

## The *Paduniella* (Trichoptera: Psychomyiidae) of China, with a phylogeny of the World species

Youwen J. Li and John C. Morse

Department of Entomology, Clemson University, Clemson, SC 29634, USA

**Abstract:** The phylogenetic relationships of the species of *Paduniella* are analyzed based on characters of larvae, pupae, and adults (mainly male genitalia). The genus is monophyletic and most closely related to *Psychomyia*, and *Metalype* in the subfamily Psychomyiinae. Nine species groups are suggested. Eight species, including six new to science, are reported from the People's Republic of China for the first time.

**Key words:** Psychomyiinae, *Psychomyia*, *Metalype*, male genitalia, female genitalia, new species

### Introduction

The genus *Paduniella* was erected by Ulmer (1913) for the species *Paduniella semarangensis* Ulmer. Ulmer (1922) established a similar genus, *Psychomyiodes*, based on *Psychomyiodes africana* Ulmer from Cameroon. Lestage (1926) established the subfamily Paduniellinae to include *Paduniella* and *Psychomyiodes* and two new closely related genera, *Mesopaduniella* and *Propaduniella*. The main character supporting *Psychomyiellodes* as genus status is the discoidal cell of the fore wing present. Actually, it is such an obscure vein that some researcher neglect it (Mosely 1936). However, this character is a plesiomorphy in this group and could not be served as evidence to support monophyletic group. Other three genera were also erected based on characters of wing venation that are very hard to see, especially for some cross veins. Consequently, published descriptions vary in their interpretations. For example, the main diagnostic character for the genus *Propaduniella* is the lack of anterior wing Fork V; for the type species *P. ceylanica*, anterior wing Fork V is absent in Ulmer's (1915) original illustration but present in Schmid's (1958) later one. Such difficulties discouraged subsequent workers from recognizing any of the genera other than *Paduniella*.

For these reasons, forty species of *Paduniella* (*sensu lato*), including the six new species in this paper, have been included in the genus from the Afrotropical (4 spp.), Oriental (34 spp.), West Palearctic (1 sp.), East Palearctic (3 spp.), and Nearctic (1 sp.) Biogeographic Regions.

In support of our higher classification of these species, this paper also analyzes the phylogeny of world *Paduniella* (*s. l.*) species based on available information, mainly characters of male genitalia, to determine any justification for recognizing *Propaduniella*, *Mesopaduniella*, and *Psychomyiodes* as distinct subgenera or genera. The phylogenetic

relationships of the genus within the family Psychomyiidae were analyzed by Li and Morse (in press). *Paduniella* is most closely related to *Psychomyia* (*s. l.*) and *Metalype*, but the relationships among these monophyletic genera remain unresolved. Malicky (1995) considered *Metalype* to be a synonym of *Psychomyia*, but did not provide phylogenetic evidence for his opinion. The latter two genera are treated as outgroups in the present phylogenetic analysis. In this paper, we add more characters to help clarify the relationships of this genus and *Psychomyia* and *Metalype*.

No species were recorded from the People's Republic of China before this research. This paper reports eight species from China, including six species new to science. All type specimens are deposited in the Department of Plant Protection, Nanjing Agricultural University, the People's Republic of China (NAU), and the Clemson University Arthropod Collection, Department of Entomology, Clemson University, South Carolina, USA (CUAC).

### *Paduniella* morphology and groundplan

**Adult.** Overall length (in following descriptions = distance from front of head to tips of folded forewings) 2.8-5.8 mm. Forewings each 2.0-5.0 mm long, yellow to yellow-brown. Forewings and hindwings acute at apex (Fig. 1). Each forewing with Forks II, III, IV, and V; each hindwing with Forks II and V. Each hindwing with acute projection on costal margin at middle. Head with several warts on vertex: pair of large oval occipital warts, pair of slender curved ocellar warts, single forked frontal wart, and inconspicuous anterior warts (Fig. 2). Each maxillary palpus 6-segmented; each labial palpus 4-segmented (Fig. 3).

**Female genitalia** (Figs. 4-5). Abdominal segment VIII (VIII) synsclerotized, its ventral posteri-

or margin broadly excised. Segment IX not evident. Segment X (X) twice as tall as long, subconical, tapering from middle to posterior, with transverse row of long setae (trans. r. set.) near base of segment, internal ventral basomesal apodeme (apodeme) forked and diverging; ventral meson cleft from posterior end to anterior 1/5 of segment, opening widest near anterior end of cleft; posteroventral margin projecting posteriad, closely appressed against ventral surface of segment IX (IX). Segment XI small, hairy, with pair of tiny, slender, one-segmented cerci (cercus).

**Male genitalia** (Figs. 7-9). Male genitalia of *Paduniella* species homogeneous, with distinctions mainly involving tergum IX (t. IX), sternum IX (S. IX), inferior appendages (inf. app.), superior appendages (sup. app.), and phallic apparatus [including paramere (para.), phallobase (phb.), and phallicata (phc.)]. Tergum IX smaller than tergum VIII, usually triangular in dorsal and lateral views, with long, slender, sclerotized, lateral bands proceeding anteriorly to juncture with corresponding strips on sternum IX. Sternum IX shape nearly like sternum VIII but broader in ventral view and with long lateral bands directed anteriorly. Lateral bands of tergum IX and sternum IX in each side, extending anteriorly and joining each other at small point in very acute angles. Superior appendages distinct posteriorly and extending well beyond tergum X; lateral bases of superior appendages extending anteriorly and indistinguishable from lateral bands of tergum IX. Pair of narrow strips from joining points of sternum IX and tergum IX directed anteroventrad and connecting these points to dorsal side of base of phallic apparatus (= phallobase region, Fig. 7), fused sclerotized strips of phallic shield and sclerotized strips of sternum IX in some Leptoceridae (Morse, 1975); similar strips also in genus *Tinodes*, except directed upward to base of phallic apparatus (They probably developed in *Tinodes* and *Paduniella* independently.). These strips in *Paduniella* sometimes not connected with phallobase. Most species with one or more median processes (med. proc.) arising between anterior ends of sternal strips above phallobase and proceeding posteriad, these processes absent in some (primitive) species. Phallic apparatus directed caudad, straight or slightly arched; phallobase broad, open in ventral view, short in some (primitive) species, half as long as phallicata or as long as phallicata in other (advanced) species; phallicata more or less compressed, with slender spine-like process arising between phallobase and phalli-

cata. [This is possibly the two lateral parameres fused, but the homology of this character is very difficult to determine. It does not exist in other genera of Psychomyiidae and Xiphocentronidae, but may occur in Hydropsychidae (*Ceratopsyche* species) and Polycentropodidae (e.g., *Polycentropus colei* Ross, 1941).] Inferior appendages each with one compressed segment and with short mesal branch.

**Larva** (Mathis and Bowles, 1995; Figs. 32-35). Larva of *P. nearctica* distinguished by two characteristics from those of other psychomyiid genera for which larvae are known: four well-developed teeth on concave margin of each anal claw [similar to those of *Psychomyia* species, but teeth lacking in *Tinodes* and *Lype* species (Wiggins, 1996)] and submental sclerites small and wider than long [like those of *Tinodes* and *Lype* species, not longer than wide as in *Psychomyia* species (Wiggins, 1996)].

**Pupae** (Mathis and Bowles, 1995). Pupa of *P. nearctica* with 6-segmented maxillary and 4-segmented labial palpi, mandibles whip-shaped, labrum with only 3 pairs of setae (rather than 5 pairs as in known pupae of other genera).

