NEW RECORDS OF ORIENTAL CTENOSTYLIDAE (DIPTERA ACALYPTRATA), WITH DISCUSSION OF THE POSITION OF THE FAMILY

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New Records of Oriental Ctenostyidae (Diptera, Acalyptrata), with Discussion of the Position of the Family.

Korneyev V. A. — Ramuliseta thaica sp. n. from Thailand is described. Nepaliseta mirabilis Barracough, 1995 is recorded for the first time from Vietnam. N. ashleyi (Barracough, 1998) comb. n. originally described from males collected in Sulawesi, Indonesia is redescribed based on a female from Taiwan. Diagnosis of the genus Nepaliseta Barracough, 1995 is reconsidered. Based on the study of new material, the phylogenetic relationships of ctenostylids recently excluded from the family Pyrgotidae, are discussed.

Key words: Diptera, Acalyptrata, Ctenostyidae, Pyrgotidae, new species, taxonomy, phylogeny, Oriental Region.

Introduction

The ctenostylids are tropical schizophorous flies of unusual appearance, and perhaps as rare in collections as they are morphologically and biologically unusual. They are nocturnal, larvivorous flies with strongly branching aristae and pictured wings, lacking ocelli and having almost transverse mesostomum, and they are distantly reminiscent of members of the Pyrgotidae, where they were tentatively placed as a subfamily Lochnotyliinae (Hendel, 1935; Lopes, 1935; Keiser, 1951; 1952; Hennig, 1952; Aczél, 1956). The nomenclature and position of the family was revised by D. K. McAlpine (1990) who has shown that the senior applicable family-group name is the Ctenostylidae, first proposed as a tribe (with ending -idea) close to Conopidae. D. K. McAlpine also stated that the group to which he assigned a family rank, Ctenostylidae, does not belong to the Pyrgotidae and apparently not even to the superfamily Tephritoidea. Further data on African and Oriental ctenostylids were recently published by Barracough (1994; 1995; 1998) who confirmed their exclusion from Pyrgotidae as a separate family. However, the superfamily placement of the Ctenostylidae is still not clear. Recently, D. K. McAlpine (1997) has reconsidered certain morphological features and phylogenetic relationships among families of the superfamily Diopsioidea, suggesting that the Ctenostylidae may somehow be related to that group. This hypothesis is discussed further in the present paper and is supported with new data obtained in the course of an analysis of phylogenetic relationships among the families of the higher Tephritoidea (Ulidiidae, Platystomatidae, Pyrgotidae and Tephritidae) (Korneyev, in prep.).

Through the kindness of Dr. Marion Kotrba and Mr. Wolfgang Schacht (Zoologische Staatssammlung München), I have examined material containing 2 specimens of ctenostylids from the Oriental Region and an additional specimen found in my collection, one specimen representing a new species, described below. Two other species are redescribed.

Material examined. The material examined is deposited in the Zoologische Staatssammlung München (ZSSM), and in my collection, Kyiv (CVK).


Abbreviations: A — apomorphy, P — plesiomorphy, H — homoplasy, SA — synapomorphy, SP — symplesiomorphy.
Family Ctenostylidae Bigot, 1882


Diagnosis. Medium-sized (wing length 4.0-9.0 mm) larviparous acalyptate flies with large head almost as bulky as short thorax, long slender legs without large setae, pictured wings, and female tergosternum 7 forming conical oviscape. Head with ocelli and proboscis always lacking, froms weakly sclerotised, with indistinctly delimited fronto-orbital plates, in males sometimes very narrow, face with sclerotised medial carina and transverse lunula, but antennal grooves very weakly chitinised, in females often completely translucent, parafacial setulose along entire length. Thorax wide, with shortened presutural portion; pro sternum transverse, sclerotised at ventral margin, widely membranous dorsal upper margins of fore coxae; postpronotum widely triangular, mostly displaced on to anterior surface; notopleuron very large, with posterior notopleural seta only; anepisternum longer than high, with vertical phragma well-developed in posterior portion; pleural wing process inflated, without swollen greater ampulla (subalar knob); anepimeron with numerous setulae and 1–3 longer setae; scutellum short, transverse, with 1–5 pairs of setae; katatergite large, swollen; sub-scute llum greatly reduced, metanotum very large and swollen, visible in dorsal view; metepimeron well-developed, metathoracal postcoxal area completely membranous medially; both anterior and posterior spiracles round, open, without fringe or setulae. Wing with 2 costal breaks, proximal (humeral) very weak but distinguishable as bare area of costa; distal (subcostal) break broad; setae on costal vein thin and moderately long; no thickened setae on costa before subcostal break; vein sc not reaching costa, ending close to vein R, before level of subcostal break; vein R_{4,5} ending posterior to wing tip; cell bm opened antero-basally, cell beu closed by arcuate or almost straight vein without any extension along vein A1; vein A_{2} developed distally of alula at least as a fold. Legs long and thin; fore coxa thick and short, with rather numerous setae on anterior surface and at ventral margin, mid coxa conspicuously smaller; hind coxa as large as fore coxa; mid tibia without apicoventral spur; pulvilli fringed; claws simple. Abdomen more or less petiolate, sternite 1 medially desclerotised, without any setae, posteriorly fused to sternite 2 with seam; male sternite 6 bare; male abdominal spiracles 6 and 7 absent; phallus simple, tubular, without glans, moderately long and coiled or very short; female sternites 3–6 without antero-medial apodemes, with pouch-like folds between them; oviscape (tergosternite 7) conical, sclerotised, not flattened, without ventro-basal apodeme; eversible membrane without any traces of taeniae; aculeus non-piercing, strongly modified into a weakly sclerotised tube with small, usually blunt bilobate cerci each bearing 2–3 strong setae.

