Phylogeny of the Genus Paramyiolia Shiraki (Diptera: Tephritidae: Trypetini) with Descriptions of Five Chinese Species

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Phylogeny of the genus *Paramyiolia* Shiraki (Diptera: Tephritidae: Trypetini) with descriptions of five Chinese species

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**Abstract**

We recognize the following 5 species of *Paramyiolia* Shiraki (Diptera: Tephritidae: Trypetini) in China: *P. atrat*, *sp. nov.*, *P. atrifasciata*, *sp. nov.*, *P. melanogaster*, *sp. nov.*, *P. nigrihumera*, *sp. nov.*, and *P. yunnana* (Wang), *comb. nov.* These species have almost identical wing patterns as Japanese *P. cornuta* (Ito), and, thus, here we refer to them jointly as the *P. cornuta* species group. Monophyly of this species group is supported by a cladistic analysis using morphological characters of all the 9 *Paramyiolia* species known in the world. Our earlier assumption about the disjunct occurrence of East Asian and North American *Paramyiolia* as a typical Arcto-Tertiary relict distribution is also strengthened by the discovery of the 5 Chinese species. In addition, we provide a revised key to the world *Paramyiolia* species and descriptions of all 5 Chinese species supplemented by their photographs including genitalic structures. We also made DNA barcoding analyses using 13 specimens representing 4 outgroup and 3 *Paramyiolia* species (*P. atra*, *P. nigricornis* (Doane), and *P. rhino* (Steyskal)). The DNA barcoding result only topologically supports the monophyly of Old and New World *Paramyiolia* together, but statistically supports the monophyly of the New World *Paramyiolia*. Interestingly, it rather clearly suggests possible existence of 2 cryptic species from the samples we identified as *P. rhino* based on the current taxonomic concept of this nominal species. Furthermore, one of these cryptic species appears to be more closely related genetically to the morphologically distinct *P. nigricornis* than to the other cryptic species.

Key Words: Chetostomatina, taxonomy, DNA barcode, cladistics

**Resumen**

Reconocemos los siguientes cinco especies de *Paramyiolia* (Diptera: Tephritidae: Trypetini) por primera vez en China: *P. atrat*, *sp. nov.*, *P. atrifasciata*, *sp. nov.*, *P. melanogaster*, *sp. nov.*, *P. nigrihumera*, *sp. nov.* y *P. yunnana* (Wang), *comb. nov.* Estas especies tienen un patrón de ala casi idéntico a la especie japonesa, *P. cornuta* (Ito), y por lo tanto, aquí nos referimos a ellos de forma conjunta como el grupo de especies *P. cornuta*. La monofilia de este grupo de especies se apoya en un análisis cladístico usando caracteres morfológicos de las 9 especies de *Paramyiolia* conocidos en el mundo. Nuestra suposición anterior sobre la ocurrencia disjunta de *Paramyiolia* en Asia del Este y América del Norte como una distribución típica antigua Arcto-Terciario también se ve reforzada por el descubrimiento de las cinco especies de China. Además, ofrecemos una clave revisada de las especies *Paramyiolia* del mundo y descripciones de los 5 especies de China complementadas por fotografías incluyendo estructuras de la genitalia. También hicimos un análisis de los códigos de barras de ADN utilizando 13 muestras que representan 4 grupos exteriores y 3 especies *Paramyiolia* (*P. atra*, *P. nigricornis* (Doane), y *P. rinoceronte* (Steyskal)). El resultado de los códigos de barras de ADN sólo topológicamente apoya la monofilia del *Paramyiolia* del Viejo y Nuevo Mundo, pero estadísticamente apoya la monofilia del *Paramyiolia* en el Nuevo Mundo. Curiosamente, se sugiere claramente la posible existencia de 2 especies crípticas en las muestras que hemos identificado como *P. rinoceronte* basado en el concepto taxonómico actual de esta especie nominal. Además, una de estas especies crípticas parece estar más estrechamente relacionada genéticamente a la morfológicamente distinta *P. nigricornis* que a las otras especies crípticas.

Palabras Clave: Chetostomatina, taxonomía, código de barras de ADN, la cladística

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*Paramyiolia* Shiraki had been a monotypic genus including a single species, *P. takeuchii* Shiraki from Japan, until Han (1992, 1996) expanded the generic limit to 3 more species from Japan and North America on the grounds that they together form a monophyletic group. Han (1996) also provided a cladogram of the 4 then known *Paramyiolia* species. The most puzzling aspect of the genus *Paramyiolia* has been their disjunct distribution pattern (2 Japanese and 2 North American species), and Han (1996, 1999) suggested this to be a typical Arcto-Tertiary relict distribution often found in higher plants (Cox & Moore 1980).