#### *Paduniella* species of China

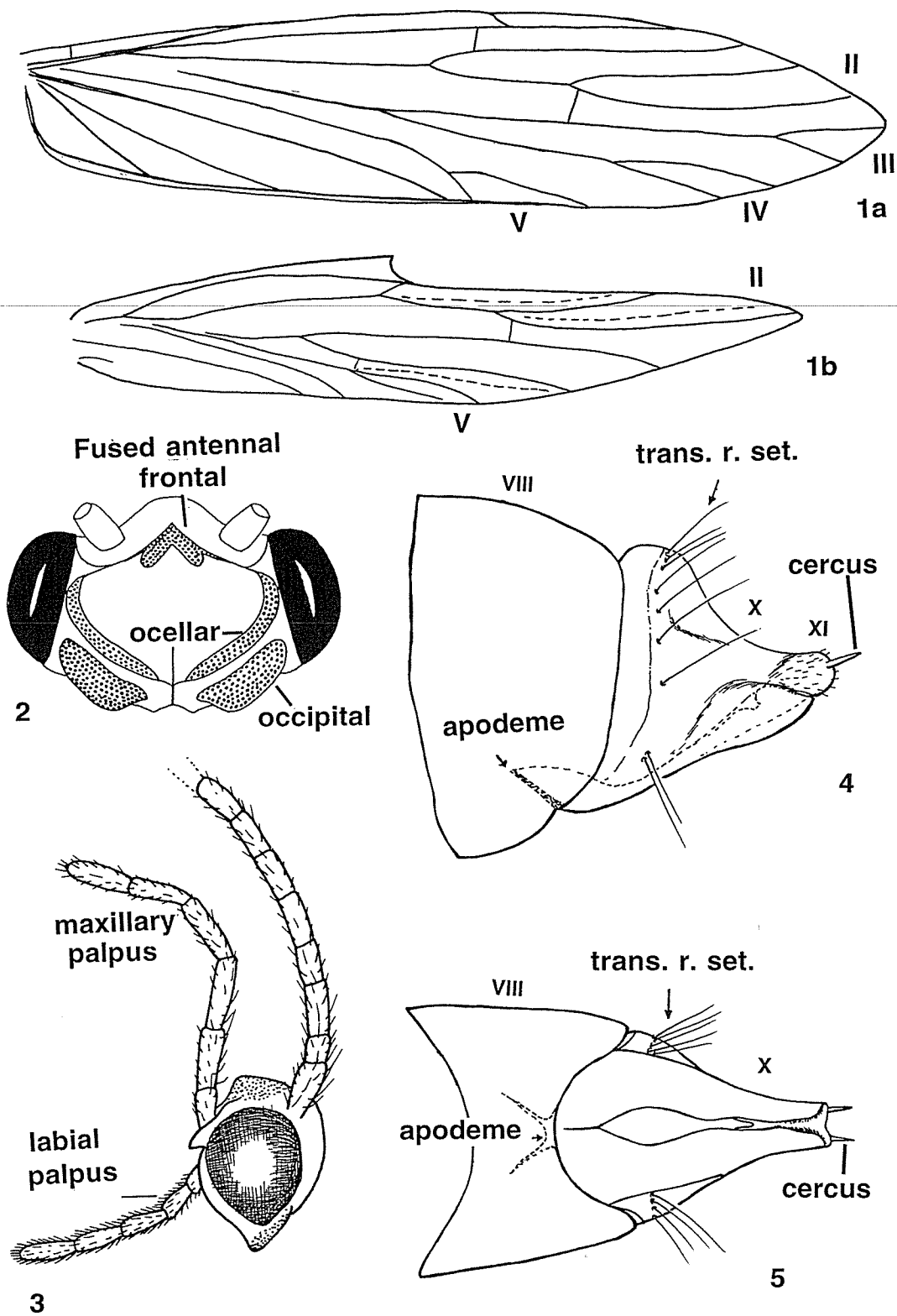
##### *Paduniella communis*, new species

(Figs. 4-5, 7-9)

Adult forewing length: 2.56-2.95 mm. Overall length: 3.06-3.42 mm. Color in alcohol uniformly pale yellow-brown, antennae annulate with brown.

**Male genitalia** (Figs. 7-9). Tergum IX broad, round at posterior margin in dorsal view. Superior appendages each oval, acute at apex, almost twice as long as tergum IX. No median process arising from sclerotized strips of segment IX. Inferior appendages each with basal third broad, abruptly narrowed to 1/3 basal thickness, then gradually enlarged and rounded at apex; mesal branch arising from near apex of mesal surface of basal part. Phallic apparatus vertical basally, then arched caudoventrad, with deep anterior incision at vertical juncture of phallobase and phallicata and sclerotized strips of segment IX; phallobase very short, about 1/8 as long as phallicata; dorsal paramere slender, arched dorsad then caudad, nearly as long as phallicata, arising from dorsal concavity close to phallobase, with short apical fork; phallicata compressed, gradually clavate, and round at apex in lateral view.

**Female genitalia** (Figures 4-5). Segment X largest in basal third, with transverse ring of long



Figs. 1-5. Adults of *Paduniella* species: 1a, forewing of *Paduniella furcata*, n.sp.; 1b, hindwing of same; 2, vertex of *Paduniella uralensis* Martynov, dorsal; 3, head of *Paduniella uralensis* Martynov, lateral; 4, female genitalia of *Paduniella communis*, n.sp., lateral; 5, same, ventral. II, III, IV, and V = Forks II, III, IV, and V; trans. r. set. = transverse row of setae.

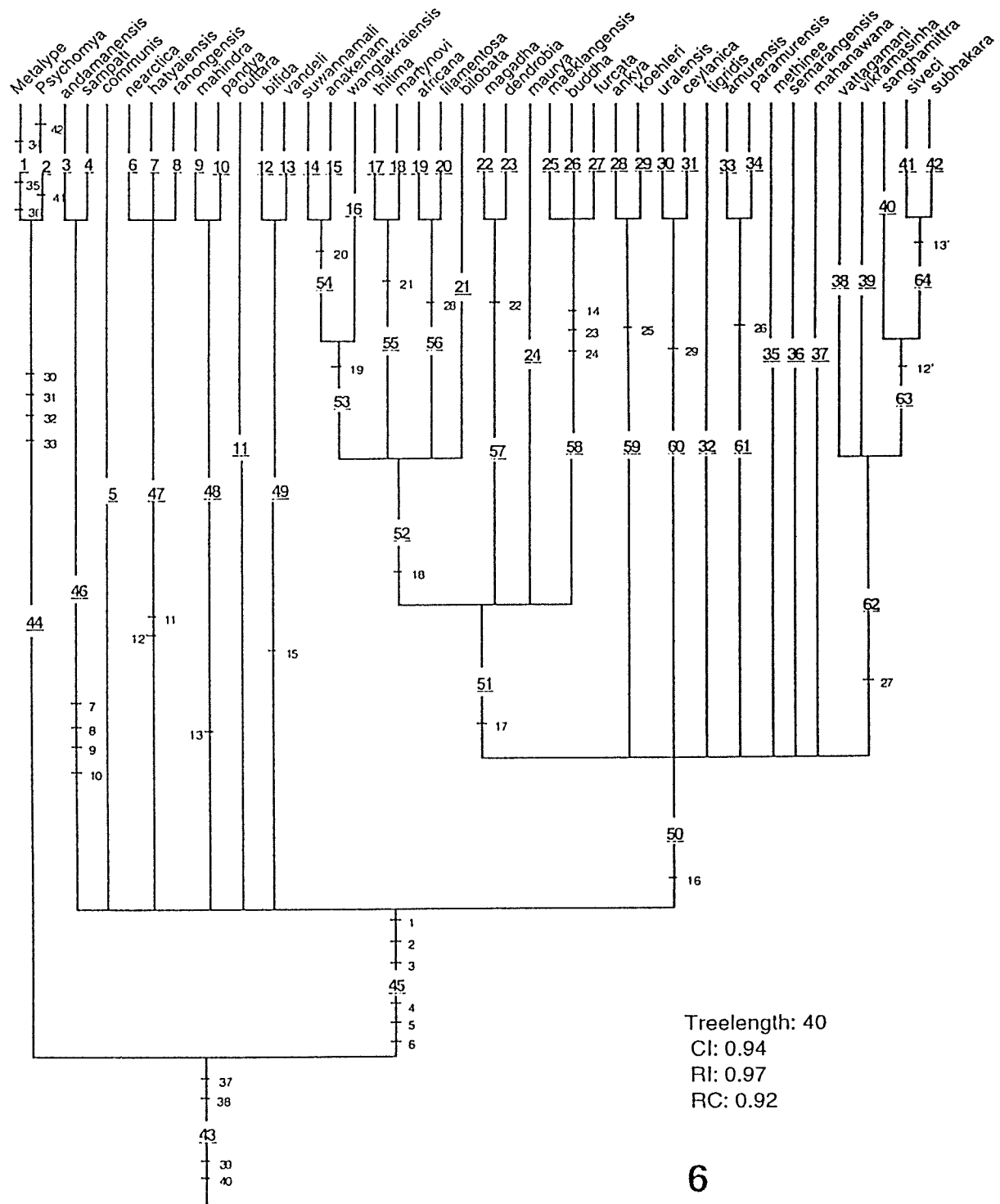
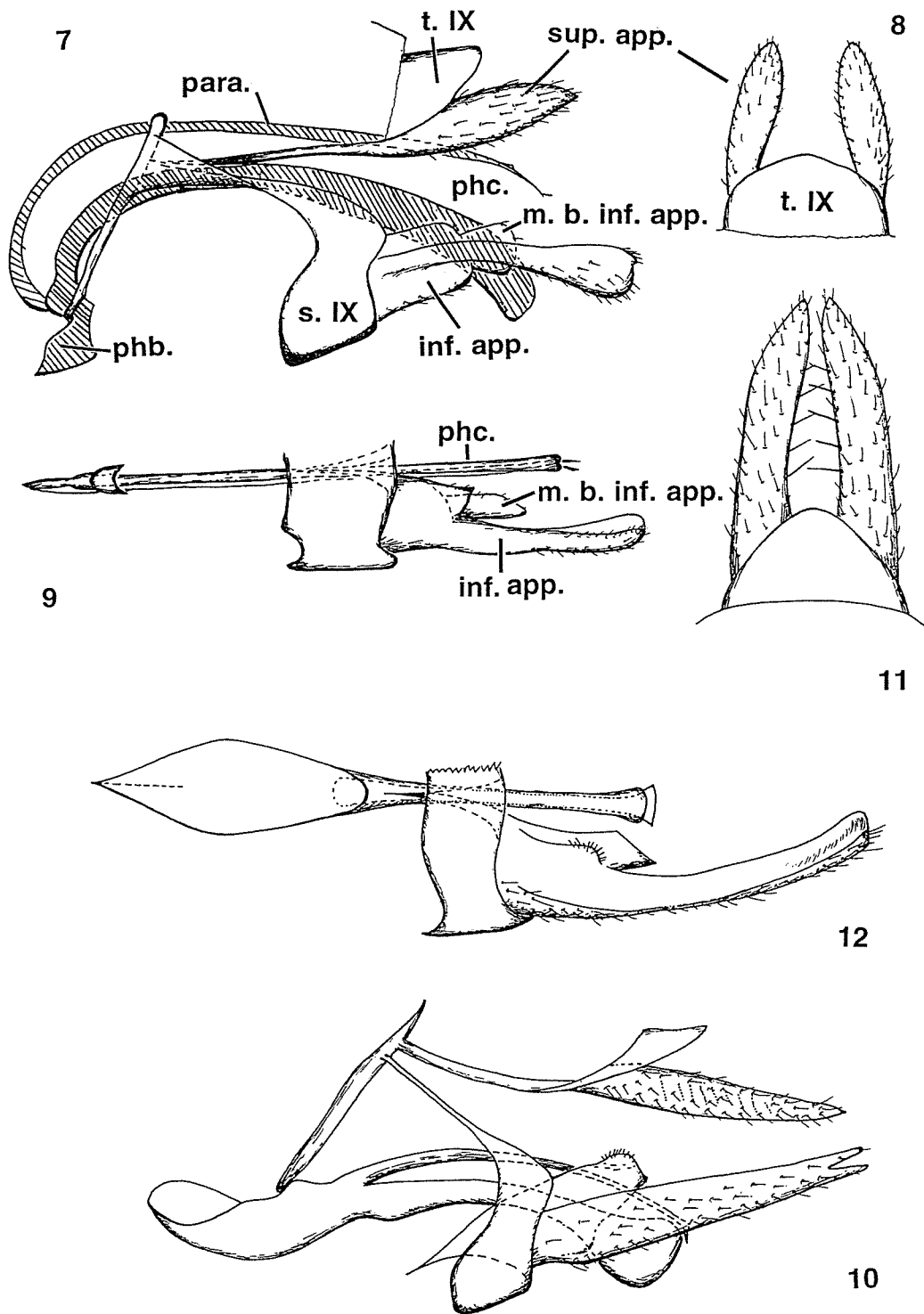


