercobrachys gen. n.
- 2 (1) Pedicel at least 1.5—2.0 times longer than scape (Fig. 172); abdominal posterolateral spines on segment VI slightly bent dorsally; eggs oval, 2—3 times longer than broad, chorion with numerous costae (Figs 246—249).

Brachycercus Curtis

Brachycercus Curtis, 1834: 122. Lestage, 1924: 61; Needham et al., 1935: 639.

Brachycercus (partim), Berner, 1950: 187. Tshernova, 1952: 284. Burks, 1953: 48. Berner, 1959: 12. Thew, 1960: 202. Leonard & Leonard, 1962: 37. Jacob, 1974: 96. Edmunds et al., 1976: 264.

Caenis (partim), Stephens, 1835: 61. Pictet, 1843—1845; 283. Eaton, 1861: 97. Eaton, 1884 (1883—1888): 141. Klapálek, 1909: 15. Esben-Petersen, 1910: 88. Lestage, 1916: 376.

Eurycaenis Bengtsson, 1917: 186. Ulmer, 1920: 122. Ulmer, 1929: 16. Schoenemund, 1930: 62. Traver, 1932: 139. Mikulski, 1936: 158.

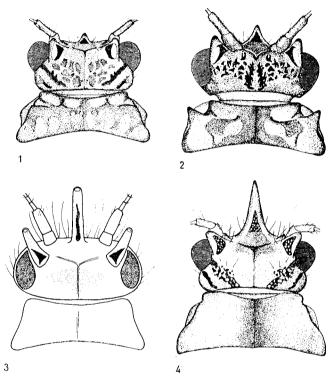
Type species: Brachycercus harrisella Curtis, by monotypy; type locality England.

Species included: B. arcticus sp. n., B. berneri sp. n., B. edmundsi sp. n., B. flavus Traver, B. floridicola sp. n., B. harrisella Curtis, B. kabyliensis sp. n., B. lacustris (Neednam), B. maculatus Berner, B. magnus Tshernova, B. nasutus sp. n., B. nitidus (Traver), B. pallidus Tshernova, B. pini sp. n., B. prudens (McDunnough), B. tuberculatus sp. n., B. tubulatus Tshernova.

Mature nymph: Body length 4-10 mm, length of cerci about 1/2 of body length. Body broad and flattened. Head with three conspicuous conical ocellar tubercles without bristles and pointed at apex and produced into distinct posterolateral lobes. Antennal pedicel at least 1.5-2.0 times as long as scape, sparsely covered with bristles. Mandibles with marginal tufts of setae. Maxillary and labial palps 2-segmented. Prosternum broader than long, fore coxae widely separated. Pronotum sometimes with a pair of lateral spines. Abdominal segments II-VI or III-VI with posterolateral spines bent dorsally, spines of segments VIII and IX absent or reduced. Legs slender, femora at most twice broader than tibiae, fore legs relatively short, middle and hind legs longer. Tibiae and tarsi approximately equal in length; claws slender, not hooked, without denticulation. First gill 2-segmented, gill cover mostly asymmetric with smooth triangular ridge, lamellate gills with fringe bifid or multifid.

Adult: Body length 3-10 mm, length of wings 3-8 mm; cerci 20-25 mm in males, 4-6 mm in females. Pedicel at least 1.5-2.0 times longer than scape not tapered toward flagellum. Prosternum twice broader than long with fore coxae

widely separated. Abdomen relatively small and contracted, lateral spines of segments V—VI prominent, bent dorsally or flat. Forceps foil-like with medial depression, pointed apex without tufts of hairs. Penis lobes almost entirely fused, base of penis with a pair of short spines. The eggs with one polar cap; chorion with a large number of costae. Micropyle linear, situated in, or adjacent to, a chorionic costa or transversing the space between two costae; sperm guide lacking (cf. Koss & EDMUNDS, 1974).

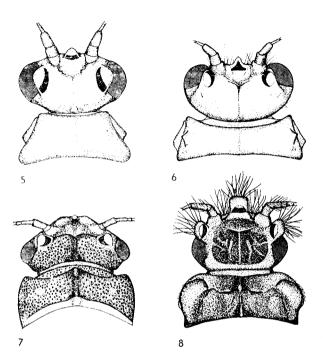


Figs 1—4: Head and pronotum of nymphs of *Brachycercus*. 1 - *B. floridicola*. 2 - *B. nitidus*. 3 - *B. tubulatus* (according to Tshernova, 1952). 4 - *B. nasutus*.

Distribution: Holarctic. In the Palaerctic known from Europe and Far East USSR(Amur basin) but undoubtedly distributed also in Western Siberia. North to Scandinavia (BRITTAIN, 1972; ITÄMIES et al., 1979) and the North Dvina river basin (TSHERNOVA, 1940). South to Balcan (Rusev, 1966a, 1966b, 1968). In the Nearctic, widespread in eastern and central regions; west to Utah and Idaho, south to Louisiana, Florida, and Georgia (BERNER, 1959; EDMUNDS et al., 1976); Some species inhabit the arctic region as well - Alaska and the Mackenzie river basin (Wiens et al., 1975). In the Nearctic the distributional patterns of *Brachycercus* resemble the upper boreal distribution.

Differential diagnosis and discussion: *Brachycercus* can be distinguished from all genera of the Caenidae by the following combination of characters. In the nymphs (1) pedicel at least 1.5 - 2.0 times longer than scape, (2) ocellar tubercles

well developed, (3) head with distinct posterolateral lobes, (4) maxillary and labial palps 2-segmented, (5) fore coxae widely separated, prosternum broad, (6) legs long and slender; femora at most twice broader than tibiae and with short bristles; tibiae approximately as long as tarsi; claws without teeth, (7) posterolateral spine of segment VI not bent medially, (8) egg chorion with costae; costae numerous;



Figs 5--8: Head and pronotum of nymphs. 5 - Cercobrachys petersorum. 6 - C. etowah. 7 - Caenoculis bishopi. 8 - Insulibrachys needhami.

one polar cap. In the imago the characters (1, 5, 7, 8) are well apparent and represent the only critical distinguishing features. The ratio of fore leg segments varies within a genus. Male genitalia of *Brachycercus* cannot be distinguished from those of the related *Cercobrachys* nor from the relatively unrelated *Tasmanocoenis* (foil-like forceps with medial depression), which have typical *Caenis*-like nymphs. As far as the wing venation is concerned, females of *B. edmundsi* (Fig. 168) cannot be separated even from females of Leptohyphinae using the MA₁ and MA₂ symmetrical fork as the only critical character (cf. EDMUNDS et al., 1976). For critical distinguishing characters between *Brachycercus* and *Insulibrachys* see discussion of the latter (p. 333).

The adult of *Brachycercus* was described by Curtis (1834), based on the finding of M. Harris (Arvy, 1980), and *B. harrisella* became the type of the genus by monotypy. Stephens (1835), erecting the genus *Caenis*, proposed two »sections«: *Caenis* (long cerci) and *Brachycercus* (short cerci). Curtis (1837) fixed the type species of

Caenis and of Brachycercus (B. harrisii = B. harrisella). Subsequent authors, because of their recognition of the length of the cerci as a secondary sexual character, included the short-tailed Brachycercus in the genus Caenis, despite priority, on the ground that the name Brachycercus was unsuitable. As shown by Jacob (1974), the name Oxycypha Burmeister, 1839, formerly synonymized with Brachycercus, is a junior synonym of Caenis Curtis, 1834. Berner (1950) discusses the relationships between the names Eurycaenis Bengtsson, 1917, Ordella Campion, 1923, and Caenis Curtis, 1834 in detail. The name Eurycaenis is a junior synonym of Brachycercus and Ordella falls into synonymy with Caenis.

The 17 species are considered here to be included in the genus *Brachycercus*. There is no information concerning the dubious species *Brachycercus tenellus* Navás from Argentina. The holotype is probably not preserved; Dr. J. Alba (pers. comm.) informed me that type material of this species does not occur in the Navás' collection in Spain. According to Thew (1960) this species may not belong to *Brachycercus* at all.

Keys to the species of Brachycercus

Mature nymphs

1 At least one protuberance near the anterior margin of metasternum present; pro- and/o metasternal tubercles present or absent	
— All thoracic sterna flat, no protuberances developed	6
2 Posterior margin of head rounded; labrum (Fig. 48) and hypopharyngeal superlinguae (Fig.	
61) produced into distinct lateral lobes; scape about 1.5 times longer than pedicel (Fig. 17)	
body yellowish pale B. pruden	
- Head with distinct posterolateral lobes; labrum oblong-shaped, without distinct lateral lobes	
hypopharyngeal superlinguae rounded; scape about twice longer than pedicel; body brow	
nish dark	
3 Posterolateral spines of abdominal segments VI and VII overlapping in dorsal view (Fig	
135, 145)	
- Posterolateral spines of abdominal segments VI ans VII not overlapping in dorsal view	
(Figs 143, 153)	
4 Gill cover asymmetric, produced posterolaterally (Fig. 86); posterolateral spine of segment 1	
reduced or inconspicuous (Fig. 135); posterior meso- and metasternal protuberance lacking.	
— Gill cover nearly symmetrical, rounded posterolaterally (Fig. 91); posterolateral spine of	
segment II conspicuous, larger than that of segment III (Fig. 145); posterior meso- and meta	
sternal protuberances well developed	
5 Posterolateral spines of segments V and VI narrow (4 times longer than wide) and well se	
parated in ventral view (Fig. 144); posterior mesosternal protuberance strongly reduced	
inconspicuous	
- Posterolateral spines of segments V and VI wide (2.5 times longer than wide) and conti	
guous in lateral view (Fig. 153); posterior mesosternal protuberance well developed, as large	
as the anterior one	í

6	Pronotum with a pair of well developed lateral spines (Fig. 2)
	Lateral spines of pronotum absent (Figs 3, 4) or pronotum with a pair of transverse rid-
	ges (Fig. 1) 9
7	Lateral ocellar tubercles longer than the eye width; gill cover nearly symmetrical, its hind
′	
	margin convex; spines of segments III—V wide (twice or 2.5 times as long as broad at base)
	and rounded at apex, those of segment VI overlapping segment VII in dorsal view, spines
	of segments VI—IX reduced or absent (Fig. 166)
	Lateral ocellar tubercles as long as the eye width; gill cover distinctly asymmetrical with
	paler posterolateral lobe, its hind margin straight (Figs 85, 229); spines of segments III-V long
	(3—5 times as long as broad at base), those of segment VI not overlapping segment VII in
	dorsal view. Spines of segments V—IX well developed, large (Figs 137, 138, 237, 238) 8
8	Body length 7.0—9.0 mm; pedicel less than twice longer than scape (3.2 : 1.7); head and
	thorax dark brown, abdominal terga brownish; no posterolateral spines of segment II, spines
	of segments III-VI 3 times as long as wide at base, spines of segment VI rounded at apex
	B. nitidus
	Body length 4.5—6.0 mm; pedicel more than twice longer than scape (2.3 : 1.1); head and
	thorax yellowish brown, abdominal terga whitish; posterolateral spines of segment II well
	developed, spines of segment VI pointed at apex (Fig. 237) B. berneri sp. n.
9	Frontal ocellar tubercle at least 1.5 times longer than lateral ones and twice as long as eye
	width, conspicuous, directed forewards (Figs 3, 4); pronotum always without transverse
	ridges
	-
	Frontal ocellar tubercle approximately as long as lateral ones, tubercles at most 1.5 times
	longer than eye width (Fig. 1); transverse ridge on pronotum absent or present 11
10	Frontal ocellar tubercle twice longer than lateral ones, tubercles conical, pointed or bluntly
	pointed at apex (Fig. 4); posterolateral spine of segment 11 larger than those of segments
	111—VII (Figs 149, 150) B. nasutus sp. n.
	Frontal ocellar tubercle 1.5 times longer than lateral ones, tubercles tubular, rounded at
	apex (Fig. 3); posterolateral spine of segment 11 reduced, much smaller than those of seg-
	ments III—VII B. tubulatus
11	Pronotum with well developed transverse lateral ridges near the anterior margin (Fig. 1) 12
	Pronotum smooth, lateral ridges absent
12	Gill cover distinctly longer than wide (length: width 1.6: 1.3) asymmetrical, produced
	posterolaterally (Fig. 87); lateral margin of segment II straight, spines of segments III—VI
	narrow, 4—5 times longer than wide at base (Figs 133, 134)
_	Gill cover very slightly longer than wide (length: width 1.9: 1.8) symmetrical, rounded
	posterolaterally (Figs 93, 227); lateral margin of segment II convex rounded with wide trian-
	gular spine (Figs 147, 235), spines of segments III-VI wider, three times longer than wide
	at base (Figs 147, 235)
13	Pedicel less than twice longer than scape (1.7:0.9) lateral ocellar tubercles bent forewards
	(fore margin concave in lateral view); spines of segment VI overlapping segment VII para-
	lelly (longitudinal axis of spines of VI paralell to that of abdomen) (Fig. 147) B. pini sp. n.
	Pedicel more than twice longer than scape (4.2: 1.9) lateral ocellar tubercles straight (fore
	margin straight or convex in lateral view); spines of segment VI overlapping distinctly over-
	lapping segment VI (longitudinal axis of spines of VI at 45° angle with the axis of abdomen)
	(Fig. 235)
	· -
14	Ocellar tubercles low, regularly triangular and equal in length at most to eye width; legs
	distinctly dark-banded on each segment (Fig. 123)
	Ocellar tubercles prominent, 1.5 times as long as eye width; legs unicolorous, without dark
	bands
1.5	
13	Spines of segment II equal in length and shape to those of segments III—VI, spines of segment

VIII well developed (Figs 139—140); gill cover with conspicuous dark spot near the base

B. flavus

Spines of segment II smaller and wider at base than those of segments III—VI, spines of segment VIII minute (Figs 141, 142); gill cover without spots, dark, unicolorous ... B. lacustris

Body pale, lateral ocellar tubercles rounded; gill cover pale with conspicuous dark brown spot; posterolateral spines of segment II equal to those of segment III: spines of segment VII overlapping segment VIII in dorsal view (Fig. 241) ... B. kabyliensis sp. n.

Body dark, lateral ocellar tubercles conical; gill cover brownish, unicolorous; posterolateral spines of segment II shorter by 1/2 than segment III, spines of segment VII not overlapping in dorsal view (Fig. 155) ... B. magnus

Adults

1	Body length 5-8 mm in males, 6-10 mm in females; abdominal terga light brown or dark
	brown, thorax pitch brown or blackish
_	sometimes with dark markings, thorax yellowish, light brown to red brown
2	Abdomen lighter than thorax, middle and hind legs whitish or yellowish; costae on chorion
	1—3 times broader than intercostal spaces (Fig. 247) B. harrisella
_	Abdomen of the same color as thorax, middle and hind legs light brown or brownish; costae on
3	chorion approximately as wide as intercostal spaces (Fig. 249)
,	lighter; penis oblong-shaped with straight lateral margins, spines near base rounded at apex
	(Fig. 178) B. nitidus
—	Abdominal terga white with dark stippling on terga I—IV or with dark spots; penis triangular
	or rounded, its lateral margins convex or concave, spines near base pointed
	Distinct lateral or medial dark spots on abdominal terga I – II and VII – X
	Abdominal terga without distinct spots with dark stippling at most
ر	conspicuous dark brown spot; posterior margin of pronotum dark brown; penis with unpaired
	pointed spine in the middle (Fig. 233)
_	Antennal pedicle slightly less than twice longer than scape; scape unicolorous, without spot,
	posterior margin of pronotum pale, penis without unpaired pointed spine in the middle 6
6	Body length about 5 mm; abdominal terga 1—II and VII—X with dark brown spots and with
	a pair of diffuse lateral spots; penis as long as wide, slightly produced anterolaterally with
	convex posterior margin (Fig. 176); costae on chorion approximately as wide as intercostal spaces (Fig. 248)
	Body length 3—4 mm; abdominal terga I—II (spots sometimes reduced) and VII—X with
	dark spots forming a band in the middle, lateral spots lacking. Penis wider than long, rounded,
	not produced anterolaterally, with posterior margin slightly arcuately incurved; costae on
	chorion wider than intercostal spaces (Fig. 244)
7	Abdominal terga I—III with dark stippling; penis only slightly produced posterolaterally
	with slightly concave posterior margin and sclerotized structure in the middle (Fig. 174);
	chorionic costae narrow, intercostal spaces 4 times wider (Fig. 246)
_	All abdominal terga white, unicolorous; penis distinctly produced into posterolateral lobes, without triangular structure in the middle, posterior margin straight or convex; chorionic
	costae at most half as wide as intercostal spaces
8	Pedicel 1.5—1.7 times longer than scape; posterolateral projections of penis rounded; thorax
	yellowish 9

- Pedicel twice the length of scape; posterolateral projections of penis bluntly pointed; thorax brownish
 B. pallidus

Brachycercus arcticus sp. n.

(Figs 10, 47, 70, 79, 112, 122, 143, 144)

Mature nymph: Body length 5.5 mm, length of cerci 2.1 mm. Head brown unicolorous with a group of dark spots on occiput. Ocellar tubercles longer than eye width, bluntly pointed, frontal tubercle more slender, narrower by 1/3-1/2 at base than lateral ones; tubercles equal in length. Some bristles on clypeus and genae. Pedicel covered with bristles as long as 1/2-3/4 of its length; ratio of pedicel: scape 1.8:0.9. Labrum about twice broad as long (width: length 3.0:1.6), not produced laterally. Outer incisors of mandibles twice broader at base than middle ones, equal in length, with 2-3 teeth; inner incisors with hardly distinguishable teeth. Hypopharyngeal superlinguae only slightly produced anterolaterally. Segment 1 of maxillary palps twice broader than segment 2; inner margin of segment 2 slightly convex with row of bristles in apical half. Segment 2 of labial palps bluntly pointed.

Pronotum with a pair of low and bluntly pointed lateral spines, light brown, paler on the sides with dark-brown dusting in the middle. Mesonotum yellowish brown with dark smudges on posterior portion and wing pads; metanotum dark brown. Sterna dark brown. Prosternum with protuberance forming transverse ridge between coxal bases; anterior mesosternal protuberance well developed and dark pigmented, posterior one inconspicuously indicated. Metasternal protuberance absent. Fore legs (ratio femur: tibia: tarsus) 5.9:3.0:3.0 middle ones 7.9:5.0:4.7, hind legs 8.4:5.3:5.0. Tibiae and tarsi wide, femora only by 1/3 broader. Claws produced into a point, slightly bent.

Abdominal terga brown, terga VII X yellowish brown. Segment II without spines. Spines of segments III—VII narrow and bluntly pointed (about 4 times as long as wide), not overlapping in c'orsal view; spines of segments VIII and IX very small. Sterna brown, with dark bands on the sides. Gill cover slightly asymmetric with slightly produced posterolateral margin; yellowish brown, triangular ridge darker. Gills 3 6 with brownish stippling, marginal fringe paler. Cerci whitish, darker at apex.

Adult and subimago unknown.

Specimen examined: Holotype, mature nymph, USA, Alaska, Birch Creek between Big Creek and Preacher's Creek, 66°00' N, 144°50' W., August 17, 1963, J. Varley, coll. UU. Holotype in alcohol, parts on slides.

Etymology: From Latin arcticus, meaning coming from or inhabiting arctic areas.

Distribution unknown except the locality of the holotype.

Differential diagnosis and discussion: Brachycercus arcticus can be distinguished from other species of Brachycercus by the following characters: (1) ocellar tubercles longer than eye width; equal in size, (2) pedicel twice the length of the scape, (3) pronotum with a pair of lateral spines, (4) spines of abdominal segments narrow, not overlapping in dorsal view, spine of segment II minute, (5) sternal tubercles present, (6) labrum and hypopharyngeal superlinguae not produced laterally, segment 2 of maxillary palps narrow (segment 1 twice as wide), (7) posterolateral portion of gill cover only slightly produced. Although adults are unknown, the nymphs show that B. tuberculatus, B. edmundsi, and B. harrisella are related in the arrangement of ocellar tubercles and presence of sternal tubercles.

Brachycercus berneri sp. n.

(Figs 174, 179, 188, 195, 204, 207, 215, 218, 229, 237, 238)

Brachycercus sp. A (part) Berner, 1950: 191. Berner, 1958: 29, Schneider, 1967: 202, Berner, 1977: 34.

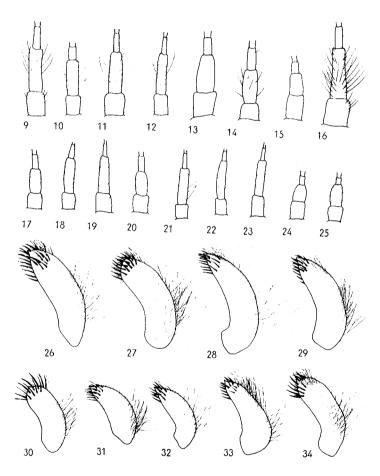
Mature nymph: Body length 5.0 (4.0 - 5.5) mm, length of cerci 2.5 (2.3 - 3.0) mm. Head whitish yellow, occiput darker with indistinct light brownish stippling. Ocellar tubercles as long as the eye width. Lateral tubercles slightly longer, but equal in width with frontal one, bluntly pointed at apex and slightly bent forewards. Genae with numerous bristles as long as scape and pedicel. Scape and pedicel whitish the ratio of pedicel: scape 1.1:2.3. Labrum more than twice as broad as long (2.9:1.3), not produced laterally. Mandibular incisors with 3 - 4 teeth, outer and middle ones approximately equal in width. Hypopharyngeal superlinguae rounded with convex lateral margins, not produced. Segment 1 of maxillary palps as long as 3/4 of segment 2. Segment 2 bluntly pointed at apex, slightly bent, inner margin concave with a row of 9—11 bristles in apical half. Segment 2 of labial palps pointed at tip with 2 transverse rows of stout spines.

Pronotum whitish of brownish yellow with a pair of small pointed spines near the anterior margin. Meso- and metanotum light brownish with numerous diffuse paler smudges. Thoracic sterna whitish yellow without protuberances. Legs whitish unicolorous with very inconspicuous darker diffuse bands near the base of each segment, outer margins of tibiae and tarsi with very long (as long as 1/2 of tarsus length) bristles, claw long, narrow and slender. Fore legs (ratio femur: tibia: tarsus) 5.7:3.2:2.7; middle legs 7.5:5.5:4.6; hind legs 8.2:6.0:5.2. Claws shorter by 1/4 than tarsus.

Abdominal terga whitish yellow, terga I, II and posterior margin of tergum X with light brown stippling; terga VII—IX whitish with very inconspicuous middle longitudinal band. Sterna of the same color as ventral side of thorax, without markings other than inconspicuous smudges. Posterolateral spines of segment II low, regularly triangular and bluntly pointed, spines of segments III—VI narrow and pointed, 4—5 times longer than wide with long bristles on the margins. No spines

overlapping abdominal segments in dorsal view. Spines of segments VII as long as those of segment III, spines of segment VII well developed. Gill cover distictly asymmetrical with produced posterolateral margin, dark brown, unicolorous, with whitish margin. Gills 3-6 oval with dark pigmented fringe. Cerci whitish or whitish yellow.