*Paramyiolia* was initially placed in an informal taxon, the Chetostoma group (Han & Freidberg 1994; Han & McPherson 1997; Han 1999) that subsequently was formally named as the subtribe Chetostomatina Han, which is one of 2 subtribes of the tribe Trypetini (Han 2006). Han (2006) also provided a preliminary cladogram showing possible phylogenetic...
relationships among all the genera of the Chetostomatina based on morphological characters. These studies suggested the genus Myoleja Ron-dani as a possible sister group of Paramyiolia. The monophyly of the subtribe Chetostomatina was also positively tested based on analyses of the mitochondrial genes (Han & McPheron 1997; Han & Ro 2009).

Paramyiolia species in East Asia are extremely rare in insect collections, but, fortunately, we were able to collect an additional Paramyiolia species represented by a single specimen in our joint-expedition to Yunnan, China in 2011. Initiated by this discovery, our subsequent examination of Chinese tephritid specimens deposited in the Institute of Zoology, Chinese Academy of Sciences, yielded 4 more congeneric species, one of which was previously described as Anomoia yunnana Wang, 1998. We here provide descriptions of these 5 Paramyiolia species (4 new species and one new combination) from China. We also provide a revised key and reanalysis of cladistic relationships of the genus Paramyiolia. In addition, we analyzed DNA barcode sequences of a single Chinese and 3 North American Paramyiolia species, along with some representative species of related genera to test their monophyly and interspecific relationships to a limited extent.

Materials and Methods

The terminology and morphological interpretations used in this article follow White et al. (1999). The following 8 ratios are used in the descriptions: frontal-head ratio (width of frons / width of head in dorsal view); eye ratio (shortest eye diameter / longest eye diameter); genal-eye ratio (genal height / longest eye diameter) - genal height is the distance between lower eye margin and lower genal margin anterior to genal seta; aristal-antennal ratio (length of arista / length of antenna excluding arista); vein R₄₋₅, ratio (length of section between basal node and r-m / length of section between r-m and apex); vein M ratio (length of section between bm-cu and r-m / length of section between r-m and dm-cu); subcostal-costal ratio (length of subcostal cell / length of costal cell, both measured along costa); wing-thorax ratio (wing length / thorax length). The morphological cladistic methods used to infer interspecific relationships of Paramyiolia are mentioned in the appropriate section. Figures in this manuscript are displayed in color in supplementary material for this article online in Florida Entomologist 98(1) (March 2015) at http://purl.fcla.edu/fcla/entomologist/browse.

Molecular methods follow Han (2000) and Han & Ro (2005). For our analysis, partial COI gene sequences (DNA barcode region) were obtained from 13 specimens representing 4 outgroup and 3 nominal Paramyiolia species (Table 1). Additional details of the DNA barcoding analysis are mentioned in the appropriate section.

All of the Chinese Paramyiolia types are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZAS). All of the voucher specimens for DNA barcoding analysis (except for the holotype of P. atrata in IZAS) are deposited in the Division of Biological Science and Technology, Yonsei University, Wonju Campus, Korea (YSUW). Species, collection and voucher data, and Genbank accession numbers are presented in Table 1.

Table 1. Collection and voucher information of the tephritid flies used in the DNA barcoding analysis. Status of the voucher specimens and Genbank accession numbers are indicated in parentheses.

Philophylla caesio (Harris). SWITZERLAND: SG 400m, Attenrhein, 4-VIII-1987, B. Merz, ♀ (both wings glued on rectangular card; YSUW94022804; GenBank Acc. Nr. KM455055).


Anomoia purmunda (Harris) – 1. SWITZERLAND: ZK 500 m, ZuK rich-Irchelpark, 8-VIII-1993, B. Merz, (both wings glued on rectangular card; YSUW95022803; GenBank Acc. Nr. KM455057).


Myoleja sinensis (Zia) – 2. KOREA: Gangwon-do, Jeongseon-aun, Jeongseon-eup, Mt. Gariwangsan from Mahangchi to 1561m peak. 7-VII-2011, H.-S. Lee et al., ♀ (specimen with abdomen detached; YSUW140201001; GenBank Acc. Nr. KM455060).

Paramyiolia atra Han & Chen sp. nov. See Holotype data (specimen with abdomen detached; YSUW130901061; GenBank Acc. Nr. KM455061).