Fig. 6. Phylogenetic cladogram of species of *Paduniella* (s. l.), with *Psychomyia* and *Metalype* as outgroups. Underlined numbers = clade numbers; plain text numbers = homologues identified in Tables 1 and 2; apostrophe (') = parallelism or convergence. Nine species groups recognized: *P. andamanensis* Group (branch #46), *P. nearctica* Group (branch #47), *P. mahindra* Group (branch #48), *P. vandeli* Group (branch #48), *P. africana* Group (branch #51), *P. ankyra* Group (branch #59), *P. uralensis* Group (branch #60), *P. amurensis* Group (branch #61), *P. subhakara* Group (branch #62).



Figs. 7-12. Male genitalia of *Paduniella* species: 7, *Paduniella communis*, n.sp., lateral; 8, same, dorsal; 9, same, right half of sternum IX and phallic apparatus with paramere and right inferior appendage, ventral; 10, *Paduniella bifida*, n.sp., lateral; 11, same, dorsal; 12, same, right half of sternum IX and phallic apparatus with paramere and right inferior appendage, ventral. inf. app. = inferior appendage, m. b. inf. app. = mesal branch of inferior appendage, para. = paramere, phb. = phallobase, phc. = phallicata, s. IX = sternum IX, supra. app. = superior appendage, t. IX = tergum IX.

setae along ridge between tapering and thick portions. Sternum X split mesally, with pair of sharp internal apodemes arising from anterior margin. Segment XI round with pair of spine-like cerci.

**Diagnosis.** The male of this new species is very similar to that of *Paduniella nearctica* Flint, 1967 in the short phallobase, the absence of a median process above the phallic apparatus, and the undivided apex of each inferior appendage. However, their differences are obvious. In the new species, tergum IX has a round posterior margin (*P. nearctica* has a mesal point), the superior appendages are twice the length of tergum IX (*P. nearctica* has superior appendages slightly longer than tergum IX), the basal part of each inferior appendage is three times as wide as the apical part (less than twice as wide in *P. nearctica*), the paramere tip is forked (unique in *Paduniella*), and the paramere is arched (straight in *P. nearctica*).

**Phylogeny.** This new species is one of the more primitive species of the genus, lacking the median sternal strip process above the phallic apparatus. Its relationship with other species in the genus remains uncertain.

**Type material.** Holotype male: Song-cun, Ding-xi-he, 33 km E. of Jin-xian, An-hui Province, 120 m elevation, 8 June 1990, collected by Morse, Yang, and Sun (NAU). Allotype Female: same data as holotype (NAU). Paratypes: AN-HUI PROVINCE: 4 Males 2 Females, Yang-jia-tan, Fengyuan-shui, She-xian, 215 m elevation, 25 May 1992, collected by Morse and Sun (CUAC); 11 Males, Yaocun, Yong-feng-he, Lang-xi-xian, 23 May 1990, collected by Morse, Yang, and Sun (NAU). JIANG-XI PROVINCE: 1 Male, Lao-dong-qiao, Gui-xi-xian, 240 m elevation, 5 June 1990, collected by Morse and Sun (NAU); 15 Males, Qin-hua-he, 57 km N. of Wu-yuan, Wu-yuan-xian, 250 m elevation, 25 May 1990, collected by Morse, Yang, and Sun (NAU). HU-BEI PROVINCE: 9 Males 1 Female, 50 km N. W. of Yin-cheng, tributary of Da-fu-shui, Ji-shan-xian, 90 m elevation, 17 July, 1990, collected by Morse (CUAC); 9 Males, 47 km N. W. of Yin-cheng, tributary of Da-fu-shui, Jin-shan-xian, 80 m elevation, 17 July, 1990, collected by Yang and Wang (NAU); 9 Males, Da-fu-shui, Tian-dian-Dam, Yicheng City, 40 m elevation, 16 July 1990, collected by Morse and Yang (NAU).

**Distribution.** The species is distributed in Hu-bei, An-hui, and Jiang-xi Provinces, Oriental Biogeographic Region of China.

**Etymology.** *communis*, Latin, meaning "common," referring to the dominance of the species in central eastern China.

*Paduniella bifida*, new species  
(Figs. 10-12)

Male forewing length 2.3-2.7 mm, overall length 2.88-3.24 mm. Color in alcohol uniformly pale yellow-brown.

**Male genitalia.** Tergum IX triangular in dorsal view. No median process arising from sclerotized strips of segment IX. Each superior appendage straight, more than twice length of tergum IX. Inferior appendages each tapering to apex, with apical incision as long as 1/8 length of inferior appendage, and short truncated mesal branch arising near base. Phallobase very thick in lateral view, about half as long as phallicata; dorsal paramere arising at juncture of phallobase and phallicata, about 1/3 distance from base of phallic apparatus, spine-like, mostly cylindrical, with apex widened, obliquely truncated, and depressed; basal 3/4 of phallicata slender, apex expanded, round in lateral view.

**Diagnosis.** The male genitalia of the species are very similar to those of *Paduniella vandeli* Décamps, 1965 in the big phallobase; the incised apex of each inferior appendage; the compressed, round, expanded apex of the phallicata; and the obliquely cut apex of the paramere in lateral view. They differ in that the apical incision of each inferior appendage is much shallower, far less than 1/4 of the length of the appendage; the inferior appendages are acute apically, much narrower in the new species than in *P. vandeli*; and the forewing length is about half that of *P. vandeli*'s.

**Phylogeny.** The species is considered most closely related to *P. vandeli* because of their uniquely shared obliquely truncated paramere spine.

**Distribution.** The species is distributed in Sichuan and Jiang-xi Provinces, part of the Oriental Biogeographic Region of China.

**Type materials.** Holotype male, Si-mian-shan, Fei-long-he, Jiang-jin-xian, Si-Chuan Province, 800 m elevation, 7 July 1990, collected by Yang (NAU). Paratypes: JIANG-XI PROVINCE: 2 Males, Xi-qihé, 10 km S. of Gui-xi, Gui-xi-xian, 30 m elevation, 4 June 1990, collected by Yang, Morse, and Sun (NAU).

**Etymology.** *bifida*, Latin, meaning "divided," referring to the incision at the apex of each inferior appendage.

***Paduniella bilobata*, new species**

(Figs. 13-15)

Male forewing length 2.52-2.88 mm; overall length 3.06-3.31 mm. Color in alcohol uniformly pale yellow-brown.

**Male genitalia.** Tergum IX triangular, with concave sides in dorsal view. Superior appendages fused with tergum IX, each with length about twice width in lateral view and about three times width in dorsal view, apex acute and pointed mesad in dorsal view and dorsad in lateral view. Inferior appendages each tapering to blunt apex, mesal branch 2/3 as long as appendage. Two median processes arising between anterior tips of sclerotized processes of segment IX almost equal length, longer process reaching apex of phallicata, each process sharp and curved ventrad at apex. Phallobase large, slightly shorter than phallicata; paramere spine-like and arising from base of phallicata, sharp at apex; phallicata compressed, slightly and gradually broader toward apex in lateral view.

**Diagnosis.** The male of this species is similar to those of *Paduniella wangtakraiensis* Malicky, 1995, *P. suwannamali* Malicky, 1993, and *P. anakenam* Malicky, 1995, in possessing two subequal median processes. However, the superior appendages of the new species are broad, each with its apicomeral corner acute and directed dorsomesad, not straight and round at the apex as in those other species.

