New genera of Tephritidae (Diptera) from Brazil and Dominican Amber, with phylogenetic analysis of the tribe Ortalotrypetini

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Abstract

The tribe Ortalotrypetini (Trypetinae) is expanded to include four genera, whose phylogenetic relationships are analyzed. The following are recognized: *Ortalotrypeta* Hendel, *Cyaforma* Wang, *Neortalotrypeta*, n. gen., proposed for *N. bicolor*, n. sp., from Brazil, and *Protortalotrypeta*, n. gen., proposed for *P. grimaldii*, n. sp., which is described from a specimen in amber from the Dominican Republic. *Ortalotrypeta ziae*, n. sp., from Taiwan, is described, and lectotypes are designated for *O. gigas* Hendel and *O. idana* Hendel. *O. macula* Wang and *O. tonkinensis* Zia are transferred to *Cyaforma*.

Resumen

El tribu Ortalotrypetini (Trypetinae) incluye: *Ortalotrypeta* Hendel, *Cyaforma* Wang, *Neortalotrypeta*, n. gen., propuesto por *N. bicolor*, sp. n., de Brasíl, y *Protortalotrypeta*, n. gen., propuesto por *P. grimaldii*, sp. n., descrito de un espécimen de ámbar de la República Dominicana. Se analizan y se discuten las relaciones filogenéticas entre estos géneros. Se describe *Ortalotrypeta ziae*, n. sp., de Taiwan, y se designan lectotipos para *O. gigas* Hendel y *O. idana* Hendel. Se transferen *O. macula* Wang y *O. tonkinensis* Zia a *Cyaforma*.

Introduction

Very few fossils of true fruit flies (Tephritidae) are known. The discovery of a well preserved tephritid specimen in amber from the Dominican Republic of at least early Miocene age is, therefore, of considerable interest. Even more intriguing are the relationships of the new genus *Protortalotrypeta* described in this paper based on this specimen. It appears to be the sister group of a clade including the Asian genera *Ortalotrypeta* Hendel and *Cyaforma* Wang, as well as *Neortalotrypeta*, another new genus from South America described in this paper. These four genera, whose host plants and biology are unknown, comprise the tribe Ortalotrypetini.

Korneyev (1982) reported the following fossil Tephritidae: *Oxyna pluvia* Durrenfeldt, from the Pliocene of Germany, *Tephritis antiqua* Heer, from the Lower Miocene of Croatia, and *Pseudacidia clotho* Korneyev, from the Miocene of the Caucasus region. All of these are compression fossils, and the latter two each consist of a wing only. Because of their poor condition, little can be determined about their phylogenetic relationships. Freidberg (1991) reported a male in good condition of a species of *Ceratitis (Pterandrus)*, possibly *rosa* (Karsch), from amber from Tanzania, probably from the Pleistocene or Pliocene (Poinar 1992; Schlüter and Von Gnielinski 1987). References to Trypetidae from the mid-Eocene Green River Formation (e.g. Grande 1984; Lewis 1989) probably all refer to the Eophlebomyiidae (Cockerell 1925). The fossil specimen described below is preserved in a piece of Dominican amber of the type discussed by Grimaldi and Mathis (1993) that is thought to be of late Oligocene or early Miocene age (ca. 25 million years old), although an Eocene age for some samples has been suggested (Poinar 1992). Because of its age and excellent condition, this specimen is perhaps the most important fossil tephritid yet encountered.

Materials and Methods

The morphological terminology used here generally follows McAlpine (1981). The following acronyms are used: AMNH - American Museum of Natural History; CNC - Canadian National Collection; and USNM - National Museum of Natural History, Smithsonian Institution. The amber fossil was examined and illustrated in mineral oil. The methods used for cladistic analysis are discussed in the "Phylogenetic Relationships" section.

Taxonomy

Tribe Ortalotrypetini

Ito (1983) proposed the tribe Ortalotrypetini in a key, with *Ortalotrypeta* Hendel as the only included genus. *Cyaforma* Wang (1989), described as being allied to *Ortalotrypeta*, and *Neortalotrypeta* Norrbom, n. gen., and *Protortalotrypeta* Norrbom, n. gen., also belong to this group, which I recognize as a tribe of the subfamily Trypetinae, although its proper classification cannot be determined until relationships among the higher taxa of the Tephritidae are clarified. Its rank and classification are subjective because the relationships among the higher taxa of Tephritidae are uncertain. The Ortalotrypetini can be diagnosed as follows: usually three scutellar setae (only two in *Neortalotrypeta*); postpronotum with two or more large setae (Fig. 1E) (except in *Neortalotrypeta* and *Ortalotrypeta singula* Wang); female abdominal syntergosternite 7 with a dorsoapical rather than apical opening (Fig. 4A-C); and female eversible membrane without basal taenia but with a large ventral area of dense dark scales (Fig. 4C). The structure of the female terminalia in the Ortalotrypetini is unique within the Tephritidae. Two postpronotal setae otherwise occur within the family only in *Blepharoneura* Loew and the related genera *Ceratodacus* Hendel, *Baryglossa* Bezzi, and *Hexaptilona* Hering, which can be easily distinguished from the Ortalotrypetini by the presence on the anepisternum of a large seta just anterior to the phragma. Very few Tephritidae other than these taxa and some genera of Acanthonevrini have three scutellar setae. The Ortalotrypetini differ from the Acanthonevrini, the group in which *Ortalotrypeta* was traditionally classified, by the characters in the diagnosis (except the number of scutellar setae), by having the ocellar seta well differentiated (although relatively small in *Protortalotrypeta* and *Neortalotrypeta*), and by having a completely fused aculeus (the tip is not "tactile" as in the Acanthonevrini).

Key to the genera of Ortalotrypetini

1. Head broad in lateral view (Fig. 1C), with anterior margin receded and with postgena broad. Postocular setae poorly differentiated from postgenal setulae. Dorsocentral seta aligned midway between postsutural supra-alar seta and postalar seta or more anteriorly. Wing elongate (Fig. 3). 2
- Head relatively narrow in lateral view (Fig. 1A), with anterior margin not receded and with postgena narrow. Postocular setae well differentiated from postgenal setulae. Dorsocentral seta aligned with postalar seta (Fig. 1E). Wing broader (Fig. 2A). (Known only from Dominican amber)..... *Protortalotrypeta* Norrbom, n. gen.

2. Paravertical seta very large, more than 2/3 length of vertical setae. Thorax with 3 scutellar setae and, except in *O. singula*, with 2-3 postpronotal setae. (Eastern Asia) 3
- Paravertical seta minute, smaller than postocellar seta. Thorax with 2 scutellar setae and 1 postpronotal seta. (Brazil) .... *Neortalotrypeta* Norrbom, n. gen.

3. Scutum dark brown, with medial yellow stripe or stripes. Wing pattern entirely brown and hyaline, without yellow areas. Cell r_{4+5} without hyaline spots..... *Cyaforma* Wang
- Scutum entirely yellow, orange or pale brown. Wing pattern with at least anterobasal yellow area (Fig. 3). Cell r_{4+5} with at least small hyaline spot or spots ..... *Ortalotrypeta* Hendel

Protortalotrypeta Norrbom, new genus

Type species, *P. grimaldii*, new species.