Paramyiolia nigricornis (Doane). USA: NC: Swain Co, Great Smoky Mountains National Park; Forney Ridge Trail below Clingmans Dome.1830 m elev. 83°29’44.4”W 35°33’13.0”N, 12-VI-2008, H.-Y. Han & K.-E. Ro, ♂ (specimen with abdomen detached; GenBank Acc. Nr. KM455062).


apically pointed with anterior-most seta largest (Figs. 1, 19–24)); 2) ocellar seta as long as or longer than ocellar triangle width; 3) with 2 pairs of orbital setae; 4) male glans without extensive sculpture pattern on dorsal and median sclerites (Figs. 30–34); and 5) female aculeus laterally flattened (Fig. 36). *Paramyiolia* males can be readily distinguished by the combination of the above character states 1-3 even without dissecting their genitalia, but females may be difficult to separate without associating with conspecific male specimens. A full description of the genus was given previously (Han 1996).

Six closely similar East Asian species (1 Japanese and 5 Chinese species), possessing almost identical wing patterns (typical *Anomoia*-type wing pattern; narrow medially interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; Figs. 1, 9–18), are here defined as the *P. cornuta* species group: *P. atra*, *sp. nov.*, *P. atrifaciata*, *sp. nov.*, *P. cornuta* (Ito), *P. melanogaster*, *sp. nov.*, *P. nigrihumera*, *sp. nov.*, and *P. yunnana* (Wang), comb. nov. See also ‘Phylogenetic relationships’ for phylogenetic justifications. These species are superficially similar to some better known species of *Anomoia* Walker, and can only be distinguished by the enlarged male frontal setae and genitalia as well as having 2 pairs of frontal setae in females (3 or more pairs in *Anomoia*). Even though females are only known for *P. cornuta* and *P. yunnana*, we assume (see ‘Phylogenetic Relationships’) that the other 4 species of the *P. cornuta* species group are likely to have 2 pairs of frontal setae in females. Additional cases of distinguishing other *Paramyiolia* species from similar looking taxa of the tribe Trypetini were considered in detail by Han (1996).

Size and shapes of *Paramyiolia* male frontal setae show substantial inter- and intra-specific variation (Figs. 19–24). Based on the examination of the better-sampled North American taxa, *P. nigricornis* (Doane) and *P. rhino* (Steyskal), we believe that their male frontal setae show typical allometric variation. Unfortunately all the Old World species are extremely rare in insect collections, and we were not able to determine

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**Fig. 1.** Strict consensus cladogram of 9 most parsimonious (MP) trees of *Paramyiolia* and related taxa (tree length = 19; consistency index = 0.736; homoplasy index = 0.263; retention index = 0.809; rescaled consistency index = 0.595). Character state changes are plotted using the fast optimization option (WinClada software). • = forward changes without homoplasy; ○ = changes with homoplasy; *Paramyiolia rhino* may contain at least 2 cryptic species (see Fig. 2). Male photographs of selected species are shown. This figure is shown in color in a supplementary document online as Suppl. Fig. 1 in Florida Entomologist 98(1) (March 2015) at http://purl.fcla.edu/floridaentomologist/browse.
variation of this potentially useful character for species distinction. It is also interesting to note that some other genera of the tribe Trypetini with male frontal modification (such as Pseudovidalia Han, Stemonocera Rondani, Strauzia Robineau-Desvoidy, and Vidalia Robineau-Desvoidy) also show such allometric variation (personal observation; see Han (2013) for an extreme case).

**DISTRIBUTION**

Japan, western China, eastern North America.

Our earlier assumption about their disjunct distribution pattern as a typical Arcto-Tertiary relict distribution (Han 1996, 1999) is strengthened by the discovery of 5 additional Chinese species. On the other hand, a recent comprehensive study of Tephritidae from the Russian Far East (Korneyev & Ovchinnikova 2004) failed to fill the distributional gap between Old and New World Paramyiolia.

**BIOLOGY**

Their host relationships are unknown, but they are likely to be fruit feeders as most other taxa of the subtribe Chetostomatina (Han 1996). Various behaviors of P. nigricornis, including lekking, mating, and oviposition have been documented in North America (Steck & Sutton, unpublished manuscript; video voucher by Steck — https://archive.org/details/ParamyioliaNigricornisBehaviorVideoVouchers).