**Distribution.** The species is distributed in southeastern (An-hui and Jiang-xi Provinces) and southwestern (Yun-nan Province) China, in the Oriental Biogeographic Region.

**Phylogeny.** The species is a member of the *Paduniella africana* Group, as suggested by the two long median processes arising between the anterior tips of the segment IX sclerotized strips, but its relationships with other species within the group are not resolved.

**Type materials.** Holotype male: Song-cun, Ding-xi-he, 33 km E. of Jin-xian, An-hui Province, 120 m elevation, 8 June 1990, collected by Morse, Sun, and Yang (NAU). Paratypes: JIANG-XI PROVINCE: 4 Males, 61 km S E of Gui-xi, Lao-dong-qiao, Xi-qi-he, Qui-xi-xian, 240 m elevation, 5 June 1990, collected by Morse and Sun (CUAC); 40 Males, 59 km S E of Gui-xi, Xi-qi-he, Gui-xi-xian, 210 m elevation, 5 June 1990, collected by Yang (NAU); 88 Males, Qi-hua-he, 57 km N of Wu-yuan, Wu-yuan, 250 m elevation, 25 May 1990, collected by Morse,

Yang, and Sun (NAU); YUN-NAN PROVINCE: 2 Males, Nan-wen-he-xiang, Nan-wen-he, Ma-li-po-xian, 600 m elevation, 12 July 1990, collected by Li and Ke (NAU).

**Etymology.** *bi-*, Latin, meaning "two," and *lobatus*, Latin, meaning "with a projection," referring to the two median processes.

***Paduniella buddha*, new species**

(Figs. 16-18)

Male forewing length 3.65 mm; overall length 4.38 mm. Color in alcohol uniformly pale yellow-brown.

**Male genitalia.** Tergum IX subdorsally incised, appearing three-lobed in dorsal view, with middle lobe acute. Superior appendages each as long as wide basally, round at apex in dorsal view, acute in lateral view, with minute ventrolateral spine basally. Inferior appendages nearly straight, slightly tapering to blunt apex, with mesal branch appearing as small hairy wart about 3/4 distance from base. Two slender median processes between anterior tips of sclerotized strips of segment IX, one process exceeding apex of phallicata, other process much shorter, 1/3 as long as first process and positioned on left side of its base; phallobase thick and nearly as long as phallicata, with ventral surface excised close to base of phallicata; paramere spine about same length and basally nearly as thick as base of phallicata; phallicata mostly slender, apex depressed to spoon shape, curved dorsad.

**Diagnosis.** The male genitalia of this species are very similar to those of *Paduniella maeklangensis* Malicky, 1993 in that the median process has a short basal lobe. However, the two species can be distinguished by the following characters: The median process has only one short lobe at its base in this species (two in *P. maeklangensis*) and the small ventrolateral process of each superior appendage is near the base of the superior appendage in this species (near the apex in *P. maeklangensis*).

**Distribution.** This species is found only at the type locality in Si-chuan Province, southwestern China, Oriental Biogeographic Region.

**Phylogeny.** The species is closely related to *P. maeklangensis* Malicky and *Paduniella furcata*, sp. n., as suggested by the subdorsal incisions of tergum IX, and the depressed and upturned apex of the phallicata uniquely shared by these species.

**Type materials.** Holotype male, E-mei-he, 8 km W of Jing-shui, E-mei-shan, Si-chuan Province,

1040 m elevation, 1 July 1990, collected by Morse and Yang (NAU).

**Etymology.** "buddha," the name of the founder of the religion of Buddhism. The type location of the species, Emei Mountain, is the holy mountain of Buddhism in China.

***Paduniella furcata*, new species**

(Figs. 1, 19-21)

Male forewing length 2.60 mm, overall length 3.17 mm. Color in alcohol uniformly pale yellow-brown.

**Male genitalia** (Figs. 19-21). Tergum IX incised subdorsally, with middle lobe narrow and apically blunt. Superior appendages each tall, height slightly more than half of length, truncated, with tiny ventrolateral tooth near apex. Inferior appendages each with large acute ventral tooth at middle, apex truncated, mesal branch 2/3 length of inferior appendage. Single median process arising at juncture of anterior apices of sclerotized strips of segment IX and posterior end of phallobase and anterior end of phallicata; curved right at apical 1/3, acute apically, and exceeding apex of phallicata. Phallobase compressed; paramere spine arising from middle of phallicata, sharp, twisted, arched, reaching apex of phallicata; phallicata slightly depressed subapically, curved dorsad at apex.

**Distribution.** The species is known only from the type locality in Jiang-xi Province, in the Oriental Biogeographic Region of China.

**Diagnosis.** The male genitalia of the species are very similar to those of *P. maeklangensis* Malicky and *P. buddha*, sp. n., in the short and rounded superior appendages each with the little ventrolateral process, the subdorsally incised tergum IX, and the spoon-like apex of the phallicata curved dorsad. However, the large tooth on the ventral side of each inferior appendage is unique in the genus.

**Phylogeny.** The species is closely related to the lineage composed of *P. maeklangensis* and *P. buddha*, sp. n.

**Type materials.** Holotype male, Xi-qi-he, 10 km S. of Gui-xi, Gui-xi-xian, Jiang-xi Province, 30 m elevation, 4 June 1990, collected by Yang, Morse, and Sun (NAU). Paratypes: 5 Males, same data as holotype (3 males, NAU; 2 males CUAC).

**Etymology.** *furca*, Latin, meaning "a fork," referring to the shape of the phallic apparatus in lateral view.

***Paduniella uralensis bicornis* Martynov**

(Figs. 2-3, 22-24)

*Paduniella uralensis* Martynov, 1914, pp. 5-10, 17, 19, 20, 21, figs. 1-5. Type locality: Ural Mountains (Lakes Ilmen and Suratkul), Russia.

*Mesopaduniella uralensis* (Martynov) — Lestage, 1926, p. 385.

*Paduniella uralensis* Martynov — Lepneva, 1928, p. 25.

*Paduniella uralensis* Martynov — Martynov, 1929, p. 30.

*Paduniella uralensis* Martynov — Martynov, 1934a, p. 207, figs. 145-146.

*Paduniella uralensis bicornis* Martynov — Martynov, 1934a, p. 208, fig. 147.

*Paduniella uralensis bicornis* Martynov — Martynov, 1934b, p. 334.

*Paduniella uralensis* Martynov — Martynov, 1948, p. 908, figs. 486c-e.

*Paduniella uralensis* Martynov — Tanida, 1993, p. 58.

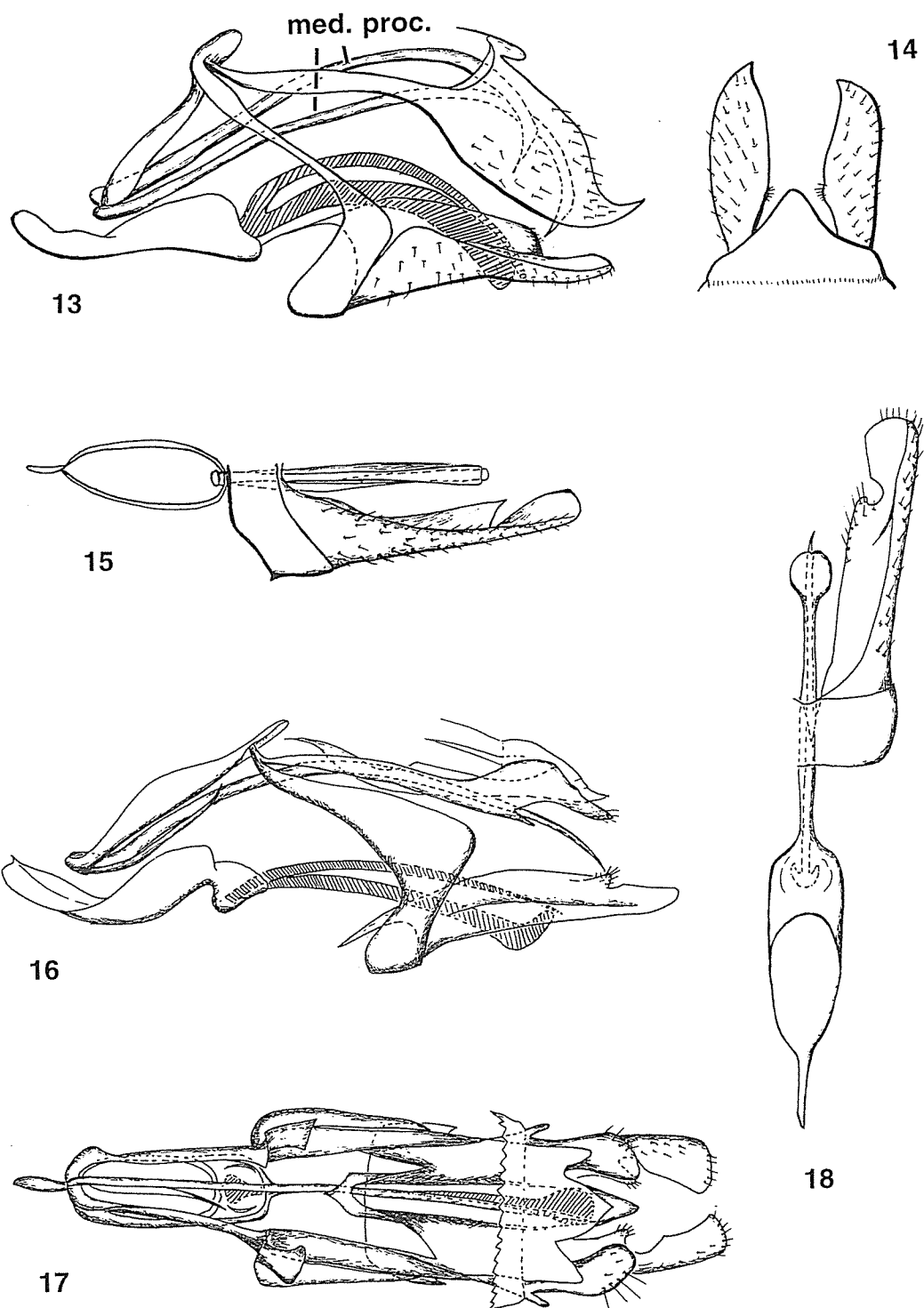
Male forewing length 2.98 mm, overall length 3.50 mm. Color in alcohol uniformly pale yellow-brown, antennae annulate with brown.