Diagnosis. *Protortalotrypeta* differs from most genera of Tephritidae (including *Neortalotrypeta*) in having 3 scutellar and 2 postpronotal setae. Of the six extant genera with more than 1 postpronotal seta, *Blepharoneura*, *Baryglossa*, *Hexaptilona* and *Ceratodacus* differ from *Protortalotrypeta* in having an anepisternal seta just anterior to the phragma, and in the normal shape of the apex of female syntergosternite 7, which has an apical rather than dorsoapical opening. Except for *Baryglossa*, these genera have a pilose or plumose, rather than bare, arista. *Ortalotrypeta* and *Cyaforma* differ from *Protortalotrypeta* in the shape of the head, facial carina, and wing, and in the location of the dorsocentral setae (see Tables 1-2).

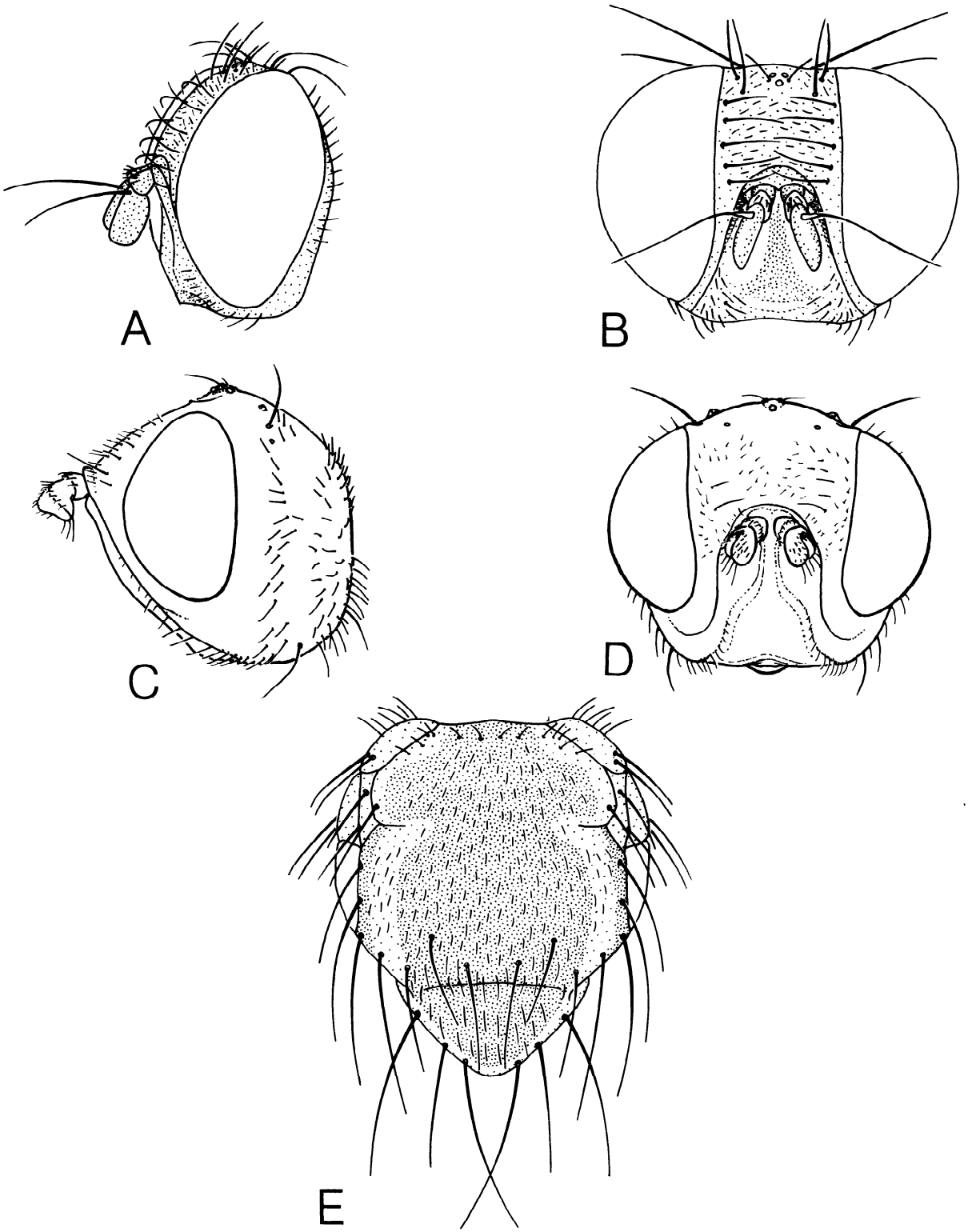

Figure 1. A,C, head, lateral view; B,D, head, anterior view; E, thorax, dorsal view; A-B,E, *P. grimaldii*, holotype; C-D, *N. bicolor*, holotype.

Description. *Head*: In lateral view (Fig. 1A), anterior margin of face and parafacial not strongly receded ventrally, postgena narrow, occiput slightly concave. Frons with 5 frontal setae and 2 orbital setae, latter nearly equal in size. Ocellar, postocellar, and paravertical setae smaller than posterior orbital seta. Postocular setae acuminate, well differentiated from postgenal setulae. Facial ridge with only small setulae. Antenna short. *Thorax*: Mesonotum (Fig. 1E) with following large setae: 2 postpronotal, 2 notopleural, 1 acrostichal, 1 dorsocentral aligned with postalar, 1 intra-alar, 1 intrapostalar, 1 presutural and 2 postsutural supra-alar, 1 postalar, and 3 scutellar. Small medial and lateral scapular setae present. Proepisternum without large setae. Anepisternum with 2 large posterior setae, without seta anterior to phragma. Katepisternal and anepimeral setae well developed. *Legs*: Mid tibia with anterodorsal seta on apical half, with row of posterodorsal setae, and with 2 large ventroapical spurlike setae. *Wing*: r-m at apical 1/3 of cell dm. Cell bcu with posteroapical lobe almost as long as broadest width of cell. Dorsally, vein R_1 completely setulose, vein R_{4+5} setulose to r-m, vein Cu_1 nonsetulose. *Female abdomen*: Syntergosternite 7 (Fig. 4A) very short, with large dorsoapical opening. Eversible membrane probably with large ventral area of dark scales.

Remarks. The dorsal view of syntergosternite 7 of the holotype of *P. grimaldii* is blurred and partially obscured by debris in the amber, but the margin of the apical opening can be seen. It extends deeply into the dorsal side, almost half way to the level of tergite 6. The eversible membrane is not everted, but a few ventral scales are protruding from the opening of syntergosternite 7, and a dark mass, probably comprising the type of dark ventral scales found in *Neortalotrypeta*, *Ortalotrypeta* and *Cyaforma*, is visible inside the apical part.

Protortalotrypeta grimaldii Norrbom new species
Figure 1A-B,E, 2A, 4A

Description. Body generally light brown, 3.70 mm long. Setae dark brown. Microtrichia absent or possibly difficult to observe. *Head* (Fig. 1A-B): Frons as broad as eye, with minute setulae medially. Ocellar seta slender and smaller than posterior orbital seta, but well differentiated from setulae. Postocellar seta half as long as posterior orbital seta. Paravertical seta about same size as ocellar seta. Face with antennal grooves and carina moderate sized. Antenna short, extended half way to ventral margin of face. Arista bare. Palpus not well exposed in holotype, but appears unconstricted basally. Proboscis obscured by air bubble. *Thorax*: Mesonotum (Fig. 1E) 1.66 mm long. Scutum mostly faint brown, with sides of presutural part and stripe from transverse suture to intra-alar seta yellowish. Apical scutellar setae crossed in apical third. Proepisternum with 2-3 setulae slightly larger than postocular setae. *Legs*: Mid tibia with anterodorsal seta at apical 3/5 (observed only on left leg); smaller ventroapical spurlike seta 2/3 as long as larger seta. *Wing*: Mostly moderate brown, with hyaline markings as shown in Fig. 2A (anal cell obscured by legs). *Female abdomen*: Terga entirely light brown, normal in width. Syntergosternite 7 (Fig. 4A) very short, 0.40 mm long, 0.24 times as long as mesonotum. Aculeus tip acute.