Descriptions of taxa

Ramuliseta Keiser, 1951

Type species: Ramuliseta palpifera Keiser, 1951, by original designation.


Redescription. Head: compound eyes dichoptic in both sexes. Lunula narrow, deep, setulose, if any present, hidden beneath anterior frontal margin; frons in both male and female wide; face with a broad and flattened medial sclerotised area in male and a narrow and low medial carina in female; palpi developed; head setae fine and rather short, irregularly developed: 0–1 lateral vertical, ocellar setae usually well-developed, 1–4 lateroclinate and 0–4 inclinate fronto-orbital setae in posterior half of frons, medial third of frons mostly bare, sides finely but rather densely setulose; male antenna; scape transverse, medially developed beyond margin of pedicel, moderately long and densely setulose; pedicel with 3–5 very
long dorso-lateral and 2–3 ventro-lateral setae; flagellomere 1 apicoventrally with finger-like process 2.5 times as long as basal part; arista short-pubescent, with rays slightly longer than width of aristomere 1 female antenna; scape, pedicel and flagellomere 1 as in male; arista basally subdivided into 2–5 main branches, which further branch into pubescent branches; palpus fine microtrichose. Thorax: proepisternal ridge without setae; mesonotum sparsely setulose, with 1 dorsocentral, 1 intraalar and 1 postalar seta, scutellum with 2–4 setae and 5–7 smaller setae at margin; anepisternum with 5–10 setae at posterior margin; anepimeron with 5–6 setae and 0–1 seta slightly longer than setae. Abdomen with narrowed tergite 1, somewhat petiolate. Male sternum 6 transverse, moderately long, half as long as sternite 5; sternite 7 mostly membranous, fused to sternite 8; the latter rather wide, setulose, typical for higher Tephritoidea; hypandrium membranous, gonites and parameres indistinguishable; phallapodeme not very long, fused to hypandrium, but without distinctive lateroventrally directed rods (vanes of phallapodeme); ejaculatory sac very broadly diamond-shaped from postventral view, with broadly rounded ejaculatory apodeme that is flattened at apex; phallus with short and weakly sclerotised basiphallus and simple, tube-like distiphallus without glans; epandrium rounded, thick and wide, with flattened lobes of subepandrial sclerite bearing numerous short setulae, but no preesistae; proctiger neither flattened, nor bilobate. Female terminalia (from Barraclough, 1994: figs 3, 5): oviscape conical, without ventro-basal apodeme; eversible membrane without sclerotised taeniae, no scales or microtrichia were figured; aculeus poorly sclerotised, cylindrical, with aperture on the apex and 2 sclerotised areas at the extreme apex on dorsal surface (obviously cerci), each bearing 2 strong setae, and small sclerite basal to them (corresponding to epiproct?); neither spermathecae nor ventral receptacle were found. Additional characters are listed in the description of R. thaica.


Ramuliseta thaica Korneyev, sp. n. (fig. 1–14)

Material examined. Holotype ♂: "Thailand, Prov. Mae Hong Son, Umg. Passhohe NW Pai (Pai nach Soppong). Lichtfang. 16.04.2000 19°27'11"N/98°18'39"E 1350 m (12/2000) H. & R. Rausch leg." (ZSSM). Holotype in fair condition: face collapsed inside head and body surface slightly covered with exudate that obscures the microtrichia; left wing and 2 legs glued to a paper rectangle pinned together with the specimen. The abdomen has been detached and placed in a plastic microvial of glycerol pinned under the insect.

Diagnosis. Similar to R. palpifera Keiser, 1951, differing in the wing venation and pattern: costal cell mostly brown, rather than with hyaline spot at middle as in R. palpifera; distance between apex of cell sc and apex of vein R2.3 at most 1.5 times longer than distance between apices of veins R2.3 and R4.5 (3.3 times as long in R. palpifera); apical portion of cell R2.3 with a large triangular hyaline incision rather than wholly brown, cell f4.5 with hyaline spot at base and smoky brown at apex rather than with 2 hyaline marks at base and a dark brown apex, vein dm-cu almost perpendicular to both M and CuA1 rather than oblique in R. palpifera.