Adult and subimago: Body length 4.5 mm, length of cerci 12 mm (male), 1.5 mm (female). Head and pronotum whitish yellow, pronotum with dark stippling. Eyes black, ocelli with conspicuous black basal ring. Antennae pale, scape and pedicel unicolorous, flagellum whitish. Thorax (meso- and metanotum) greyish brown, pronotum paler. Abdomen whitish, terga and sterna I—III with dark-brown stippling,



Figs 9—34: Scape and pedicel of antennae (9—25) and segment 2 of labial palps (26—34)·9 - Brachycercus edmundsi. 10 - B. arcticus. 11, 26 - B. nitidus. 12, 34 - B. floridicola. 13, 32 - Cercobrachys petersorum. 14 - Caenoculis bishopi. 15 - Cercobrachys etowah. 16, 27 - Insulibrachys needhami. 17, 29 - B. prudens. 18, 30 - B. nasutus. 19 - B. pallidus. 20, 28 - B. tuberculatus. 21 - B. lacustris. 22 - B. pini. 23 - B. flavus. 24 - C. serpentis. 25, 31 - C. minutus. 33 - C. peruanicus.

terga and sterna IV—IX unicolorous. Wings greyish, membranes C and Sc brownish in the basal half. Fore and middle legs with inconspicuous dark stippling, hing legs paler, the ratio femur: tibia: tarsus (male) 1.5:3.0:1.5 (fore legs), middle legs 2.0:1.1:1.1, and 2.0:1.2:1.2 for hind legs. Thorax darker in females, wings translucent and colorless, stippling of first abdominal segments not so pronounced as in males. Penis longer than wide, slightly produced posterolaterally with slightly concave posterior margin. Spines near base pointed, sclerotized triangular structure apparent in the middle of penis (Fig. 174). Ornamenting of chorion unknown.

Specimens examined: Holotype, mature nymph, Florida, Liberty Co., Sweetwater Creck, April 30, 1946, L. Berner No. 2034.0 coll. FSCA; 13 nymphs, same data, coll. FSCA; paratypes: adult male, Florida, Liberty Co., Cat. No. 2-349-3, L. Berner No. 3924.0; adult female, Florida, Liberty Co., Sweetwater Cr. Cat. No. IV-1451-1, April 14, 1951, L. Berner No. 3336.1 coll. FSCA, Holotype in alcohol, parts of holotype and paratypes (male) on slides.

Etymology: Species named for Dr. L. Berner, University of Florida, Gainesville, who discovered this species many years ago.

Distribution: Southeastern Nearctic species distributed in Florida, Alabama, Georgia, and South Carolina, inhabiting the Coastal Plain, Piedmont, and Valley and Ridge physiographic provinces as defined by Berner (1977). All the localities known so far are summarized by Berner (1950, 1958, 1977) and Schneider (1967). Judging from the small number of specimens collected, this species seems to be solitary to rare where it occurs.

Differential diagnosis and discussion: B. berneri can be distinguished from the other species of *Brachycercus* by the following combination of characters: in nymphs (1) ocellar tubercles low as long as the eye width, (2) pedicel twice as long as scape, (3) pronotum with a pair of low lateral spines, (4) sternal projections lacking, (5) spines of segment II developed, spines of segments III VII long, narrow and pointed, not overlapping abdominal terga in dorsal view, (6) labrum without lateral projections, hypopharyngeal superliguae rounded, not produced, (7) gill cover asymmetric produced posterolaterally; in adults (1) antennae unicolorous, pedicel more than twice as long as scape, (2) abdominal sterna white, sterna I III with dark stippling, (3) penis longer than wide, slightly produced posterolaterally, its posterior margin concave, with sclerotized triangular structure in the middle and pointed spine near base. Adults and nymphs were associated by rearing (L. Berner). This species is related to B. pallidus (ocellar tubercles longer than the eye width, gill cover symmetrical, spines of segment VI overlapping segment VII), and B. nitidus (pedicel less than twice as long as scape; no posterolateral spines on segment II, body and abdomen darker). B. berneri can be easily distinguished from the other Florida species (B. floridicola, B. pini, B. maculatus) by presence of pronotal spines.

For a long time, there was only one species of *Brachycercus* recognized in Florida although this genus shows large species diversity just in this and closely adjacent areas. Synonymy of the Florida species described here (B. floridicola, B. pini and B. berneri) is therefore rather tentative since the names »B. maculatus«, »Brachycercus sp. A« and »Brachycercus sp.« were used indiscriminately everywhere. Recently I have received the original material of Dr. Berner enabling to redescribe true

B. maculatus and Brachycercus sp. A, of Berner (1950). However, the Berner's (1950: 192), figure of nymph of B. sp. A actually refers to a new species (B. pini) described below (no pronotal spines, symmetric gill covers with rounded posterolateral margin and spines of segment VI overlapping segment VII). I take pleasure to redescribe and to name for Dr. Berner the species Brachycercus sp. A of Berner (1950) according to original nymphal material (Sweetwat Creek, Liberty Co.) and the original description (pronotal spines mentioned) not taking into account the figure.

Brachycercus edmundsi sp. n.

(Figs 9, 51, 86, 115, 135, 136, 168, 173, 245)

Brachycercus sp. (possibly prudens McDunnough) Edmunds et al., 1963: 47.

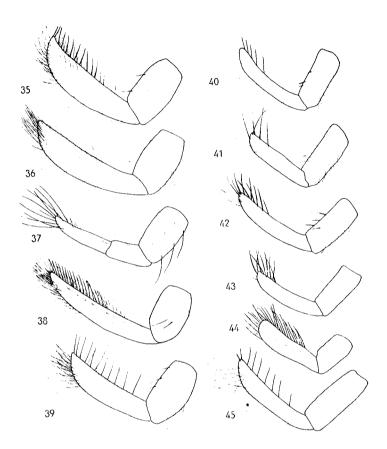
Brachycercus sp. Berner, 1959: 12. Woodbury & Argyle, 1963: 28. Edmunds et al., 1976: 256.

Mature nymph: Body length 6.9 mm, length of cerci 2.5 mm. Head dark brown with blackish brown scattered groups of spots on occiput and diffuse triangular dark spot at base of frontal tubercle. Lateral ocellar tubercles straight, frontal tubercle of the same length. Tubercles longer than the eye width, yellowish brown. Bristles on occiput, clypcus and genae slightly shorter than ocellar tubercles. Scape with fine bristles; pedicel with setae as long as a half of its length; the ratio scape: pedicel 1.3:2.2. Labrum about twice as long as broad (4.0:1.7), moderately produced anterolaterally (Fig. 51) with conspicuous marginal spines. Outer and middle incisors of mandibles approximately equal in length and width at base, inner incisors branched. Hypopharyngeal superlinguae only slightly produced. Segment 1 of maxillary palps twice as broad as segment 2. Segment 2 with straight or slightly concave inner margin with bristles.

Pronotum dark brown with darker smudges near the anterior margin. A pair of lateral spines on pronotum well developed. Meso- and metanotum with wing pads dark or pitch brown with paler smudges. Thoracic sterna light brown. Pr sternal protuberance pointed but low, anterior mesosternal one wide and rounded at apex, posterior mesosternal protuberance absent. Legs pale brown, fore legs (ratio femur: tibia: tarsus) 7.8:4.1:3.9, mic'dl: legs 10.7:7.2:6.5, hind legs 7.5:5.5:4.9. Claws of middle and hind legs short, as long as 1/3 of the length of tarsi, nearly straight.

Abdominal terga I and II light brown, terga VII—X paler, with dis olved darker band in the middle. Spines of segment II rounded and very short, visible in ventral view. Spines of segment III—VII long, narrow and pointed, spines of segments VIII and IX bluntly pointed, well developed. Sterna brown, sterna VII and IX slightly darker. Gill cover asymmetrical, with apparently produced posterolateral margin, brownish, unicolorous. Cerci pale yellowish.

Adult and subimago: Body length 9.1 mm, length of cerci 3.3 mm (female). Head dark brown, diffuse black spot between lateral ocelli. Eyes greyish black, ocelli light grey. Scape and pedicel brown, apical portion of flagellum whitish, pedicel twice as long as scape. Pronotum blackish brown or dark brown, slightly paler on sides, meso- and metanotum pitch brown. Wings translucent with browhish grey



Figs 35—45: Maxillary palp of nymphs. 35 - Brachycercus tuberculatus. 36 - B. prudens. 37 - Caenoculis bishopi. 38 - Cercobrachys peruanicus. 39 - C. etowah. 40 - B. pini. 41 - B. magnus. 42 - B. lacustris. 43 - B. nasutus. 44 - C. petersorum. 45 - B. floridicola.

longitudinal veins. Coxae brown, femora of fore legs with brown longitudinal stripes, middle and hind femora whitish. Abdominal segments brown or yellowish brown, segments I—III darker. Cerci white. Body of subimago yellowish brown or brown, thorax darker, last abdominal segments paler. Wings brownish grey or grey with fringe of setae of the same color, longitudinal veins in anterior half of wing darker. Posterolateral spines strongly bent upwards, very narrow and pointed; spines on segments III—VI as long as two segments. Eggs with chorionic costae apparently

wider than intercostal area (about 2 2.5 times). Costae often interrupted or ending in the equatorial area of the eggs, some of them connected (Fig. 245).

Adult male: unknown.

Specimens examined: Holotype, mature nymph, Wyoming, Green Riv., Sweetwater Co., June 30, 1959, G. Smith, G. Musser, coll. UU; paratype, mature nymph, same data, July 3, 1959, coll. UU, paratypes, 2 partially molted female adults, Colorado, Grand Co., Colorado Riv., Kremling, September 3, 1967, C. R. Meck, coll. FAMU; Holotype in alcohol, parts of paratypes (nymph, adult female) on slides. Further material examined: Utah, Hideout Co., Green Riv., September 5, 1948, G. F. Edmunds, coll. UU (1 nymph); Idaho, Lincoln Co., North Gooding Canal, 6 mi N of Shoeshone, July 24, 1964, S. L. Jensen, P. S. Lombardi, F. D. Isenberg, coll. UU (1 nymph).

Etymology: Species named for Dr. G. F. Edmunds, University of Utah, Salt Lake City, who discovered it a good many years ago.

Distribution: Distributed in the northwestern and southwestern states of the USA, namely in Idaho, Wyoming, Colorado and Utah (Berner, 1959; Edmunds et al., 1976) and probably also in southwestern Canada.

Differential diagnosis and discussion: B. edmundsi can be distinguished from remaining species of *Brachycercus* by the following combination of characters: (1) ocellar tubercles longer than eye width, equal length, (2) pedicel nearly twice as long as scape, (3) pronotum with lateral spines, (4) spines of abdominal segments VII - VIII overlapping in dorsal view, spines of segment II large and low, (5) prosternal and anterior mesosternal protuberances present, (6) gill cover asymmetric, produced posterolaterally. Nymphs are related to those of B. arcticus, B. tuberculatus and B. harrisella. They differ mainly in overlapping abdominal spines from B. arcticus and B. harrisella and in absence of metasternal protuberance and in body length from B. tuberculatus. Adults and nymphs of B. edmundsi were associated according to chorionic sculpturing. Adult male of this species remains unknown. Females are easily distinguishable from all known species, except for B. harrisella, by considerably larger body size (approximately 9-10 mm) and apparently darker, brownish or blackish coloration as well as by different arrangement of chorionic costae. Females of B. harrisella differ in the pale abdomen and some details of ornamentation of egg chorion.

Brachycercus flavus Traver

(Figs 23, 63, 74, 82, 89, 99, 109, 123, 139, 140, 244)

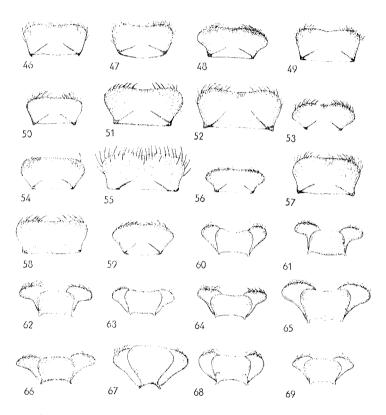
Brachycercus flavus Traver in Needham et al., 1935: 640. Berner, 1950: 189; 1959: 12. Edmunds et al., 1976: 266.

Brachycercus lacustris, Burks, 1953: 48 (nec Needham, 1918: 249).

Brachycercus species (part), BERNER, 1977: 33.

Mature nymph: Body length 4.3 (4.0-4.5) mm, length of cerci 2.1 (2.0-2.5) mm. Head dark brownish with darker diffuse spots near the eye bases. Epicranial suture bordered with light, diffuse paler spots of irregular shape on vertex and occiput. Head tubercles equal in size, as long as 1/2-2/3 of the eye width; frontal tubercle

more pointed; antennae whitish yellow, pedicel about twice longer than scape (2.8:1.5). Labrum with slight lateral lobes, its lateral margins straight or slightly concave, twice broader than long (length: width 0.6:1.4). Outer and middle mandibular incisors equal in lenth and width at base, with 2 3 bluntly pointed teeth. Segment 2 of maxillary palps as broad as 2/3 of segment 1 with sparse bristles in apical half of slightly concave inner margin. Hypopharyngeal superlinguae rounded, slightly produced laterally, lingua oblong-shaped. Segment 2 of labial palps bent and bluntly pointed at apex.



Figs 46—69: Labrum (46—49) and hypopharynx (60—69) of nymphs. 46, 68 - Brachycercus pini. 47 - B. arcticus. 48, 61 - B. prudens. 49 - B. pallidus. 50, 60 - B. nasutus. 51 - B. edmundsi. 52, 65 - B. harrisella. 53, 62 - B. tuberculatus. 54 - Cercobrachys petersorum. 55 - Caenoculis bishopi. 56, 66 - Cercobrachys minutus. 57, 67 - Insulibrachys needhami. 58 - B. nitidus. 59 - C. peruanicus. 63 - B. flavus. 64 - B. lacustris. 69 - C. etowah.

Pronotum three times broader than long, dark brownish with inconspicuous smudges on the sides and a pair of transverse ridges in the middle. Meso- and metanotum dark brownish, unicolorous. Thoracic sterna flat, brownish, anterior margin of mesosternum darker and prominent, but not forming protuberance. Legs whitish

yellow with brown stripes on femora, tibiae and tarsi (the latter stripes sometimes diffuse), coxae brown. The ratio femur: tibia: tarsus 2.2:1.3:1.3 for fore legs, 3.5:2.0:2.3 for middle ones and 4.0:2.3:2.5 for hind legs; claws brownish.

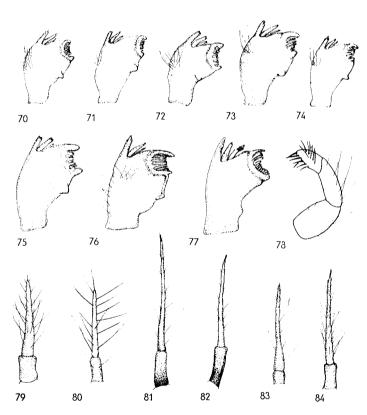
Abdominal terga light yellowish brown or yellowish, terga I, II, VIII, IX and X with medial brown band which may lack in some terga in some specimens; sterna yellowish brown with lateral brownish spots forming a pair of submarginal darker bands. Spines of segment II as long as 1/2 of that of segment III, asymmetrical, bluntly pointed. Spines of segments II—VI 2.5 times as long as broad at base, pointed at apex, spines of segment VI slightly overlapping segment VII in dorsal view. Gill I with dark brown stripe at base. Gill cover dark brownish, as long as wide, asymmetric with straight inner margin. Outer fork of triangular ridge with dark brown, alongated, conspicuous spot. Cerci yellowish brown.

Adult and subimago: Body length 4.0 (3.0 4.5) mm, length of cerci 15 (14 to 15) mm (male), 2.3 mm (subimago). Head light yellowish with slightly darker frons and blackish brown strips near the base of eyes; eyes black, ocelli greyish. Pronotum pale, brownish yellow with faint purplish brown in the middle. Meso- and metanotum light yellow, medial suture black bordered. Wings semi-hyaline whitish, transparent, Sc and R brownish, other veins pale, colorless. Wings of subimago milky greyish. Fore legs with brownish femora and tibiae, tarsi whitish yellow; middle and hind legs whitish, unicolorous. Abdominal sterna whitish yellow, sterna I III shaded with smoky brown in the middle, in some specimens with medial dark brownish stripes, terga IV, V, VI paler, unicolorous, terga VII - X with darker medial stripe. Sterna whitish yellow with a pair of submarginal greyish brown bands in subimago. Abdomen of female more whitish. Penis broad, about twice broader than long, without lateral lobes, its posterior margin rounded, slightly incurved in the middle. Forceps longer by 1/2 than penis. Polar cap of egg wide, as broad as the egg width; costae 2 3 times broader than intercostal spaces, not interrupted or forked in equatorial area.

Specimens examined: 3 paratypes, adults, Louisiana, Sabine River Ferry opp. Orange, Texas, leg. C. U. Biological Expedition, June 20, 1917, coll. CU (No. 1363.3-7). 10 nymphs, 1 male subimago, Alabama, Dallas Co., Cedar Creek 5 mi N of Minter, June 26—27, 1968, W. L. & J. G. Peters, P. T. P. Tsui, M. L. Pescador, coll. FAMU; 1 female, 2 males, Alabama, Dallas Co., Cat. No. 6-2356-3, L. Berner No. 3908.6 coll. FSCA; 2 nymphs, Georgia, Dawson Co., Cat. No. 6-2455-1, L. Berner No. 3718.9 coll. FSCA; 2 females, Georgia, Monree Ce., Cat. No. 7-1255-1 L. Berner No. 3750.6 coll. FSCA; 5 nymphs, South Carolina, Florence Co., UF Cat. No. 6-1255-1, L. Berner No. 3567-17; 1 nymph, Mississippi, Harrison Co., UF Cat. No. 8-22-54-1, L. Berner, No. 3650.2; 1 female, Mississippi, Lowndes Co., UF Cat. No. 6-1156-1, L. Berner No. 3880.18; 2 females, Mississippi, Lawrence Co., UF Cat. No. 8-1654-22, L. Berner No. 3639.4, coll. FSCA; nymph, Indiana, Arland, Greasy Creek, July 10, 1929, H. T. Spieth, coll. UU.

Distribution: Nearctic species, distributed in southeastern and northeastern areas of the USA. Originally known only from Louisiana (Louisiana-Texas border) but nymphs were collected also in Alabama, Georgia, Florida, Mississippi and South Carolina, and from an one isolated locality in Indiana. Burks (1953) found this species in Illinois.

Differential diagnosis and discussion: Critical characters distinguishing this species from other species of the genus *Brachycercus* are as follows: in nymphs (1) ocellar tubercles smaller than eye width, (2) pedicel twice longer than scape, (3) pronotum with a pair of transverse ridges, no lateral spines, (4) sternal projections lacking, fore margin of mesosternum prominent, (5) spines of segment II well developed (1/2 of those of segment III), (6) hypopharyngeal superlinguae rounded, segment 2 of maxillary palps 1.5 times broader than segment 1, (7) gill cover as long as wide with dark spot near the base; in adults (1) antennae unicolorous, pedicel twice longer than scape, (2) abdominal terga whitish with dark stripes in the middle of terga VII – X, (3) penis broader than long, rounded, without posterolateral lobes, its hind margin convex with incurvation in the middle, (4) costae on chorion 2–3 times broader than intercostal spaces. Adults and nymphs are related to *B. herneri*, *B. floridicola* and especially *B. lacustris*. Adults are easily distinguishable by the structure of the penis, nymphs are well characterized by the arrangement of posterolateral



Figs 70—84: Mandible (70—77), labial palp (78) and gill 1 (79—84) of nymphs. 70, 79 - Brachycercus arcticus. 74 - B. pini. 72 - Cercobrachys minutus. 73 - B. nitidus. 74 82 - B. flavus. 75, 83 - C. petersorum. 76 - Insulibrachys needhami. 77, 78, 80 - Caenoculis bishopi. 81 - B. lacustris. 84 - B. magnus.

abdominal spines (spines of segment II large) and gill cover (quadrate, as long as broad).

Adults and nymphs were associated by comparison of a dissected subimago from a mature nymph with the paratype material. Although all the characters of genitalia and body coloration are identical (except the presence of dark medial stripe on first abdominal segment which varies also in nymph) there are some differences in body size of adults in comparison with paratype material. This differences can be caused by dessication of pinned paratype material (see discussion of *B. lacustris* and *B. prudens*). Judging from Burks' (1953) figure of a whole nymph (see shape of posterolateral abdominal spines and gill cover), actually the species *B. flavus* is in question (instead of *B. lacustris*).

Brachycercus floridicola sp. n.

(Figs 1, 12, 34, 45, 87, 95, 106, 121, 133, 134)

Brachycercus sp., Berner, 1958: 29. Peters & Jones, 1973: 193. Pescador & Peters, 1974: 193. Brachycercus species (part), Berner 1977: 33.

Mature nymph: Body length 5.0 (4.5 – 5.5) mm, length of cerci 2.5 (2.5 – 3.0) mm. Head yellowish or yellowish brown with numerous diffuse darker smudges in the middle of occiput (may be inconspicuous or absent in some specimens) and two pairs of posterolateral oblique dark-brownish bands. Ocellar tubercles of the same color. Frontal tubercle very small (as long as 1/3 of the length of lateral ones) and bluntly pointed. Lateral tubercles regularly triangular, as long as or slightly shorter than eye width. Genae and frons with sparse setae slightly longer than frontal tubercle. Scape and pedicel narrow, yellowish, the ratio pedicel: scape 3.1 - 1.5. Labrum twice broader then long (width: length 1.4:0.6) not produced laterally with straight or slightly concave lateral margins. Middle mandibular incisors longer than outer ones, mandibles with sparce lateral bristles. Hypopharyngeal superlinguae moderately produced, their outer margins concave. Segment 2 of maxillary palps 1.5 times longer than segment 1, bluntly pointed at apex; its inner margin concave, bearing regular row of 8-10 bristles. Segment 2 of labial palps not tapered apically.

Pronotum yellowish brown or light brown with paler smudges and a pair of transversal lateral ridges. Meso- and metanotum brownish with diffuse smudges. Thoracic sterna unicolorous, without any protuberances. Fore legs (ratio femur: tibia: tarsus) 3.2:1.5:1.6, middle legs 4.5:3.2:2.7, hind legs 4.5:2.5:2.6. Legs yellowish or whitish yellow, sometimes with inconspicuous smudges, claws relatively very long and slender, tarsi twice as broad as claws at base.