**Male genitalia** (Figs. 22-24). Tergum IX very short, deeply notched mesally. Superior appendages each slender, suddenly curved mesad subapically, slightly exceeding inferior appendages. Inferior appendages each thick basally, slightly more slender in middle, apically blunt, with mesal branch taller than base of appendage. Single median process between anterior apices of sclerotized strips of segment IX twisted, apex acute, extending slightly beyond phallic apparatus. Phallobase short, about 1/4 as long as phallicata; paramere spine arising at juncture of phallobase and phallicata, straight, very sharp at apex; phallicata straight, slender, compressed and shaped like battle-axe at apex, with acute apicodorsal and apicoventral points.

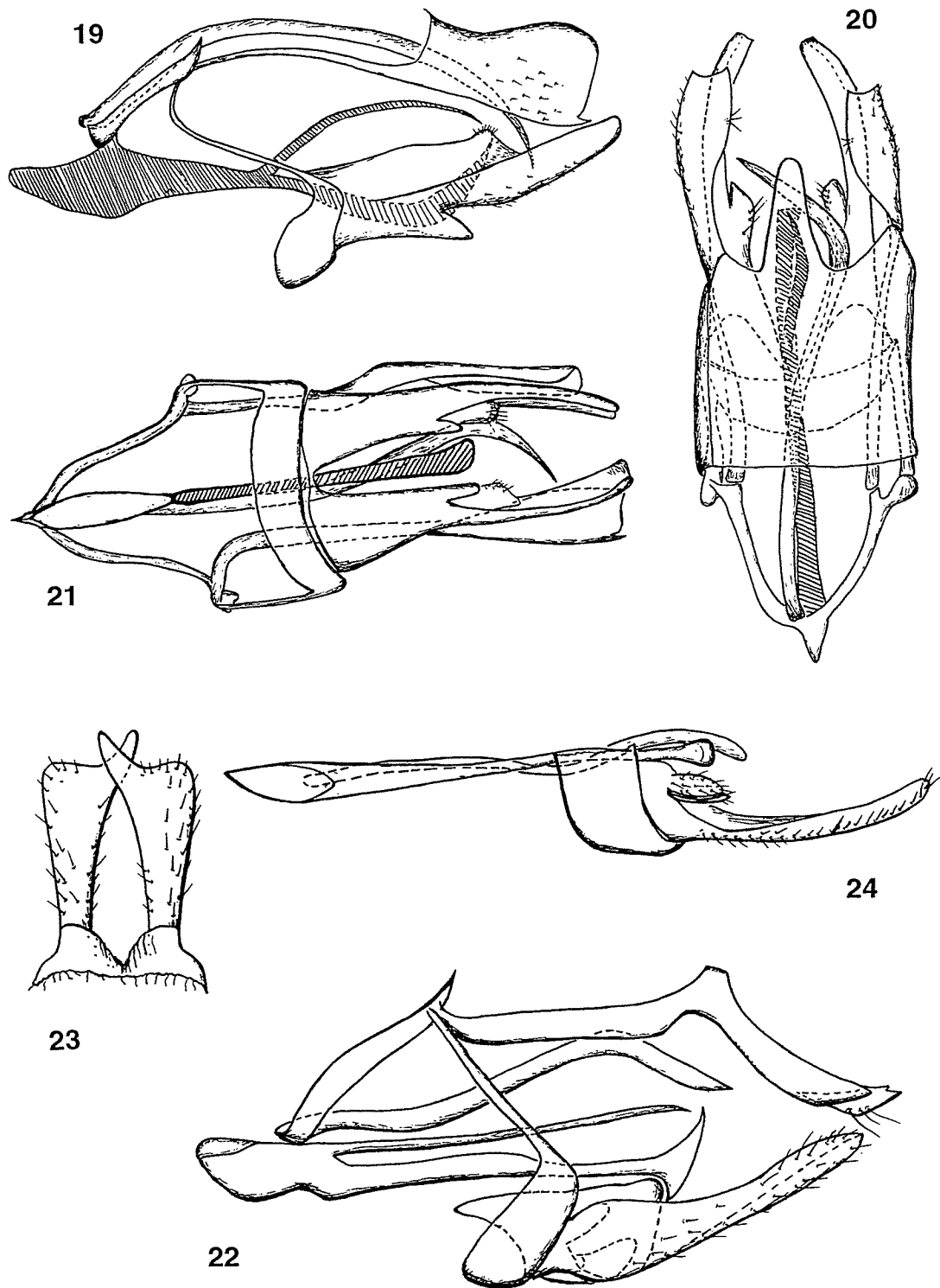
**Distribution.** The species is distributed in the East Palearctic Biogeographic Region from the Ural Mountains through the southern Ussuri River region of Russia to northeastern China. The nominate subspecies occurs in the western end of this range and the subspecies *P. uralensis bicornis* Martynov, 1934 in the eastern end.

**Diagnosis.** The male of this species is similar to that of *Paduniella ceylanica* Ulmer, 1915, in having the phallicata with an apicodorsal vertical extension at its apex and its apicoventral angle is acute. However, the apex of the phallicata in *P. uralensis* extends ventrad, unlike that of *P. ceylanica*. Also, the superior appendages of *P. uralensis* are curved mesad (straight, tapering to apices in *P. ceylanica*) and tergum IX is concave mesally in *P.*