Description. Head (fig. 1–3). Length:height:width ratio=1 : 1 : 1.03. Unicolorous, brownish yellow; microtrichia often indistinguishable in the holotype. Froms densely brown setulose, except bare postero-medial triangular impressed area between vertical plates in front of ocellar setae. Vertical plate sparsely microtrichose, with 5 (2 pro-laterocline and 3 pro-incline) orbital setae. Ocelli indistinguishable; ocellar setae as long as orbital setae. Medial and lateral vertical setae well-developed, subequal. Face membranous, flat, slightly shagreened, in holotype apparently non-translucent. Scape and pedicel dark yellow, rather densely dark brown or black setulose; pedicel with 1 long and several shorter thin dorsal setae in addition to minute setae. Flagellomere 1 yellowish, rather short, wide at base, extremely narrow, finger-like in apical 0.7 of its length, with arista inserted in dorsal surface at its base. Arista not branching, simple, long pubescent, with rays at most twice as long as basal aristal width; extreme tips of both aristae broken off. All setae and setulae brownish-black. Parafacial very narrow, setulose. Mouthparts rudimentary. Palpus present.

Thorax (fig. 1, 4). Ground colour (including disc of scutellum) yellowish-brown. Thorax length from anterior margin of prothorax to the posterior end of postnotum slightly (1.1 times) exceeding its width. Mesonotal scutum measured between notopleural setae as wide as long. At most 1 prescutellar acrostichal, 1 dorsocentral, 1 notopleural, 1 intraalar and 1 postalar seta distinguishable. Mesonotal setulae brown; poststatural acrostichal setae forming 4–6 very irregular rows. Postpronotal lobe without setae, but 5–6 small setae. Notopleuron with 3–4 rather long setae. Scutellum 3 times as wide as long, with 2 pairs of setae (basal and apical) and with at least 2–6 distinguishable setae on each side. Prosternum poorly visible, transverse, apparently sclerotised only at postnoteral margin. Proepisternum without setae or setulae. Aneupisternum wrinkled in antero-ventral portion, on posterior margin with 4–5 setae half as long as notopleural or katepisternal seta, major setae either broken off or absent. Katepisternum with a strong seta inserted in
antero-ventral area, medially of fore coxa margin; postero-ventral margin adjacent to mid coxa bare; latero-dorsal area with 1—2 setae and 6—7 smaller setulae. Ancpimeron with 1 seta and 3–4 setulae.

Legs (fig. 5–8) yellow, with brownish-black setulae. Fore coxa (fig. 4) robust, slightly compressed in antero-dorsal direction, antero-lateral margin with 14—16 setae arranged in 2 rows, antero-medial margin with 12–15 setae, and antero-distal margin with 8–9 setae; remaining part of anterior surface bare; posterior surface with 6—8 setae at distal margin. Fore trochanter with 2 appressed setulae. Fore femur and tibia (fig. 5) without strong and long setae, with brown setulae only. Fore tarsus as long as tibia, yellowish-brown setulose; tarsomere 2 slightly more than half as long as tarsomere 1; empodium pennate (fig. 8). Mid coxa conspicuously smaller than fore and hind coxa; eucoxite (anterior) surface with submarginal! row of 11 — 12 setulae; disticoxite (posterior) surface with 9—10 setulae; midcoxal prong fine, lamelliform. Mid trochanter with 2 setulae on dorsolateral surface. Mid femur, tibia and tarsus as in fig. 6; tibia without any thickened setae at apex. Hind coxa large, almost cylindrical, slightly narrowed apically, finely setulose on anterior surface and on sides, posterior surface mostly bare. Hind trochanter with 8—10 fine setulae on posterior surface. Hind femur, tibia and tarsus as in figure 7.

Fig. 2–3. Ramuliseta thaica, ♂: 2 — head, anterior aspect; 3 — same, lateral. Scale: 1 mm.

New Records of Oriental Ctenostylidae.

Fig. 4–8. Ramuliseta thaica, ♂: 4 — thorax, lateral aspect; 5 — fore leg (coxa and trochanter removed), anterior aspect; 6 — mid leg, same; 7 — hind leg, same; 8 — last tarsomere of fore leg, enlarged.

Рис. 4–8. Ramuliseta thaica, ♂: 4 — грудь, вид сбоку; 5 — передняя нога (тазик и вертлуг не показаны), вид спереди; 6 — средняя нога, то же; 7 — задняя нога, то же; 8 — последний тарзомер передней ноги, увеличено.