**PHYLOGENETIC RELATIONSHIPS**

Han (1996) made an earlier cladistic analysis of Paramyiolia already, but it has become necessary to reanalyze their phylogenetic relationships since the number of species doubled in this study. We used the same set of characters as Han (1996) with slight modification (Table 2 – Characters 1-11) plus 3 new characters (Characters 12-14). We used Anomoia purmunda (Harris) and Myoleja sinensis (Zia) as outgroups based on previous studies (Han 1996, 2006). All of the characters were treated as unordered and equally likely for forward and reverse changes. Table 3 shows their character state distribution. An exhaustive search using the PAUP* package (Swofford 2001) recovered 9 most parsimonious (MP) trees, and their strict consensus tree is shown in Fig. 1. The character state changes were plotted using the fast optimization option of WinClada software (Nixon 1999). The following discussions are based on a hypothesized character evolution in this strict consensus cladogram.

As in an earlier study (Han 1996), Paramyiolia is divided into 2 relatively robust monophyletic groups (Fig. 1). The North American group (P. nigricornis and P. rhina) is supported by 2 synapomorphies, of which the character state 10-1 (loss of subapical lobe of glans) is unambiguous. So far as known, this state is unique within the subtribe Chetostomatina (Han 2006). In addition, the overall structures of their glans are almost identical to each other (Han 1996, Figs. 28 vs. 29), convincingly supporting their close relationship.

The monophyly of the East Asian group is also supported by 2 synapomorphies, of which the character state 2-1 (4 pairs of male frontal setae) is unambiguous. Except for P. takeuchii, the 6 remaining East Asian species are again grouped based on 2 unambiguous synapomorphies (here defined as the P. cornuta group; see also DIAGNOSIS). The character state 13-1 (2 pairs of frontal setae in female), however, is only observed in 2 species (P. cornuta and P. yunnana) and marked as uncertain for the other 4 species (Table 3). We nevertheless believe that unknown females of these 4 species are likely to have 2 frontal setae, because the observed external body structures (including genitalia) of the P. cornuta group closely resemble each other except for body coloration and pattern (Figs. 3–8).

It is interesting to note that all of the species of the P. cornuta group have almost identical wing patterns, which are also very similar to those of the genus Anomoia (see A. purmunda and P. atra in Fig. 1). That is why P. cornuta and P. yunnana were initially described under the genus Anomoia (Ito 1984; Wang 1998). We believe that the Anomoia-type wing pattern could either have been derived by convergence or be a remnant of a plesiomorphic wing pattern present in the common ancestor of Anomoia and Paramyiolia (possibly in Myoleja too). At least, the WinClada fast character optimization option suggested the former (Fig. 1). A similar case of wing pattern convergence was previously reported for another trypetine genus Philophyta (Han & Norrbom 2008).

**DNA BARCODING ANALYSIS**

We were able to obtain fresh samples of P. atra, P. nigricornis, and P. rhina, as well as 2 outgroup taxa, A. purmunda and M. sinensis. We also added 2 species of the genus Philophyta, which was suggested as a basal group within the Chetostomatina in recent molecular phylogenetic analyses (Han & Ro 2009; Han 2012). Even though the taxon sampling is limited, it provided us an opportunity to examine their genetic relationships. We sequenced COI barcode regions for a preliminary phylogenetic analysis. We used multiple samples for each species when available, and the pairwise proportional distances among 13
samples are shown in Table 4. The neighbor-joining (NJ) tree based on Kimura two-parameter distances (Fig. 2) shows the following relationships.

Monophyly of the East Asian, *P. atra*, and North American *Para-
myiolia* is only topologically supported (poorly supported by 80/66% standard error and bootstrap test values). *Paramyiolia atra* shows 9.0-9.7% barcode distance from North American congeners, and 11.5-12.3% from similarly wing-patterned *Anomoia pumunda*. Therefore, the almost identical wing patterns found both in *Paramyiolia* and *Ano-
moia* do not seem to reflect a corresponding close genetic relationship in this case.

As expected, the North American species form a strong monophyletic group supported by 99/100% standard error and bootstrap values with the maximum pairwise barcode distance at 3.4%. Furthermore, 3 nodes within this monophyletic group are strongly supported, suggesting that the taxon we have called *P. rhino* may include at least 2 distinct biological species (tentatively called *P. sp-A* and *sp-B* cf. *rhino*). Interestingly, based on COI, *P. sp-A* is more closely related to *P. nigricornis* (average 1.4% barcode distance) than to the morphologically indistinguishable *P. sp-B* (average 3.3% barcode distance). If these barcode differences truly reflect their specific differences, we could say that the common ancestor of these 3 species once had a *rhino*-like appearance and the drastically different wing and body patterns in *P. nigricornis* have evolved since it split from the *P. sp-A* lineage. We initially thought there might be some sequencing errors involved but 16S ribosomal RNA gene sequences also support the same topology (Han, unpublished data). Previous morphological studies of *Paramyiolia*, including Han (1992, 1996), failed to recognize any cryptic species involving *P. rhino*. In order to resolve this problem using both morphological and molecular approaches, HYH is currently conducting a collaborative project with 2 Florida entomologists, Gary Steck and Bruce Sutton, who have sampled North American *Paramyiolia* extensively over a long period of time.