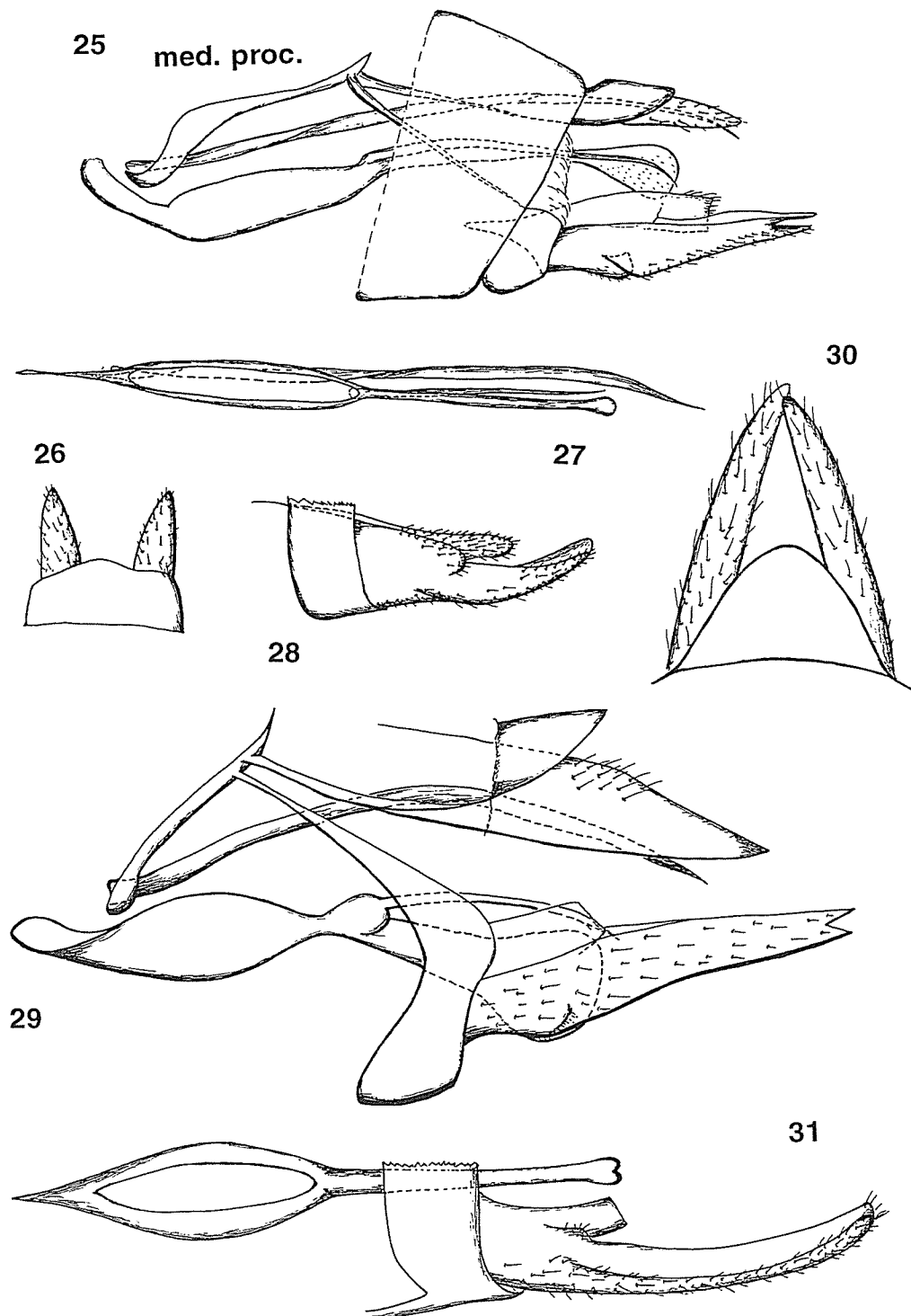




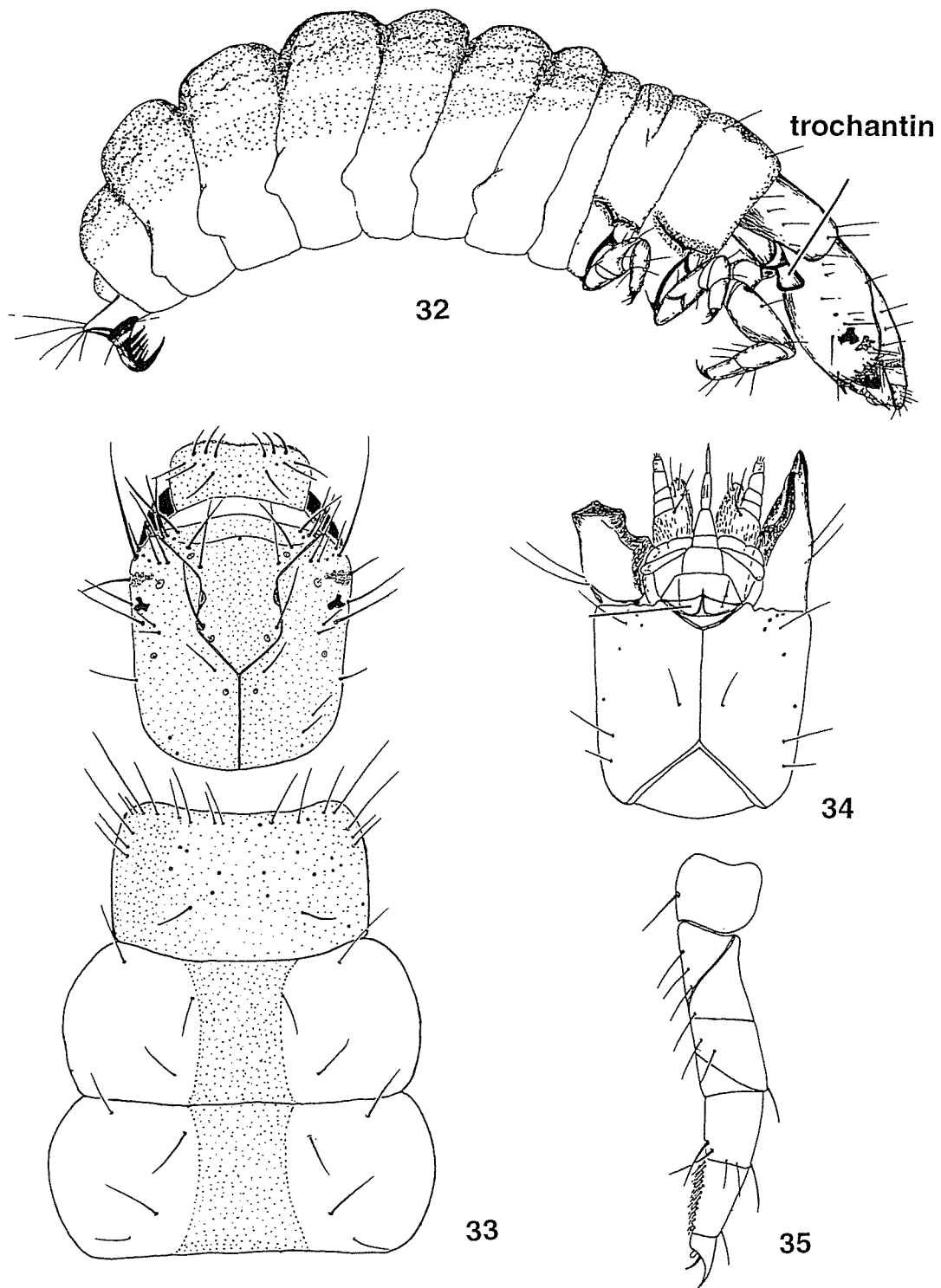
Figs. 13-18. Male genitalia of *Paduniella* species: 13, *Paduniella bilobata*, n.sp., lateral; 14, same, dorsal; 15, same, right half of sternum IX and phallic apparatus with paramere and right inferior appendage, ventral; 16, *Paduniella buddha*, n.sp., lateral; 17, same, dorsal; 18, same, right half of sternum IX and phallic apparatus with paramere and right inferior appendage, ventral. m. p. = median process.



Figs. 19-24. Male genitalia of *Paduniella* species: 19, *Paduniella furcata*, n.sp., lateral; 20, same, dorsal; 21, same, ventral; 22, *Paduniella uralensis* Martynov, left lateral; 23, same, superior appendages and tergum IX, dorsal; 24, same, right half of sternum IX and phallic apparatus with paramere and right inferior appendage, ventral.



Figs. 25-31. Male genitalia of *Paduniella* species: 25, *Paduniella paramurensis*, n.sp., left lateral; 26, same, superior appendages and tergum IX, dorsal; 27, same, right half of sternum IX and phallic apparatus, with paramere and median process; 28, same, right inferior appendage, ventral; 29, *Paduniella amurensis* Martynov, left lateral; 30, same, superior appendages and tergum IX, dorsal; 31, same, right half of sternum IX and phallic apparatus and right inferior appendage, ventral.



Figs. 32-35. Larva of *Paduniella nearctica* Flint: 32, right lateral view; 33, head and thorax, dorsal view; 34, head, ventral view; 35, right metathoracic leg, posterior view.

*uralensis* (convex in *P. ceylanica*). The difference between *Paduniella uralensis uralensis* and *P. uralensis bicornis* is that the superior appendages of specimens from the Ural Mountains are more distinctively excised behind, with the lateral corner also is somewhat produced in dorsal view. In our specimens, the superior appendages are not produced at their lateral corners, placing them in the subspecies *P. uralensis bicornis*.

**Phylogeny.** *Paduniella uralensis* is a sister species of *P. ceylanica*, as suggested by the dorsally extended apex of the phallicata and its acute apicoventral angle.

**Materials examined.** 2 males, 14 females, A-shi River, Mao-er-shan Town, Shang-zhi-xian, Heilong-jiang, 300 m elevation, 13 July 1993, collected by Li and Sun (NAU).

*Paduniella paramurensis*, sp. n.

(Figs. 25-28)

Male forewing length 2.81-2.95 mm, overall length 3.31-3.53 mm. Color in alcohol uniformly pale yellow-brown, antennae annulate with brown, eyes black.

**Male genitalia.** Tergum IX with posterior margin sinuous, almost straight, in dorsal view. Superior appendages triangular, about as long as tergum IX. Inferior appendages each with short basoventral tooth, mesal branch extending beyond middle of appendage, appendage tapering to incised apex. Single median process arising between anterior apices of sclerotized strips of segment IX slender and sharp, twisted, exceeding apex of phallicata. Phallobase nearly as long as phallicata; paramere arising at their juncture, needle-like, as long as phallicata; phallicata slender before enlarged, compressed apex almost as tall as phallobase, rounded in lateral view.

**Diagnosis.** The male genitalia of this species are very similar to those of *Paduniella amurensis* Martynov, 1934a, b in that superior appendages are straight and tapering, the inferior appendages are incised apically and each has a truncated mesal branch and a round ventromesal branch at middle length; the single median process is twisted, long, slender and very sharp; the phallobase is nearly as long as the phallicata; and the phallicata is expanded and compressed laterally at its apex. The species can be distinguished from *P. amurensis* by four characters: (1) the phallicata is more slender and its length is more than ten times its width at the middle in lateral view (length about four times the

width in lateral view in *P. amurensis*), (2) the superior appendages are about as long as broad basally in dorsal view (much longer in *P. amurensis*), (3) tergum IX is almost quadrate in dorsal view (triangular in *P. amurensis*), and (4) the mesal branch of each inferior appendage exceeds the middle of the appendage (not reaching the middle of the appendage in *P. amurensis*).

**Distribution.** The new species is distributed in Jiang-xi Province, southern China, Oriental Biogeographic Region.

**Phylogeny.** The species is closely related to *Paduniella amurensis* Martynov, as suggested by the truncated mesal branch of each inferior appendage.

**Type materials.** Holotype male, Xi-qi-he, 10 km S of Gui-xi, Gui-xi-xian, Jiang-xi Province, 30 m elevation, 4 June 1990, collected by Yang, Morse, and Sun (NAU). Paratypes: 43 Males, same data as holotype (41 males, NAU; 2 males CUAC).