Abdominal terga yellowish or yellowish brown; terga I, II, and VIII—IX sometimes with transverse diffuse dark-brown spots. Spines of segment II well developed and bluntly pointed, bent but not overlapping the lateral margin of segment. Spines of segments III—VI long and slender (4—5 times longer than wide), pointed, spines of segment VI overlapping that of segment VII; spines of segment VII as long as 3/4

of the segment length, bluntly pointed. Gill cover asymmetric, produced posterolaterally, covered with diffuse dark-brown or blackish-brown spots, paler near posterolateral projection; triangular ridge slightly darker; gills 3—5 nearly symmetric, oval with dark brown stippling, marginal fringe darker. Cerci whitish or whitish yellow.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph, Florida, Gadsden Co., Bear Creek on dirt road at bridge 8 mi S of St. Hwy 268, February 7, 1974, J. Jones, coll. FAMU; paratypes, 3 nymphs, same data, June 6, 1974, June 24, 1974, J. Jones; paratypes, 4 nymphs, same data June 2, 1969, M. L. Pescador; paratypes, 3 nymphs, Florida, Gadsden Co., Rocky Comfort Creek at 2nd bridge on dirt road, 6 mi S of St. Hwy 268, June 7, 1968, August 15, 1967, G. Cooper, J. Jones; paratypes, 2 nymphs, same data, May 21—25, 1968. M. L. Pescador, J. Jones; paratype, 1 nymph, same data, April 24, 1968. W. L. Peters, P. T. P. Tsui, J. Jones, coll. FAMU; Further material examined: Florida, Okaloosa Co., Shoal Riv., on Hwy 393 at Dorces, August 28, 1973, leg. J. Jones, G. Cooper and W. L. Peters, coll. FAMU (1 nymph); parts of nymphs paratypes on slides, holotype in alcohol.

Etymology: From Latin floridicola, meaning inhabiting the area of Florida, USA.

Distribution: Southeastern Nearctic species distributed mainly in the Coastal Plain province. Localities so far only in Florida (central and northwestern regions) but species undoubtedly distributed also in Georgia and Alabama (cf. Berner, 1977). Judging from a small number of specimens collected at known localities this species seems to be solitary to rare where it occurs.

Differential diagnosis and discussion: B. floridicola sp. n. has the following critical distinguishing characters: (1) ocellar tubercles low, slightly shorter than eye width, inequal in length (frontal tubercle much smaller), (2) pedicel twice as long as scape, (3) pronotum with a pair of transverse ridges, (4) sternal protuberance lacking, (5) labrum without lateral projections, hypopharyngeal superlinguae moderately produced, (6) spines of segment II well developed, spines of segment III – V bent but not overlapping, (7) gill cover asymmetric, produced posterolaterally. This species is related to B. lacustris, B. flavus and B. magnus (broad and small abdominal spines in all these species, spines of segment II mostly well developed) and closely related to B. herneri (symmetric gill cover, head tubercles equal in length, abdominal spines broader).

Brachycercus harrisella Curtis

(Figs 52, 65, 153, 154, 242, 247)

Brachycercus Harrisella Curtis, 1834: 3.

Caenis Harrisella, Stephens, 1835: 61. Pictet, 1843—1845: 286. Walker, 1853: 583. Eaton, 1884 (1883—1888): 146. Klapálek, 1909: 15. Esben-Petersen, 1910: 89. Lestage, 1916: 383. Pawlik, 1933: 112.

Caenis luctuosa, Eaton, 1871: 97 (nec Burmeister, 1839: 797).

Eurycaenis harrisella, Bengtsson, 1917: 186. Ulmer, 1920: 122. Lestage, 1922: 257. Ulmer,: 1927: 256, 1929: 16. Schoenenmund, 1930: 62, 102. Haberman, 1922; 225. Lehmann, 1934, 110. Mikulski, 1936: 158. Lestage, 1945: 88. Siemińska, 1954: 185. Smissaert, 1956: 89. Zelinka 1956: 389. Keffermüller, 1957; 255. Bogoescu, 1958: 98. Keffermüller, 1959: 19. Kazlauskas, 1959: 170.

Brachycercus harrisella, Pazciczky, 1914: 78. Pongrácz, 1914: 178. Lestage, 1924: 61. Tshernova, 1941: 215. Berner, 1950: 187. Kimmins, 1954: 37. Macan, 1955: 127. Landa, 1957: 363. Ujhelyi, 1959: 36. Keffermüller, 1960: 38. Macan, 1961: 10. Sowa, 1961: 10. Kazlauskas & Sanvajtite, 1962: 37. Rusev, 1962: 124. Kazlauskas, 1964: 165. Tshernova, 1964: 135. Kazlauskas, 1965: 201. Rusev, 1966a: 105; 1966b: 231. Wojcik, 1966: 112. Illies, 1967: 219. Zelinka & Rothschein, 1967: 63. Rusev, 1968: 297. Landa, 1968: 281, 1969a: 259; 1969b: 292. Remm, 1971: 39. Kachalova & Scrube, 1971: 19. Kimmins, 1971: 318. Brittain, 1972: 171. Jacob, 1974: 96. Sowa, 1975: 257, 344. Landa, 1977: 25. Puthz, 1978: 262. Itäimes et al., 1979: 89. Soldán, 1979: 226; 1981: 24.

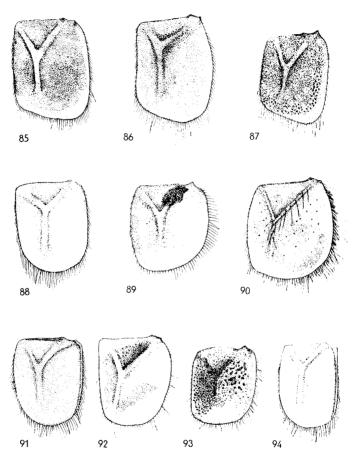
Mature nymph: Body length 7.5 (6.0-11) mm, length of cerci 3.5 (2.5-4) mm. Head brown, occiput and frons darker, epicranial suture with pale bordering. Ocellar tubercles equal in length, bluntly pointed at apex, frontal tubercle more slender. Lateral tubercles slightly bent, as long as or longer than the eye width. Antennae light yellowish, pedicel more than twice longer than scape (1.3-0.5) with numerous long bristles. Bristles on genae as long as frontal tubercle. Labrum more than twice as broad as long (6.5:2.6), convex, anterior margin with stout setae and fine bristles. Outer mandibular incisors twice as broad as middle ones at base; middle incisors as long as or longer than outer. Incisors with 1-3 bluntly pointed teeth. Inner incisors narrow (shorter by 1/3 than the middle one) with numerous bristles, lateral bristles of mandibules well apparent. Hypopharyngeal superlinguae triangular, lateral margins slightly concave, bearing regular row of stout bristles in apical half. Segment 2 of labial palps nearly symmetrical, tapered apically, with tip produced into a point.

Pronotum with a pair of well-developed lateral spines, some specimens also with a pair of transverse ridges in the middle, dark brown with diffuse paler smudges. Meso- and metanotum darker, wing pads paler. Thoracic sterna brownish. Transverse prosternal protuberance well developed, covered with long bristles; anterior mesosternal protuberance narrow; symmetric and lower with a very wide base; metasternal protuberance lacking or very slightly indicated. Fore legs (ratio femur: tibia: tarsus) 1.7:0.8:0.8, middle ones 2.3:1.5:1.4, hind legs 2.7:1.5:1.5. Legs yellowish brown, claws darker, relatively short (1/3 of tarsi) and wide at base.

Abdominal terga light brown or yellowish brown, terga I-II darker. Spines of abdominal segment II triangular, low with wide base, sharp spines near gill cover base well developed; spines of segments III-VII wide, asymmetrical and not overlapping in dorsal view, about 3 times longer than wide, Gill cover slightly asymmetrical, posterolateral lobe inconspicuous, dark brown, lighter near outer margin, triangular ridge prominent, well developed. Hind margin slightly concave in some specimens; gills 3-6 triangular, bluntly pointed, anterior margin straight with marginal and fringe dark brown stipling. Cerci yellowish brown, darker at base, with paler setae.

Adult and subimago: Body length 7.5 (5.5-9) mm, length of cerci 25 (22-38) mm (male), 4.5 (4-6.5) mm (female). Head and pronotum dark brown, frons blackish. Eyes black, ocelli with conspicuous black rings. Antennae brown (scape and pedicel

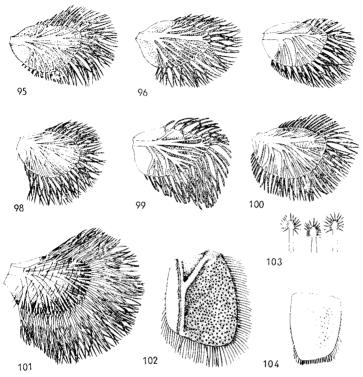
with paler smudges) flagellum whitish except base. Thorax dark brown, sterna paler with yellowish lateral margins and coxal areas. Wings translucent (grey in subimago), membranes C and Sc also translucent or slightly milky, veins C, Sc and Rs brownish, other veins greyish. Legs yellowish or light brownish, femora dark bordered, especially those of fore legs. Legs of female whitish; legs of subimago dark brown. The



Figs 85—94: Gill cover of nymphs, 85 - Brachycercus nitidus, 86 - B. edmundsi. 87 - B. floridicola. 88 - B. prudens. 89 - B. flavus. 90 - Insulibrachys needhami. 91 - B. tuberculatus. 92 - B. nasutus. 93 - B. pini. 94 - Cercobrachys serpentis.

ratio femur: tibia: tarsus (male) 1.5: 4.0: 2.5 for fore legs, 1.6: 0.8: 0.7 for middle ones, 2.0: 1.0: 1.1 for hind legs. Abdominal terga I-VI of male and subimago light brown with numerous minute lighter spots, and paler sides, terga VII-IX of the same color with a pair of oval light spots on sides. Sterna brown with blackish stippling, unicolorous, sternum IX darker. Abdomen in females whitish yellow, unicolorous. Posterolateral spines of segments IV-VI not overlapping, longer than segment length. Forceps base with a pair of anteriorly directed, pointed spines

and a pair of longitudinal, triangular whitish spots. Penis broader than long with distinct posterolateral rounded lobes, its posterior margin convex. Penis ornamented with blackish markings in the middle. Forceps about 1.5 times longer than penis, darker at base, pointed at apex. Chorion with longitudinal costae 2-3 times broader than intercostal spaces. Costae straight, only exceptionally connected or interrupted in the equatorial area (Fig. 247).



Figs 95—104: Gill 3 (95—101), gill cover (102, 104) and branched setae on gill cover (103). 95 - Brachycercus floridicola. 96 - B. nasutus. 97 - B. lacustris. 98 - Cercobrachys etowah. 99 - B. flavus. 100, 102, 103 - Caenoculis bishopi. 101 - Insulibrachys needhami. 104 - Cercobrachys petersorum.

Specimens examined: 3 males, 2 females, 5 subimagos, 40 nymphs, Czechosłovakia, South Slovakia, Ipel Riv., Lela, May 25, 1975, T. Soldán; 1 female, 8 nymphs, East Slovakia, Latorica Riv., Leles, July 1, 1974; T. Soldán; 10 nymphs, North Bohemia, Ploučnice Riv., Mimoň, May 20, 1954, V. Landa, coll. IE; 130 nymphs, 2 subimagos, USSR, Usa Riv., Batchandi, July 5, 1965, V. N. Novikov, coll. IE.

Distribution: Widely distributed all over the Europe except true Mediterranean area (reported only from France by Lestage, 1924) but present in Balcan (Rusev, 1962, 1966a, 1966b). Many localities from Central Europe given by Lestage (1924), Lehmann, (1934), Schoenemund (1930), Mikulski (1936), Keffermüller (1957, 1959, 1960), Landa (1969), especially from Poland, Germany, and Czechoslovakia. Distributed also in Estonia, Lithuania and Latvia (Kazlauskas, 1964, 1965; Remm, 1971). Its occurrence in the Alps and adjacent region doubtful (cf. Puthz,

1978). In Scandinavia known from Norway (BRITTAIN, 1972) and from localities near the Polar circle (Oulu) in Finland (ITÄIMES et al., 1979). TSHERNOVA (1941) reports this species from the Petchora river basin. Eastern and southeastern limits of distribution of *B. harrisellus* unknown. Most probably distributed also in the Volga basin, USSR, According to Sowa (1975) the distribution of this species bolongs to North-Central European type.

Differential diagnosis and discussion: B. harrisella differs from other Brachycercus species by the following combination of characters: in nymphs (1) ocellar tubercles longer than eve width, equal in length, (2) pedicel more than twice longer than scape, (3) pronotum with lateral spines, (4) spine of segment II large and low, spines of segments VI-VIII not overlapping in dorsal view, (5) prosternal and anterior mesosternal protuberance present, (6) gill cover nearly symmetrical; in adults (1) antennae with brown scape and pedicel, flagellum whitish, (2) abdominal sterna brown in males, whitish or yellowish in females, (3) penis broader than long with distinct posterolateral lobes and convex hind margin, two spines at base, (4) costae on chorion 2-3 times broader than intercostal spaces. Presence of thoracic sternal protuberances in nymphs shows that this species is related to B. arcticus, B. tuberculatus, B. prudens and especially to B. edmundsi (abdominal spines overlapping in dorsal view, gill cover apparently asymmetrical). Nymphs differ from B. tuberculatus in absence of metathoracic protuberance, from B. arcticus in large body size and the arrangement of posterolateral abdominal spines. Known adult males of remaining species can be distinguished from males of B. harrisella by considerably smaller (3-5 mm) body size, paler coloration of abdomen and different arrangement of posterolateral penis projections. Males of B. pallidus, although having brownish abdominal terga, differ by having a straight posterior margin of penis, which is whitish without markings, and by coloration of sterna. Females of B. edmundsi differ from those of B. harrisella in paler coloration of abdomen; females of other species differ in smaller body size and different arrangement of chorionic costae.

Brachycercus kabyliensis sp. n. (Figs 180, 181, 187, 201, 208, 214, 217, 228, 241)

Mature nymph: Body length 5.9 mm, length of cerci 3.1 mm. Head whitish yellow, occipital suture dark brownish bordered. Lateral ocellar tubercles slightly bent anteriorly, frontal tubercle shorter by 1/5. Tubercles longer than the eye width, brownish. Bristles on genae longer than ocellar tubercles. Scape without bristles; pedicel with setae as long as 1/3 of its length; the ratio scape: pedicel 6.7: 1.5. Labrum more than twice as broad as long (2.6: 1.2), moderately produced anteriorly with conspicuous marginal spines. Outer and middle incisors approximately equal in length and width at base, inner incisors branched. Hypopharyngeal superlinguae only slightly produced. Segment 1 of maxillary palps moderately broader than segment 2. Segment 2 with apparently concave inner margin with 9-10 bristles.

Pronotum unicolorous, whitish yellow, with inconspicuous darker smudges. Pro-

notal spines absent. Meso- and metanotum with wing pads of the same color, metanotum with brown stippling in the middle. Sternal protuberances absent; prosternum with a group of stout bristles in the middle. Legs whitish, unicolorous, fore legs (ratio femur: tibia: tarsus) 5.0:2.7:2.7, middle legs 7.5:4.9:4.5, hind legs 7.6:4.5:4.7. Claws of middle and hind legs short, as long as 1/3 of the length of tarsi, nearly straight.

Abdomen whitish, unicolorous. Spines of segments II-V approximately equal in size, pointed and bent posteriorly; spines of segments VI and VII strongly bent, medially overlapping segments VII and VIII in dorsal view; segment VII and IX with reduced posterolateral spines. Gill cover nearly symmetrical, with slightly produced inner margin, behind triangular ridge intensively dark brown medial spot. Cerci whitish, apical part with dark brown stippling.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph, Algeria, Wilaya de Tizi-Ouzu, Oued Isser, Isser-ville, October 5, 1981, T. Soldán, coll. IE; paratype, younger nymph, Alger, Wilaya de Tlemcen, C2-A, J. Gagneur, coll. IE. Holotype in alcohol, parts on slide.

Etymology: From Latin Kabylia, a name of the costal region in central Algeria.

Distribution: Apparently restricted to a maritime humid zone of North Africa, probably very fare.

Differential diagnosis and discussion: B. kabyliensis can be distinguished from remaining species of Brachycercus by the following combination of characters: (1) ocellar tubercles longer than eye width, frontal tubercle shorter, (2) pedicel twice as long as scape, (3) pronotum without lateral spines, (4) spines of segment II well developed, spines of segments VI and VII overlapping in dorsal view, (5) sternal protuberances absent, (6) gill cover nearly symmetrical, produced posteromedially. This species is related to Palearctic species B. magnus and Nearctic species B. pini, B. floridicola and B. flavus. It can be distinguished mainly by pale body color, long head tubercles, overlapping spines of abdominal segments and the arrangement of gill cover and pronotum.

Brachycercus lacustris (NEEDHAM)

(Figs 24, 42, 64, 81, 97, 105, 141, 142, 176, 248)

Ephemerclla sp., Needham, 1908: 263.

Caenis lacustris NEEDHAM, 1918: 249.

Eurycaenis pallida IDE, 1930: 218 (nec Tshernova, 1928: 114, preoccupied name). McDunnough, 1931: 264. Traver, 1932: 139.

Eurycaenis idei LESTAGE, 1931: 119 (new name for pallida IDE).

Brachycercus idei, Needham et al., 1935: 641. Lyman, 1944: 3 (idei — lacustris). Berner, 1950: 190; 1959: 12. Leonard & Leonard, 1962: 38. Koss & Edmunds, 1974: 341. Edmunds et al., 1976: 266.

Mature nymph: Body length 5.0 (4.5-6.5) mm, length of cerci 1.8 (1.5-2.8) mm. Head brownish black or pitch brown, occiput light brown, epicranial suture bordered yellow. Ocellar tubercles triangular, low, at most as long as the eye width, yellowish

brown. Lateral tubercles bluntly pointed or rounded, frontal one pointed. Antennae pale, pedicel with several long bristles. The ratio scape: pedicel 0.7:1.8. Labrum nearly three times broader than long (3.4:1.2) with a pair of anterolateral groups of branched bristles. Outer and middle incisors of maxillae equal in length and nearly equal in width at base; inner incisors wide, shorter by 1/3 than middle ones and distally rugged. Hypopharyngeal superlinguae with produced and rounded anterolateral portions. Segment 2 of maxillary palps with convex outer margin and slightly concave inner one; a group of bristles on bluntly pointed apical portion. Segment 2 of labial palps produced into a point with a group of stout bristles at apex forming only a single irregular transverse row.

Pronotum yellowish brown or light brown without lateral spines, more than three times broader than long (width: length 3.8:1.2). Meso- and metanotum yellowish brown with diffuse darker smudges, wing pads of the same color. Thoracic sterna flat, without protuberances, mesosternum dark brown, metasternum paler. Fore legs (ratio femur: tibia: tarsus) 6.1:3.4:3.4, middle ones 8.4:5.5:5.5, hind legs 8.0:5.1:5.1. Coxae and femora light brown in basal half, tibiae and tarsi yellowish or whitish with brown stripes at base. Claws pale, bent and about 1/3-1/2 as long as tarsi.

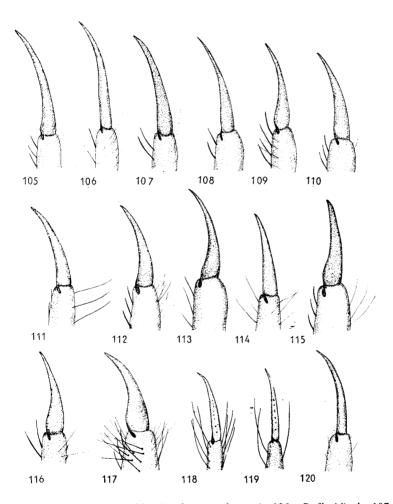
Abdominal terga whitish yellow, terga I and II darker. Dark brown triangular spots in the middle of terga I, II, VII-IX, a pair of rust brown strokes situated anterolaterally on terga VII-IX. Segment II with triangular rounded spines as long as 1/3 of those of segment III. Spines of segments III-VI pointed, spines of segment VI not overlapping segment VII in dorsal view. Terga II-IX yellowish brown with dark brown stippling. Gill cover light brown, whitish around the margin, anterior portion of triangular ridge dark brown or pitch brown, asymmetrical, its inner margins nearly straight, outer margins rounded, convex; gill 3-6 rounded, nearly oval with dark stippling. Cerci unicolorous, yellowish brown.

Adult and subimago: Body length 4.5 (4.0-4.5) mm, length of cerci 17 (15-18) mm (male), 4.0 (3-4) mm (female). Head and pronotum whitish yellow, occiput with a pair of v-shaped diffuse spots on sides near eye bases, antennae yellowish, unicolorous. Thorax darker, light brown, mesonotum with a pair of short dark brown strips. Prosternum with transverse dark-brown stippling in the middle, meso- and metasternum brownish. Wings translucent or slightly milky, veins C, Sc and R dark bordered, membrane C and Sc greyish; other veins translucent. Legs whitish yellow, coxae darker, fore femora brownish. The ratio femur: tibia: tarsus (male) 1.5:3.8:2.6 for fore legs, 2.6:1.5:1.5 for middle ones and 2.7:1.5:1.5 for hind legs. Abdominal terga whitish, terga I-II and VII-IX with dark band in the middle, terga III-IX with darker sides and darker posterior margins. Sterna whitish, unicolorous without markings, sternum IX slightly darker. Posterolateral spines of segments IV-VI very narrow, 1.5 times longer than segment length, pale. Penis oblong-shaped with concave lateral margins, only slightly broader at apex than at base, with narrow posterolateral lobes; posterior margin of penis convex; a pair

of bent and divergent bluntly pointed spines near the base; forceps dark brown at base, paler in apical half, longer by 1/3 than penis. Chorion with intercostal spaces as wide as costae, costae not fused or interrupted in equatorial area. Cerci white, unicolorous.

Specimens examined: 3 nymphs, Maine, Washington Co., Schoodie brook South, August 16, 1973. T. M. Mingo, coll. FAMU; 6 males, 1 female, Michigan, St. Claire Riv., without further data, coll. UU.

Distribution: Nearctic species, distributed in the USA (NE, C) (Berner, 1959; EDMUNDS et al., 1976) and Canada (IDE, 1930); so far known from Maine, Michigan, New York, and Ontario. This species seems to have an upper boreal distribution. Report of its occurrence in Illinois (Burks, 1953) seems to be doubtful (see discussion of *B. flavus*).



Figs 105—120: Nymphal claws. 105 - Brachycercus lacustris. 106 - B. floridicola. 107 - B. prudens. 108 - B. nasutus. 109 - B. flavus. 110 - B. pallidus. 111 - Cercobrachys petersorum. 112 - B. arcticus. 113 - B. magnus. 114 - B. tuberculatus. 115 - B. edmundsi. 116 - Caenoculis bishopi. 117 - Insulibrachys needhami. 118 - Cercobrachys serpentis. 119 - C. etowah. 120 - C. peruanicus.