Wing as in figure 1. Costa thickened, with costal break, weak humeral break at middle of cell c, and broad subcostal break. Humeral vein joining subcostal vein somewhat distal of its separation from R_{1}. Subcostal vein broken at apex. Vein R_{1} setulose along its whole length on dorsal side; cell R_{2+3} apically widened; vein R_{4+5} bare; vein M almost parallel to R_{4+5}, ratio of its 3 last sections: M_{2}:M_{3}:M_{4}=1:1.5:1.6, i. c. penultimate section almost as long as ultimate and much longer than second one. Wing pattern, as in most ctenostylines, with brown basal cells and well-developed pattern in apical two thirds. Apical portion of cell R_{2+3} with very narrow dark stripe along costal vein and large hyaline sector between it and vein R_{4+5}. Brown subapical spot gradually fading to greyish shading at apices of cells R_{4+5} and M. Cell cua, and postero-medial corner of anal lobe pale greyish. Vein Cu_{A2}+Cu_{A1} in apical 2/5 of its length fold-like, but visible to its extreme tip. Alula narrow, hyaline, slightly darkened on anterior margin. Upper calypter narrow, with fringe of rather long and sparse microtrichia; lower calypter almost linear. Haltere brownish-yellow, with large sparsely microrichose knob, in dry specimen somewhat bent, giving L-shaped appearance to whole haltere.


Female not known.

Measurements (length in mm). Body 5.6, wing 5.0.

Discussion. R. thaica is the second member of the genus Ramuliseta known from the male (Ramuliseta ashleyi Barraclough is transferred to the genus Nepaliseta), while R. madagasacariensis Hennig is known from females only. Taking into account the sexual dimorphism of the wing pattern known in some related genera, certain differences in the wing pattern of the female can be expected. However, the wing venation usually shows no such dimorphism, and the length of the penultimate section of the costal vein is considered to be a consistent character of this species. This character is not known elsewhere in the Ctenostylidae, except in the new genus described below. The new species shares this character, as well as the long phallicus, with species of the genus Nepaliseta, differing by having ocellar setae and at most 1 dorsocentral and 2 scutel-lar setae on each side.
Fig. 9-14. *Ramuliseta thaica*, ♂: 9 — male abdomen, ventral aspect; 10 — male postabdomen, ventro-lateral aspect; 11 — male genitalia, right lateral aspect; 12 — hypandrium and phallapodeme; 13 — sperm pump, lateral; 14 — same, ventral aspect.


*Nepaliseta* Barraclough, 1995

Type species: *Nepaliseta mirabilis* Barraclough, 1995, by original designation.


**Diagnosis.** This genus fits near *Ramuliseta* Keiser and *Furciseta* AczéI, sharing with them the low bare lunula (A?), well-developed palpi (P) and almost parallel veins R_{4+5} and M (P), and differing in lacking a ventroapical projection on female flagellomere 1 (A) and ocellar setae (A) and possessing 3—4 pairs of scutellar setae (unresolved polarity). Having 3 pairs of dorsocentral setae, as in *Furciseta* (unlike 1 pair in *Ramuliseta*) is also of unresolved polarity. In the key to the genera of Ctenostyliidae (D. K. McAlpine, 1990: 369), it runs near *Ramuliseta*, differing from the latter by the presence of more than 1 pair of dorsocentral setae and more than 2 pairs of scutellar setae, and the rounded, short flagellomere 1 of female without a finger-like projection.

**Redescription.** Head: compound eyes almost holoptic in male, dichoptic in female; lunula rather low, bare, wide in male and rather narrow in male; in female frons wide, in male strongly narrowed; face with broad and flattened medial sclerotised area in male and narrow and low medial carina in female; palpi developed; head setae fine and rather short, irregularly developed: 0 postocellar, 0—1 medial vertical, 0—2 lateral vertical, ocellar setae absent, 3—4 lateroclineate and 2—3 inclinate fronto-orbital setae in posterior half of female frons, (1—2 lateroclineate and 0—1 inclinate fronto-orbital setae in posterior half of male frons), medial third of female frons depressed, mostly bare, sides slightly raised, finely but rather densely setulose; ptilinal suture long, distinct as far as lower eye margin or more; parafacial setulose along entire length; female
antenna: scape transverse, medially extended beyond margin of pedicel, very long and densely setulose; pedicel with 2—3 very long dorso-lateral, 1—2 ventro-medial and 4—5 ventro-lateral setae; flagellomere 1 short and rounded, apicoventrally without finger-like process; aristata basally subdivided into 2-5 main branches, which divide further into pubescent branches; male antenna: scape i-shaped, medially and ventrally extended almost beyond margins of pedicel, moderately setulose, less than in female; pedicel with 2-3 very long setae; flagellomere 1 short and rounded, apicoventrally with long finger-like process; aristata simple, pubescent, but not subdivided into branches (like in *Ramuliseta* male); palpus finely microtrichose; prothoracic valva: gena setulose; occipital sclerite bare, without distinctive supracervical setae; occipital setae forming 4-5 irregular rows. Thorax: prothorax bare, transverse, broadly membranous with a ventral sclerotised area and lateral arms joined laterally to proepisternum; proepisternal ridge without setae; cervical sclerite large, triangular in profile; postpronotum small, flattened, without setae, bearing 2—3 setulae; mesonotum presuturally mostly setulose and much more densely setulose postseturally; 6 cross-tics, 3 dorso-central setae (anterior close to nuture, posterior in line with intraalar), 1 intraalar and 1 posta-lar seta, scutellum with 6—10 setae and numerous setulae over most of its disc; anepisternum with distinct vertical phragma; prephragmal area of its disc with 12—15, and area posterior phragma with 5—8 setulae and 1-2 somewhat longer setulae; anepimeron with 10-12 setulae and 0-1 slightly longer seta; katepisternum with 1—3 setae inserted in antero-ventral area, and mediially of fore coxa margin; its postero-ventral margin adjacent to mid coxa at most with 1 seta, latero-dorsal area with 1 seta and 8–10 setulae. Wing as in other ctenostylids, Sc incomplete; R, setulose; cell r, without crossveins between R, and costa; R, bare, almost straight; M moderately curved posteriorly, R, and M rather divergent; vein Cu1+A, well-developed in proximal half and at least as fold in distal half; vein A2 distinct, distal of alula, as fold. Alula and upper calypter well-developed; lower calypter linear. Haltere as in *Ramuliseta*, with a large, elongate knob which gives a L-shaped shape to whole haltere. Abdomen with narrowed tergite 1, somewhat petiolute. Sternite microtrichose elongate, weakly sclerotised except lateral margins; sternite 2 elongate, without desclerotised window at anterior margin, fused to sternum 1; sternite 3—6 with anterior- medial apodemes. Female terminalia: oviscape conical, without ventro-basal apodeme; eversible membrane without sclerotised taeniae, covered with microtrichia; aculeus poorly sclerotised, cylindrical, with aperture at the apex and sclerotised areas at extreme apex on dorsal surface (obviously cerci), each bearing 2 strong setae, and small sclerite basal to them (corresponding to epiroct?)... neither spermatheca nor ventral receptacle found. Vagina full of eggs containing 1st