Etymology. This species is named for David A. Grimaldi, who recognized the holotype as a tephritid and made it available to me for study.

Holotype. Female (AMNH), DOMINICAN REPUBLIC: El Valle region, in 0.7 x 0.7 x 2.0 cm piece of amber, probably of early Miocene or late Oligocene age.

Neortalotrypeta Norrbom, new genus

Type species, *P. bicolor*, new species.

Diagnosis. *Neortalotrypeta* probably runs to *Pseudophorellia* Lima or *Oedicarena* Loew in the the most recent keys to Neotropical genera of Tephritidae (Foote 1980). Because some couplets are based on antennal characters and the antennae are missing in the holotype of *N. bicolor*, this cannot be stated with certainty. *Pseudophorellia* differs in lacking ocellar and acrostichal setae, in having the base of vein Cu setulose dorsally, and in having a large lateral seta on abdominal syntergite 1+2. *Oedicarena* differs in having 2 orbital setae and a mostly hyaline wing with narrow bands. The shape of syntergosternite 7 separates the female of *Neortalotrypeta* from that of all tephritid genera except *Protortalotrypeta*, *Ortalotrypeta* and *Cyaforma*. *Neortalotrypeta* differs from *Protortalotrypeta* in the shape of the head and facial carina, wing size and shape, and in having poorly differentiated postocular setae. It is easily

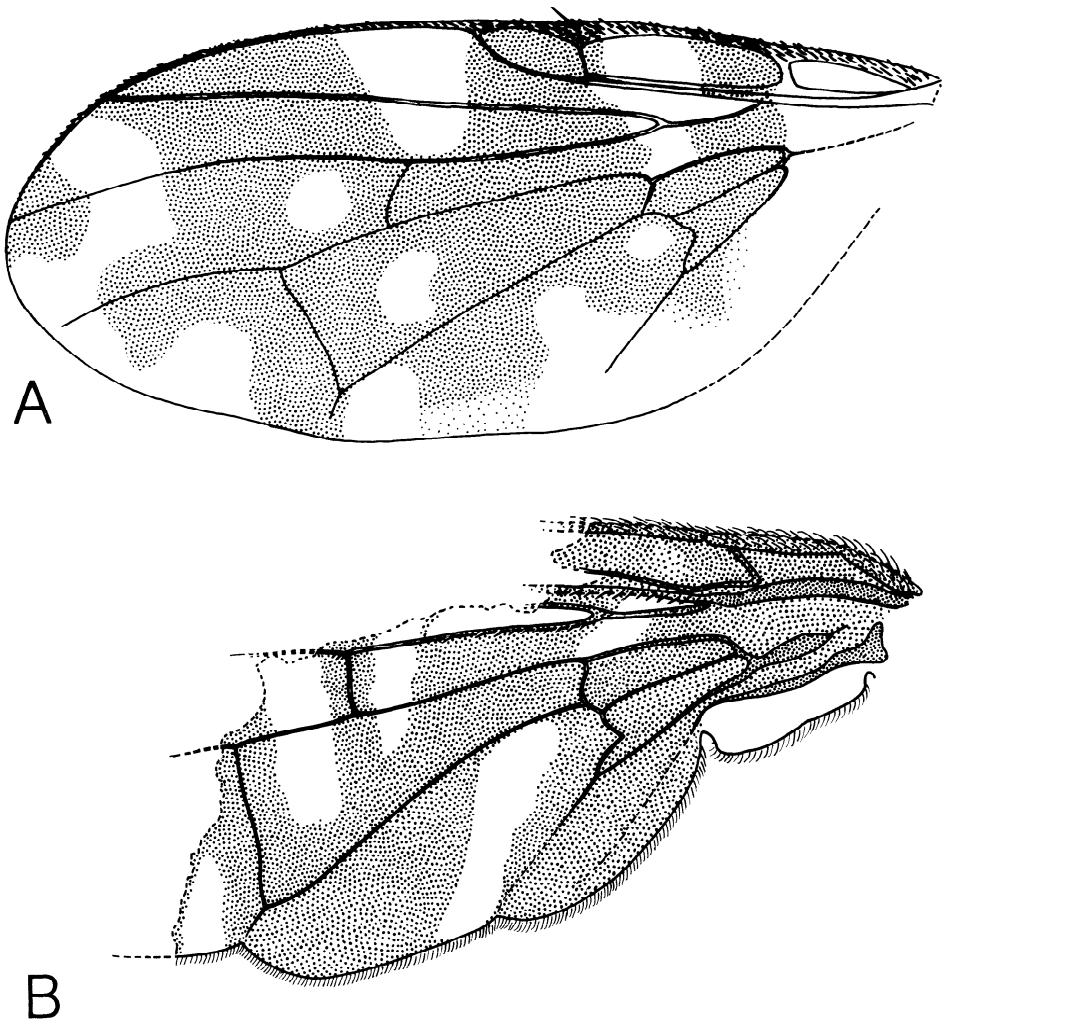

Figure 2. A, right wing, ventral view, *P. grimaldii*, holotype; B, remaining part of left wing, dorsal view, *N. bicolor*, holotype.

distinguished from all three genera by having only 1 orbital, 1 postpronotal, 1 postsutural supra-alar, 0 intrapostalar, and 2 scutellar setae, whereas *Protortalotrypeta*, *Ortalotrypeta* and *Cyaforma* have 2, 2-3 (rarely 1), 1-2, 0-1, and 3 of these setae, respectively. *Ortalotrypeta* and *Cyaforma* also have a large paravertical seta (minute in *N. bicolor*), several enlarged setae on the facial ridge, and a further anteriorly displaced dorsocentral seta.

Description. *Head*: In lateral view (Fig. 1C), anterior margin of face and parafacial strongly receded ventrally. Postgena, gena, and frons broad. Occiput slightly convex. Facial carina with ventral half broad, emarginate. Facial ridge with only small setulae. Frons twice as broad as eye, with minute setulae medially, 1 frontal seta, and 1 orbital seta. Ocellar seta present. Postocellar seta absent. Paravertical seta minute, no larger than postgenal setulae. Postocular setae weak, poorly differentiated from postgenal setulae. Palpus unconstricted basally. Labium small, not strongly convex. Labella without spinules or sclerotized ridges. *Thorax*: Mostly microtrichose. Mesonotum with following large setae: 1 postpronotal, 2 notopleural, 1 acrostichal, 1 dorsocentral aligned midway between supra-alar and postalar setae, 1

intra-alar, 0 intrapostalar, 1 presutural and 1 postsutural supra-alar, 1 postalar, and 2 scutellar. Scutellum very slightly convex, microtrichose and setulose dorsally, apical setae crossed. Medial and lateral scapular setae present. Proepisternum with numerous small subequal setulae. Anepisternum with 1 large posterior seta, without seta anterior to phragma. Katepisternal and anepimeral setae well developed. *Legs*: Mid tibia with anterodorsal seta on apical half, with row of posterodorsal setae, and with 2 large ventroapical spurlike setae. *Wing*: Elongate. r-m at apical 3/5 of cell dm. Cell bcu with posteroapical lobe almost as long as broadest width of cell. Dorsally, vein R_1 setulose (at least on basal half), vein R_{4+5} setulose at least to r-m, vein Cu_1 nonsetulose. *Female abdomen*: Terga normal in width. Syntergosternite 7 (Fig. 4B-C) short, with large dorsoapical opening. Eversible membrane (Fig. 4C) with large ventral area of dark scales. Aculeus (Fig. 4D) strongly dorsally curved; tip completely fused to main part of aculeus. 3 spermathecae (Fig. 4E) spherical or subspherical, with basal apodeme, and with elongate, slender base; surface with minute, acute projections.