Differential diagnosis and discussion: Nymphs can be distinguished from other nymphs of Brachycercus by the following combination of characters: (1) head tubercles low, at most as long as the eye width, equal in length, (2) pedicel more than twice longer than scape, (3) pronotum without lateral spines, (4) thoracic sterna without protuberances, (5) spines of abdominal segments small, as long as the segment length, spines of segment II low, triangular with wide base, (6) labrum without lateral projections, legs with dark stripes, (7) gill cover nearly symmetrical with rounded and convex outer margin. Nymphs are related to those of B. pini, B. magnus, B. floridicola and closely related to B. flavus. They can be distinguished especially by the absence of pronotal ridge (from B. pini and B. floridicola), the arrangement of head tubercles and stripes on legs (from B. magnus) and by the arrangement of posterolateral abdominal spines and gill cover (from B. flavus). Adults are characterized by these characters: (1) body and antennae pale, pedicel more than twice longer than scape, (2) penis with small posterolateral lobes and a pair of divergent, bluntly pointed teeth at base, (3) chorion with costae as wide as intercostal spaces. Body coloration of adults similar to that of B. berneri, B. nasutus, B. flavus and B. prudens, but the arrangement of penis characters clearly separates them.

I have observed few differences in the color patterns of the abdomen in adults of material studied (St. Claire Riv.). Although the head coloration has characteristic spots near occiput (cf. IDE, 1930: 218 - »vertex pale medially, dark cinnamon toward the eyes«). Neither IDE (1930) nor Lyman (1944) (the only authors who studied adults) report spots on abdominal terga. There are also some differences in body length (4.0-4.5 mm) in the material studied in alcohol. IDE (1930) gives the body length 3.5 mm, length of cerci 16 mm and length of fore wing 4.5 mm for dried males so that the differences might be caused by drying. Lyman (1944), who associated nymphs of *B. lacustris* and adults of *B. idei* by rearing, does not give any measurements. The material studied by me was associated according to the arrangement of chorion. Leonard & Leonard (1962) report this species from Michigan. Their figure of a *Brachycercus* wing undoubtedly belong neither to *B. lacustris* nor any other species of *Brachycercus*. Judging from numerous cross veins it seems to refer to the genus *Tricorythodes* (Tricorythidae).

Brachycercus maculatus Berner

(Figs 183, 190, 194, 198, 202, 206, 211, 219, 221, 227, 233-236)

Brachycercus maculatus Berner, 1946: 78. Pescador & Peters, 1974: 193, 195.

Mature nymph: Body length 6.0 (5.5-6.0) mm, length of cerci 2.5 (2.5-3.0) mm. Head dark yellowish with large darker diffuse spot in the middle of frons and two pairs of posterolateral oblique dark brownish bands (inner bands large, outer ones narrow, diffuse). Ocellar tubercles yellowish. Frontal tubercle smaller (as long as 1/2 of the length of lateral ones), bluntly pointed, equal in width at base with lateral

tubercles. Lateral tubercles regularly triangular, as long as or slightly longer than eye width, straight, not bent forwards. Genae and frons with sparse setae slightly longer than lateral tubercles. Scape and pedicel narrow light yellowish; the ratio pedicel: scape 4.2: 1.9 (pedicel with several long bristles). Labrum more than twice as broad as long (width: length 3.4: 1.5), not produced laterally with straight lateral margins. Middle mandibular incisors as long as outer ones. Outer incisors twice broader at base than middle ones. Inner incisors wide, slightly shorter than middle ones. Mandibles with sparce lateral bristles. Hypopharyngeal superlinguae moderately produced laterally, their outer margin concave. Segment 2 of maxillary palps 1.5 times longer than segment 1 with stout bristles in apical third and very slightly concave inner margin; segment 1 with a group of short anteromedial bristles. Segment 2 of labial palps pointed at apex with two apical rows of stout flat bristles.

Pronotum 2.5 times broader than long, with dark anterolateral brown diffuse bands and a pair of well developed transversal ridges in anterior third of pronotum length. Meso- and metanotum light brownish with diffuse smudges. Thoracic sterna unicolorous without any protuberances. Fore legs (ratio femur: tibia: tarsus) 6.0:2.9:3.1, middle legs 7.6:4.4:5.0, hind legs 8.4:4.7:5.3. Legs yellowish, slightly darker at base of each segment, claws long and slender.

Abdominal terga yellowish with dark brown band in the middle and brownish stippling near the posterior margins. Lateral spines of segment II low and rounded. Posterolateral spines of segments III-VI wide (3.0-3.5 times longer than broad at base), bluntly pointed, considerably bent dorsally. Spines of segment VI overlapping segment VII, bent medially (their axis and body axis at 45° angle). Spines of segments VII and VIII well developed, as long as 1/3 of the segment length. Gill cover yellowish (triangular ridge with intensive dark brown stippling) nearly symmetrical with rounded posterolateral margin; gills 3-5 nearly symmetrical oval with brownish stippling, marginal fringe darker. Cerci whitish or whitish yellow.

Adult and subimago: Body length 5.0 (5.0-5.5) mm, length of ccrci 12.8 mm (male), 2.5 mm (subimago male). Head whitish yellow, frons dark brown, occiput with dark brown posterior margin, epicranial suture paralelled with brownish band, large dark brownish spots between eyes and lateral ocelli. Scape with brown spot on outer side. Thorax dark yellowish or slight yellowish brown, pronotum mottled with purplish brown, its posterior margin dark brown. Thoracic sterna brownish with darker stippling in the middle. Wings semihyaline whitish; Sc and Rs haevily shaded with purplish brown in basal half, other veins translucent (adult), wings whitish grey in subimago, fore veins of the same color. Legs light brown with smoky shading, fore femora shaded with purplish brown on outer margin, fore tibiae smoky. Abdominal terga whitish with medial transversal band and dark brown stippling near the posterior margins. Abdominal color patterns well apparent on sterna I-III, on posterior segments more diffuse. Abdominal sterna whitish or light yellowish without markings, anterior margins with dark shadings. Postero-

iateral spines of segments III-VII very well apparent in subimagoes, those of segments IV-V as long as segment VII. Forceps light brown, straight, exceeding by 1/3 posterior margin of penis; posterior margin of subgenital plate slightly convex. Penis oval with unpaired pointed spine in the middle, twice broader than long, expanded posteriorly, penis lobes nearly not distinguished in the middle of posterior penis margin. Spines near penis base pointed, 2.5 times longer than broad at base. Cerci whitish, unicolorous.

Specimens examined: 2 male subimagoes, 2 nymphs and 2 exuviae, Florida, Alachua Co., Santa Fe River, May 8, 1947, L. Berner, No. 3055.0, coll. FSCA.

Distribution: Southeastern Nearctic species so far know only from Florida (Berner, 1946, 1950, 1977; Pescador & Peters, 1974) but undoubtedly distributed also in Georgia and Alabama. Berner's (1950) map shows distribution of this species in the middle of the Florida peninsula south to Silver Springs. Pescador & Peters (1974) found *B. maculatus* also in Bear Creek and Rocky Confort Creek in Gadsden Co. This species seems to be moderately abundant where it occurs.

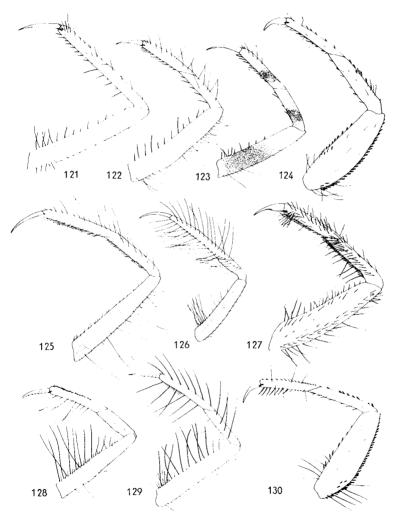
Differential diagnosis and discussion: Adults and nymphs of this species were associated by rearing (L. Berner). B. maculatus differs from the other Brachycercus species by the following combination of characters: in nymphs (1) smaller ocellar tubercles slightly longer than eye width, not bent forewards, from tubercle, (2) pedicel more than twice as long as scape, (3) pronotum with a pair of transversal ridges, (4) sternal protuberances lacking, (5) spines of segment II low and rounded, spines of segment III-VI strongly bent dorsally, those of segment VII overlapping and bent medially in dorsal view, (6) labrum without lateral projections, hypopharyngeal superlinguae moderately produced, (7) gill cover nearly symmetrical with rounded posterolateral margin; in adults (1) pedicel more than twice longer than scape with dark brown spot, (2) abdominal sterna pale with spots forming medial band, (3) penis broader than long with distinct posterolateral lobes and unpaired pointed spine in the middle. Nymphs of B. maculatus are related to nymphs of the other Florida species, closely related to those of B. pini. They are distinguished mainly by absence of pronotal spines (from B. berneri) and the arrangement of gill cover (from B. floridicola) and the arrangement of spines of abdominal segments (from B. floridicola and B. pini). Adults of B. maculatus are related to those of B. flavus and B. lacustris (abdominal spots on sterga) from which they are distinguished by the arrangement of antennae and penis (scape-pedicel ratio, coloration, presence of penis spine). Spot on scape and presence of penis spine approaches B. maculatus to B. nasutus and B. berneri, respectively. B. maculatus can by distinguished by different abdominal color patterns, pedicel-scape ratio and shape of penis from these species. The species was originally found by BERNER (1946) and correctly associated with nymphal exuviae from the same locality. Then the name B. maculatus, since it was the only known Florida species for a long time, was applied also to related species B. floridicola and B. pini. These findings have to be re-examined (cf. discussion of B. berneri).

Brachycercus magnus Tshernova

(Figs 41, 84, 113, 115, 156)

Brachycercus magnus Tshernova, 1952: 284; 1958: 64. Sukatskene, 1962: 113.

Mature nymph: Body length 5.3 mm, length of cerci 3.2 mm. Head dark brown, occiput brown blackish, eyes black. Ocellar tubercles rounded at apex; medial tubercle equal in length, lateral ones broader by 1/2 at base. Setae on genae and clypeus shorter than frontal tubercle. Scape and pedical covered with fine setae,



Figs 121—130: Fore (126, 130) and middle (121—125, 127—129) legs of nymphs. 121 - Brachycercus floridicola. 122 - B. arcticus. 123 - B. flavus. 124, 130 - Caenoculis bishopi. 125 - Cercobrachys peruanicus. 126 - C. petersorum. 127 - Insulibrachys needhami. 128 - C. serpentis. 129 - C. etowah.

the ratio scape: pedicel 0.7: 1.1. Labrum oval, about twice as broad as long with slightly concave lateral margins. Outer mandibular incisors triangular, as long as middle ones, twice broader at base. Hypopharyngeal superlinguae only moderately produced anterolaterally, rounded. Both inner and outer margins of segment 2 of maxillary palps straight, segment rounded in apical portion, not expanded apically. A group of 8-10 bristles in apical half of segment 2. Segment 2 of labial palps rounded with two transverse rows of stout bristles at apex.

Pronotum dark brown, unicolorous, more than twice as broad as long (width: length 4.0: 1.6), without lateral spines; transverse ridge well apparent in the middle. Meso- and metanotum brownish or dark brown with inconspicuous pales smudges, wind pads lighter. Prosternal protuberance absent, posterior margin of prosternum forming inconspicuous marginal ridge. Fore legs (ratio femur: tibia: tarsus) 8.0: 3.7: 3.3, middle ones 8.6: 5.7: 5.4, hind legs 9.3: 6.4: 5.5. Claws long and bent, as long as 1/3-1/2 of tarsus.

Abdominal terga unicolorous, dark brownish, terga VIII-X lighter brown, paler in the middle. Segment II with triangular, bluntly pointed posterolateral spines as long as 1/2 of those of segment III; spines of segments III-V pointed; spines of segment VI rounded and apex and broad (twice longer than broad), not overlapping segment VII in dorsal view. Sterna brown; sterna VIII-IX yellowish brown. Gill cover light brown (triangular ridge darker), asymmetrical, nearly as long as wide (length: width 8.5: 7.5), with slightly produced posterolateral portion. Gills 3-6 oval, brownish with paler marginal fringe. Cerci yellowish brown.

Adult and subimago unknown.

Specimen examined: mature nymph, USSR, Amur Riv., Makki (locality No. 44 of Tshernova, 1952), August 1948, O. A. Tshernova, coll. IE.

Distribution: So far known only from Far East, USSR. Reported from the Amur tasin (TSHERNOVA, 1952, 1958) and from the river Angara (SUKATSKENE, 1962). TSHERNOVA (1958) considers this species to be an endemic to the Amur.

Differential diagnosis and discussion: Critical characters distinguishing nymphs of this species are as follows: (1) ocellar tubercles equal in length, 1.5 times longer than eye width, (2) pedicel about 1.8 times longer than scape, (3) only short transverse ridges on pronotum, (4) sternal protuberances lacking, (5) posterolateral spines of abdominal segments wide and asymmetric, not overlapping in dorsal view, spines of segment II triangular, pointed, (6) labrum without lateral projections, (7) gill cover asymmetric, nearly as long as wide. This species is related to *B. kabyliensis*, and to Nearctic species *B. lacustris*, *B. pini*, *B. floridicola* and *B. flavus*; it can be distinguished mainly by the arrangement of head tubercles, pronotum and posterolateral spines of abdominal segments.

Brachycercus nasutus sp. n.

(Figs 4, 18, 30, 43, 50, 60, 92, 108, 149, 150)

Brachycercus sp., Schneider, 1967: 202. Brachycercus species (part), Berner, 1977: 33.

Mature nymph: Body length 4.2 (4.0-4.8) mm, length of cerci 2.5 (2.0-3.0) mm. Head yellow or yellowish brown, occiput with two pairs of posterolateral oblique dark brown stripes and diffuse dark-brown spots around the epicranial suture. Ocellar tubercles yellowish; lateral tubercles as long as eye width, rounded at apex. Frontal tubercle twice longer than lateral ones, pointed and directed forwards. Antennae pale, ratio scape: pedicel 1.0: 1.8, pedicel with a few fine hairs. Labrum twice broader than long (length: width 1.3: 2.8) with anterior margin straight, fringed with branched bristles. Outer mandibular incisors slightly longer than middle ones, equal in width, with 2-3 rounded teeth; inner incisors wide and branched at apex. Hypopharyngeal superlinguae rounded, not produced. Segment 2 of maxillary palps cylindrical with convex outer margin and apical group of bristles. Segment 2 of labial palps oval, with two transverse rows of stout apical bristles.

Pronotum whitish yellow, unicolorous, without lateral spines, about three times broader than long (3.8:1.2 length: width). Meso- and metanotum yellowish brown with inconspicuous darker smudges and bands. Diffuse dark-brown spots near the base of wing pads. Thoracic sterna including prosternum flat, without protuberance, with dark brown dusting. Fore legs (ratio femur: tibia: tarsus) 4.7:2.8:2.5, middle ones 7.8:5.3:4.8, hind legs 8.1:5.3:5.1; legs yellowish or whitish yellow, coxae and basal half of femora light brown, tibiae and tarsi with diffuse wide dark stripes near the bases. Small, circular dark-brown spots at apex of femora. Claws very slender and pointed, longer than 1/2 tarsi, yellowish.

Abdominal terga whitish yellow with dark-brown band in the middle. Both anterior and posterior margins of terga I, II, VII-IX bordered dark; tergum X with dark brown transverse stripe. Posterolateral spines of segment II conspicuous, wide at base, longer or as long as those of segment III, bluntly pointed. Spines of segments III-IV with straight posterior margins, pointed and bent at apex. Abdomen as a whole broader than thorax. Abdominal sterna whitish yellow or yellowish, sterna I-VI with triangular dark brown diffuse spots in the middle, sterna VI-IX without markings. Gill cover slightly tapered apically, whitish yellow with conspicuous triangular dark brown spot on triangular ridge and diffuse posterior brownish smudge, nearly symmetrical, outer margin more convex than inner one; gills 3-7 oval, bluntly pointed at apex with dark brown stippling. Cerci yellowish, unicolorous.

Adult and subimago: Body length 3.2 mm (male), 3.3 mm (female), length of cerci 14 mm (male), 0.9 mm (female). Thorax yellowish brown, head slightly darker, eyes black, ocelli with conspicuous black basal ring. Antennae whitish, scape and pedicel unicolorous, pedicel about 1.5-1.7 times longer than scape. Head (vertex) and pedic l of female with conspicuous dark-brown stippling. Wings trans-

lucent, C and Sc fields with respective veins darker, other veins translucent. Legs whitish yellow, femora of fore legs darker, brownish. The ratio femur: tibia: tarsus (male) 1.5:2.5:1.9, for fore legs, 2.5:1.4:1.2 for middle ones and 2.7:1.5:1.1 for hind legs. Abdomen greyish white, unicolorous, terga as well as sterna without markings. Tergum X darker, with dark-brown hind margin. Abdomen of female translucent. Penis approximately as long as wide, with conspicuous and bluntly pointed posterolateral lobes; its lateral and posterior margin slightly convex. Forceps whitish yellow, produced into a sharp point, longer by 1/3 than penis.

Specimens examined: Holotype, mature nymph, Alabama, Escambia Co., Conekuh Riv., S of Pollard, April 28, 1967, W. L. and J. G. Peters, coll. FAMU; paratype, nymph, same data, coll. FAMU; paratypes, 4 females, 1 adult male, Florida, Escambia Co., Cat. No. 8-2454-2, L. Berner No. 3656.4, coll. FSCA; Further material examined: Florida, Escambia Co., Cat. No. 8-1254-2, L. Berner No. 3630.10, coll. FSCA (1 nymph); Florida, Escambia Co., Cat. No. 8-1254-2, L. Berner No. 3630.4, coll. FSCA (1 nymph, 1 female). Holotype in alcohol, parts on slides.

Etymology: From Latin nasutus, meaning having conspicuous nose, here conspicuous and prominent frontal tubercle.

Distribution: Southeastern Nearctic species, so far known only from Florida and South Alabama (Escambia Co.) (Schneider, 1967; Berner, 1977).

Differential diagnosis and discussion: B. nasutus can be distinguished from other Brachycercus species by the following combination of characters: in nymphs (1) frontal tubercle twice longer than lateral ones and 3-4 times longer than the eye width, (2) pedicel less than twice as long as scape, (3) pronotum without spines or ridges, (4) sternal protuberances lacking, (5) posterolateral spines of segment II larger than those of segments III-VII, (6) labrum without lateral projections, (7) gill cover nearly symmetrical, tapered apically; in adults: (1) pedicel about 1.5-1.7 times longer than scape, (2) abdomen whitish without markings, (3) penis as long as wide with well developed posterolateral lobes. Adults and nymphs were associated by rearing (L. Berner). Nymphs are related in morphological characters only to B. tubulatus since the unique arrangement of head tubercles and well developed posterolateral spines of segment II single them out from all remaining known species. Well developed posterolateral lobes of penis of B. nasutus resemble those of B. harrisella and B. pallidus, species from which B. nasutus can be easily distinguished by body coloration and size.

Brachycercus nitidus (TRAVER)
(Figs 2, 11, 26, 58, 73, 85, 137, 138, 178, 243, 249)

Eurycaenis nitida TRAVER, 1932: 139.

Brachycercus nitidus, Smith in Needham et al., 1935: 82. Needham et al., 1935: 641. Wurz & Roback, 1955: 167. Berner, 1959: 12. Landa, 1969b: 292. Edmunds et al., 1976: 266. Berner, 1977: 33. Soldán, 1981: 24.

Mature nymph: Body length 7.0 (6.0-9.5) mm, length of cerci 3.2 (3.5-4.5) mm. Head yellowish brown, paler on sides, frons dark brown; vertex and occiput with

irregular dark brown spots surrounding the epicranial suture. Head tubercles equal in length, slightly longer or as long as eye width; frontal tubercle bluntly pointed, lateral ones more rounded. Genae and frons with sparce bristles as long as frontal tubercle. Antennae yellowish, the ratio scape: pedicel 1.7: 3.2. Labrum more than twice as broad as long with slightly concave lateral margins without projections. Mandibular incisors equal in length, outer ones slightly broader at base, distally rugged. Lateral group of bristles on mandibles well apparent. Segment 2 of maxillary palps, longer by 1/3 than segment 1, asymmetrical with concave inner margin, bearing bristles in apical half. Hypopharyngeal superlinguae triangular, rounded, with nearly straight lateral margins. Segment 2 of labial palps tapered apically, nearly straight.

Pronotum brown with paler smudges, darker in the middle, with a pair of well-developed, anteriorly directed lateral spines, meso- and metanotum dark brownish. Thoracic sterna brown, without protuberances. Legs brownish yellow or greyish yellow, without stripes. The ratio femur: tibia: tarsus 3.7: 1.8: 1.6 for fore legs, 5.0: 3.2: 2.8 for middle ones, 5.4: 3.5: 3.0 for hind legs. Claws 1/3 length of tarsi.

Abdominal terga I, II, VI-VIII brownish yellow with diffuse paler smudges, darker in the middle, tergum IX pale yellow, brownish near the anterior margin, tergum X dark brown. Sterna brown, unicolorous. No spines on segment II although spines near the base of gill cover well developed. Spines of segments III-V narrow, 3-4 times longer than wide at base and pointed at apex, not overlapping in dorsal view. Spines of segment VI bluntly pointed. Gill cover dark brown with paler or whitish outer margin, distinctly asymmetrical, posterolateral lobe well apparent, triangular ridge darker; gills 3-6 rounded, asymmetrical, with dark brown dusting. Cerci yellowish brown with pale bristles.

Adult and subimago: Body length 4.8 (4.5-5.8) mm, length of cerci 19 (15-20) mm (male), 3.0 (2.8-3.8) mm (female). Head and pronotum yellowish or greyish brown, eyes black, ocelli grey, frons darker, antennae greyish brown, unicolorous. Pronotum paler laterally with diffuse spots in the middle. Meso- and metanotum reddish brown. Wings translucent, greyish in C, Sc a R fields, veins C and Sc dark bordered; wings of subimago dark grey, blackish near the base. Legs yellowish grey, femora dark bordered. The ratio femur: tibia: tarsus (male) 3.1:7.1:4.0 for fore legs, 3.8:2.6:2.1 for middle ones and 4.0:2.8:2.1 for hind legs. Abdominal terga I-III purplish black, terga IV-VI greyish with paler sides, terga VIII-X paler, tergum X dark grey. Sterna brownish grey with numerous tiny paler spots, abdomen of subimago much darker, deep grey. Penis oblong-shaped, without any posterolateral lobes, with lateral as well as posterior margins straight, about 1.5 longer than wide with a pair of rounded teeth at base. Forceps longer by 1/4 than penis. Intercostal spaces on chorion slightly broader than costae; costae prominent and conspicuous, only rarely fused or interrupted in equatorial area.

Specimens examined: I male, I female, I subimago, South Carolina, Aiken Co., Upper Three Run Creek at SRL, June 14—15, 1976 (light trap 8.30—6.30) W. L. and J. G. Peters; 4

nymphs, South Carolina, Oconee Co., Chattooga Riv., Burrels Ford, Rec. Area, June 16—17, 1977 W. L. and J. G. Peters; 5 nymphs, South Carolina, Pickens Co., Six Mile Creek, Clemson, May 26, 1968, P. H. Carlson; 4 nymphs, Georgia, Cherokee Co., Etowah R., 6.5 mi ESE of Ball Ground, August 22—25, 1971, W. L. and J. G. Peters, L. Berner, coll. FAMU; 3 nymphs, North Carolina, Macon Co., Cullasaja Riv., July 5, 1965 V. Landa, coll. IE; 2 nymphs, Massachusetts, Amherest, July 23, 1951 O. Flint; 3 nymphs, South Carolina, Sawmill Riv., July 9, 1959; 1 nymph, North Carolina, Murphy, July 27, 1930 leg. H. T. Spieth, coll. UU.