**Key to species of the genus **Nepaliseta**

**Таблица для определения видов рода Nepaliseta**

1. Hyaline interval between two brownish-yellow spots in cell r1; short, at most as wide as long at anterior margin (fig. 20) — *N. ashleyi* (Barraclough)
   — Hyaline interval between two brownish-yellow spots in cell r1; twice as long as wide (fig. 26) ...

**Nepaliseta ashleyi** (Barraclough), comb. n. (fig. 15—20)


**Diagnosis.** Differs from *N. mirabilis* only in details of wing pattern as noted in the key above.

**Redescription.** Body and setae uniformly brownish-yellow in colour. Mesonotum with 2 submedian longitudinal vittae and 4 rounded spots of darkened cuticle at the points where muscles attach.

**Female (first description).** Head as in figures 15—18. Area of annulus grooves completely translucent. Height:length:width ratio = 1.08:1.07. Vertical plate with 4—5 latrocline and 2—4 inclinate orbital setae. Vertex with second major seta distally of lateral vertical setae on each side. Thorax as in figure 19. Mesonotum length (without scutellum) to width (measured between notopleural setae) ratio = 0.9. Wing 2.67 times longer than wide, with brownish-yellow wing pattern, as in figure 20; anal lobe, alula and upper calypter with brown stripe. Haltere with brownish knob. Female abdomen unicolorous, not dissected.

**Measurements (length in mm).** Female. Body 6.0, wing 6.0, oviscape 1.0.

**Discussion.** This species was described from a male and originally placed in the genus *Ramuliseta*; however, Barraclough (1998) has noted in the end of its description: "The wing patterning and venation of *R. ashleyi* differ strongly from *R. madagascarensis* and *R. palpifera*... but are similar to that of *Nepaliseta mirabilis* Barraclough... *Nepaliseta mirabilis* differ mainly in having much broader hyaline region on the apical half of wing, just beyond its mid-length". Discovery of the female that possess all the important characters of the male, except for terminalia structure and the frons broad (certainly a sexually dimorphic character, which is common in the Ctenostylidae), and is similar to females of *N. mirabilis* in all the main features, shows that *R. ashleyi* is another species of the genus *Nepaliseta*. Both species of the latter genus share the ocellar setae.
Fig. 15—18. *Nepaliseta ashleyi*, ♀, head: 15 — lateral left aspect; 16 — dorsal aspect; 17 — posterior aspect (upper portion of occiput and vertex); 18 — anterior aspect.

Рис. 15—18. *Nepaliseta ashleyi*, ♀, голова: 15 — вид слева; 16 — вид сверху; 17 — вид сзади (верхняя часть затылка и темя); 18 — вид спереди.

Fig. 19-20. *Nepaliseta ashleyi*, ♀: 19 — thorax, dorsal aspect; 20 — right wing. Рис.


lacking and numerous scutellar setae (3—5 pairs) and setulae. However, males of *N. ashleyi* have the finger-like projection of the flagellomere 1 well-developed, whereas in the female described above, such an appendix is absent like in *N. mirabilis*, which is believed to be a sexually dimorphic feature.