Neortalotrypeta bicolor Norrbom new species
Figure 1C-D, 2B, 4B-E

Description. 8.25 mm long. Dark brown except for bright yellow head. Setae black. *Head* (Fig. 1C-D): Gena broad, height almost 2/5 long diameter of eye. Frons twice as broad as eye, with minute setulae medially, and with 1 weak frontal seta near anterior margin. 1 orbital seta (broken in holotype, but probably large). Ocellar seta slender and shorter than distance between ocelli and eye, but well differentiated from setulae. *Thorax*: Mostly microtrichose except postpronotal lobe, anterior 2/3 of anepisternum, and most of presutural and medial postsutural areas of scutum (perhaps rubbed off of scutum on holotype). Mesonotum 3.04 mm long. Apical scutellar setae crossed (at basal fifth in holotype). Small medial and 2 slightly larger lateral scapular setae present. *Wing* (Fig. 2B): Basal half mostly dark brown, including all of base except alula and hyaline spot across base of cell r_{2+3} and middle of cell br. Cell cu_1 brown except large subbasal hyaline band. Middle of wing with 2 hyaline bands, 1 across cell r_{2+3} and subapically across cell br, almost to middle of cell dm, the other across cell r_{4+5} subbasally, extended well into cell dm subapically.

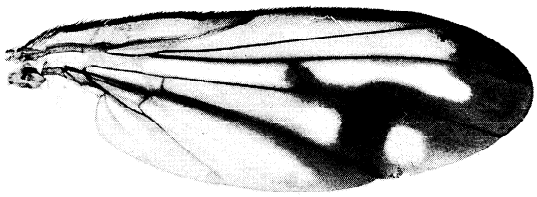

Figure 3. Left wing, *Ortalotrypeta ziae*, holotype.

Female abdomen: Terga entirely microtrichose. Syntergosternite 7 (Fig. 4B-C) 1.37 mm long, 0.45 times as long as mesonotum. Aculeus 0.71 mm long, strongly dorsally curved basal to tip; tip (Fig. 4D) elongate, slightly sagittate, very finely serrate.

Remarks. The holotype of *N. bicolor* is in poor condition, with the following parts missing: antennae, right hind leg, right wing, and anteroapical third of left wing. I am describing it only because of the significance of *Neortalotrypeta* to the analysis of relationships of the Ortalotrypetini. The labels of the holotype have only the following data: "Corumbá"; "April"; "S.W. Williston Collection". Papavero (1971:378-380) provides a summary of Smith's travels in southern Brazil and a short description of the type locality.

Etymology. The name of this species refers to the distinctly different color of the head versus the rest of the body.

Holotype. Female (AMNH), [BRAZIL: Mato Grosso do Sul:] Corumbá, April, [1882, H.H. Smith].

Genus *Ortalotrypeta* Hendel

Ortalotrypeta Hendel 1927:55 (Type species, *idana* Hendel, by original designation).

Description. *Head*: In lateral view similar to Fig. 1C (also see Hendel 1927:55, Fig. 16), anterior margin of face and parafacial strongly receded ventrally. Postgena broad. Occiput slightly convex. Genal height 1/3-1/2 long diameter of eye. Facial carina well developed, usually slightly emarginate, ventral 1/3-2/5 broad. Facial ridge with 1-3 vibrissalike setae in addition to smaller setulae. Frons 1.3 times as broad as eye, with minute setulae medially, 2-4 frontal setae, and 2 large

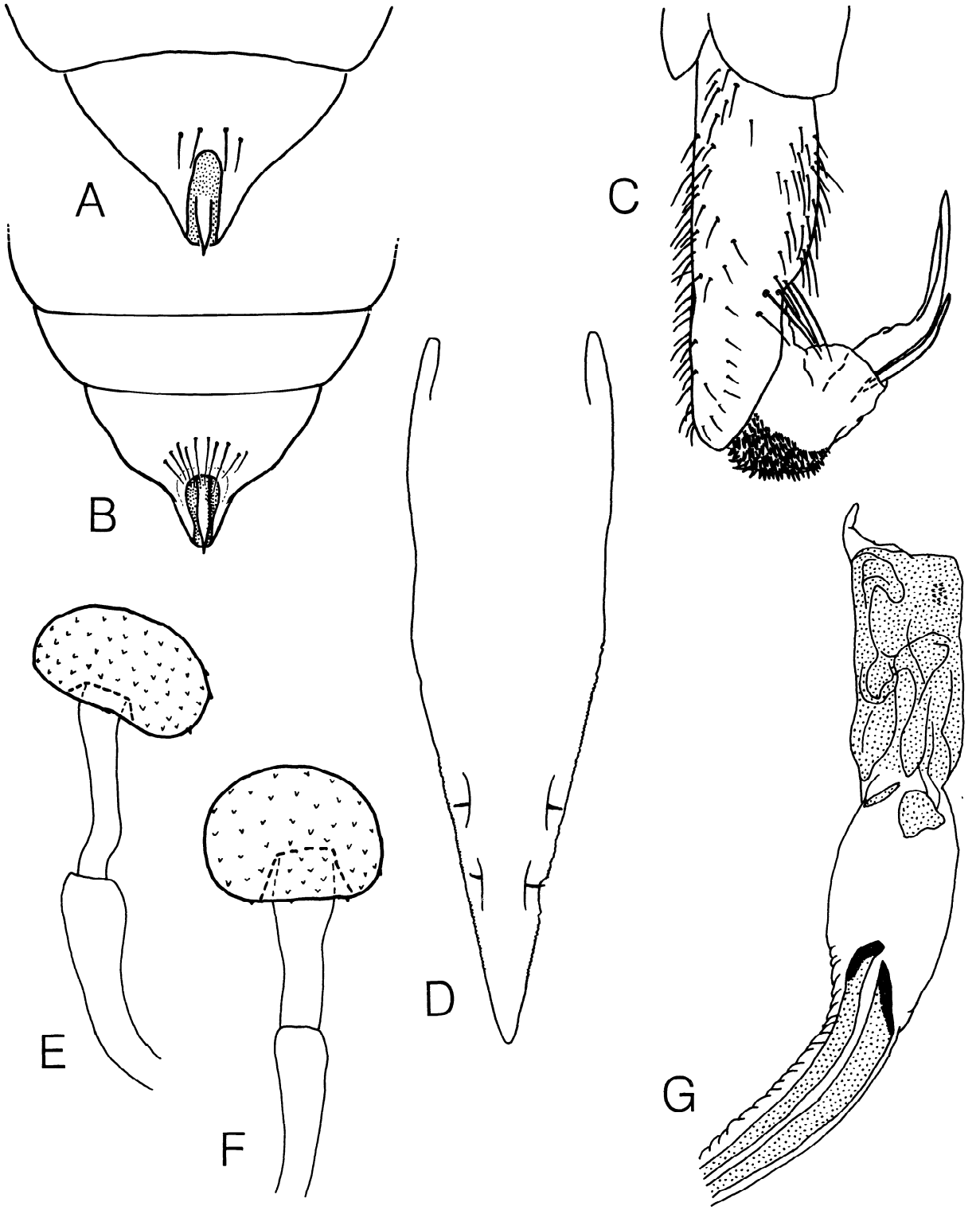

Figure 4. Terminalia: A-B, apex of female abdomen, dorsal view (most setae not shown); C, same, with aculeus and eversible membrane everted from syntergosternite 7, lateral view; D, aculeus, ventral view (internal channels not shown); E-F, spermathecae (1 of 3); G, distiphallus; A, *P. grimaldii*, holotype; B-E, *N. bicolor*, holotype; F, *Cyaforma shenonica*, paratype; G, *Ortalotrypeta idanina*, paratype.