**Revised Key to Species of World *Paramyiolia***

1. Wing without narrow subapical to apical C-band; crossvein DM-Cu not oblique ........................................... 2
   — Wing with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R_{1+2}; crossvein DM-Cu oblique, resulting cell dm apically pointed (Figs. 9–18) ........................................... 4

2. Apical half of cell r_{3+4} with some hyaline area (Fig. 1); NORTH AMERICA .............................. *P. rhino* (Steykskal)
   — Apical half of cell r_{3+4} without hyaline area .................................................................................. 3

3. Mediotergite dark brown; cell r_{1+2} with 3 hyaline spots (Fig. 1); JAPAN .................................................. *P. takeuchii* Shiraki
   — Mediotergite yellow to orange brown; cell r_{1+2} with single hyaline spot (Fig. 1); NORTH AMERICA .................... *P. nigricornis* (Doane)

4. Scutum and preabdominal tergites entirely dark brown (Fig. 3); femora predominantly dark brown (Fig. 10); CHINA ................................................................. *P. atra, sp. nov.* (§ unknown)
   — Scutum and preabdominal tergites at least with some yellow brown areas (Figs. 4–8); femora yellow brown (Figs. 11–18) ......................... 5

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Table 3. Character state distribution of characters used in the cladistic analysis of *Paramyiolia*. *?* = uncertain state.
5. Scutum with 4 wide dark brown longitudinal bands with lateral pair interrupted medially (Fig. 4); CHINA .............................................................. P. atrifasciata, sp. nov. (♀ unknown)
—. Scutum without such longitudinal bands .................................................. 6

6. Abdominal tergites 1-5 entirely brown, distinctly darker than scutum (Fig. 5); CHINA .................................................. P. melanogaster, sp. nov. (♀ unknown)
—. At least abdominal syntergite 1+2 entirely yellow brown, concolorous with scutum .......................... 7

7. Abdominal tergites 3-5 entirely dark brown; scutal area behind postpronotal lobe with large dark brown speck (Figs. 6, 15); CHINA .............................................................. P. nigriventer, sp. nov. (♀ unknown)
—. At least abdominal tergite 3 entirely yellow brown; scutum entirely yellow brown .......................... 8

8. Abdominal tergite 4 in male (Fig. 7) and tergite 5 in female with a pair of large dark specks; CHINA .................................................. P. yunnana (Wang)
—. Abdominal tergite 4 in male (Fig. 8) and tergite 5 in female entirely yellow brown; JAPAN .................................................. P. cornuta (Ito)

Descriptions of Chinese Paramyiolia

Paramyiolia atra Han & Chen sp. nov. (Figs. 3, 9, 10, 19, 25, 30).

TYPE MATERIAL
HOLOTYPE: ♂, CHINA: Yunnan, Honghe, Pingbian, Mt. Dawei Nature Reserve, along stream, N22°54'57.6" E103°41'46.4", 2026 m, 7-VII-2011, H.-Y. Han and S.-W. Suk.

DIAGNOSIS

Paramyiolia atra is readily distinguishable from its congeners by the almost completely dark brown body coloration (Figs. 3, 9, 10). This species can be diagnosed as follows: 1) wing with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; 2) scutum, mediotergite, preabdominal tergites dark brown; and 3) femora predominantly dark brown. In addition, this species has the most differently shaped male gleans (Fig. 30; acrophallus widely open and relatively long without any narrowed portion, directed downward at about a 45 degree angle) compared to those of the other Paramyiolia species group, which have similarly shaped gleans (Figs. 31–34; acrophallus abruptly narrowed near apex, directed downward at about a 75 degree angle).