Distribution: Nearctic species distributed in Southeastern area of the USA; so far recorded from North Carolina (Traver, 1932, Needham et al., 1935; Berner, 1977), Florida (Wurz & Roback, 1956) and Georgia (Berner, 1977) inhabiting Piemont and Blue Ridge physiographical provinces. Material from Massachusetts shows certain north extension of range; a species with probably mid- or upper austral distribution in North America.

Differential diagnosis and discussion: The following characters distinguish this species from remaining species of the genus *Brachycercus*: in nymph (1) ocellar tubercles equal in length, as long as or slightly longer than eye width, (2) pedicel less than twice longer than scape, (3) pronotum with a pair of lateral spines, (4) no spines on segment II, spines of other segments long, pointed and not overlapping in dorsal view, (5) labrum without lateral projections, lateral margins of hypopharyngeal superlinguae straight, (6) gill cover distinctly asymmetrical with paler posterolateral lobe, in adults (1) antennae unicolorous, pedicel less than twice longer than scape, (2) abdominal terga greyish with blackish purple coloring, (3) penis oblong-shaped with straight margins and bluntly pointed basal teeth, (4) intercostal spaces on chorion slightly broader than costae. Nymphs are related to those o *B. prudens* and *B. pallidus* but are distinguished by the arrangement of mouthparts (from *B. prudens*) and abdominal spines (from *B. pallidus*) and also by body length and coloration. Adults are easily distinguishable by unique structure of penis and by characteristical greyish color from adults of all remaining species.

Brachycercus pallidus Tshernova

(Figs 19, 49, 110, 166)

Brachycercus pallidus Tshernova, 1928: 114 (nec 1de, 1930: 218). Kazlauskas, 1965: 201. Sowa, 1975: 257, 344. Puthz, 1978: 272.

Brachycercus harrisella, ILLIES, 1967: 219 (nec Curtis, 1834: 3).

Mature namph: Body length 4.7 (4.5) mm, length of cerci 2.4 (2.8) mm. Head brown without spots, frons darker. Lateral tubercles shorter by 1/4 than frontal one and slightly broader at base. Antennae light yellowish, pedicel more than twice longer than scape (5.0: 2.2) with sparse bristles. Bristles on genae and frons shorter than frontal tubercle. Labrum more than twice broader than long (length: width. 2.3: 6.2), its lateral margins slightly concave, without lateral projections. Outer and middle mandibular incisors with 3-4 distal teeth, equal in length and width. Group of lateral bristles on mandibles clearly apparent. Segment 2 of maxillary palps 1.5 times longer than segment 1, with slightly concave inner margin (bristles

1.

in apical half). Hypopharyngeal superlinguae triangular with nearly straight lateral margins. Segment 2 of labial palps symmetrical, slightly bent and tapered at apex.

Pronotum brownish with a pair of conspicuous lateral spines, transverse ridges in the middle lacking. Meso- and metanotum brown with diffuse paler smudges. Pronotum more than twice as broad as long (4.4:1.6). Thoracic sterna brownish, unicolorous, without protuberances. Legs yellowish brown without rings, claws slender, as long as 1/3-1/2 of tarsi. The ratio femur: tibia: tarsus 1.5:0.5:0.6 for fore legs, 2.2:1.5:1.4 for middle ones and 2.6:1.4:1.4 for hind legs.

Abdominal terga light or yellowish brown, terga I, II and X darker. Sterna yellowish, unicolorous. Posterolateral spines of segment II triangular, bluntly pointed with concave lateral margins. Spines of segment III-V asymmetric, about 2.5 times longer than wide at base; spines of segment VI overlapping segment VII in dorsal view; spines of segments VIII and IX very small, inconspicuous. Gill cover brown, nearly symmetrical, with hind margin convex and darker triangular ridge. Cerci yellowish with transparent bristles.

Adult and subimago: Body length 4.8 (4.5-6.0) mm, length of cerci 15 (14-19) mm (male), 3.1 (2.9-3.3) mm (female). Head light yellowish brown, frons with large diffuse brown spot, ocelli black. Antennae whitish brown, unicolorous, pedicel more than twice longer than scape. Thorax yellowish brown, metathorax darker. Sterna brownish, unicolorous, without paler areas on the sides (as present in B. harrisella). Wings translucent, fields C and Sc milky, respective veins slightly darker, other veins translucent. Wings of subimago milky greyish. Legs pale, yellowish brown, femora and basal portions of tibiae darker. The ratio femur: tibia: tarsus (male) 1.3:3.7:2.3 for fore legs, 1.5:0.8:0.6 for middle ones, and 1.8:0.8:0.9 for hind legs. Abdominal terga pale yellowish, slightly darker on sides, terga VIII and IX with brownish hind margins. Sterna unicolorous, whitish yellow, last sternum darker. Forceps base whitish with round dark spots in the middle. Forceps yellowish, longer by 1/3 than penis. Penis whitish, without markings about as long as wide, with well developed posterolateral lobes; lobes rounded, lateral margins of penis concave, posterior margin straight. Spines near the penis base identical with those of B. harrisella. Cerci whitish, without rings, cerci of subimago darker.

Specimens examined: 3 nymphs, 1 male, 1 female, 2 subimagos, USSR, Usa Riv., Batchandi, July 4, 1965 leg. V. Novikov, coll. IE.

Distribution: B. pallidus is known from the European part of the USSR (Volga Riv. basin and Lithuania) (TSHERNOVA, 1928; KAZLAUSKAS, 1965); recently found also in Poland, the Vistula basin (Sowa, 1975). This species (probably of mid-boreal origin) seems to have wide Eurasian distribution but only a few localities have been reported so far.

Differential diagnosis and discussion: This species differs in the following critical characters from the remaining species of the genus *Brachycercus*: in nymphs (1) head tubercles longer than the eye widths, frontal tubercle longer by 1/4 than lateral ones, (2) pedicel more than twice longer than scape, (3) pronotum with a pair of lateral spines, (4) posterolateral abdominal spines wide and rounded, those of

segment VI overlapping segment VII in dorsal view, spines of segment II with concave lateral margins, (5) sternal protuberances of thorax missing, (6) gill cover nearly symmetrical; its hind margin convex; in adults (1) antennae whitish, pedicel more than twice longer than scape, (2) abdomen yellowish, thorax yellowish brown, (3) penis with distinct posterolateral lobes, whitish, with straight hind margin. The presence of pronotal spines and absence of sternal protuberances on thorax approach in appearance nymphs of B. prudens and B. nitidus. They can be distinguished especially by the arrangement of mouthparts and gill cover (from B. prudens) and by body size and the arrangement of posterolateral abdominal spines (from B. nitidus). Adults are related to those of B. prudens, B. flavus and B. nasutus, differing in the arrangement of penis, forceps and antennae, and are closely related to B. harrisella, differing especially in the shape of penis, coloration of thoracic sterna and different body size. In B. harrisella sternal thoracic protuberance (lacking in B. pallidus) may be present also in adults.

Brachycercus pini sp. n.

(Figs 22, 40, 46, 68, 71, 93, 147, 148, 183)

Brachycercus sp. A (part), BERNER 1950: 191.

Mature nymph: Body length 5.0 (4.8-5.5) mm, length of cerci 2.5 (2.3-3.0) mm. Head yellowish or yellowish brown with darker frons. Two pairs of diffuse oblique dark-brown stripes on occiput. Ocellar tubercles paler, as long as the eye width. Lateral tubercles slightly longer but equal in width at base with frontal one. Genae and frons almost without bristles. Scape and pedicel narrow and whitish yellow, the ratio pedicel: scape 1.7: 0.9. Labrum twice as broad as long (3.7: 1.7), not produced laterally. Mandibular incisors with 2-3 teeth, outer and middle ones approximately equal in width, middle incisors slightly longer. A few bristles present on the lateral margins of mandibles. Hypopharyngeal superlinguae rounded with convex lateral margins, not produced. Segment 1 of maxillary palps twice as broad as than segment 2. Segment 2 somewhat rounded at apex, inner margin concave with few bristles in apical half. Segment 2 of labial palps rounded at apex but produced into a point at tip.

Pronotum yellowish brown or light brown, with a pair of transverse lateral ridges near the anterior margin. Meso- and metanotum brownish with diffuse dark smudges. Thoracic sterna yellowish brown without protuberances. Legs yellowish with diffuse dark-brown bands near the base of each segment, almost without bristles. Fore legs (ratio femur: tibia: tarsus) 5.5: 2.5: 2.7; middle legs 7.2: 4.6: 4.9; hind legs 8.1: 4.7: 4.9. Claws relatively wide at base, half as long as tarsus.

Abdominal terga yellow or light yellowish brown, terga I, II and VII-IX with transverse diffuse dark band near the anterior margins. Anteromedial spot usually present on terga VII-IX. Sterna the same color as ventral side of thorax; without markings other than inconspicuous darker smudges. Posterolateral spines of segment

II low and rather rounded, spines of segments III-VI wide, three times longer than wide, pointed or bluntly pointed. Spines of segment VI overlapping segment VII and VIII well developed. Gill cover nearly symmetrical, light brown or yellowish brown with diffused dark brown spot on triangular ridge, gills 3-6 oval with dark pigmented fringe. Cerci whitish or whitish yellow. Costae on chorion very narrow, intercostal areas at least 4 times broader.

Specimens examined: Holotype, mature nymph, Florida, Washington Co., Pine Log Creek, 1.5 mi S of Ebro, April 23. 1967, paratypes, 2 nymphs, same data as holotype; paratype, nymph, Florida, Okaloosa Co., Blackwater River at Bryant Bridge 2.5 miles W of Holt, July 11, 1967, W. L. and J. G. Peters, G. Cooper, J. Jones, P. T. P. Tsui, coll. FAMU; paratype, 1 nymph, Florida, Walton Co., Sandy Creek, Hwy 181, September 5, 1970, P. H. Carlson; paratype, 1 nymph, Florida, Bay Co., Pine Log Creek, Hwy 79, June 20, 1971, E. Farmer, E. D. Kaplan, P. H. Carlson; paratype, 1 nymph, Florida, Jackson Co., Waddeles Mill Creek, November 28, 1960, W. M. Beck; paratype, 1 nymph, Florida, Pasco Co., Withlacoochee River (Southern), April 7, 1955 W. M. Beck; paratypes, 2 nymphs, Washington Co., Mill Creek, Hwy 284, September 5, 1970 P. H. Carlson, coll. FAMU. Holotype in alcohol, parts of paratypes on slides.

Differential diagnosis and discussion: *B. pini* can be distinguished from the other species of *Brachycercus* by the following combination of characters: in nymphs (1) ocellar tubercles low, as long as the eye width, (2) pedicel less than twice as long as scape, (3) pronotum with a pair of transverse ridges, (4) sternal projections lacking, (5) spines of segment II low, spines of segment III-VI wide at base, spines of segment VI overlapping segment VII in dorsal view, (6) labrum without lateral projections, hypopharyngeal superlinguae rounded, not produced, segment 1 of maxillary palps twice as broad as segment 1, (7) gill cover nearly symmetrical, rounded post rolaterally. This species is related to *B. lacustris* and *B. flavus*, and closely related to *B. floridicola* from which it is distinguished mainly by the arrangement of abdominal posterolateral spines and gill cover. *B. pini* is illustrated by BERNER (1950: 192) as a figure of *Brachycercus* sp. A (see discussion of *B. berneri*).

Brachycercus prudens (McDunnough)

(Figs 17, 29, 36, 48, 61, 88, 107, 151, 152)

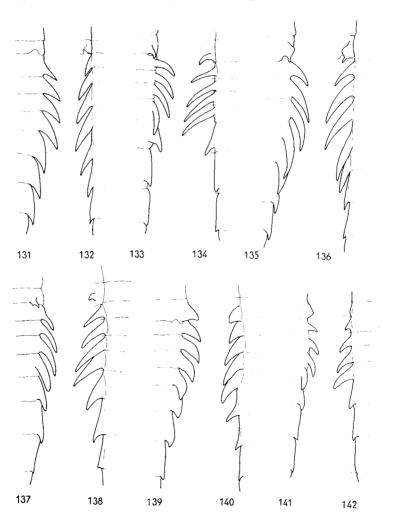
Eurycaenis prudens McDunnough, 1931: 264.

Brachycercus prudens, Needham et al., 1935: 642. Berner, 1950: 189. Burks, 1953: 49. Berner, 1959: 12. Edmunds et al., 1976: 266. Berner, 1977: 33.

Mature nymph: Body length 5.6 mm, length of cerci 2.2 mm. Head oval with only slightly developed posterolateral lobes, dark yellowish, tubercles whitish. Tubercles longer than eye width, frontal tubercle slightly longer but equal in width. Antennae pale whitish, unicolorous, pedicel about 1.5 times broader than long (scape: pedicel 1.2: 1.9). Labrum oval with well developed and rounded lateral lobes, twice broader than long (5.5: 2.2). Middle mandibular incisors as long as or slightly longer than outer ones; incisors equal in width with 1-2 pointed teeth. Segment 2 of maxillary palps extended and covered with fine bristles in apical half,

nearly as broad as segment 1, with straight inner margin. Hypopharyngeal super-linguae oval or nearly bluntly pointed, conspicuously produced laterally, their outer margin bent at a right angle; lingua oblong-shaped, rounded. Segment 2 of labial palps tapered and pointed at apex with stout setae at tip.

Pronotum dark yellow or yellowish brown, about three times broader than long (length: width 1.4:4.5) with a pair of flat lateral spines and a pair of short transverse ridges in the middle. Meso- and metanotum, as well as the wing pads light brown, unicolorous. Thoracic sterna of the same color, bearing four protuberances. Anterior mesosternal protuberance flat with very broad base; posterior mesosternal and meta-



Figs 131—142: Dorsal (131, 133, 135, 139, 141) and lateral (132, 134, 136, 138, 140, 142) view of posterolateral spines of abdominal segments in nymphs. 131, 132 - *Insulibrachys needhami*. 133, 134 - *Brachycercus floridicola*. 135, 136 - *B. edmundsi*. 137, 138 - *B. nitidus*. 139, 140 - *B. flavus*. 141, 142 - *B. lacustris*.

sternal protuberance prominent, produced into blunt point, approximately equal in size. Legs pale whitish yellow, unicolorous, without rings. The ratio femur: tibia: : tarsus 3.5:1.8:2.1 for fore legs, 4.5:2.8:2.8 for middle legs and 4.8:3.2:3.2 for hind legs.

Abdominal terga as well as sterna light whitish yellow, unicolorous. Spines of segment II well developed as long as those of segment III, spines of segments IV—V bluntly pointed, asymmetrical, 2.5—3 times longer than wide at base. Spines of segment VI bluntly pointed, overlapping segment VII in dorsal view. Gill cover of the same color as abdomen, symmetrical, with darker triangular ridge. Gills 3—6 pale without stippling. Cerci whitish.

Adult and subimago: Body length 4.5 (3.0-3.5) mm, length of cerci 2.1 mm (subimago), 14.2 (13-16) mm (male). Head dark yellow, frons with inconspicuous darker stippling, eyes black, ocelli grey with dark brown rings. Pronotum dark yellow, faintly tinged medially; meso- and metanotum light brown, unicolorous. Thoracic sterna of the same color, base of coxae lighter. Legs whitish yellow, femora of fore legs slightly darker. Legs of subimago yellowish gr.y. Wings semi-hyaline whitish, Sc and R veins dark except apical position. Wings of subimago whitish grey, fore veins darker. Abdomen entirely pale yellowish white without any markings. Penis with distinct posterolateral lobes, approximately as long as wide with concave lateral margins and straight or slightly concave posterior margin. Forceps yellowish, longer by 1/3 than penis. A pair of relatively very long (5 times longer than wide at base) and parallel spines near the base of penis. Forceps base yellowish with spots fused in the middle with yellowish bordered anterior margin of sternum IX.

Material examined: 5 adult male paratypes, Canada, Saskatchewan, Saskatoon, September 9, 1930 leg. K. M. King (No. 3235), coll. Biosystematics Research Institute, Ottawa; 1 nymph, USA, Wyoming, Sweetwater Co., Black's Fork Riv. at interst. Hwy 80, 6 mi E of Little America, July 21, 1971 leg. S. L. Jensen and A. V. Provonsha, coll. UU; 5 nymphs, Wyoming, Sweetwater Co., Black's Fork Riv. W of Green River City, August 2—3, 1969, leg. A. V. Provonsha, coll. UU; 1 nymph, 1 adult subimago, same data, August 3, 1968 leg. R. Koss and W. P. McCafferty, coll. UU.

Distribution: Originally known only from Saskatchewan, Canada, and Kansas, USA; Burks (1953) records this species from Illinois. Taking into account also localities in Wyoming it seems to be a species with upper or mid-boreal distribution. Berner (1977) reports this species also from Alabama but the material might in fact belong to *B. nasutus* or to *B. flavus*.

Differential diagnosis and discussion: This species can be distinguished from other species of the genus *Brachycercus* by the following combination of characters in nymphs: (1) ocellar tubercles longer than the eye width, (2) pedicel 1.5 times longer than scape, (3) pronotum with a pair of flat lateral spines, (4) four sternal thoracic protuberances present, (5) spines of segment II well developed, spines of segment VI overlapping in dorsal view, (6) both labrum and hypopharyngeal superlinguae with distinct lateral lobes, segment 2 of maxillary palps nearly as broad as segment 1, (7) gill cover symmetrical; in adults (1) antennae unicolorous, pedicel 1.5 times longer than scape, (2) abdomen whitish, unicolorous, (3) penis with rounded,

well developed posterolateral lobes, posterior margin straight or slightly convex; basal spines pointed and parallel, 5 times longer than wide at base. This species occupies a relatively isolated position among other species of *Brachycercus*, especially in nymphal characters. The arrangement of mouthparts (labrum, maxillary palps, hypopharynx) antennae (pedicel: scape ratio) and symmetrical gill cover approach those to the nymphs of the genus *Cercobrachys* but the arrangement of thoracic sterna (presence of protuberances) and posterolateral abdominal spines, as well as imaginal characters, are clearly those of true *Brachycercus*; the four protuberances on thoracic sterna are like those of nymphs of *B. tuberculatus* but all remaining nymphal characters are quite different. Adults are related to those of *B. berneri*, *B. pallidus* and especially *B. nasutus* in body coloration but they differ in the structure of the penis and other characters (scape-pedicel relatio, coloration of scape).

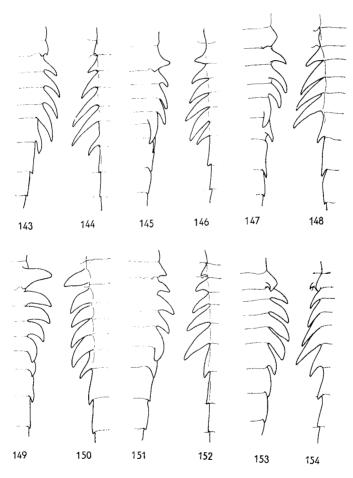
Subimago and nymphs in material studied were associated by rearing (R. W. Koss and W. P. McCafferty). The subimago is identical with adult paratype material in all characters except some details in the arrangement of penis and body size. The size differences (1.0—1.5 mm) are probably due to dessication (paratypes pinned). Preparation of penis of the paratype material damaged by dessication does not enable correct comparison with the preparation of penis of the subimago from Wyoming. I did not observe the division of original penis lobes apparent in the figure of McDunnough (1931) and Needham et al. (1935) in subimaginal exuviae of the holotype (holotype is probably patially molted subimago). Otherwise most characters of penis are identical, including long and pointed basal spines not figured or mentioned in original description. Despite these small differences I believe that the redescribed material actually represents *B. prudens* (McDunnough, 1931).

Brachycercus tuberculatus sp. n. (Figs 20, 28, 35, 53, 91, 114, 145, 146)

Mature nymph: Body length 5.2 mm, length of cerci 2.5 mm. Head yellowish brown, darker around the epicranial suture, eyes black. Head tubercles equal in length, longer than eye width, bluntly pointed at apex. Bristles on clypeus and genae as long as frontal tubercle. Scape with fine bristles, antennae yellowish brown, ratio pedicel: scape 1.3:0.8. Labrum about twice broader than long, without lateral projections. Middle mandibular incisors slightly longer than the outer ones, equal in width; inner incisors represented by a single stout seta. Hypopharyngeal superlinguae conspicuously produced laterally, their outer margins bent nearly at right angles. Segment 2 of maxillary palps with straight inner margins and outer margin covered with fine bristles. Segments of labial palps with fine hairs, segment 2 with two rows of stout bristles.

Pronotum light brown, slightly darker at posterior margin, three times broader than long with a pair of low and bluntly pointed lateral spines. Meso- and metanotum of the same color, wing pads paler. Prosternum with wide rounded protuberances bearing long hairs between bases of coxae; anterior mesosternal protuberance similar to prosternal one, posterior mesosternal protuberance higher and bluntly pointed; metasternal protuberance lower, rounded at apex. Fore legs (ratio femur: tibia: tarsus) 6.5:3.5:4.0, middle ones 8.5:5.5:5.5, hind legs 9.0:6.0:5.7, legs whitish yellow, without darker markings.

Abdominal terga whitish yellow, terga VIII—X paler, terga I—II paler at the midline. Posterolateral spines of segment II triangular, pointed, spines of segment VI overlapping segment VII in dorsal view. Sterna light brown, whitish in the middle, with a pair of inconspicuous darker bands on the sides, sternum IX and hind margin of sternum VIII whitish. Gill cover symmetrical, light brown, triangular ridge slightly



Figs 143—154: Dorsal (143, 145, 147, 149, 151, 153) and lateral (144, 146, 148, 150, 152, 154) view of posterolateral spines of abdominal segments in nymphs. 143, 144 - *Brachycercus arcticus*. 154, 146 - *B. tuberculatus*. 147, 148 - *B. pini*. 149, 150 - *B. nasutus*. 151—152 - *B. prudens*. 153, 154 - *B. harrisella*.

darker; marginal ridge distinct especially on the outer margin; gills 3 7 rounded, whitish. Cerci whitish at base, brownish at apex.

Subimago and adult unknown.

Specimens examined: Holotype, mature nymph, USA, Utah, Provo Riv., Midway, Wasatch Co., June 11, 1965 V. Landa, coll. UU; paratype, mature larva labelled »Brachycercus sp.« without further data, coll. UU. Holotype in alcohol, parts on slides. As to the type locality, there was a certain doubt although the holotype was undoubtedly collected in Utah. Dr. Edmunds believes this specimen may be mislabeled and that it actually may have been collected in the Green River or Yampa River at Echo Park, Dinosaur National Monument, Colorado by Dr. Landa in June, 1965. The genus Brachycercus is not known from the Great Basin and habitats at the Provo River are not typical for the western USA localities for the genus.

Distribution: Probably mid- or upper boreal species distributed in NW states of the USA.