orbital setae. Ocellar and paravertical setae 3/4 as large to subequal to outer vertical seta. Postocellar seta small, as large as postocular setae. Postocular setae weak, poorly differentiated from postgenal setulae. Antenna short. Arista pubescent. Palpus unconstricted basally. Labium small, not strongly convex. Labella without spinules or sclerotized ridges. *Thorax*: Mesonotum with following large setae: 2-3 postpronotal (except 1 in *singula*), 2 notopleural, 1 acrostichal, 1 dorsocentral (more or less aligned with anterior postsutural supra-alar), 1 intra-alar, 0-1 intrapostalar, 1 presutural and 2 postsutural supra-alar, 1 postalar, and 3 scutellar. Apical scutellar setae usually crossed. Small medial and larger lateral scapular setae present. Scutellum very slightly convex, setulose dorsally. Proepisternum usually with 1 to several setae and numerous setulae. Anepisternum with 2-3 large posterior setae, without seta anterior to phragma. Katepisternal and anepimeral setae well developed. *Legs*: Mid tibia with 1-4 anterodorsal setae on apical 3/5, with row of posterodorsal setae, and with 2 large ventroapical spurlike setae. *Wing*: Elongate. r-m at apical 3/5-2/3 of cell dm. Cell bcu with posteroapical lobe 1/3-1/2 as long as broadest width of cell. Dorsally, vein R_1 setulose, vein R_{4+5} densely setulose to beyond level of dm-cu, vein Cu_1 nonsetulose. *Male abdomen*: Lateral sclerites long, fused to hypandrium at base only. Surstyli slightly elongated. Interparameral sclerite with only 1 bridge. Aedeagal apodeme with arms unfused basally. Basiphallus with minute microtrichia ventrally, apically with 2 strong, narrow sclerites (Fig. 4G). Distiphallus (Fig. 4G) membranous basally, well sclerotized apically. *Female abdomen*: Syntergosternite 7 short, with large dorsoapical opening. Eversible membrane with large ventral area of dark scales. Aculeus strongly dorsally curved; tip completely fused to main part of aculeus. 3 spermathecae similar to Fig. 4E-F, spherical or subspherical, with basal apodeme, and with elongate, slender base; surface with minute, acute projections.

Remarks. Ten species have been described in *Ortalotrypeta*, two of which, *macula* Wang (1988) and *tonkinensis* Zia (1955), are transfered here to *Cyaforma*. With the addition of *ziae*, n. sp., described below, there are now nine included species in *Ortalotrypeta*. I have not examined specimens of *tibeta* Wang, *gansuica* Zia, nor *singula* Wang, and have seen limited material of the other species, but the following key is presented in an attempt to update that of Zia (1963).

Key to the species of *Ortalotrypeta*

1. Thorax with 1 postpronotal seta. Cell r_1 entirely dark brown apical to stigma ..... *singula* Wang
- Thorax with 2-3 postpronotal setae. Cell r_1 with yellow or hyaline areas apical to stigma 2

2. Thorax with 2 postpronotal setae 3
- Thorax with 3 postpronotal setae 5

3. Dark brown areas at wing apex and bordering crossvein dm-cu not connected along vein M. Vein Cu_1 without dark brown border. Cells r_1 and r_{2+3} without hyaline spots ..... *trypetoides* Chen
- Dark brown areas at wing apex and bordering crossvein dm-cu connected along vein M. Vein Cu_1 with dark brown border. At least cell r_1 with hyaline spot 4

4. Wing with dark brown band bordering crossvein r-m and extended across cell dm to brown border along vein Cu_1. Cell r_1 with large hyaline spot ..... *idana* Hendel
- Area bordering crossvein r-m yellow. Cell dm yellow except brown bands bordering vein Cu_1 and crossvein dm-cu. Cell r_1 with small hyaline spot or without hyaline spot ..... *idanina* Zia

5. Cell dm crossed by dark brown subapical band extended from crossband r-m. Subbasal hyaline spot in cell r_{4+5} and subapical hyaline spot in cell dm connected across vein M. Cell r_1 with marginal hyaline spot 6
- Cell dm without dark brown band extended from crossvein r-m. Subbasal hyaline spot in cell r_{4+5} and subapical hyaline spot in cell dm separated by yellow or brown border along vein M. Cell r_1 without hyaline spot 8

6. Apical half of cell r_{4+5} with medial hyaline spot or yellow area. Stigma brown 7
- Apical half of cell r_{4+5} entirely dark brown, without medial hyaline spot or yellow area. Stigma yellow ..... *gigas* Hendel

7. Dark brown apical areas along veins R_{4+5} and M connected basally as well as apically to surround subapical hyaline spot in cell r_{4+5}. Only apical half of vein Cu_1 bordered by dark brown ..... *tibeta* Wang
- Dark brown apical areas along veins R_{4+5} and M connected only apically, separated basally by yellow area in cell r_{4+5}. All of vein Cu_1 narrowly bordered by brown ..... *gansuica* Zia

8. Brown marks along crossveins r-m and dm-cu not connected by brown along vein M. Only apices of veins R_{4+5} and Cu_1 bordered by brown. Cell r_1 entirely yellow or with brown areas restricted to extreme apex or area bordering stigma .... *isshikii* (Matsumura)

- Brown marks along crossveins r-m and dm-cu connected by brown along vein M (Fig. 3). Most of vein R_{4+5} with narrow brown border (extended basally well beyond crossvein r-m). All of vein Cu_1 with broad brown border. Cell r_1 with narrow brown margin along costa..... ..... *ziae* Norrbom, n. sp.

Ortalotrypeta gigas Hendel

Ortalotrypeta gigas Hendel 1927:55.

Remarks. Hendel described this species from an unstated number of males from Mt. Omei. The only specimen of ***gigas*** now in the USNM from this locality is designated lectotype. Its left wing, presumably that photographed by Hendel (Taf. II, Fig. 7), is lacking.

Specimens examined. Lectotype male [here designated] (USNM), CHINA: Szechuan: Mt. Omei, D.C. Graham; also with red label with "Type No. 41875 U.S.N.M." [added at USNM] and white label with "Ortalotrypeta gigas Hend." [hand written by Aldrich]).

Ortalotrypeta idana Hendel

Ortalotrypeta idana Hendel 1927:56.

Remarks. This species was described from an unstated number of specimens of both sexes from "Tatsiculu [sic], 8500-13000 Fuss". Two males in the USNM are apparently syntypes. That designated lectotype is without its left wing, which presumably was that photographed by Hendel (Taf. II, Fig. 6). I found no female syntypes in the USNM nor in the exotic collection of the Naturhistorisches Museum Wien during a visit there.

Specimens examined. Lectotype male [here designated] (USNM), CHINA: Szechuan: 9 mi. SW of Tatsienlu, 8500-13000 ft., 25-27.VI.1923, D.C. Graham; also with red label with "Type No. 41876 U.S.N.M." [added at USNM] and white label with "Ortalotrypeta idana Hend." [hand written by Aldrich]. 1 paralectotype (USNM) with same data as lectotype, except without hand written label, and red label with "Paratype" instead of "Type".