**Etymology.** *para-*, Greek, meaning "close, near," and Amur, area of Far East Russia adjacent to China.

*Paduniella amurensis* Martynov

(Figs. 29-31)

*Paduniella amurensis* Martynov, 1934a, pp. 206, 208-210, 334-335, figs. 148-149.

*Paduniella amurensis* Martynov — Martynov, 1934b, pp. 334-335.

*Paduniella amurensis* Martynov — Martynov, 1935, pp. 151, 206.

*Paduniella amurensis* Martynov — Lepneva, 1953, p. 419.

*Paduniella amurensis* Martynov — Tanida, 1993, p. 58.

*Paduniella amurensis* Martynov — Vshivkova, 1995, p. 56.

Male forewing length 3.0 mm, overall length 3.5 mm. Color in alcohol uniformly yellow-brown.

**Male genitalia.** Tergum IX triangular, blunt apically. Superior appendages each broad at base, tapering to apex, more than twice as long as tergum IX. Inferior appendages each with basoventral tooth inconspicuous, mesal branch obliquely truncated well before middle of appendage, appendage tapering to incised apex. Single median process arising between anterior apices of sclerotized strips of segment IX slender, sharp, exceeding apex of phallicata. Phallobase longer than phallicata; paramere spine nearly straight, acute, reaching apex of phallicata; phallicata compressed and round at apex in lateral view, width at middle 1/4 length.

**Diagnosis.** The species is similar to *Paduniella paramurensis*, new species, resembling it and differing from it as explained in its diagnosis above.

**Distribution.** In addition to Si-chuan Province of China, Oriental Biogeographic Region, the species is distributed widely over the Amur region of Far East Russia and North Korea (East Palaearctic Biogeographic Region) and in India (Oriental Biogeographic Region), although we are not convinced that the Indian specimens represent the same species.

**Phylogeny.** The species is closely related to *Paduniella paramurensis*, n.sp., for reasons cited above for that species.

**Materials examined.** Si-Chuan Province: 1 male, 17 km E of Ping-wu, tributary of Fu-jiang, Ping-wu-xian, 1060 m elevation, 27 June 1990, collected by Yang and Li (NAU). 1 male 19 km E. of Ping-wu, tributary of Fu-jiang, Ping-wu-xian, 1090 m elevation, 27 June 1990, collected by Morse (CUAC).

#### Key to males of *Paduniella* species from China

1. Median processes absent above phallic apparatus (Fig. 7) ..... 2
- 1' Median process or processes arising between anterior ends of sclerotized strips of segment IX (Fig. 13) ..... 3
- 2(1). Phallobase more than half as long as phallicata (Fig. 7) ..... *Paduniella communis*, n.sp.
- 2'. Phallobase about 1/8 length of phallicata (Fig. 10) ..... *Paduniella bifida*, n.sp.
- 3(1'). Two median processes present (Fig. 13) ..... 4
- 3'. One median process present (Fig. 19) ..... 5
- 4(3). Median processes subequal in length (Fig. 13) ..... *Paduniella bilobata*, n.sp.
- 4'. One median process much shorter than the other one (Fig. 16) ..... *Paduniella buddha*, n.sp.
- 5(3'). Phallicata depressed and curved dorsad apically; inferior appendages each with apex entire (Fig. 19) ..... 6
- 5'. Phallicata compressed and expanded at apex; inferior appendages each with apex forked (Fig. 25) ... 7
- 6(5). Tergum IX concave subdorsally (Fig. 20) ..... *Paduniella furcata*, n.sp.
- 6'. Tergum IX concave mesally (Fig. 23) ..... *Paduniella uralensis bicornis* Martynov

- 7(5'). Phallicata about 1/12 as wide in middle as long (Fig. 25) ..... *Paduniella paramurensis*, n.sp.
- 7'. Phallicata about 1/3 as wide in middle as long (Fig. 29) ..... *Paduniella amurensis* Martynov

#### Phylogeny of world *Paduniella* species

To analyze the phylogeny of world *Paduniella* species, 42 homologues were chosen from 40 of the 44 species of the genus (Tables 1 and 2). The homologous condition for each of these characters was inferred by reference to the above groundplan. The computer program PAUP (Swofford, 1993) version 3.1, with its heuristic searching method, was used to infer the phylogeny, employing the following assumptions: all characters unordered; base weight of each character 1.

A single cladogram was inferred with tree-length 40 (with base weight of each character = 1), CI 0.94, RI 0.97, RC 0.92 is depicted in Fig. 6.

Homologues 37-40 suggest that *Paduniella* is most closely related to the monophyletic lineage of *Metalype* and *Psychomyia*. *Metalype* and *Psychomyia* share the four homologues 30-33.

Six homologues (1-6) strongly suggested that *Paduniella* is a monophyletic group. However, the males, at least, are rather homogeneous within the genus, such that discovery of informative infrageneric homologues was difficult. Therefore, the cladogram of the species still has several unresolved polytomies.

At the base of the cladogram for the genus, the *P. andamanensis* Group (branch #46, including *Paduniella andamanensis* Malicky, 1979, and *Paduniella sampati* Malicky, 1979) is monophyletic as indicated by homologues 7-10. The *P. nearctica* Group (branch #47, including *P. nearctica* Flint, *Paduniella hatyaiensis* Malicky, 1993 and *Paduniella ranogensis* Malicky, 1993, is supported by homologues 11, 12. The *Paduniella mahindra* Group (branch #48, including *Paduniella mahindra* Schmid, 1958 and *Paduniella pandya* Schmid, 1958) is suggested by homologue 13. The *Paduniella vandeli* Group (branch #49, including *Paduniella bifida*, sp. n. and *Paduniella vandeli* Decamps) is supported by homologue 15. No homologue has been found to associate these four Groups or *Paduniella communis* sp. n. and *Paduniella outtara* Schmid, 1961 with other species in this clade. The remaining species of the genus belong to a monophyletic group (branch #50) suggested by homologue 16. This latter group is composed of nine unresolved components: *Paduniella mahanawana*

Schmid, 1958, *Paduniella semarangensis* Ulmer, *Paduniella methinee* Chantaramongkol and Malicky, 1986, *Paduniella tigridis* Malicky, 1993, the *Paduniella subhakara* Group (branch #62, suggested by homologue 27), *Paduniella amurensis* Group (branch #61, suggested by homologue 26), *Paduniella uralensis* Group (branch #60, suggested by homologue 29), *Paduniella ankyra* Group (branch #59, suggested by homologue 25), and *Paduniella africana* group composed of the rest of the species (branch #51, suggested by homologue 17).

Homologue 12 appears independently twice (branches #47 and 63) and homologue 13 twice (branches #48 and 64).

#### Discussion and taxonomic conclusions - superspecific taxonomy

From the cladogram, nine monophyletic species groups are recognized. The type species of the four genera mentioned in the beginning of this paper are all in the monophyletic group, branch #50. The type species of *Mesopaduniella* (*Paduniella uralensis*) (branch #30) and the type species of *Propaduniella* (*Paduniella ceylanica*) (branch #31) are sister species in the *P. uralensis* Group (branch #60); of these two genera, *Propaduniella* has page priority. The type species of *Psychomyiodes* (*P. africana*) is in the *Paduniella africana* Group (branch #51). The relationships of the type species of *Paduniella* (*P. semarangensis*) with these two lineages and with other species in the monophyletic group suggested by homologue 16 remain unresolved.

Our purpose in inferring the relationships of the *Paduniella* species has been to establish working hypotheses for subsequent biological work. We prefer to reflect our conclusions in the higher classification of the group. If the included 44 species are treated as a subfamily, then *Paduniella*, *Psychomyiodes*, and *Propaduniella* would likely be considered different genera and many more generic names would be needed and *Mesopaduniella* as synonym of *Propaduniella* should not be used. If the 44 species are treated as a genus, these genus-group names could be afforded subgeneric rank. However, there are still many unresolved branches in our cladogram. Furthermore, there are some character parallelisms and convergences that weaken our arguments. Therefore, to minimize future changes of species combinations, we prefer to retain all 44 species in a genus *Paduniella*, with only informal

species-group names attached to those that presently seem to us most convincingly monophyletic.

#### Checklist of *Paduniella* species

For each species in the following checklist, the type country is noted, followed by an indication of the major biogeographical region(s) from which the species has been reported, where AT = Afrotropical, EP = East Palearctic, NA = Nearctic, OL = Oriental, and WP = West Palearctic.