*Nepaliseta mirabilis* Barraclough (fig. 21—30)


Material examined. ♀: «Вьетнам, Хошонбинь, Бави, 10 VI 1986, Горохов» [Vietnam, Hochon-bin: Bavi, Gorokhov leg.](CVK). In fair condition. 2 hind legs and 1 fore leg are missing; left wing partially broken and glued; abdomen has been detached and placed in a plastic microvial with glycerol pinned under the insect.


Female. Head as in figures 21–22. Height : length : width ratio = 1.0 : 1.0 : 1.0. Vertical plate with 4–6 latero-clinate and 0 inclinate orbital setae. Lateral vertical sets on each side and additional sets close to it absent. Thorax as in figures 24-25. Mesonotum length (without scutellum) to width (measured between notopleural
Fig. 21—27. *Nepaliseta mirabilis*, ♀: 21 — head, lateral left aspect; 22 — same, dorsal aspect; 23 — left antenna, lateral aspect; 24 — thorax, lateral aspect; 25 — same, dorsal aspect; 26 — right wing; 27 — right calypter.

Fig. 21-27. *Nepaliseta mirabilis*, ♀: 21 — голова, вид слева; 22 — то же, вид сверху; 23 — левая антenna, вид сбоку; 24 — грудь, вид сбоку; 25 — то же, вид сверху; 26 — правое крыло; 27 — правое жужжалце.

setae) ratio = 0.8. Wing 2.86 times as long as wide, with brownish-yellow pattern as in figure 26, hyaline crossband broad, anal lobe, alula and upper calypter with brown stripe. Haltere (fig. 27) with brownish knob. Female abdomen unicolorous, as in figures 28—29.

Measurements (length in mm). Female. Body 2.7–5.4, wing 4.0–5.3, oviscape 0.8.

Relationships of Ctenostylidae

The fact that ctenostylid species were originally assigned to the family Pyrgotidae seems reasonable, taking into account the absence of ocelli, receding face profile, pictured wings with two costal breaks, setulose vein R, and posteriorly bowed R_{4+5} and M, fused abdominal sternites 1 and 2, male subepandrial sclerite finely setulose without prensisetae, conical oviscape and finally, nocturnal activity, attraction to light and apparently zoophagous larvae. In the Pyrgotidae, the genus *Toxopyrgota* Hendel, 1914, shares certain features with the Ctenostylidae such as the very oblique face profile, short mesonotum, long legs and arched vein closing cell buc, but otherwise is a typical
pyrgotide, quite different from ctenostylids (Steyskal, 1972: Figs 11-15). The similarity of ctenostylids and pyrgotids is so strong that it encourages the hypothesis that the inconsistency of other characters is the result of strong secondary modification, which has considerable credibility because of the extremely aberrant appearance of ctenostylids. However, detailed study shows that many "homologies" in ctenostylids and pyrgotids are actually homoplasies.

The characters supporting and contradicting the assignment of the Ctenostylidae to the Tephritoidea, were discussed by D. K. McAlpine (1990). He arrived at the general conclusion that ctenostylids are not tephritoids at all, and he supported this hypothesis with the following arguments: 1) male preabdomen with a well-developed tergite and sternite 6, whereas segments 7 and 8 are vestigial; 2) phallus short and simple rather than long, coiled and bearing terminal glans; 3) in female, terminal structure of the telescopic ovipositor non-sclerotised, except for apical structures dorsally of the gonopore with strong setae which McAlpine (1990) considered to be cerci.

In the Tephritoidea, these three characters are all present in the derived state. The male tergite 6 is vestigial in some Lonchaeidae (see Morge, 1963: Figs 58, 59, 62) and completely absent in other Tephritoidea that consists one of synapomorphies of that superfamily. Commonly, and apparently in the ground plan of the subfamily Tephritoidea, the phalli are ribbon-like, but short pipe-like or non-ribbon-like phalli are known in some Lonchaeidae (see Morge, 1963: Figs 65—66) and a few Platystomatidae and Pyrgotidae (D. K. McAlpine, 1973; 1990). However, in Ramuliseta thaica (fig. 9), which I dissected, the protandrial sclerites were rather soft and shrivelled, and I cannot support nor disprove that the setulose sclerite postero-dorsad of the epandrium is the tergite 6 rather than the sternite 8 as it is in Pyrgotidae and other higher Tephritoidea; the asymmetrical position of this sclerite may indicate that it is sternite 8 rather than tergite 6. Moreover, in this species and in Nepaliseta ashleyi (see Barraclough, 1998: Figs 8—9) the phallus is long and somewhat coiled, but has no terminal glans. The latter feature does not contradict the placement of ctenostylids in the Pyrgotidae: it is rather similar to this in at least Cardiacera miliacea Hendel. However, the structure of the terminal portion of the telescopic ovipositor in ctenostylids cannot be treated as a derived state of the sclerotised, elongate complex aculeus that forms another synapomorphy of the Tephritoidea (Korneyev, 1999).