Ortalotrypeta sp., possibly *ishikii* (Matsumura)

Remarks. Because of the great difference in range, I have doubts that the five specimens I examined from Nepal are conspecific with *ishikii*, which is otherwise known only from Japan. But they are remarkably similar to the single specimen from Japan I examined. The only differences I observed are that the Nepalese specimens have a more distinct pterostigmal dark spot that extends into cell r_1, and there is a broader and more distinct gray border between the hyaline spot and the posterior margin of cell m, but these characters may vary in *ishikii*. Without a better understanding of the variation in the latter species, the status of the Nepalese specimens is difficult to determine. They are the first specimens of *Ortalotrypeta* reported from Nepal.

Specimens examined. NEPAL: Ktmd. Pulchauki, 8000 ft., 27.VII or 6, 7, or 17.VIII.1967, Can. Nepal Exped., 2 males 3 females (CNC, USNM).

Ortalotrypeta ziae Norrbom, n. sp. Figure 3

Diagnosis. *O. ziae* differs from all other species of *Ortalotrypeta* as follows: the brown markings on r-m and dm-cu are connected by a brown border along vein M; cell r_1 is narrowly brown along the costa (other species have basal and/or apical brown areas or are entirely brown or yellow); and vein R_{4+5} has a narrow brown border. The other species, except *O. gigas* Hendel, also have the stigma mostly dark brown.

Description. 8.07-8.81 mm long. Generally light orangebrown. Setae black. *Thorax*: Entirely light orangebrown. Lightly microtrichose except anterior half of anepisternum. Mesonotum 3.41-3.62 mm long, with 3 (1 anterior, 2 posterior) postpronotal setae. Intrapostalar seta strong. Proepisternum with 2-3 large setae in addition to setulae. *Legs*: Mid tibia with 2-4 anterodorsal setae on apical 3/5. *Wing* (Fig. 3): Cells bc, c, stigma, br, r_1 and r_{2+3} mostly yellowish, without hyaline spots. Stigma with only apex dark brown. Cell r_1 with narrow dark brown border along costa, gradually narrowed

basally. Vein R_{4+5} narrowly, and veins r-m, M beyond r-m, Cu_1 and dm-cu, and apices of cells r_{2+3}, r_{4+5} and m broadly bordered by dark brown, all of which is connected. Cell r_{4+5} with elongate hyaline mark extended 7/10 length of cell. Cell dm mostly yellowish except dark brown areas and subapical hyaline spot. Cell m with large hyaline spot. Cubital and anal cells mostly faint yellowish. *Male abdomen*: Tergites entirely orangebrown. Genitalia not dissected.

Remarks. This is the first species of *Ortalotrypeta* reported from Taiwan.

Etymology. This species is named for Y. Zia, whose numerous descriptions of Tephritidae included several species of *Ortalotrypeta*.

Holotype. Male (USNM), [TAIWAN] (Formosa): Musha, 21.V.1932; Melander Collection. **Paratype.** male 1 (USNM), [TAIWAN]: Arisan, 6.VI.1932; Melander Collection.

Genus *Cyaforma* Wang

Cyaforma Wang 1989:358 (Type species, *shenonica* Wang, by original designation).

Description. Similar to *Ortalotrypeta*. Differing as follows: *Thorax*: Mesonotum dark brown, with medial yellow stripe or pair of stripes. Scutellum sometimes entirely brown. 1-2 postsutural supra-alar setae. *Wing*: Cell bcu sometimes with posteroapical lobe very small and poorly differentiated. Wing pattern mostly dark brown, without yellow areas, at most with following hyaline areas: marginal spot in cell r_1; subapical spot in cell r_{2+3}; subapical spot in cell dm; large triangular posterior area in cell m; and large posterior areas in alula, anal cells and cell cu_1.

Remarks. Wang (1989) proposed *Cyaforma* as a monotypic genus. I am transferring two additional species from *Ortalotrypeta*, *C. macula* (Wang), n. comb., and *C. tonkinensis* (Zia), n. comb.

Key to the species of *Cyaforma*

1. Wing with basal marginal hyaline spot in cell r_1 and subapical hyaline spot in cell dm. Scutum with single broad medial yellow stripe, extended to posterior margin. Scutum with 2 postsutural supra-alar setae 2
- Wing with cells r_1 and dm entirely brown, without hyaline spots. Scutum with pair of submedial yellow stripes, sometimes connected anteriorly, not extended to posterior margin. Scutum with only one postsutural supra-alar seta ..... *shenonica* Wang

2. Wing with subapical hyaline spot in cell r_{2+3}. Thorax with 3 postpronotal .. setae. Scutellum brown ..... *macula* (Wang)
- Wing without subapical hyaline spot in cell r_{2+3}. Thorax with 2 postpronotal setae. Scutellum yellow ..... *tonkinensis* (Zia)

Phylogenetic Relationships

The cladistic relationships of the species of Ortalotrypetini were analyzed using Hennig86 (Farris 1988; Fitzhugh 1989). The implicit enumeration option (ie*) was used in all analyses. The characters analyzed are listed in Table 1, and the distributions of their states are shown in Table 2. Fig. 5 shows the possible relationships within the group.

The outgroup taxa (the top three taxa in Table 2) were assigned unknown character states (?) for characters 16-26 involving wing pattern, because their wing patterns are very different from those in the Ortalotrypetini, and homologies could not be established. Character states shown in bold in Table 2 are uncertain. They were coded based on assumptions (e.g., that *N. bicolor* does not have yellow areas on the parts of the wing missing in the holotype, because there are none on the part that is present), on the basis of statements in the literature that a particular species is generally like another species, or on comparative statements in descriptions of other species. For example, Wang (1989) stated that *Cyaforma shenonica* differs from the species of *Ortalotrypeta* (including the two that are here transferred to *Cyaforma*) in having 1 postsutural supra-alar seta, so the species that were not examined and for which this character was not explicitly described are coded state 1 (2 setae present) for character 9.

The sister group of the Ortalotrypetini is unknown. *Ortalotrypeta* was traditionally included in the Acanthonevrini, which previously comprised all genera with three scutellar setae (e.g., see Hardy 1986). Hancock (1986) redefined the Acanthonevrini to include only those genera (some with only two scutellar setae) that have a reduced ocellar seta (presumably an apomorphic state),

Table 1. Characters and states used in phylogenetic analysis of Ortalotrypetini.