DESCRIPTION

Body (Figs. 3, 9, 10) predominantly dark brown with brown head and yellow brown tibiae and tarsi; setae and setulue dark brown to brown; wing length 4.5 mm and thorax length 1.9 mm. Male head (Fig. 19) largely brown except dark brown occellar triangle and occiput; frons brown, sparsely covered with fine dark brown setulae, deeply concave with highly modified frontal setae; anterior 2 frontal setae greatly enlarged with 2nd seta slightly shorter than and about half as thick as 1st seta; posterior 2 frontal setae normal, about 0.7x as long as 1st seta; fronto-orbital plate associated with enlarged setae sharply elevated; frontal-head ratio 0.41, eye ratio 0.78 and genal-eye ratio 0.08; inner vertical seta 0.8x longest diameter of eye; outer vertical seta 0.6x as long as inner vertical seta; postocellar seta 0.4x as long as inner vertical seta; paraventral seta 0.5x as long as postocellar seta; ocellar triangle dark brown; ocellar seta 1.5x as long as ocellar triangle; antenna with aristal-antennal ratio 1.61; scape and pedicel with dark brown setulae; arista short pubescent, dark brown except yellow brown base; parafacial very narrow, about 0.2x as wide as flagellomere 1; facial ridge with short fine pale setulae; genal seta dark brown; postgena moderately swollen with long dark brown setulae; postocellar setae extended 0.7x distance from upper eye margin to lower eye margin; median occiput entirely dark brown; lateral occiput with dark brown upper half and brown lower half; supracervical setulae yellow brown; maxillary palp with dark brown apical and subapical setulae. Thorax almost entirely dark brown with dark brown setae and setulae; scutum heavily pruinose dark brown with brown postpronotal lobe; dorsocentral seta about 0.4x distance from level of intra-alar seta to poststatural supraalar setulae; scutellum slightly convex, almost bare with few tiny marginal setulue, basal seta 2.3x as long as scutellum and apical setulae 1.2x as long as scutellum; proepisternum densely covered with long yellow brown setulae; anepisternum with lower seta hair-like, about 0.3x as long as upper seta; mediotergite shiny dark brown. Legs with femora dark brown, tibiae and tarsi yellow brown; fore femur with 4 posteroventral setae; midtibial spur 1.3x as long as midtibia width. Wing (Fig. 9) hyaline with dark brown to brown pattern; typical Anomoia-type pattern with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; crossovein DM-Cu strongly oblique forming apically pointed cell dm; basal area enclosed by pterostigma, crossovein R-M, and basal half of cell DM-Cu almost entirely dark brown except for hyaline spot covering middle 1/3 of cell c; wing-thorax ratio 2.4, vein R4+5 ratio 2.6, vein M ratio 0.48 and subcostal-costal ratio 0.54; R4+5 with 8 tiny setulae between node and crossovein R-M.

Male abdomen (Fig. 3) about as long as wide, entirely subshiny dark brown; epandrium (Fig. 25) dark brown and surstylus brown; lateral surstylus with both anterior and posterior lobes angular, truncate apically in lateral view; glans (Fig. 30) with distinct subapical lobe; acrophallus widely open and relatively long without any narrowed portion.
directed downward at about 45 degree angle; dorsal sclerite without extensive sculpture pattern found in most other genera of the subtribe Chetostomatina; vesica relatively short, about 1/8 as long as sclerotized portion of glans.

Female unknown.

DISTRIBUTION
China (Yunnan).

ETYMOLOGY
The specific epithet is an adjective from the Latin ‘atra’, meaning black, referring to the predominantly dark body coloration.

*Paramyiolia atrifasciata* Han & Chen sp. nov. (Figs. 4, 11, 12, 20, 26, 31).

TYPE MATERIAL
HOLOTYPE: ♂, CHINA: Sichuan: Mt. Emei, Qingyinge, 800-1000 m, 10-V-1957, Z.Y. Wang. Specimen in poor condition with left wing missing and right wing damaged apically (Figs. 11, 12).

DIAGNOSIS
*Paramyiolia atrifasciata* is the only species of the genus with 4 wide longitudinal stripes (lateral pair medially interrupted) on scutum (Fig. 4). This species can be diagnosed as follows: 1) wing narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; 2) scutum with 4 wide dark brown longitudinal stripes; and 3) abdominal tergites 3-5 dark brown (female unknown).