#### Genus *Paduniella* Ulmer, 1913, p. 80;

- type species: *Paduniella semarangensis* Ulmer (monobasic);  
 synonym *Mesopaduniella* Lestage, 1926, p. 383, 384 (Martynov, 1934a, p. 206); type species: *Paduniella uralensis* Martynov (monobasic);  
 synonym *Propaduniella* Lestage, 1926, p. 383, 384 (Martynov, 1935, pp. 151, 206); type species: *Paduniella ceylanica* Ulmer (monobasic);  
 synonym *Psychomyiodes* Ulmer, 1922, p. 50 (AV Martynov, 1934a, p. 206); type species: *Psychomyiodes africana* Ulmer (original designation).  
*africana* (Ulmer, 1922, p. 52, figs. 3-7), *Psychomyiodes*; Cameroon; AT.  
*amurensis* Martynov, 1934a, pp. 206, 208-210, 334-335, figs. 148-149a-c; Russia (S Ussuri); EP.  
*anakenam* Malicky and Chantaramongkol, 1995, p. 23; Thailand; OL.  
*andamanensis* Malicky, 1979, p. 98, figs.; Andaman Islands; OL.  
*angusta* Banks, 1939, pp. 143-144, pl. 1 figs. 3, 5, 6; Philippines; OL.  
*ankya* Mosely, 1939, pp. 29-30, figs. 85-90; Uganda; AT.  
*bifida*, new species; People's Republic of China (Sichuan Province); OL.  
*bilobata*, new species; People's Republic of China (Anhui Province); OL.  
*borneensis* Banks, 1931, p. 426; Malaysia (Sabah); OL.  
*buddha*, new species; People's Republic of China (Sichuan Province); OL.  
*capensis* Barnard, 1940, pp. 655-656, figs. 18a-e; Republic of South Africa; AT.  
*ceylanica* Ulmer, 1915, pp. 42-43, 73, figs. 4-5; Sri Lanka; OL.  
*communis*, new species; People's Republic of China (Anhui Province); OL.  
*dendrobia* Malicky and Chantaramongkol, 1993, p. 1159, figs.; Thailand; OL.  
*filamentosa* Jacquemart and Statzner, 1981, p. 10, figs.; Zaire; AT.  
*fissa* Martynov, 1935, pp. 150-151, 206, figs. 51a-c; India; OL.

- furcata*, new species; People's Republic of China (Jiangxi Province); OL.
- hatyaiensis* Malicky and Chantaramongkol, 1993, p. 1157, figs.; Thailand; OL.
- koehleri* Malicky, 1995, p. 24; Indonesia (Bali); OL.
- maeklangensis* Malicky and Chantaramongkol, 1993, p. 1158, figs.; Thailand; OL.
- magadha* Schmid, 1961, p. 197, pl. 16 figs. 5-6; Pakistan; OL.
- mahanawana* Schmid, 1958, pp. 8, 9, 10, 11, 15, 16, 18, 19, 20, 24, 28, 30, 36, 104-105, pl. 18 figs. 17-20; Sri Lanka; OL.
- mahindra* Schmid, 1958, pp. 18, 20, 24, 30, 36, 103, pl. 18 figs. 12-14; Sri Lanka; OL.
- martyнови* Kumanski, 1992, Korean People's Democratic Republic; EP.
- maurya* Schmid, 1961, pp. 197-198, pl. 16 figs. 7-8; Pakistan; OL.
- methinee* Chantaramongkol and Malicky, 1986, p. 526, figs.; Sri Lanka; OL.
- nearctica* Flint, 1967, pp. 310-311, figs. 1-4; United States of America; NA.
- outtara* Schmid, 1961, pp. 196-197, pl. 16 figs. 3-4; Pakistan; OL.
- pandya* Schmid, 1958, pp. 5, 6, 10, 13, 19, 25, 26, 28, 36, 102-103, pl. 18 figs. 9-11; Sri Lanka; OL.
- paramurensis*, new species; People's Republic of China (Jiangxi Province); OL.
- ranongensis* Malicky and Chantaramongkol, 1993, p. 1157, figs.; Thailand; OL.
- sampati* Malicky and Chantaramongkol, 1993, p. 1156, figs.; Thailand; OL.
- sanghamittra* Schmid, 1958, pp. 7, 11, 12, 13, 16, 18, 26, 28, 36, 104, pl. 18 figs. 15-16; Sri Lanka; OL.
- semarangensis* Ulmer, 1913, pp. 81-82, figs. 2-3; Indonesia (Java); OL.
- siveci* Chantaramongkol and Malicky, 1986, p. 526, figs.; Sri Lanka; OL.
- subhahara* Schmid, 1958, pp. 9, 10, 13, 16, 19, 20, 22, 25, 28, 30, 32, 36, 103-104, pl. 18 figs. 21; Sri Lanka; OL.
- suwannamali* Malicky and Chantaramongkol, 1993, p. 1157, figs.; Thailand; OL.
- thitima* Chantaramongkol and Malicky, 1986, p. 526, figs.; Sri Lanka; OL.
- tigridis* Malicky and Chantaramongkol, 1993, p. 1159, figs.; Thailand; OL.
- uralensis* Martynov, 1914, pp. 5-10, 17, 19, 20, 21, figs. 1-5; Russia (S Ural); EP and WP;  
subspecies *Paduniella uralensis bicornis* Martynov, 1934a, p. 208, fig. 147; Russia (S Ussuri).
- vandeli* Décamps, 1965, p. 239, figs.; France; WP.
- vattagamani* Schmid, 1958, pp. 5, 15, 36, 102, pl. 18 figs. 6-8; Sri Lanka; OL.
- vikramasinha* Schmid, 1958, pp. 4, 18, 20, 21, 29, 30, 36, 105-106, pl. 19 figs. 1-6; Sri Lanka; OL.
- wangtakraiensis* Malicky and Chantaramongkol, 1993, pp. 1158, figs.; Thailand; OL.

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**Table 1.** Characters used to infer a phylogeny of species in the genus *Paduniella* (s. l.). 0 = plesiomorphy, 1 = homologue.

1. Each maxillary palpus 5-segmented = 0; each maxillary palpus 6-segmented = 1.
2. Each labial palpus 3-segmented = 1; each labial palpus 4-segmented = 1.
3. Each hindwing with Fork III present = 0; each hindwing with Fork III absent = 1.
4. Inferior appendages 2-segmented, without mesal branch = 0; inferior appendages compressed, 1-segmented, each with small mesal branch = 1.
5. No narrow transverse strips connecting dorsolateral edges of sternum IX = 0; narrow transverse strips connecting dorsolateral edges of sternum IX, ventrally approaching phallobase = 1.
6. Pupa with 5 pairs of labral setae = 0; pupa with 3 pairs of labral setae = 1.
7. Paramere spine present = 0; paramere spine absent = 1.
8. Superior appendages short, broad, and apically blunt = 0; superior appendages long, slender, and acute = 1.
9. Superior appendages without long lateral basal process = 0; superior appendages with long lateral basal process = 1.
10. Phallicata short, thick, and apically blunt = 0; phallicata long, slender, and acute = 1.
11. Superior appendages round at apex = 0; superior appendages truncate at apex = 1.
12. Phallobase straight ventrally = 0; phallobase concave ventrally = 1.
13. Paramere spine of phallicata dorsal = 0; paramere spine of phallicata lateral = 1.
14. Apex of phallus compressed = 0; apex of phallus depressed = 1.
15. Apex of paramere spine not truncate at apex = 0; apex of paramere spine obliquely truncate at apex = 1.
16. Sternal strips without long median process = 0; sternal strips with long median process = 1.
17. Sternal strip median process with one long lobe = 0; sternal strip median process divided, with one short lobe and one long lobe = 1.
18. Sternal strip median process with one long lobe = 0; sternal strip median process with two long lobes = 1.
19. Inferior appendages without teeth at middle of dorsal edges = 0; inferior appendages each with small tooth at middle of dorsal edge = 1.
20. Inferior appendages without lateral teeth on mesal branch = 0; inferior appendages each with small lateral tooth on mesal branch = 1.
21. Sternal strip processes without short dents basally = 0; sternal strip processes each with several short dents basally = 1.
22. Paramere spine arising from base of phallicata = 0; paramere spine arising from middle of phallicata (with some species having it even closer to apex) = 1.
23. Tergum IX not divided subdorsally = 0; tergum IX divided subdorsally = 1.
24. Superior appendages without lateral teeth = 0; superior appendages each with lateral tooth = 1.
25. Inferior appendages without conspicuous ventral projections = 0; inferior appendages each with conspicuous ventral projection = 1.
26. Mesal branch of each inferior appendage round = 0; mesal branch of each inferior appendage truncate = 1.
27. Phallobase separated from phallicata = 0; phallobase fused with phallicata = 1.
28. Sternal strip median process with less than three long lobes = 0; sternal strip median process with three long lobes = 1.
29. Phallicata apex with ventral angle obtuse = 0; phallicata apex with ventral angle acute and curved dorsad = 1.
30. Hindwing m-cu crossvein present = 0; hindwing m-cu crossvein absent = 1.
31. Phallus straight at apex = 0; phallus "J-shaped" at apex = 1.
32. Ocellar warts separated = 1; ocellar warts contiguous = 1.
33. Male tergum X triangular = 0; male tergum X deeply divided into two lateral parts = 1.
34. Superior appendages without mesal apical spines = 0; superior appendages each with mesal apical spine = 1.
35. Basal half of each inferior appendage not expanded mesally, straight, and with anterior surface sclerotized = 0; basal half of each inferior appendage more or less expanded mesally and twisted slightly anteriorly at mesal edge, with anterior surface membranous = 1.
36. Phallobase complete, without deep lateral excision = 0; phallobase extended dorsally and ventrally, with deep lateral excision = 1.
37. Hindwing without prominent costal point = 0; hindwing with prominent costal point = 1.
38. Larva anal claw without teeth = 0; larva anal claw with teeth = 1.
39. Female abdominal segment X about same length as other abdominal segments = 0; Female segment X elongated = 1.
40. Male phallic apodeme short = 0; male phallic apodeme well developed = 1.
41. Female with transverse row of setae on tergum X = 0; female without transverse row of setae on tergum X = 1.
42. Male tergum X lateral parts separated with superior appendages = 0; male tergum X lateral parts fused with superior appendages for 1/2 length = 1.