On the other hand, ctenostylids share certain features with families usually referred to the superfamily Diopsioidea: Psilidae, Nothychidae, Tanypezidae and others. Some of them are so similar that the diopsoid hypothesis of ctenostylid relationships is worth serious consideration. The morphological characters and some phylogenetic hypotheses about Diopsioidea families were recently considered by D. K. McAlpine (1997), facilitating further discussion of both the pyrgotid and the diopsoid hypotheses of the origin of the Ctenostylidae.
### Comparison of Key Characters of Ctenostylidae and Allied Taxa
Сравнение ключевых признаков Ctenostylidae с таковыми ближайших таксонов

<table>
<thead>
<tr>
<th>N</th>
<th>Ctenostylidae</th>
<th>Diopsioidea and allied families</th>
<th>Pyrgotidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Head. Ocellar triangle vestigial; ocelli always absent. AA or SA with some Pyrgotidae</td>
<td>Ocellar triangle always large, usually reaching anterior margin of frons, with well-developed ocelli.</td>
<td>Ocellar triangle small or vestigial; ocelli present in the ground-plan of the family.</td>
</tr>
<tr>
<td>2</td>
<td>Head. Vertical plate in female rather long and wide, extending into anterior third of frons. SP with Psilidae and other Diopsioidea?</td>
<td>Vertical plate in females rather long and wide, joined to eye, extending into anterior third of frons in Psilidae; with some reservations, also in Diopsidae and Tanypezidae; not in Nothybidae, Gobryidae.</td>
<td>Vertical plate in both sexes quite short, more or less separated from eye margin, restricted to posterior third of frons.</td>
</tr>
<tr>
<td>3</td>
<td>Head. Postocular seta equal to well-developed lateral vertical seta in (Nepaliseta). SA or convergence with Psilidae</td>
<td>Postocular seta equal to well-developed lateral vertical seta in Nothybidae and Psilidae.</td>
<td>No large postocular setae.</td>
</tr>
<tr>
<td>4</td>
<td>Head. No series of postocular setae can be distinguished from occipital setulae. SA or convergence with Psilidae</td>
<td>Differentiated series of postocular setae absent in Psilidae, Diopsidae, and allied families, but not in Tanypezidae.</td>
<td>Series of postocular setae well differentiated.</td>
</tr>
<tr>
<td>5</td>
<td>Head. Vertical plate in female with 3—5 partially lateroclinate setae poorly distinguishable among frontal setulae. SP with Psilidae and other Diopsioidea?</td>
<td>Vertical plate with 2—5 partially lateroclinate setae poorly distinguishable among frontal setulae at least in Psilidae; apparently similar in Tanypezidae</td>
<td>1—2 strong reclinate orbital setae.</td>
</tr>
<tr>
<td>6</td>
<td>Head. Arista (in males) with short erect pubescence. SP with Psilidae and Tanypezidae?</td>
<td>Arista (in both sexes) with short erect pubescence in Psilidae; also in Tanypezidae</td>
<td>Arista almost bare.</td>
</tr>
<tr>
<td>7</td>
<td>Thorax. Precoxal prothoracal bridge not developed; precoxal area membraneous. P</td>
<td>In Psilidae prothorax normally developed, but not forming sclero-tised precoxal bridge; in other families (including Tanypezidae) precoxal bridge well-developed (synapomorphies or convergence).</td>
<td>Precoxal prothoracal bridge not developed; precoxal area membraneous.</td>
</tr>
<tr>
<td>8</td>
<td>Thorax. Proepisternum without row of strong setae. P</td>
<td>Proepisternum without row of strong setae.</td>
<td>Proepisternum with a distinct row of strong setae, at least in the subfamily Pygoticinae (including Toxhrini).</td>
</tr>
<tr>
<td>10</td>
<td>Thorax. Prothoracic spiracle circular, almost devoid of hairs on its margins. SA or SP with Psilidae and Nothybidae</td>
<td>In Psilidae and Nothybidae pro-thoracic spiracle circular, almost devoid of hairs on its outer margins. In Diopsidae, Syringogastriidae, Gobryidae and Tanypezidae various, but neither circular, nor almost bare</td>
<td>Prothoracic spiracle vertical, with fine hairs on its margins.</td>
</tr>
<tr>
<td>11</td>
<td>Thorax. Notopleuron setulose. SP with Psilidae</td>
<td>Notopleuron setulose in Psilidae; bare in Tanypezidae.</td>
<td>Notopleuron without setulae. SA of Tephritoidae or Tephritoidea +Tanypezidae. (Reversal in some Platystomatidae.)</td>
</tr>
<tr>
<td>12</td>
<td>Thorax. Anterior notopleural seta absent. SA or HP with most Diopsioidea, except Tanypezidae</td>
<td>Anterior notopleural seta absent in Psilidae, Diopsidae, Gobryidae and Nothybidae.</td>
<td>Anterior notopleural seta present. P</td>
</tr>
</tbody>
</table>
13. **Thorax.** Anepisternum with setae on postero-dorsal margin. SA or HP with Tephritoidea and Tanypezidae

14. **Thorax.** Anepimeron setulose. SA or convergence with Platystomatidae, Pyrgotidae and Tephritoidea

15. **Thorax.** Katepisternal setae present. P

16. **Thorax.** Metathoracic post-coxal bridge not developed. P

17. **Wing.** Vein Sc broken at apex. SA either with Psilidae or with Pyrgotidae, or AA (convergence)

18. **Wing.** Vein R, setulose. SA or AA convergent with Platystomatidae, Pyrgotidae and Tephritoidea

19. **Wing.** Vein A2 developed distally of alula at least as a fold. P

20. **Legs.** Fore femur without series of postero-ventral erect setae. SA with Diopsidae or Tanypezidae?