DESCRIPTION
Body (Figs. 4, 11, 12) yellow brown ground color except for dark brown scutal stripes and abdominal tergites; setae brown to dark brown and setulae mostly yellow brown; wing length approximately 4.5 mm (both wings broken in the only available specimen) and thorax length 1.8 mm. Male head (Fig. 20) almost entirely yellow brown except dark brown ocellar triangle; frons sparsely covered with fine yellow brown setulae, deeply concave with highly modified frontal setae; anterior 2 frontal setae greatly enlarged with 2nd seta slightly shorter and about 0.7x as thick as 1st one; posterior 2 frontal setae normal, about half as long as 1st seta; fronto-orbital plate associated with enlarged setae sharply elevated; frontal-head ratio 0.38, eye ratio 0.72 and genal-eye ratio 0.11; inner vertical seta broken off; outer vertical seta about as long as posterior-most frontal seta; postoccular seta slightly shorter than outer vertical seta; paravertical seta 0.6x as long as postocellar seta; ocellar triangle dark brown; ocellar seta about as long as ocellar triangle; antenna with arista-antennal ratio 1.7; scape and pedicel with yellow brown setulae; arista short pubescent, entirely yellow brown; parafacial very narrow, about 0.2x as wide as flagellomere 1; facial ridge with short fine pale setulae; genal seta brown; postgena moderately swollen with long yellow brown setulae; postocular setae extended 0.7x distance from upper eye margin to lower eye margin; supracervical setulae yellow brown; maxillary palp with brown apical and subapical setulae. Thorax yellow brown ground color with brown setae and setulae; scutum heavily pruinose yellow brown with 4 wide dark brown longitudinal stripes, lateral stripes interrupted near transverse suture; dorsocentral seta about 0.4x distance from level of intra-alar seta to postsutural supra-alar seta; scutellum slightly convex, almost bare with few tiny marginal setulae, basal seta 2.4x as long as scutellum and apical seta 1.6x as long as scutellum; proepisternum densely covered with long yellow brown setulae; anepisternum with lower seta about half as long as upper seta; mediotergite shiny brown. Legs entirely yellow brown with brown to yellow brown setae and setulae; fore femur with 5 posteroventral setae; midtibial spur 1.2x as long as midtibia width. Wing (Fig. 11) hyaline with brown to yellow brown pattern; typical *Anomoia*-type pattern with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; crossvein DM-Cu strongly oblique forming apically pointed cell dm; basal area enclosed by pterostigma, crossvein R-M, and basal half of cell DM-Cu almost entirely brown except for hyaline spot covering middle 1/3 of cell c; vein M ratio 0.40; R4+5 with 10 tiny setulae between node and crossvein R-M.

Male abdomen (Fig. 4) about as long as wide, tergite 1 yellow brown with pair of large sublateral brown specks; tergite 2 brown; tergites 3-5 subshiny dark brown; sternites 1-4 yellow brown; sternite 5 brown; epandrium (Fig. 26) dark brown and surstylus brown; lateral
surstylus with both anterior and posterior lobes angular, truncate apically in lateral view; glans (Fig. 31) with distinct subapical lobe; acro-

phallus abruptly narrowed near apex, directed downward at about 75 degree angle; dorsal sclerite without extensive sculpture pattern found

Figs. 9–18. Chinese *Paramyiolia* species in lateral and dorsal views (all male holotype specimens). (9, 10) *P. atra*; (11, 12) *P. atrifasciata*; (13, 14) *P. melanagaster*; (15, 16) *P. nigrihumer*; (17, 18) *P. yunnana*. This figure is shown in color in a supplementary document online as Suppl. Figs. 9–18 in Florida Entomologist 98(1) (March 2015) at http://purl.fcla.edu/fcla/entomologist/browse.
Paramyiolia melanogaster Han & Chen sp. nov. (Figs. 5, 13, 14, 21, 27, 32).

TYPE MATERIAL


ETYMOLOGY

The specific epithet is an adjective derived from the Latin ‘ater’, meaning black, and ‘fasciata’, meaning striped, referring to the striped scutum.

Paramyiolia melanogaster Han & Chen sp. nov. (Figs. 5, 13, 14, 21, 27, 32).

DIAGNOSIS

Paramyiolia melanogaster can be distinguished from its congeners by the following combination of characteristics: 1) wing with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; 2) head and thorax including legs almost completely yellow brown; and 3) abdominal tergites 1-5 brown, distinctly darker than head and thorax (female unknown).