Differential diagnosis and discussion: This species is distinguished by the following characters from remaining species of the genus *Brachycercus*: (1) ocellar tubercles equal in length, longer than the eye width, (2) pedicel 1.5 times longer than scape, (3) pronotum with a pair of lateral spines, (4) four thoracic sternal protuberance present, (5) posterolateral spines of segment II well developed, those of segment VI overlapping segment VII in dorsal view, (6) hypopharyngeal superlinguae produced laterally, (7) gill cover nearly symmetrical, marginal ridge well apparent. This species is related to *B. harrisella*, *B. edmundsi*, *B. arcticus* and *B. prudens* in nymphal characters. It can be distinguished by the arrangement of thoracic sternal protuberances, posterolateral spines and scape-pedicel relation. From *B. prudens* (also four thoracic protuberances) it differs in the arrangement of mouthparts, ocellar tubercles and posterolateral abdominal spines.

Brachycercus tubulatus Tshernova

(Fig. 3)

Brachycercus tubulatus Tshernova, 1952: 285; 1958: 64. Sukatskene, 1962: 113. Baykova & Varykhanova, 1978: 121.

Mature nymph. Body length 6 mm, length of cerci 4 mm. Head and thorax light yellowish; head oval without distinct posterolateral lobes, occiput with rectangular dark spot in the middle. Frontal tubercle long and slender, tube-like, somewhat rounded at apex, as long as the distance between its base and posterior margin of head. Lateral tubercles shorter by 1/3 - 1/4 than frontal ones and slightly bent. Frontal tubercles with stripe-like marking, lateral ones with triangular dark spots. Antennal pedicel 2.5 times longer than scape. Posterior margin of pronotum apparently longer than the anterior one, pronotum approximately 3 times broader than long, smooth, without any lateral spines or ridges in the middle. Posterolateral spines of abdominal segments similar to those of *B. harrisella*, spines of segment VIII small, inconspicuous. Description of nymph according to the original description and figures by TSHERNOVA (1952).

Adult and subimago unknown.

Distribution: So far known only from Far East USSR (the Angara and Amur Riv. basins). According to TSHERNOVA (1958) endemic to this region. BAYKOVA & VARYKHANOVA (1978) record nymphs from Mongolia.

Differential diagnosis and discussion: This species was described from a single specimen (mature nymph) collected in lower region of the Amur basin (Far East). I have had no opportunity to study this specimen. Except for records by SUKATSKENE (1962) and BAYKOVA & VARYKHANOVA (1978) no further specimens are known. Nymphs can be easily distinguished by tube-like tubercles on head, absence of pronotal spines and pedicel 2.5 times longer than scape from all other species of the genus *Brachycercus* (note also the unique position of ocelli in original Tshernova's figure on apex of tubercles). Long, tubular frontal tubercle approaches *B. tubulatus* to *B. nasutus* (frontal tubercle triangular, different arrangement of posterolateral spines of abdomen).

Insulibrachys gen. n.

Type species: *Insulibrachys needhami* sp. n. by original designation; type locality Cuba. Species included: *I. needhami* sp. n.

Mature nymph: Head with cylindrical ocellar tubercles widely rounded at apex, bearing numerous long apical bristles. Pronotum with a pair of rounded lateral projections. Abdominal segments III - VI with wide posterolateral spines only slightly bent dorsally, spines of segments VII - IX well developed, as long as 1/2 - 2/3 of segment length. Legs covered with submarginal bristles and stout setae resembling spines; submarginal rows of spines on inner margins of tibiae and tarsi. Gill cover symmetrical, nearly circular, triangular ridge with row of setae. Fringed margins of gills 3 6 pale, longer than the gill width. For further nymphal characteristics see *I. needhami*.

Adult: Ocelli large and prominent. Pedicel conical, tapered toward to flagellum, with straight lateral margins. Pronotum with indicated lateral rounded projections as in nymph. Posterolateral spines of abdominal segments V and VI flat, not bent dorsally, spines of segments VIII and IX as long as 1/2 of segment length. Subimago, male genitalia and chorion ornamentation unknown.

Etymology: *Insulibrachys* (m.), from Latin insula meaning island and *Cercobrachys*, a related genus.

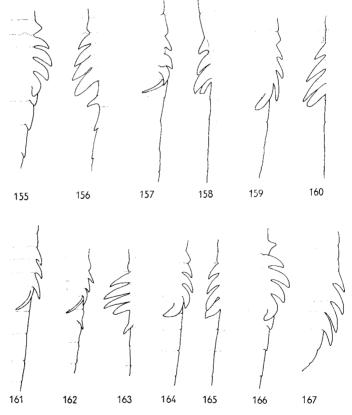
Distribution: Known only from Cuba, probably endemic to West Indies or Central America.

Discussion: This genus comprises only a single species. Nymph (only a single specimen is known) shows a set (see generic characteristics) of unique morphological characters which singles this species out of all known species of caenids with ocellar tubercles in the nymphal stage. These characters undoubtedly justify the establishment of a new genus within the family Caenidae although there are certain close relationships to the genus *Brachycercus*. There is little doubt that the female studied, although

having some distinguishing characters, actually does not belong to some undescribed species of true *Brachycercus*. On the other hand, probably no species of true *Brachycercus* lives either in South Florida or in Cuba and, moreover, no caenid species living in Florida has managed to colonize the West Indies and vice versa (cf. Berner, 1950; Peters, 1971).

Insulibrachys needhami sp. n. (Figs 8, 16, 27, 57, 67, 76, 90, 101, 117, 127, 131, 132, 170, 172)

Mature nymph: Body length 7.6 mm, length of cerci 3.7 mm. Head dark yellowish brown with large dark brown spots in the middle of vertex and occiput. Epicranial suture light bordered, with dark spot with lighter stripes, eyes black. Ocellar tubercles equal in length, frontal tubercle slightly broader, symmetrical, lateral tubercles slightly asymmetrical, setae at apex and setae on genae longer by 1/3 1/2 than tubercles. Antennae yellowish brown, flagellum paler at apex, pedicel twice longer than scape



Figs 155—167: Dorsal (155, 157, 159, 161, 162, 164, 166, 167) and lateral (156, 158, 160, 163-165) view of posterolateral spines of abdominal segments in nymphs. 155, 156 - Brachycercus magnus. 157, 158 - Cercobrachys etowah. 159, 160 - C. peruanicus. 161 - C. minutus. 162, 163 - C. petersorum. 164, 165 - C. serpentis. 166 - B. pallidus. 167 - Caenoculis bishopi.

(3.9:2.0) with numerous stout bristles as long as 1/2 of pedicel. Labrum about twice broader than long (width: length 5.3:2.7) with slight lateral lobes, lateral margins concave. Outer incisors with three bluntly pointed teeth, twice as broad as middle ones. Middle incisors as long as outer ones. Segment 2 of maxillary palps with concave inner margin bearing a row of 10-11 bristles, outer margins of maxillae conspicuously convex, rounded. Hypopharyngeal superlinguae with rounded lateral projections, lingua nearly triangular, rounded. Segment 2 of labial palps bent and rounded at apex.

Pronotum dark brown with paler smudges especially on the sides, about three times as broad as long (9.5:3.2) with a pair of lateral projections and a pair of short transverse ridges in the middle. Meso- and metanotum dark brown with inconspicuous lighter spots near the wing pads. Thoracic sterna flat, paler, unicolorous. Legs yellowish brown, covered with marginal bristles and a row of stout setae. The ratio femur: tibia: tarsus 3.4:2.5:1.8 for fore legs, 4.3:3.5:1.9 for middle ones and 5.0:4.2:2.3 for hind legs. Claws stout and relatively short, slightly bent.

Abdominal terga dark brown with whitish yellow sides and pale longitudinal smudges in the middle, tergum X darker. Sterna light brown, paler in the middle with a pair of blackish brown round spots on sides. Posterolateral spines of abdominal segments flat, sharply pointed, not overlapping in dorsal view. Spines of segment II very low, nearly absent, those of segments III—VII about 3—4 times longer than wide at base, spines of segments VIII—IX conspicuous, as long as 1/2 of segment length. Gill cover rounded, nearly circular, dark brown, gills 3—6 with numerous pale fringe. Cerci whitish yellow with pale bristles.

Adult female (assigned to I. needhami): Body length 5.8 mm, length of cerci 2.4 mm. Head dark brown with darker posterior margin and numerous minute paler spots near the epicranial suture, eyes black, ocelli greyish. Vertex with a pair of flat tubercles with rounded tip, ocelli prominent, as long as 1/2 of the eye width. Antennae yellowish brown, scape slightly darker without spots, flagellum darker at base. Pedicel conical, twice as broad at base than at apex, with straight or slightly concave lateral margins, about twice longer than scape (0.6:1.1). Pronotum resembles that of nymph, black brown, with well indicated lateral protuberances and paler spots in the middle. Meso- and metanotum pitch brown, unicolorous. Wings transparent, slightly brownish, first veins dark brown, respective fields with dark brown stippling, other veins brownish with paler apical portions. Fore legs light brown, femora dark bordered. Middle and hind legs yellowish brown, femora slightly darker. The ratio femur: tibia: tarsus 3.7:2.1:1.1 for fore legs, 4.2:3.4:1.1 for middle ones and 4.8:4.5:1.6 for hind legs. Abdominal terga brownish, unicolorous, spines of abdominal segments long, narrow and pointed, straight and well developed on segments III-IX.

Adult male and subimago unknown.

Specimens examined: Holotype, mature female nymph, Cuba, Pinar del Rio Prov., Santa Cruz de los Banos, March 28, 1939, J. G. Needham, coll. UU; paratype, adult female, Cuba,

Pinar del Rio Prov., Soroa, dead specimen atracted to light in garden swimming pool, October 12, 1964, V. Landa, coll. IE. Holotype in alcohol, parts on slides.

Etymology: Species named for the late Dr. J. G. Needham, a distinguished specialist in Nearctic aquatic insects, who collected holotype.

Differential diagnosis and discussion: Critical characters distinguishing this species are apparent from the characters of the genus; nymphs can be easily distinguished from all known species of the Caenidae. As indicated above, the nymph and adult female of material studied cannot be associated without doubt since they do not contain any eggs. On the other hand, the arrangement of pronotum (lateral rounded projections), head (broad prominent ocelli) and posterolateral spines of abdominal segments permit me to associate this female with nymph. Also the leg measurements are comparable, being clearly different from the species of *Brachycercus*. At present, additional nymphs cannot be collected at the type locality in Cuba because of heavy pollution of water (no mayflies were found here in 1980, Gelbič, pers.comm.). Adults seem to be extremely rare; there was only a single specimen among several thousands of caenids in Landa's collection from Cuba.

Cercobrachys gen. n.

Brachycercus (partim), Tshernova, 1952: 284; Edmunds, Traver, 1954: 239; Demoulin, 1958: 11; Berner, 1959: 12; Burks, 1953: 48; Ujhelyi, 1959: 36; Thew, 1960: 102; Leonard & Leonard, 1962: 37; Landa, 1969: 258; Tshernova, 1970: 144; Jacob, 1974: 96; Edmunds et al., 1976: 264:

Eurycaenis (part), Bogoescu, 1958: 86.

Type species: Cercobrachys etowah sp. n., by original designation; type locality Florida.

Species included: C. etowah sp. n.; C. colombianus sp. n.; C. minutus (TSHERNOVA) comb. n.; C. peruanicus sp. n.; C. petersorum sp. n.; C. serpentis sp. n.

Mature nymph: Body length about 4—7 mm, length of cerci about 1/2 of body length. Body slender and only slightly flattened dorsally. Antennal pedicel as long as scape or slightly longer: Labrum with well developed lateral lobes, its lateral margins concave. Mandibles without lateral groups of bristles, at most several scattered hairs on lateral margins. Maxillary and labial palps 2-segmented, segment 2 of maxillary palps nearly as broad as segment 1. Prosternum broader than long, fore coxae widely separated. Pronotum usually with a pair of low lateral spines or a pair submarginal ridges. Abdominal segments II—IIV or III—VI with well developed spines considerably bent dorsally; spines of segment VI bent medially, continuous in the middle of tergum and forming **gill* basket**. Legs slender, femora at most twice as broad as tibiae, covered with very long (mostly as long as tibiae) setae; middle and hind legs longer, tibiae shorter than tarsi; claws very long and slender, in some species with two rows of minute rounded denticles. Gill 1 2-segmented, gill cover mostly symmetrical, lamellate gills with fringe bifid or multifid.

Adult: Body length 3-5 mm, length of wing 2.8-4.0 mm, length of cerci 15 to

20 mm in males, 3—4 mm in females. Pedicel about as long as scape. Prosternum about 2—3 times broader than long with fore coxae widely separated. Abdomen relatively small and contracted, lateral spines distinct and conspicuously bent dorsally. Forceps foil-like with medial depression, pointed apex without tufts of hairs. Penis lobes almost entirely fused; a pair of sclerotized formations near the base of penis (different from spines in *Brachycercus*) present. The eggs with one polar cap, chorion ornamented with 3—4 large, rounded costae covered with small tubercles. Micropyle linear, transversing the space between costae, sperm guide lacking.

Etymology: Cercobrachys (m.), an anagram to Brachycercus, related genus.

Distribution: Holarctic, Neotropical, Oriental. In the Palearctic known from Europe (Poland, Czechoslovakia, USSR) and from Far East USSR (Amur basin). In the Nearctic, distributed in Georgia, Alabama, South Carolina, and Florida (C. etowah) and in Idaho (C. serpentis). Further species found in Peru, Colombia, and Thailand. Although the distributional data are very restricted, this genus seems to have an upper austral distribution in the Nearctic and Transpalearctic distribution in Eurasia.

Differential diagnosis and discussion: Cercobrachys gen. n. can be distinguished from all genera of Caenidae by the following combination of characters: in nymph (1) pedicel at most 1.1-1.3 times longer than scape, (2) ocellar tubercles low but well apparent, (3) head without distinct posterolateral lobes, (4) maxillary and labial palps 2-segmented, (5) fore coxae widely separated, prosternum broad, mesosternum with prominent anterior margin bearing cranially directed long bristles, (6) legs long and slender with very long setae, tibiae usually as long as or shorter than tarsi, claws can have minute teeth, (7) spines of segment VI of abdomen considerably bent medially, nearly continuous in the middle, (8) egg chorion with 3-4 large costae with small tubercles, one polar cap. In adults some characters (1, 5, 7, 8) are easily apparent and represent useful distinguishing features. There are no characters distinguishing this genus in wing venation and the segment ratios in legs in adults. Nymphs of the genus Cercobrachys distinctly differ from those of Brachycercus in many characters. These differences are much greater than those between nymphs of some Caenis-like genera (e. g. Caenis, Caenodes, Tasmanocoenis, Caenomedea and others). TSHERNOVA (1952) points out the difference between true Brachycercus and C. minutus from the Amur basin. Since the adults of Cercobrachys are mostly unknown the only reliable distinguishing characters are the scape-pedicel ratio and the arrangement of chorion in females. The new genus is established in order to separate distinct group of species with a xgill basket« and specialized legs. These species are characterized by different distributional patterns (occurrence also in the Oriental and Neotropic) and probably also by a slightly different biology.

Keys to the species of Cercobrachys

Mature nymphs

1 (2) Tibiae of fore and middle legs 2.6 times shorter than tarsi (Fig. 162) segment VII with a pair of posterolateral spines (Figs 162, 163); as long as those of segment III; segment 2

- 2 (1) Tibiae of fore and middle legs longer or at most 1.8 times shorter than tarsi (Figs 125, 128); segment VII without posterolateral spines (Figs 157, 159, 161, 164) or spines shorter by 1/2 than those of segment III (Fig. 240); segment 2 of maxillary palps tapered apically, pointed or bluntly pointed (Figs 38, 39); abdominal sterna without setae, at most with fine bristles
- 3 (6) Pronotum smooth, without lateral spines or spines very obtuse, forming submarginal longitudinal ridge; claws without denticles (Figs 120, 216).

- 6 (3) Pronotum with a pair of pointed or rounded lateral spines (Fig. 6); claws with minute denticles (Figs 118, 119)
- 8 (7) Tarsi of hind legs equal in length or slightly (1.1—1.2 times) longer than tibiae; gill cover without submarginal ridge on inner margin, 1.1—1.2 times longer than wide; spines of segment VI narrow, more than 6 times longer than broad in dorsal view (Figs 157, 161); head unicolorous, without spot.
- 9(10) Body pale yellowish, eyes positioned anterolaterally on head, directed forewards (Fig. 6); pronotum with distinct, right-angled lateral spines (Fig. 6); posterolateral spines of segment V overlapping segment VI in dorsal view (Fig. 157); inner margin of segment 2 of maxillary palps slightly concave, with row of stout setae and fine bristles (Fig. 39) C. etowah sp. n.

Adults

Cercobrachys etowah sp. n.

(Figs 6, 15, 39, 69, 119, 129, 157, 158, 169, 177, 251)

Mature nymph: Body length 4.5 (4.5-5.5) mm, length of cerci 1.5 (1.3 to 2.1) mm. Head whitish yellow, unicolorous with rounded posterior margin, eyes directed forwards. Lateral ocellar tubercles low (shorter by 1/3 than the eye wodth), frontal tubercle as long as 2/3 of lateral ones. Antennae pale, the ratio scape: pedicel 1.7: 1.9. Labrum with distinct lateral lobes, three times broader than long (1.3:0.4). Outer mandibular incisors as long as middle ones, broader by 1/2 at base. Segment 2 of maxillary palps 1.5 times longer than segment 1, asymmetrical, pointed at apex. Hypopharyngeal superlinguae triangular, only slightly produced. Segment 2 of labial palps tapered apically, pointed.

Thorax pale yellow without markings, pronotum 3-4 times broader than long, with a pair of low, right-angled lateral spines. Anterior margins of pro- and mesosternum prominent, bearing stout and long setae. Legs pale yellowish, without stripes, covered with rows of marginal setae twice longer than width of the femur. The ratio femur: tibia: tarsus 2.1:1.2:1.6 for fore legs, 3.2:2.8:1.5 for middle ones and 3.2:2.1:2.4 for hind legs. Claws shorter by 1/2 than tarsi, slightly bent at apex with two rows of 5-8 minute teeth.

Abdomen pale yellow, unicolorous, without markings. Posterolateral spines of segment II only indicated, rounded, those of segment III as long as segment length, bluntly pointed. Spines of segment III as long as segment length, bluntly pointed. Spines of segments IV and V overlapping in dorsal view, twice as long as segment length, asymmetrical, bluntly pointed, no spines on segments VII—X. Gill cover pale yellowish, symmetrical, rounded posteriorly, gills 3—6 rounded, without dark stippling. Cerci whitish yellow.

Adult and subimago: Body length: 5.0 (4.5-5.0) mm, length of cerci 14 (11 to 15) mm (male), 2.0 (2.0-3.0) mm (female). Head dark brownish; frons blackish brown, epicranial suture bordered black, posterior head margin also black. Blackish diffuse spots near the base of ocelli. Scape yellowish brown with dark brown outer smudge; pedicel yellowish, flagellum paler. Pronotum yellowish or light brown with a pair of darker purplish brown smudges. Meso- and metanotum brown, paler on sides. Metanotum with finger-like medial projection on posterior margin. Thoracic sterna brownish, paler in the middle; sternal transverse sutures dark bordered. Wings translucent, semi-hyaline whitish, first 3-4 longitudinal veins dark brown in basal half, other veins translucent; C and Sc membranes slightly milky greyish. Legs brownish yellow, fore femora darker, dark purplish bordered. The ratio femur: : tibia : tarsus (male) 2.2 : 3.8 : 2.2 for fore legs, 5.0 : 4.0 : 3.0 for middle ones and 5.0: 4.0: 3.2 for hind legs. Legs and wings of subimago greyish. Abdominal terga I and II with blackish stippling, terga III-VI pale yellow with very slight brownish dusting, terga VII-IX paler, tergum X dark yellowish. Sterna whitish yellow, sternum IX and forceps darker, yellowish brown. Penis approximately as

long as wide, with distinct posterolateral rounded lobes; its lateral margins convex, posterior margin concave, conspicuously arcuately incurved in middle. Oblong-shaped dark brown spot in the middle of penis. Forceps by 1/4 - 1/3 longer than penis. Eggs slender, 3 -4 times longer than wide. Chorion of egg with 3 5 broad costae sculptured as in Fig. 250. Both costae and intercostal spaces covered with small tubercles (Fig. 251).

Material examined: Holotype, mature nymph, paratypes 5 nymphs, Georgia, Cherokee Co., Etowah Riv. at junction of Hwy 681, 6.5 mi ESE of Ball Ground, June 22 –25, 1971 L. Berner, W. M. Beck, P. T. P. Tsui, M. Pescador, W. L. and J. G. Peters; paratypes 11 nymphs, Florida, Gadsden Co., Monroe Creek at bridge on St. Hwy 286, June 6—August 15, 1967 G. Cooper, J. Jones; paratypes, 2 nymph, Florida, De Soto Co., Nocatee Peace Riv., August 4, 1950, No. 3382, H. P. Nicholson, coll. UF; paratype, 1 nymph, Florida, Gadsden Co., Flat Cr. on St. Hwy 270A, 6 mi SE Chattahoochee, July 24, 1967, G. Cooper and J. Jones; paratype, 1 nymph, Florida, Gadsden Co., Rocky Comfort Creek 3.5 mi SW of Quincy on St. Hwy 274, June 20, 1967 G. Cooper, J. Jones, and B. Owens; paratype, 1 nymph, Florida, Gadsden Co., Bear Creek at bridge on St. Hwy 267, June 21, 1967 G. Cooper, J. Jones, and B. Owens; paratypes, 25 males, 4 females, 32 subimagoes, Florida, Dixie, Levy, Gilchrist Co., Suwanee Riv., Hwy 27, May 9, 1975, P. Carlson. All specimens coll. FAMU, holotype in alcohol, parts of paratypes on slides.

Etymology: Named after the locality of the holotype (Etowah Riv.)

Distribution: Nearctic species so far known only from Florida, inhabiting Costal Plain physiographic province (Berner, 1977); undoubtedly distributed also in Georgia and Alabama. This species seems to be abundant where it occurs since large collections of adults are available from several Florida localities (Apalachicola Riv., Suwanee Riv., and others).

Differential diagnosis and discussion: Nymphs of this species can be separated from other species of *Cercobrachys* by the following combination of characters: (1) ocellar tubercles as long as 2/3 of eye width, frontal tubercle shorter, (2) segment 2 of maxillary palps pointed, 1.5 times longer than segment 1, (3) pronotal spines present, (4) tibiae of fore legs shorter by 1/3 1/4 than tarsi, (5) claws with denticles, (6) spines of segment 2 only indicated, spines of segment V overlapping in dorsal view, (7) gill cover symmetrical with rounded apical portion, 1.2 times longer than wide. Nymphs are related to those of *C. serpentis* and closely related to those of *C. minutus*. They differ mainly in brighter coloration of body, arrangement of mouth-parts (maxillary palps) and posterolateral abdominal spines and nearly circular gill cover. Adults can be compared only with adults of *C. minutus*; their differential diagnosis is apparent from the key.

Cercobrachys colombianus sp. n.