21. **Legs.** Tibiae without dorsal preapical setae. Apparently SA with Nerioidae, Diopsidae, Tanypezidae and Tephritoidea

22. **Legs.** Mid tibia without ventroapical seta (“mid-tibial spur”). AA of Ctenostyldidae

23. **Abdomen.** Sternite 1 bare. AA of Ctenostyldidae

24. **Abdomen.** Sternite 2 lacking anterior membranous window, fused to sternite 1. SA or convergence with Pyrgotidae

25. **Abdomen.** Male sternite 6 bare. SA or convergence with Pyrgotidae and other higher Tephritoidea

26. **Abdomen.** Male tergite 6 well-developed, setulose, symmetrical. (?) SP with Diopsidae
27. Abdomen. Female tergite and sternite 7 forming conical oviscape (tergosternite 7). SA or convergence with Pyrgotidae and other Tephritoidea

28. Abdomen. Female cerci not fused with tergite 8. P

The relationships of the Ctenostylidae, though still not clear, may be restricted to a narrower list of superfamilies. First, despite the setulose parafacial, a character known mostly in the Calyptrata (and a few genera of Platystomatidae), and the almost holoptic eyes in males of some species, they do not belong in the calyptrate series, because of the almost inconspicuous transverse thoracic suture and tibiae completely devoid of any setae. They apparently belong to the group of acalyprate superfamilies in which the dorsal preapical setae on tibiae are absent (synapomorphy of Nerioidea, Diopsioidea, Tanypezidae and Tephritoidea?). In the Nerioidea, Tanypezidae and Diopsioidea, any traces of A2 distad of the alula vein are absent (synapomorphy), while in ctenostylids this vein is quite well-developed. This may mean that the Ctenostylidae is the sister-group of the Nerioidea + Diopsioidea + Tanypezidae, but it is also probable that A2 was lost in some of these groups independently. The presence of rather numerous features shared by the Ctenostylidae and Psilidae (Diopsioidea) makes such a hypothesis rather more credible.

The possible relationship of Ctenostylidae and Diopsioidea sensu D. K. McAlpine (1997) is supported by the round almost bare prothoracic spiracles, fore femora lacking posteroventral setae, occiput without a series of postocular setulae but with the postocular seta next to lateral vertical seta, similar structure and chaetotaxy (lateroclinate setae present) of the vertical plate of frons, as well as having only posterior notopleural seta and incomplete subcosta; all these characters are either synapomorphies of Psilidae, or of Psilidae and allied Diopsioidea, or of larger range of taxa, with a high probability of homoplasy.

The combination of the presence of vein A2, the plesiomorphous state characterising the Ctenostylidae, with numerous autapomorphies (reduction of ocellar triangle, with frontal vitta medially unsclerotized; well sclerotised, transverse, setulose lunula; short and robust form of thorax; setose anepisternum, katepisternum and anepimeron; bare male sternite 6; reduction of gonites and parameres; and finally, fusion of female tergite and sternite 6 into a tergosternite) may be considered to contradict an assignment to the Diopsioidea. However, the independent disappearance of A2 in Psilidae and other Diopsioidea is one of the most believable assumptions.

The possibility of a relationship between the Ctenostylidae and Tephritoidea is not to be ruled out completely as the identity of the male protandrial sclerites remains vague. If they belong in the Tephritoidea, they certainly are the members of the Higher Tephritoidea, and of the cluster Platystomatidae + Pyrgotidae + Tephritidae, however they do not belong to any of these families.

Furthermore, no reliable results from a computer cladistic parsimony analysis can be expected until the homologies of the structures discussed above are explicitly proved and the outgroup is determined.

Conclusion. The results of a more detailed morphological comparison of ctenostylids with other cyclorrhaphous Diptera show that they are related to the Nerioidea + Diopsioidea + Tanypezidae + Tephritoidea group of superfamilies. There are several almost equal alternative hypotheses of sister-group relationships of the Ctenostylidae. Of the hypothesised taxa, those most supported by possible synapomorphies are the Psilidae (of the Diopsioidea) and the Pyrgotidae (of the Tephritoidea). Some of presumed synapomorphies may actually be homoplasies, and further cladistic
analysis must involve more detailed and extensive morphological studies to serve as a basis for further phylogenetic reconstructions. This is unlikely to be possible until more extensive material is collected or becomes available for study and analysis.

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