1. Head shape, lateral view - 0) anterior margin not strongly receded, postgena narrow; 1) anterior margin strongly receded, postgena broad.
2. Facial carina - 0) ventral half not strongly expanded ventrally; 1) ventral half strongly expanded.
3. Facial ridge - 0) with only small setulae; 1) with one to several larger setae.
4. Paravertical seta - 0) smaller than or approximately as large as postocellar seta; 1) much larger than postocellar seta.
5. Postocular setae - 0) well differentiated from postgenal setulae; 1) poorly differentiated from postgenal setulae.
6. Thorax and abdomen color - 0) entirely yellow, orange or pale brown; 1) mostly dark brown.
7. Scutum color - 0) unicolorous; 1) brown, with medial yellow stripe or stripes.
8. Number of postpronotal setae - 0) 1; 1) 2; 2) 3.
9. Number of postsutural supra-alar setae - 0) 1; 1) 2.
10. Intrapostalar seta - 0) absent; 1) present.
11. Dorsocentral seta - 0) aligned with postalar seta; 1) approximately midway between postalar seta and postsutural supra-alar seta; 2) aligned close to postsutural supra-alar seta (if 2 postsutural supra-alars, the more posterior one).
12. Number of marginal scutellar setae - 0) 2; 1) 3; 2) 4-5.
13. Apical scutellar setae - 0) usually not crossed; 1) usually crossed.
14. Mid tibia - 0) without anterodorsal seta on apical half; 1) with anterodorsal seta(e) on apical half.
15. Wing shape - 0) short, moderately broad; 1) elongate, relatively slender.
16. Wing color - 0) hyaline and dark brown only; 1) at least anterobasal part mostly yellow.
17. Stigma color - 0) mostly brown; 1) entirely or mostly yellow.
18. Cell r_1 color - 0) entirely brown or hyaline; 1) partly or entirely yellow.
19. r-m with dark brown border - 0) yes; 1) no.
20. r-m dark brown border connected to border on Cu1 across cell dm - 0) yes; 1) no.
21. Brown area along apex of vein R_{4+5} - 0) connected to brown area along vein M near level of dm-cu; 1) not connected near level of dm-cu (but may be connected apically).
22. Vein Cu1 - 0) entirely bordered by dark brown; 1) not bordered or only apical part bordered by dark brown.
23. Cell r1 - 0) with large marginal hyaline spot; 1) without hyaline spot. 24. Cell r2+3 with subapical or apical hyaline spot - 0) yes; 1) no.
25. Cell R_{4+5} - 0) with subapical and usually subbasal hyaline spots (sometimes fused); 1) with only basal hyaline spot; 2) without hyaline spots.
26. Hyaline spot spot in cell dm - 0) not connected to basal spot in cell r_{4+5}; 1) connected to basal spot in cell r_{4+5}.
27. Distiphallus - 0) with membranous basal lateral lobe; 1) without membranous basal lateral lobe.
28. Syntergosternite 7 opening - 0) apical; 1) dorsoapical.
29. Eversible membrane scales - 0) similar dorsally and ventrally; 1) with large ventral area of small dark scales. *Protortalotrypeta* appears to have state 1, but this character is not clearly visible in the single known specimen.
30. Eversible membrane - 0) basal taenia present; 1) basal taenia absent.

three spermathecae (plesiomorphic), and an incompletely fused aculeus, with the tip free or delimited from tergite 8 by a suture (plesiomorphic). The Ortalotrypetini have a completely fused aculeus and therefore do not belong in the Acanthonevrini. A spermathecal character also indicates that these two tribes are not closely related (V.A. Korneyev, pers. comm.). Among other Tephritidae, the *Blepharoneura* group (*Blepharoneura* Loew, *Ceratodacus* Hendel, *Baryglossa* Bezzi, and *Hexaptilona* Hering) might be the sister group of the Ortalotrypetini. They are the only other tephritid genera with two postpronotal setae (apomorphic), and are among the few taxa outside of the Acanthonevrini that have three scutellar setae, although the latter may be plesiomorphic for the family (see below). A spermathecal character discovered by Korneyev (pers. comm.) suggests that the *Blepharoneura* group and the Ortalotrypetini are not closely related, however.

Because the sister group of the Ortalotrypetini is uncertain, I ran several separate analyses using *Paraterellia* Foote, *Blepharoneura*, or *Xarnuta* Walker as the outgroup. The latter two taxa share some characters with the Ortalotrypetini and might be fairly closely related, whereas *Paraterellia* was selected as a typical genus of Trypetinae. The results probably would be similar with any other taxon of Tephritidae substituted as outgroup, althought the polarity of some characters and their distribution on the trees might vary, as they do depending upon which of the three above taxa is used.

In all three analyses, two trees with the same topology result. They differ from the Nelson consensus tree (Fig. 5) only in that the trichotomy within *Ortalotrypeta* is resolved; in one, *O. ziae* and *O. ishikii* are sister taxa with character 8 state 2 a synapomorphy, whereas in the other, *O. ishikii* and *O. trypetoides* are sister taxa, with character 22 as a synapomorphy. With *Paraterellia* as outgroup, the trees were 55 steps long (consistency index = 60, retention index = 69). The Nelson tree in Fig. 5 based on this analysis is one step longer. Alternate

distributions other than those shown are equally likely for some character states (e.g., character 3 could be an independent apomorphy for *Ortalotrypeta* and for *C. shenonica* + *C. tonkinensis*; character 6 could be a synapomorphy for *Neortalotrypeta* + *Cyaforma* + *Ortalotrypeta*, with reversal to state 0 in *Ortalotrypeta*; and characters 8 (state 1), 9, 10 and 12 each could be independent apomorphies in *Protortalotrypeta* and in *Cyaforma* + *Ortalotrypeta*). With *Xarnuta* as outgroup the resulting trees were 54 steps long (ci = 62, ri = 71), and with *Blepharoneura* they were 52 steps (ci = 63, ri = 72). If *Xarnuta* is the outgroup, character 10 is not a synapomorphy for the Ortalotrypetini, and if *Blepharoneura* is the outgroup, characters 8 (state 1), 10, and 12 are not synapomorphies for the group because the polarity of these characters is reversed.

The monophyly of the Ortalotrypetini is indicated by several synapomorphies. The shape of syntergosternite 7, which has a dorsoapical, rather than apical, opening (Fig. 4A-C) (character 28) and the large ventral area of dark scales on the eversible membrane (Fig. 4C) (character 29) are complex characters apparently unique to these four genera within the Tephritidae. The presence of the ventral area of scales is not confirmed with certainty in *Protortalotrypeta*, but it is a synapomorphy at least for *Neortalotrypeta*, *Ortalotrypeta*, and *Cyaforma*. The absence of taenia on the eversible membrane (character 30) probably also is a synapomorphy for all four genera, but its condition in *Protortalotrypeta* is unknown. The shapes of the aculeus and its tip also appear to be similar in these four taxa, although this is also difficult to see in the single specimen of *Protortalotrypeta*. The presence of an outstanding anterodorsal seta or setae on the mid tibia (character 14) and the orientation of the apical scutellar setae (character 13), which usually are crossed rather than parallel or diverging, are other autapomorphies of the Ortalotrypetini.

Characters 8 (state 1), 9, 10, and 12 also might be autapomorphies for the Ortalotrypetini depending upon which taxon is its sister group and whether or not the plesiomorphic states present in *Neortalotrypeta* are due to reversal, as is shown in Fig. 5, or the apomorphic states arose independently in *Protortalotrypeta* and *Cyaforma* + *Ortalotrypeta*. State 1 of characters 10 and 12 might be plesiomorphic for the Tephritidae because the *Blepharoneura* group and many genera of Acanthonevrini, as well as the Tachinsicidae and some Platystomatidae and Pyrgotidae also have three or more scutellar setae (D.A. Hancock, pers. comm.), and many of them have an intrapostalar seta. The polarity of these characters and their significance for the Ortalotrypetini cannot be determined until the sister taxon of the group is identified.

Table 2. Character state distributions in species of Ortalotrypetini and taxa used as outgroups. Character states in bold are uncertain (see text for explanation).

	Characters 1111111111222222222223
Taxa	12345678901234567890123456789O
Blepharoneura	000000010101000????????????0000
Parateretlia	000000000000000????????????0000
Xarnuta	000000000102000????????????0000
P. grimaldii	00000001110111000000000000?11?
N. bicolor	11001100001011100**0**00?**0**0??1?111
O. gansuica	1111**1**0021?211111010010011**1**????
O. gigas	11111002112111111100000111111
O. tibeta	**1111**10021?**2111**1010001000 1????
O. idana	11111001112111110100100000 1???
O. singula	**1111**10001?**2111**1100111010000????
O. idanina	11111001112111110111010001111
O. isshikii	11111002112111110101111100 1???
O. trypetoides	11111001102111110101111100 1111
O. ziae	11111002112111111101101100 1???
C. macula	**1**101111211211**1**10000000020????
C. shenonica	11111111002111100000001120 1111
C. tonkinensis	1111111**1**1211110000000120?1??