(Figs 189, 192, 200, 205, 212, 216, 225, 239, 240)

Mature nymph: Body length 4.0 mm, length of cerci 1.8 mm. Head and thorax dark yellowish or yellowish brown with inconspicuous darker smudges. Dark brown stippling of fore gut well apparent through head and thoracic integument. Lateral ocellar tubercles large, regularly triangular, bluntly pointed at apex, as long as the

eye width, their width at base equal to width of eyes; frontal tubercle shorter by 1/2, equal in shape with lateral ones. Sparse short bristles on genae. Antennae yellowish brown, unicolorous, the ratio pedicel: scape 0.9:0.6. Labrum twice as broad as long, length: width 0.9:2.1, oblong shaped, not produced laterally, with numerous short bristles on the anterior margin. Outer maxillary incisors slightly longer than middle ones but 2.5-3 times broader at base. Segment 2 of maxillary palps twice as long as segment 1, slightly extended apically, asymmetrical and bluntly pointed, its inner margin straight with bristles in last two thirds. Segment 2 of labial palps pointed at apex with two slightly oblique subapical rows of short and flat bristles.

Pronotum more than twice broader than long without lateral spines, its lateral margins moderately convex, rounded. Thoracic sterna with inconspicuous darker stippling; their anterior margin with sparce (prosternum) or without (meso- and metasternum) bristles. Legs whitish yellow, unicolorous, without markings, tibiae and tarsi covered with long bristles. The ratio femur: tibia: tarsus 4.0:2.0:2.4 fore legs, 5.8:3.7:3.7 middle legs, 6.2:4.1:4.8 for hind legs. Claws slightly but slender as long as 1/3 of tarsus, without denticulation.

Abdominal terga dark yellowish, terga I, II and VII—IX with dark brown medial band. Sterna unicolorous, slightly dark with brownish stippling. Posterolateral spines of segment I, II and VII—IX lacking, those of segments III as long as wide, triangular, pointed; spines of segments IV and V 2.5—3 times longer than wide, spines of segment VI very large rounded 1.5 times as long as wide, continuous in the middle of segment IX. Gill cover yellowish symmetrical (length: width 4.7: 3.7); triangular ridge not pigmented. Cerci yellowish brown, slightly darker apically.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph, Colombia, Tolima Prov., Quebrada Riv. between Armero and Lerida, 11.7 km from Lerida, April 4, 1969 W. P. McCafferty; paratype, I nymph, same data as helotype, coll. UU.

Etymology: From Latin colombianus, meaning inhabiting or coming from the state Colombia

Distribution: Neotropic, distribution unknown except the locality of holotype.

Differential diagnosis and discussion: C. colombianus can be distinguished from the other species of Cercobrachys by the following combination of characters: (1) ocellar tubercles large, regularly triangular, wide at base, (2) segment 2 of maxillary palps twice longer than segment 1, (3) pronotal spines absent, (4) tibiae of fore legs shorter than tarsi, (5) claws without denticles, (6) spines of segments II and VII—IX absent, those of segments 6 large continuous in the middle of the segment V, (7) gill cover symmetrical, 1.3 times longer than wide.

Cercobrachys minutus (Tshernova) comb. n.

(Figs 25, 31, 59, 120, 125, 159, 160)

Brachycercus minutus Tshernova, 1952: 285. 1958: 64. Keffermüller, 1960: 36. Tshernova, 1964: 135. Kazlauskas, 1964: 169. 174; 1965: 201. Wojcik, 1966: 112. Rusev, 1968: 297; 1970:

113. Sowa, 1975: 257. Puthz, 1978: 272. Baykova & Varykhanova, 1978: 121. Soldán, 1978: 326.

Eurycaenis minutus, KAZLAUSKAS, 1962: 3.

Mature nymph: Body length 4.7 (4.5) mm, length of cerci 1.1 (1.2) mm. Head brown with slightly darker occiput and frons. Lateral ocellar tubercles rounded, as long as the eye width, frontal tubercle pointed, regularly triangular, shorter by 1/4 than laterals. Bristles on genae as long as head. Antennae yellowish brown, unicolorous, the ratio pedicel: scape 1.6:1.2. Labrum with well developed antenolateral lobes and slightly incurved anterior margin, twice broader than long (length: width 1.3:2.4). Outer and middle mandibular incisors equal in length with 3--4 bluntly pointed teeth; mandibles with relatively numerous marginal setae. Segment 2 of maxillary palps longer by 1/2 than segment 1, equal in width; convex inner margin covered with fine bristles. Hypopharyngeal superlinguae produced laterally and bluntly pointed. Segment 3 of labial palps tapered apically and pointed.

Pronotum dark brown with a pair of very obtuse, low lateral spines forming submarginal ridge, 3 times broader than long; meso- and metanotum dark brown with paler smudges, medial suture black bordered. Thoracic sterna dark pitch brown, unicolorous, paler in the middle, anterior margin of mesosternum only slightly produced. Legs yellowish brown with darker femora, covered with long bristles. The ratio femur: tibia: tarsus 2.2:0.8:1.1 for fore legs, 3.4:2.1:2.2 for middle ones and 4.0:2.1:2.2 for hind legs. Claws slightly bent with minute denticulation.

Abdominal terga I and II dark pitch brown, unicolorous, terga VII—X yellowish brown, a pair of darker smudges on terga VII and VIII; sterna I - VII dark brown, darker on sides, sterna VIII—IX paler. Posterolateral spines on segment II and VII—X lacking, those of segments III—V pointed, not overlapping in dorsal view; spines of segment VI narrow and pointed in dorsal view. Gill cover brown, lighter posteriorly, with dark pigmented triangular ridge. Cerci brownish, paler in the apical half.

Adult and subimago: Body length 4.0 (3.5-4.0) mm (male), 5.0 mm (female) (Keffermüller, 1960), length of cerci 13 (12.0-15.0) mm (male), 3.5 (female, subimago). Head light brown, darker in medial area near the epicranial suture and near posterior margin, dark brown spots near the base of ocelli. Antennae with deep brown scape and pedicel and paler flagellum with basal darker ring. The ratio scape: pedicel the same as in nymph. Antennae of subimago paler, dark ring on flagellum not apparent. Thorax dark brown, pronotum with conspicuous smudges, thoracic sterna dark, paler on sides. Wings translucent, semi-hyaline whitish, first 3-4 longitudinal veins dark brown near base, respective membranes slightly milky with some dark brown dusting. Legs brownish yellow, fore legs and femora of middle and hind ones darker, fore femora dark bordered. The ratio femur: tibia: tarsus (male) 2.5: 4.2: 2.2 for fore legs, 4.4: 3.2: 2.8 for middle ones and 4.6: 3.3: 3.0 for hind legs. Abdomen brownish yellow, first abdominal terga darker with blackish stippling, segment IX and X paler. Penis slightly broader than long with distinct

posterolateral rounded lobes, its lateral margins straight or convex, posterior margin straight. Triangular dark brown spot in the middle of penis. Forceps brown, longer by 1/3-1/2 than penis.

Material examined: 3 nymphs, 1 male, 1 subimago, Czechoslovakia, South Slovakia, Ipel Riv., Lela, May 25, 1975 T. Soldán, coll. IE.

Distribution: Widely distributed Transpalearctic species; originally considered as endemic to the Amur basin, Far East (Tshernova, 1952, 1958). Later found also in Poland (Keffermüller, 1960 and others), Lithuania (Kazlauskas, 1965), Czechoslovakia (Soldán, 1978) and Bulgaria (Rusey, 1968); also in Mongolia (Baykova & Varykhanova, 1978).

Differential diagnosis and discussion: The following combination of characters distinguishes this species from remaining species of the genus Cercobrachys: (1) ocellar tubercles as long as eye width, frontal tubercle smaller, (2) segment 2 of maxillary palps pointed, 1.5 times longer than segment 1, (3) pronotal spines obtuse, forming submarginal ridge, (4) tibiae of fore legs shorter by 1/2 than tarsi, (5) claws with minute denticles, (6) posterolateral spines of segments II and VII absent, those of segment V not overlapping in dorsal view, (7) gill cover symmetrical, approximately 1.3 times longer than wide. Nymphs of C. minutus are related to C. serpentis and closely related to those of C. etowah; they differ mainly in the arrangement of characters (6) and (7). Adults can be compared only with C. etowah. They are distinguished by the structure of penis and some details in coloration (see key).

Cercobrachys peruanicus sp. n. (Figs 33, 38, 59, 120, 125, 159, 160)

Brachycercus sp., EDMUNDS et al., 1976: 226.

Mature nymph: Body length 4.5 (4.5—4.7) mm, length of cerci 1.4 (1.3—1.4) mm. Head pale yellowish, whitish between ocelli; frons, vertex and occiput yellowish brown. Lateral ocellar tubercles rounded, as long as the eye width, frontal tubercle smaller, more pointed. A group of about 10—15 setae longer than head on genae. Antennae unicolorous, brownish yellow, ratio scape: pedicel 1.0:1.1. Labrum more than twice as broad as long (width: length 2.5:1.1). Outer incisors 2—3 times broader than middle ones, equal in length. Segment 2 of maxillary palps asymmetrical, bluntly pointed and more than twice the length of segment 1 which is twice broader and rounded. Segment 2 with dense setae and numerous bristles on inner margin. Hypopharyngeal superlinguae apparently produced into round:d lobes, lingua oblong-shaped. Segment 2 of labial palps tapered toward to apex, pointed.

Pronotum yellowish white with inconspicuous darker smudges on sides and a pair of very low and obtuse lateral spines forming submarginal ridges. Meso- and metanotum yellowish white with light brownish stippling in the middle, two diffuse darker stripes near the base of wing pads, wing pads whitish with brownish outer margins. Thoracic sterna whitish, prosternal and marginal mesosternal bristles long, conspicuous. Legs whitish yellow with long pale setae, the ratio femur: tibia: tarsus 5.5:

: 3.0 : 3.8 for fore legs, 6.0 : 4.5 : 4.0 for middle ones, and 6.5 : 5.0 : 4.2 for hind ones. Claws slender, conspicuously bent at apex, without denticulation.

Abdominal terga I and II with slight dark brown stippling, terga VII—IX paler, whitish, tergum X darker. Sterna whitish with brownish stippling. Posterolateral spine of segment II well developed, obtuse; spines of segments III—V nearly symmetrical, pointed; spines of segment VII rounded at apex, segment VII—X without spines. Gill cover long and narrow (length: width 5.5:3.4) with straight lateral margins; submarginal outer ridge slightly indicated. Cerci pale, unicolorous. The eggs (dissected from mature larva) measuring $200-250\,\mu\mathrm{m}$ with 4 large, rounded costae and conspicuously tapered toward the polar cap, 3 times longer than broad.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph; paratypes 4 nymphs, Peru, San Martin Prov., Rio Tulumayo, 20 km E of Tingo María, July 1963 W. L. Peters, coll. UU; paratype, nymph, Peru, Loreto, Rio Yurac, July 1963 W. L. Peters, coll. UU. Parts of holotype on slides, holotype in alcohol.

Etymology: From latin peruanicus, meaning inhabiting or coming from the state Peru. Distribution unknown except the above localities, Neotropical.

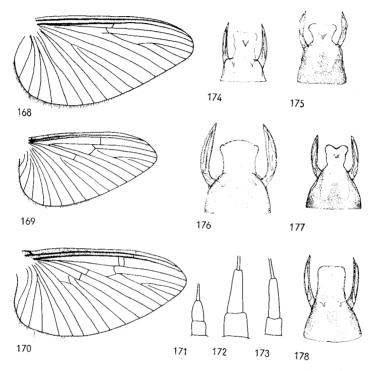
Differential diagnosis and discussion: C. peruanicus can be distinguished by the following combination of characters: (1) ocellar tubercles rounded, as long as the eye width, (2) segment 2 of maxillary palps pointed, more than twice longer than segment 1, (3) pronotal spines very obtuse, forming submarginal ridge, (4) tibiae of fore legs slightly shorter than tarsi, (5) claws without denticles, (6) spines of segment II well developed, those of segment VI rounded in dorsal view, spines lacking from segments VII—X, (7) gill cover elongated (1.6 times longer than wide) without marginal ridges. The characters (2, 5, 6, 7) singles this species out from C. minutus, C. etowah and C. serpentis; eggs are different from those of C. etowah and C. petersonum in shape and arrangement of costae.

Cercobrachys petersorum sp. n. (Figs 5, 13, 32, 44, 54, 75, 83, 104, 111, 126, 162, 163)

Mature nymph: Body length 5.7 (5.2—6.3) mm, length of cerci 2.0 (1.8—2.1) mm. Head oval with slightly concave posterolateral margins, pale yellowish with slightly darker frons and vertex behind the lateral tubercles. Lateral ocellar tubercles shorter than the eye width, rounded. Frontal tubercle shorter by 1/2, low and wide, nearly circular. Antennae pale yellowish, unicolorous, the ratio scape: pedicel 0.6:0.8. Setae on genae shorter than head. Labrum oval with rounded lateral lobes, twice broader than long (width: length 1.8:0.9) and with anterolateral groups of bristles. Outer and middle mandibular incisors equal in length and width, spatulate, not tapered apically, with bluntly pointed teeth; inner incisors of right mandible reduced, setose. Segment 2 of maxillary palps club-shaped, rounded at apex, as wide as segment 1 and about 1.5—1.8 times longer. Hypopharyngeal superlinguae produced into

rounded lateral lobes with concave lateral margins. Segment 2 of labial palps only slightly tapered apically.

Pronotum whitish yellow, unicolorous, twice broader than long (width: length 6.5:3.0) without any lateral spines or ridges. Meso- and metanotum of the same color with dark brown dusting in the middle and paler wing pads. Sterna pale, whitish. Prosternum and anterior margins of meso- and metasternum with numerous, cranially directed bristles. Sterna with 2 3 wave-like indicated protuberances. Legs pale, unicolorous, fore legs with conspicuously long setae; a group of setae near the base



Figs 168—178: Wing (168—170), penis in ventral view (174—178) and base of antennae (171 to 173) in adults. 168, 173 - Brachycercus edmundsi. 169, 177 - Cercobrachys etowah. 170, 172 - Insulibrachys needhami. 171, 175 - Cercobrachys minutus. 174 - B. berneri. 176 - B. lacustris. 178 - B. nitidus.

of femora, setae on tibiae and tarsi arranged into submarginal rows. The ratio femur: tibia: tarsus 5.8:2.0:5.2 for fore legs, 3.7:1.3:3.4 for middle ones and 4.2:2.0:3.2 for hind legs. Claws bent, without denticulation.

Abdominal sterna I and II with heavy dark brown dusting, terga VII—X pale brownish yellow. Sterna whitish yellow, unicolorous, sterna I—VII with a pair of rounded submarginal spots and conspicuous spine-like setae near the posterior margins. Segment II with convex lateral margin, posterolateral spines of segment III—V pointed, nearly symmetric, 3—4 times longer than broad at base; segment VII with

a pair of well developed spines. Gill cover pale yellowish with slightly produced mediolateral margin and hind margin with flat rounded setae; short setae also on gill cover surface, triangular ridge only indicated. Cerci unicolorous, pale whitish. The eggs (dissected from female nymphs) ellipsoidal, 4 times longer than broad with several rounded costae and polar cap as wide as the eggs.

Adult and subimago unknown.

Material examined: Holotype, mature nymph, paratypes 2 nymphs, Thailand, Chiengmai Prov., Mae Ping, Chiengmai, November 17, 1964 W. L. and J. G. Peters, coll. UU; parts of holotype on slides, holotype in alcohol.

Etymology: This species is named for Dr. W. L. Peters and Mrs. J. G. Peters who collected the type material in Thailand.

Distribution: Oriental, distribution unknown except the locality of holotype.

Differential diagnosis and discussion: C. petersorum differs from the remaining species of Cercobrachys by the following combination of characters: (1) ocellar tubercles low, rounded, shorter than the eye width, (2) segment 2 of maxillary palps club-shaped, rounded at apex and 1.5—1.8 times longer than segment 1, (3) pronotal spines absent, (4) tibiae of fore legs more than twice shorter than tarsi, (5) claws without denticles, (6) posterolateral spines of segment VII well developed, (7) gill cover asymmetrical with stout setae on the posterior margin. The species occupies a quite isolated position among species of the genus Cercobrachys. The arrangement of most characters (2, 3, 4, and 7) is unique within the genus. On the other hand, the arrangement of posterolateral spines of segment III—VI, antennae, head tubercles, and thoracic sterna ally this species to the genus Cercobrachys until other Oriental species are found.

Cercobrachys serpentis sp. n. (Figs 24, 94, 118, 128, 164, 165)

Mature nymph: Body length 3.7 mm, length of cerci 1.6 mm. Head brownish yellow with large dark spot on vertex and occiput, epicranial suture light bordered. Lateral tubercles shorter by 1/3 than the eye width, frontal tubercle slightly longer and more pointed. Antennae pale yellowish, pedicel about as long as scape (1.3:1.2). Labrum with well developed lateral lobes. Outer mandibular incisors slightly broader than middle one, equal in length; incisors with 3—4 bluntly pointed teeth. Segment 2 of maxillary palps pointed at apex, nearly as wide as segment 1 and longer by 1/2, with concave inner margin bearing numerous long bristles in apical half. Hypopharyngeal superlinguae only slightly produced laterally, bluntly pointed.

Pronotum yellowish brown, darker smudges in the middle; a pair of very obtuse and inconspicuous lateral spines present. Meso- and metanotum light brown or yellowish brown with diffuse darker spots and smudges near wing pads bases, posterior margin of metanotum darker. Thoracic sterna light brown, prosternum and prominent anterior margin of mesosternum with long bristles. Legs pale yellowish, setae

on inner margins of tibiae as long as 1/2 femur, tibiae without longer setae. The ratio femur: tibia: tarsus 2.4:0.9:1.6 for fore legs, 2.8:1.2:2.0 for middle ones and 3.0:1.5:2.5 for hind legs, claws as long as 1/2 of tibiae, bent at apex, with two rows of 6-7 teeth.

Abdominal terga yellowish brown, unicolorous, tergum X slightly darker. Posterolateral spines of segment II very low and rounded; those of segments III—V pointed, asymmetrical, not overlapping in dorsal view, spines of segment VI wide, twice longer than broad in dorsal view; spines of segment VII missing. Sterna yellowish brown, sterna I—IV paler in the middle. Gill cover slightly asymmetrical with straight inner margin and clearly defined submarginal ridge, triangular ridge brownish. Cerci yellowish, unicolorous.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph; paratype nymph, <u>Idaho</u>, Payette Co., Snake Riv., Payette, August 7, 1965 G. F. Edmunds, coll. UU. Parts of holotype on slides, holotype in alcohol.

Etymology: From Latin serpens, meaning snake; named after the type locality.

Distribution: Nearctic, probably widespread in NW states of the USA. Morphologically similar nymphs found also in Nebraska (coll. UU).

Differential diagnosis and discussion: The following combination of characters distinguishes this species from remaining species of the genus *Cercobrachys*: (1) ocellar tubercles bluntly pointed, shorter by 1/3 than the eye width, (2) segment 2 of maxillary palps pointed, 1.5 times longer than segment 1, (3) pronotal spines present, forming submarginal ridge, (4) tarsi of fore legs about 1.8 times longer than tibiae, (5) claws with denticles, (6) posterolateral spines of segments III—V not overlapping in dorsal view, those of segment VI wide, spines of segment VII missing, (7) gill cover 1.4 times longer than wide with apparent inner submarginal ridge. *C. serpentis* is related to *C. etowah* and *C. minutus*; it differs mainly in the arrangement of abdominal spines, gill cover and head coloration (see key).

Caenoculis gen. n.

Type species: Caenoculis bishopi sp. n., by original designation; type locality Malaysia.

Species included: Caenoculis bishopi sp. n., C. dangi sp. n., C. nhahoensis sp. n.

Mature nymph: Body length approximately 4 mm, length of cerci 2/3 of body length. Body cylindrical, not flattened, head with three low and rounded ocellar tubercles, produced into distinct posterolateral lobes. Antennal pedicel approximately twice as long as scape. Mandibles without lateral bristles. Maxillary and labial palps 3-segmented. Pronotum without lateral spines; fore coxae nearly contiguous. Abdominal segments (IV—VII or IV—VIII) with flat posterolateral spines, not bent dorsally. Femora three times broader than tibiae, middle and hind legs only slightly longer than fore legs, tibiae and tarsi approximately of the same length; claws of fore

legs slender, bent, claws of hind and middle legs stout, hooked, with or without denticulation. Gill 1 2-segmented, gill cover symmetrical or asymmetrical, produced posterolaterally, triangular ridge present but asymmetrical; ventral side of gill cover with submarginal row of spines like in *Caenis*; lamellate gills with fringe bifid or multifid.

Adult and subimago unknown.

Etymology: Caenoculis (m.), from Caenis, related genus and Latin oculi, meaning eyes. Distribution: Oriental, Malaysia, Vietnam.

Differential diagnosis and discussion: Caenoculis can be distinguished from all remaining genera of the family Caenidae by the following combination of nymphal characters: (1) pedicel about twice as long as scape, (2) occllar tubercles well developed, (3) head with distinct posterolateral lobes, (4) maxillary and labial palps 3-segmented, (5) fore coxae nearly continuous, (6) femora three times as broader as tibiae, tibiae approximately as long as tarsi, (8) posterolateral spines of segment VI not bent medially, (9) gill cover with ventral subimaginal row of spines, (10) body covered with scales. The genus in the nymphal stage is very well defined and easily distinguishable from all genera of the Caenidae on comparison of the characters of Brachycercus and Cercobrachys (1, 2, 7, 9, 10) with those of the Caenis-like genera and Clypeocaenis (3, 4, 5, 6, 8, 10).

Key to the species of Caenoculis

Mature nymphs

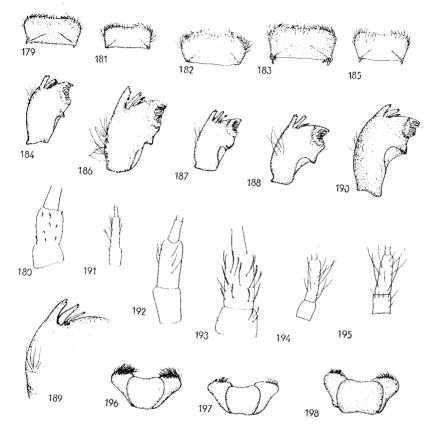
- 2 (1) Body brown, unicolorous; pronotum and mesothorax with conspicuous medial ridge; frontal ocellar tubercle well apparent; gill cover asymmetrical, covered at least partially with branched scales; fore femora and tibiae with short scales (Figs 124, 130, 209); fore legs shorter than middle ones.

Caenoculis bishopi sp. n.