Neortalotrypeta shares a number of apomorphic character states with *Ortalotrypeta* and *Cyaforma*, including: the shape of the head (character 1); the shape of the facial carina (character 2); the poor differentiation of the postocular setae (character 5); the anterior displacement of the dorsocentral seta (character 11), which occurs convergently in many other tephritid genera; and the elongate shape of the wing (character 15). The bare arista is an autapomorphy of *P. grimaldii*.

Ortalotrypeta and *Cyaforma* share at least two apomorphies: the extremely large paravertical seta (character 4); and a further anteriorly displaced dorsocentral seta (character 11, state 2). The presence of one to several large setae on the facial ridge (character 3) may be an additional synapomorphy, but it also could be an independent apomorphy for *Ortalotrypeta* and for *C. shenonica* + *C. tonkinensis*. I am unsure of the state of this character in some species; no outstanding setae are present on the facial ridge in Wang's figure of the head of *C. macula*. The absence of a basal membranous lobe on the distiphallus (character 27) is another apomorphy shared by *Cyaforma* and *Ortalotrypeta*, but this character is unknown for *Protortalotrypeta* and *Neortalotrypeta*, so it may be a synapomorphy lower on the tree than is shown in Fig. 5. The

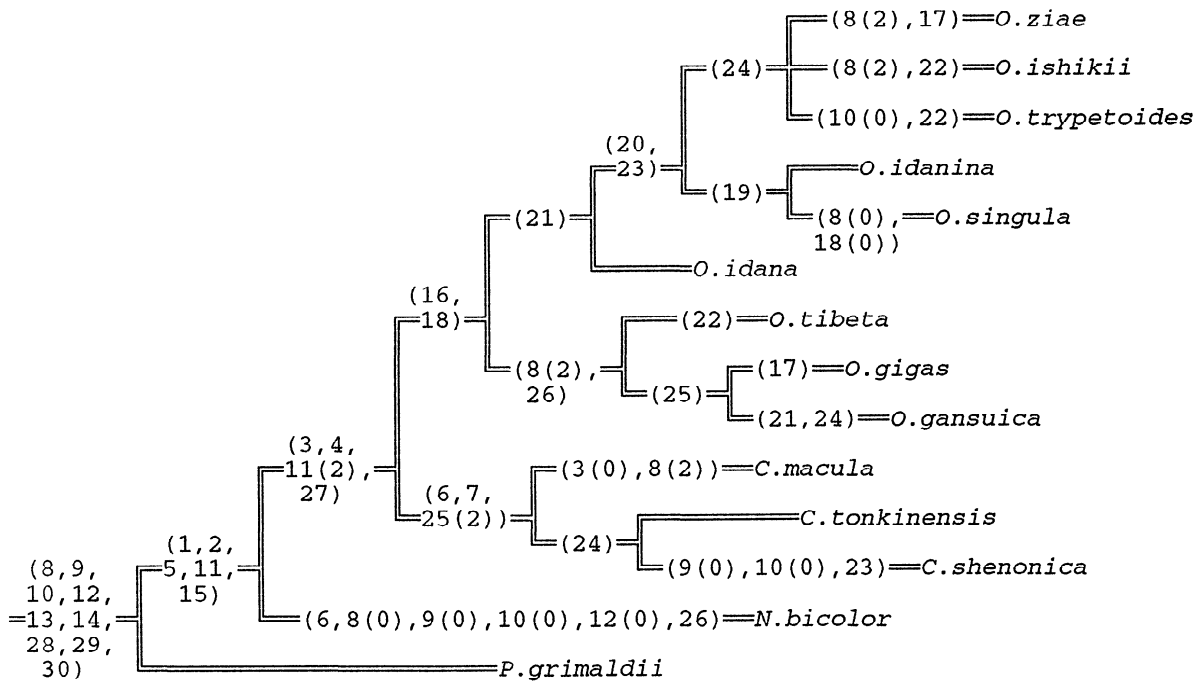

Figure 5. Cladistic relationships among species of Ortalotrypetini (Nelson consensus tree, with *Paraterellia* as outgroup). Numbers separated by commas refer to characters listed in Table 1. State 1 is assumed unless character number is followed by an alternative state in parentheses.

presence of only one frontal seta and one orbital seta in *N. bicolor* are autapomorphies.

Wang (1989) proposed *Cyaforma* as a monotypic genus for *C. shenonica*, in part based on the presence of a second postsutural supra-alar seta (character 9) in *Ortalotrypeta* and the other species here placed in *Cyaforma*. Other characters, such as thorax color (character 6), scutal color pattern (character 7), and absence of the subapical hyaline spot in cell r_{4+5} (character 25 state 2) suggest that *C. shenonica* is closely related to *C. macula* and *C. tonkinensis*, and that the absence of the second postsutural supra-alar seta in *C. shenonica* is because of reversal. The other characters used by Wang to diagnose *Cyaforma* from *Ortalotrypeta* (wing especially elongate, lobe on cell bcu short) are autapomorphies of *C. shenonica*, as is the absence of the hyaline spot in cell dm.

The hypothesis that *Ortalotrypeta* (not including *macula* and *tonkinensis*) is monophyletic is supported by its partially yellow wing pattern (character 16). Detailed analysis of the relationships among the species of the genus was not the intent of this study, as some species were not examined. Most of the characters that appear useful to resolve their relationships involve wing pattern, which was difficult to divide into characters and states. The brown border on vein R_{4+5} and that on vein M between r-m and dm-cu are regarded as autapomorphies of *O. ziae* and are not included in the matrix of Table 2.

Zoogeography

Considering its distribution and relationships to other families, the Tephritidae probably is post-Gondwanan. The family presumably originated in the Paleotropics because of the greater diversity of its higher taxa now found there. The Ortalotrypetini, however, appear to have originated in the New World, because *Protortalotrypeta* and *Neortalotrypeta*, the two basalmost taxa, are from the Neotropical Region. Under this hypothesis, the *Cyaforma* + *Ortalotrypeta* lineage was a secondary introduction to Asia, and extinction of the group in North America is assumed (the latter is likely whatever origin of the group is hypoth-

esized). The only other taxon of Tephritidae known to have similar zoogeographic and cladistic relationships is the *Blepharoneura* group (Norrbom and Condon, in prep.), although other taxa such as the subtribe Carpomyina may have originated and diversified in the New World, with subsequent reinvasion of the Palearctic Region. Bush (1966) suggested a late Oligocene or early Miocene date for the introduction to North America of the carpomyine genus *Rhagoletis* Loew. The age of the holotype of *Protortalotrypeta grimaldii* indicates that the Ortalotrypetini had already spread to the Neotropics by the early Miocene, and would seem to support Bush's hypothesis. Ancestors of other taxa, such as the *Blepharoneura* group, the tribe Toxotrypanini, and perhaps some groups within the Tephritinae may also have been introduced to the New World at this time.

Acknowledgments

The holotype of *P. grimaldii* was identified as a tephritid by D.A. Grimaldi, who kindly allowed me to study it. I also am grateful to him for the loan of the holotype of *N. bicolor*, and to X.-J. Wang for the loan of paratypes of *Cyaforma shenonica*. C.C. Labandeira kindly provided information from the paleontological literature and he and H.-Y. Han, D.L. Hancock, A. Freidberg, M.A. Condon, R.W. Poole and N.E. Woodley reviewed the manuscript. L. Lawrence and T.B. Griswold drew or photographed Fig. 1-3, and L. Roberts drew Fig. 4C.

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