(Figs 7, 14, 37, 55, 77, 78, 80, 100, 102, 103, 116, 124, 130, 167)

Mature nymph: Body length 4.1 mm, length of cerci 2.1 mm. Head brownish, evently covered with branched scales on posterior half; from slightly lighter. Lateral occilar tubercles low (as long as 1/2-2/3 of the eye width) and rounded; frontal

tubercle smaller by 1/3 than lateral ones. Antennae brownish, unicolorous, pedicel twice longer than scape (2.5:1.2). Labrum oblong-shaped with small anterolateral lobes, more than twice broader than long (length: width 2.6:6.3) with slightly incurved fore margin covered with stout setae. All mandibular incisors approximately equal in width, outer incisors longest; inner incisors with subapical bundle of fine



Figs 179—198: Antennal scape and pedicel (180, 191—195), labrum (179, 181—185), mandible (184, 186—190) and hypopharynx (196—198) of nymphs. 179, 188, 195 - *Brachycercus berneri*. 183, 190, 194, 198 - *B. maculatus*. 184, 185, 191, 197 - *Brachycercus kabyliensis*. 180, 181, 187 - *Caenoculis nhahoensis*. 182, 186, 193, 196 - *C. dangi*. 189, 192 - *Cercobrachys colombianus*.

bristles. Segment 3 of maxillary palps as long as segment 1, longer than segment 2. Hypopharyngcal superlinguae only slightly produced laterally. Segment 3 of labial palps triangular with row of stout spines on inner margin and a group of bristles in the middle, shorter by 1/2 than segment 2.

Pronotum brown, unicolorous, three times broader than long with a pair of paler spots on sides and conspicuous medial ridge, evenly covered with branched scales. Meso- and metanotum brown as well, with scales and inconspicuous paler smudges. Ventral side of thorax light brown, legs yellowish brown. Femora with outer marginal

row of drop-like scales and several bristles at base, tarsi with bristles and longer spines on margins. The ratio femur: tibia: tarsus 7.5:5.0:4.4 for fore legs, 8.2:5.8:4.0 for middle ones and 8.2:5.8:4.9 for hind legs; claws of fore legs bent.

Abdominal terga light brown with darker stippling, sterna yellowish brown without markings. Posterolateral spines of segments IV – VII twice longer than broad at base, bent, asymmetrical and pointed. Gill cover asymmetrical, dark brown, evenly covered with branched scales except for the inner margin behind triangular ridge; inner fork of triangular ridge with row of short, pointed spines; gills 3—6 rounded and nearly symmetrical with dark brownish intertracheal spaces and marginal fringe. Cerci yellowish, unicolorous.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph, Malaysia, Gombak Riv. near Kuala-Lumpur, J. Bishop, coll. FAMU. Holotype in alcohol, parts on slides.

Etymology: Species named for Dr. J. Bishop who collected the type specimen in Malaysia.

Differential diagnosis and discussion: This species seems to be closely related to *C. nhahoensis*. It can be distinguished mainly by the arrangement of ocellar tubercles and posterolateral spines of abdominal segments.

Caenoculis dangi sp. n.

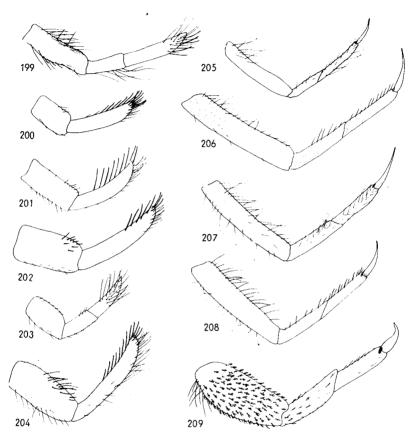
(Figs 182, 186, 193, 196, 199, 210, 222, 224, 230)

Mature nymph: Body length 4.4 mm, length of cerci 3.2 mm. Head dark brown with a pair of large pale spots on vertex and evenly covered with branched scales. Ocellar tubercles very low, rounded, frontal tubercles hardly distinguishable. Antennae pale unicolorous, pedicel more than twice longer than scape (1.2:0.5) with numerous short and stout bristles. Labrum oval with rounded incurvation in the middle of fore margin, more than twice broader than long (length: width 1.6:3.8) and with stout and numerous marginal setae. Middle mandibular incisors distinctly narrower than outer ones, slightly longer; inner incisors shorter by 1/3. Segment 3 of maxillary palps distinctly shorter than segment 1. Hypopharyngeal superlinguae circular. Segment 3 of labial palps triangular, bluntly pointed, shorter by 1/4 than segment 2, with marginal row of stout spines.

Pronotum dark brown with numerous pale spots, narrow, produced anterolaterally, ratio length: width 0.6: 2.3; medial ridge not developed. Meso- and metanotum dark brown with numerous pairs of large pale spots. Thoracic nota evenly covered with relatively small branched scales. Legs brownish yellow, with bristles longer than the femur width, tibiae and tarsi of fore legs conspicuously dark brown ringed. The ratio femur: tibia: tarsus 7.7: 5.3: 4.5 for fore legs, 7.0: 4.5: 3.8 for middle legs, and 7.5: 5.5: 4.0 for hind legs. Claws of fore legs long, slender, slightly bent; claws of middle and hind legs stout, hooked, with very minute teeth.

Abdominal terga I, III and VIII—X brownish, other terga paler. Posterolateral spines of segments IV—VIII long and pointed, at least 3—4 times longer than wide at base. Posterior margin of tergum II with small medial spine, margins of other terga smooth. Gill cover symmetrical with several very small branched scales, gills 3—6 rounded with brownish stippling. Cerci whitish, transparent, with conspicuous bristles.

Adult and subimago unknown.



Figs 199—209: Maxillary palpus (199—204) and middle leg (205—209) of nymphs. 199—Caenoculis dangi. 200, 205—Cercobrachys colombianus. 201, 208—Brachycercus kabyliensis. 202, 206—B. maculatus. 204, 207—B. berneri. 203, 209—Caenoculis nhahoensis.

Specimen examined: Holotype, mature nymph, Vietnam, Thuan-hai Prov., Cau Song Pha, 50 km W of Phan-rang, April 20, 1982 T. Soldán, coll. IE. Holotype in alcohol, parts on slides.

Etymology: Named for a distinguished Vietnamese hydrobiologist, Dr. Dang Ngoc Thanh. Distribution: Oriental, unknown except for the type locality.

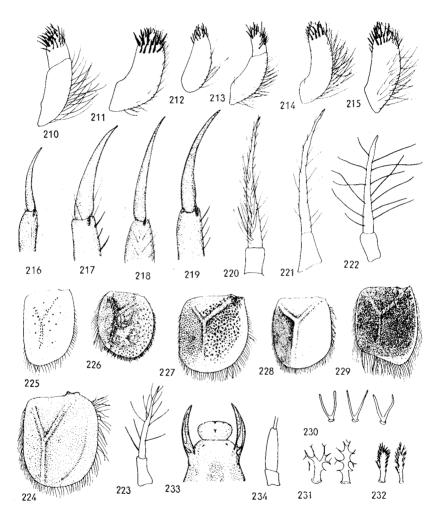
Differential diagnosis and discussion: This species occuppies an independent position, critical distinguishing characters are apparent from the key.

Remaining species of the genus *Caenoculis* differ mainly in the arrangement of gill cover and thoracic nota.

Caenoculis nhahoensis sp. n.

(Figs 180, 181, 187, 203, 209, 213, 223, 226, 231, 232)

Mature nymph: Body length 3.9 (3.5 4.0) mm; length of cerci 2.8 (2.5 2.9) mm. Head dark brown or blackish brown, evenly covered with branched scales.



Figs 210—234: Distal part of labial palp (210—215), claws (216—219), gill 1 (220—223), gill cover (224—229) and spines of middle femora (231) and gill cover (230, 232) of nymphs, and base of antenna and male genitalia of adult (234, 233). 210, 222, 224, 230 - Caenoculis dangi. 213, 223, 226, 231, 232 - C. nhahoensis. 212, 216, 225 - Cercobrachys colombianus. 211, 219, 221, 227, 233, 234 - Brachycercus maculatus. 214, 217, 228 - B. kabyliensis. 215, 218, 220, 229 - B. berneri.

)

Lateral ocellar tubercles regularly triangular, as long as eye width, frontal tubercle smaller by 1/2 than lateral ones. Antennae with paler unicolorous pedicel less than twice longer than scape (0.9:0.5). Labrum three times as broad as long, with nearly straight fore margin. Middle mandibular incisors slightly narrower than outer ones, approximately of the same length; inner incisors with subapical bundle of short fine bristles. Segment 3 of maxillary palps as long as segment 1. Hypopharyngeal superlinguae distinctly produced laterally. Segment 3 of labial palps rounded with apex produced into a blunt point, shorter by 1/2 than segment 2, with stout marginal spines.

Pronotum dark brown, unicolorous, oblong shaped, 3—4 times as broad as long, with conspicuous medial ridge. Meso- and metanotum of the same colour, medial ridge well apparent. Legs brownish yellow; tibiae and tarsi with inconspicuous darker rings; covered with branched scales. The ratio femur: tibia: tarsus 4.3: 3.0: 2.8 for fore legs, 4.5: 3.0: 3.0 for middle legs, 4.7: 3.2: 3.0 for hind legs. Claws of middle and hind legs more hooked, without denticles.

Abdominal terga dark brown; terga VIII—X covered with scales, medial teeth apparent on the posterior margin of terga I, II, VIII and IX. Posterolateral spines on segments IV VIII, long and pointed 3—4 times longer than wide at base. Gill cover asymmetrical, evenly covered with scales, gills 3—6 oval, 1.3—1.5 times longer than wide. Cerci yellowish, unicolorous.

Adult and subimago unknown.

Specimens examined: Holotype, mature nymph, Vietnam, Thuan hai Prov., Kinl:-Dinh Riv., Nha-ho near Phan Rang, April 18, 1982 T. Soldán, coll. IE; paratypes, 4 nymphs, same d ita. Holotype in alcohol, parts on slides.

Etymology: Named after the type locality, Nha-ho.

Distribution: Oriental; unknown except the type locality.

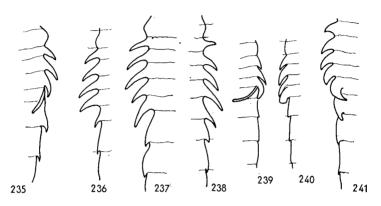
Differential diagnosis: Related to C. bishopi; critical distinguishing characters are apparent from the key.

Notes on the biology of Caenidae with ocellar tubercles

Since the biology of most species studied remains quite unknown, the following data concern mostly the well-known European species, *Brachycercus harrisella*, and some American species of the same genus. There are no data concerning *Insulibrachys needhami* and *Caenoculis bishopi*.

Nymphal habitats. Nymphs of *Brachycercus* and *Cercobrachys* have a relatively very wide ecological range. In the Palearctic, nymphs of *Brachycercus* inhabit mainly slow flowing, large, continental rivers. Brittain (1972) found nymphs in the 400 m wide river Blomma in Norway and Rusev (1966a, 1966b, 1968) in the Danube at a depth of 3.60 m (current speed 0.37 m.sec⁻¹) about 850 m from the banks. Tshernova (1952) reports finding of nymphs of *Brachycercus* at depths of 1.3—4.0 m; those of *B. tubulatus* from as much as 3.0—8.0 m in the Amur river basin. Also

Dr. Berner (pers. comm.) informed me that the nymphs of *C. etowah* from the Peace Riv. in Florida were collected in 20 feet of water (about 6 m). Lehmann (1935), Siemińska (1954), Keffermüller (1957, 1960) and Landa (1957, 1969) found the nymphs of *B. harrisella* and *C. minutus* in smaller rivers and stream pools at depth of 0.10—0.25 m with current speeds of 0.35—0.43 m.sec⁻¹ (Keffermüller, 1957) or 0.40—0.78 m.sec⁻¹ (Landa, 1957). Nymphs are generally found in lowland and highland localities, Landa (1957) reports the localities at altitudes of 278, 427, 447 and 523 m in Czechoslovakia. In the Nearctic the nymphs of *Brachycercus* and *Cercobrachys* inhabit larger lowlands rivers (e.g. Appalachicola Riv. in Flo-



Figs 235—241: Dorsal (235, 237, 239, 241) and lateral (236, 238, 240) view of posterolateral spines of abdominal segments in nymphs. 235, 236 - *Brachycercus maculatus*. 237, 238 - *B. berneri*. 241 - *B. kabyliensis*. 239, 240 - *Cercobrachys colombianus*.

rida - Berner, 1950; Schneider, 1967) as well as in smaller streams (e.g. Pescador & Peters, 1974). Traver (1932) reports B. nitidus from small rivers and mountains streams, Peters & Jones (1973) collected Brachycercus nymphs from a clean, shifting-sand river. Some species, e.g. B. lacustris, have been reported from the shores of lakes (NEEDHAM, 1908, and others). Water temperatures where nymphs of Brachycercus occur range between 6-25 degrees centigrade. According to Berner (1950) nymphs of B. maculatus prefer slightly alkaline streams, living at a depth of only several inches; LANDA (1957) reports a pH range of 6.9-7.4 for B. harrisella. Nymphs of Brachycercus prefer silty or fine muddy microhabitats. In stream with shifting-sand habitats they live close on top of the sand with a very thin overburden of silt (Berner, 1950; Edmunds et al., 1976). Spieth (1938) reported the nymphs of Brachycercus from »the clean sand of a bar in about one foot of water«. SUKATS-KENE (1962) found nymphs of B. magnus and B. tubulatus among submerged vascular plants (I have collected nymphs of B. harrisella in the same microhabitats at several localities in Czechoslovakia as well). The Vietnamese Caenoculis species inhabit similar microhabitat.

Nymphal habits. Nymphs are usually at least partially covered with silt and

are very difficult to see. Nymphs of *B. harrisella* dig in mud, sometimes even not being exposed above the mud surface; they move very slowly (Landa, 1957). Berner (1950) observed the nymphs of *B. berneri* sprawling on the sand. When collected the nymphs raise their cerci over the abdomen and move with a slow wriggling motion; their progress is hardly perceptible (Edmunds et al., 1976). Nymphs undoubtedly feed on fine detritus.

Life cycle. Brachycercus harrisella is a typical summer« species (cf. LANDA, 1968) having a single generation a year in Europe. Embryonic diapause occurs during winter. Older larvae can be found from May to August (LANDA, 1968, 1969a; Sowa, 1975); adults fly from the end of May to the beginning of September. The development of nymphs, even of those from the same population, is irregular in most localities in Czechoslovakia so that the flying period is rather prolonged. Judging from the time of finding mature nymphs of C. minutus and B. pallidus, these species have a similar type of life cycle (cf. KAZLAUSKAS, 1965; WOJCIK, 1966; Sowa, 1975). In the Nearctic, the emergence of northwestern species is restricted to the warm summer months; emergence in Idaho and Canada has been recorded even as late as September (EDMUNDS et al., 1976). Longer emergence periods occur in the south. Southeastern species (B. berneri, B. pini, B. floridicola, B. maculatus) most probably emerge throughout the year. The development of nymphs is continuous, perhaps with the ceasing of nymphal growth in December and January (cf. Berner, 1950; Edmunds et al., 1976). Pescador & Peters (1974) record one generation a year for B. maculatus (nymphs present from April to the end of October, adults in September and October in Rocky Comfort Creek in Florida). Winter emergence (e.g. February 28; April 6) of this species is recorded by Berner (1950) from Silver Springs and the Santa Fe River in Florida.

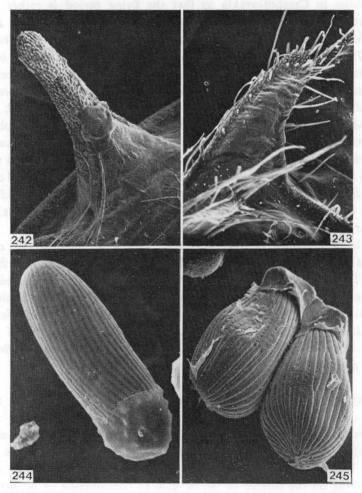
Adult habits. Landa (1969) observed the emergence of subimagos of *B. harrisella* in the evening, molting into adults after 1—2 hours, and a mating flight round midnight. The adult stage lasts 4—10 hours. Keffermüller (1957) noted the emergence of reared nymphs after midnight. Also, Eaton (1884) states that adults probably fly at night. I have observed an early morning mating flight of *B. harrisella* in Eastern Slovakia. Ide (1930) describes also an early morning mating flight of *B. prudens* in Ontario. Edmunds et al. (1976) refer to a mid-morning mating flight of *Brachycercus* in Florida and Wyoming, and flight after dark in Idaho.

Phylogeny and relationships of the Caenidae with ocellar tubercles

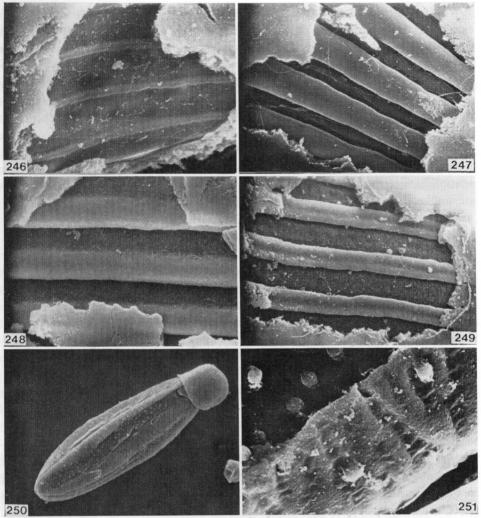
As indicated above, the caenids with ocellar tubercles in the nymphal stage represent a morphologically as well as biologically well-defined group within the family Caenidae. This group is characterized by graduate specialization for digging or semi-burrowing on the surface of silt or mud (a combination of ocellar tubercles, thoracic sternal protuberances, posterolateral spines on the abdominal segments and bristles on the legs protects the nymph from silt). Contrary to most other may-

flies, the adults of Caenidae in general represent extremely reduced stages. While in the nymphs there are at least 10-12 critical distinguishing characters, only two characters (separated fore coxae, bent posterolateral spines on abdomen) separate these genera from other Caenidae. Nymphal adaptations are only clearly reflected in adult structures. Because of the very reduced adult structures (such as wings); and insufficiently known biology and distribution, the interrelationships of these genera can at present be evaluated mainly on the base of nymphal characters.

All caenids with ocellar tubercles possess certain derived similarities in nymphal stage so that they most probably represent a common phyletic line which evolved from an unspecialized pre-Caenis ancestor (Fig. 252). Another line is represented



Figs 242—245: Frontal head ocellar tubercle (242), posterolateral spine of abdominal segment VI (243) of nymphs and mature eggs (244, 245). 242 - *Brachycercus harrisella*. 243 - *B. nitidus*. 244 - *B. flavus*. 245 - *B. edmundsi*. (Critical point dried, gold-coated, 20 kV electronmicrographs).



Figs 246—251: Mature eggs (250) and details of chorion (246—249, 251). 246 - Brachycercus pini. 247 - B. harrisella. 248 - B. lacustris. 249 - B. nitidus. 250, 251 - Cercobrachys etowah. (Critical point dried, gold-coaled, 20 kV electronmicrographs).

by the genus Caenis and related genera (e.g. Caenodes, Tasmanocoenis, Caenomedea, Caenopsella and others). This line is apparently more primitive in comparison with line of caenids with ocellar tubercles (nymphs without any adaptation for silty microhabitats). Only the Ethiopian genus Austrocaenis shares one common character with the Brachycercus line (arrangement of fore coxae). Nymphs of the recently described Oriental genus Clypeocaenis evolved a unique, secondary specialization of mouthparts and fore legs for straining food from the current (SOLDÁN, 1978, 1983). This genus undoubtedly represents a further derived line which evolved from the phyletic line of Caenis-like genera.

Within the *Brachycercus* line, the most primitive lineage consists of the genus *Caenoculis* the nymphs of which share several common characters with the *Caenis*-like genera (3-segmented maxillary and labial palps, nearly continuous fore coxae, wide femora, body not dersally flattened) as well as with the Brachycercus-like genera (head tubercles, claws almost without denticles, posterolateral spines of abdomen, gill cover with typical triangular ridge). This combination of characters can be considered as a partial specialization for silty microhabitats. Unique branched setae on the body surface and gill cover probably help to protect them from silt since long bristles, characteristic for *Brachycercus* and *Cercobrachys*, are not developed.

On the other land, there is a doubt if *Caenoculis* actually possesses any close relationships to the *Brachycercus* and *Cercobrachys* line. The small ocellar tubercles are unlike the *Brachycercus* line, and the narrowly separated coxae also occur in *Austrocaenis*. Nevertheless, according to my opinion, the phylogeny diagram presented in Fig. 252 seems to be very probable.

Another derived lineage comprises the genera Brachycercus and Insulibrachys. Judging from the morphological characters of nymphs, the genus *Insulibrachys* is more primitive (ocellar tubercles rounded and cylindrical, abdominal spines not specialized for protecting gills, no adaptations of thoracic strrna), but the degree of head specialization in this unique form is unclear because of presence of stout setae on the tubercles which are not present in any species of Brachycercus of Cercobrachys. The geographic isolation of Insulibrachys undoubtedly played an important role in the evolution of this genus. This isolation seems to be relatively very old; Berner (1950) and Peters (1971) pointed out that there are no faunistic similarities between the mayflies of Cuba and Florida because of the considerable coological differences between the predominantly stony mountain streams in Cuba and absence of swiftly flowing streams in South Florida. The case of Brachycercus and Insulibrachys supports this conclusion although the biology of Insulibrachys is unknown; type locality of Insulibrachys is quite different from sandy stream localities included in Florida where species of the genus Brachycercus occur. Brachycercus possesses s. str. ecologically very successful nymphs which inhabit a very large spectrum of Holarctic biotopes despite their morphological specializations. There are two groups of species; the first group includes nymphs which do not possess thoracic protuberances and are brighter in color (B. berneri, B. pini, B. floridicola, B. nitidus and others) living in a sandy biotopes usually. In the Nearctic, these species represent a southeastern extension of an upper boreal distribution of the genus. The second group consists of species with specialized thoracic sterna (mostly the pronotum) for digging in predominantly muddy (e.g. B. harrisella) biotopes. They are distributed in much colder regions (B. harrisella, B. edmundsi, B. tuberculatus, B. arcticus, B. prudens). Of these species, B. prudens shows distinct relationships with the genus Cercobrachys in the arrangement of mouthparts and antennae.

The most derived lineage of the *Brachycercus* line is represented by the genus *Cercobrachys* (Fig. 252). The specialization for silty habitats is more advanced than

that of *Brachycercus*. Posterolateral spines of the abdominal segments are strongly bent forming a closed »gill basket« and tegether with symmetrical and continuous gill covers they protect the lamellate gill very effectively. Legs bear very long protecting bristles and the pro- and mesosternum (fore margin) is also very specialized (long bristles directed anteriorly help to protect the mouthparts). On the other hand,

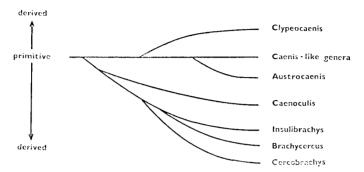


Fig. 252: A tentative diagram of phylogeny of the Caenidae.

head tubercles and pronotal spines are less developed than in *Brachycercus*. The genus *Cercobrachys* seems to be more cosmopolitan in distribution than *Brachycercus* being also Oriental (*C. petersorum*) and Neotropic (*C. peruanicus*, *C. colombianus*).

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