DESCRIPTION

Body (Figs. 5, 13, 14) with head and thorax yellow brown and abdomen brown; setae brown to dark brown and setulae mostly yellow brown; wing length 3.9 mm and thorax length 1.7 mm. Male head (Fig. 21) largely yellow brown except dark brown ocellar triangle; frons sparsely covered with fine yellow brown setulae, deeply concave with highly modified frontal setae; anterior 2 frontal setae enlarged with 2nd seta slightly shorter than and about 0.7x as thick as 1st seta; posterior 2 frontal setae normal, less than 0.5x as long as 1st seta; fronto-orbital plate associated with enlarged setae sharply elevated; frontal-head ratio 0.35, eye ratio 0.77 and genal-eye ratio 0.08; inner vertical seta 0.8x longest diameter of eye; outer vertical seta 0.6x as long as inner vertical seta; postocellar seta 0.4x as long as inner vertical seta; paravertical seta 0.5x as long as postocellar seta; ocellar triangle dark brown; ocellar seta 1.8x as long as ocellar triangle; antenna with scape and pedicel with dark brown setulae; parafacial very narrow, less than 0.2x as wide as flagellomere 1; facial ridge with short fine pale setulae; genal seta yellow brown; postgena moderately swollen with long
Han and Chen: Phylogeny of *Paramyiolia*, a tephritid genus

yellow brown setulae; postocular setae extended 0.6x distance from upper eye margin to lower eye margin; supracingual setulae yellow brown; maxillary palp with brown apical and subapical setulae. Thorax entirely yellow brown with brown to dark brown setae and yellow brown setulae; scutum heavily pruinose; dorsocentral seta about 4x distance from level of intra-alar seta to postsutural supra-alar seta; scutellum slightly convex, almost bare with few tiny marginal setulae, basal seta 2.2x as long as scutellum and apical seta 1.5x as long as scutellum; proepisternum densely covered with long yellow brown setulae; anepisternum with lower seta hair-like, about 0.7x as long as upper seta; mediotergite shiny yellow brown. Legs yellow brown; fore femur with 4 posteroventral setae; midtibial spur as long as midtibia width. Wing (Fig. 13) hyaline with brown to yellow brown pattern; typical Anomoia-type pattern narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; crossvein DM-Cu strongly oblique forming apically pointed cell dm; basal area enclosed by pterostigma, crossvein R-M, and basal half of cell DM-Cu almost entirely brown except for hyaline spot covering middle 1/3 of cell c; wing-thorax ratio 2.3, vein R4+5 ratio 2.3, vein M ratio 0.58 and subcostal-costal ratio 0.52; R5+6 with 10 tiny setulae between node and crossvein R-M.

Figs. 25–29. Epandrial complexes of Chinese *Paramyiolia* in caudal and lateral views (all from holotypes). (25) *P. atra*; (26) *P. atrifasciata*; (27) *P. melanogaster*; (28) *P. nigrihumera*; (29) *P. yunnana*. This figure is shown in color in a supplementary document online as Suppl. Figs. 25–29 in Florida Entomologist 98(1) (March 2015) at http://purl.fcla.edu/fcla/entomologist/browse.
Male abdomen (Fig. 5) about as long as wide with tergites 1-5 brown and sternites 1-5 yellow brown; epandrium (Fig. 27) brown and surstylius yellow brown; lateral surstylus with both anterior and posterior lobes angular, truncate apically in lateral view; glans (Fig. 32) with distinct sub-apical lobe; acrophallus abruptly narrowed near apex, directed downward at about 75 degree angle; dorsal sclerite without extensive sculptural pattern found in most other genera of the subtribe Chetostomatina; vesica relatively large, about half as long as sclerotized portion of glans.

Female unknown.

**DISTRIBUTION**
China (Sichuan).

**ETYMOLOGY**

The specific epithet is a noun derived from the Greek 'melanos', meaning dark, and 'gaster', meaning belly, referring to the dark abdomen.

*Paramyioliia nigrihumera* Han & Chen **sp. nov.** (Figs. 6, 15, 16, 22, 28, 33).

**TYPE MATERIAL**

**HOLOTYPE:** ♂, CHINA: Sichuan: Mt. Emei, 550-750 m, 2-V-1957, Z.Y. Wang; **PARATYPES:** 1 ♂, Sichuan: Mt. Emei, Temple Baoguo, 600 m, 9-V-1957, L.Y. Zheng and H.H. Cheng; 1 ♂, Yunnan: Xishuangbanna, 650 m, 7-IV-1958, S.Y. Wang.

**DIAGNOSIS**

*Paramyioliia nigrihumera* can be easily distinguished by the following combination of characteristics: 1) wing with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; 2) scutum predominantly yellow brown with large triangular dark brown speck behind postpronotal lobe (Fig. 6); 3) mediotergite shiny brown, distinctly darker than yellow brown scutellum; and 4) abdominal syntergite 1+2 yellow brown and tergites 3-5 dark brown (Fig. 6; female unknown).

**DESCRIPTION**

Body (Figs. 6, 15, 16) yellow brown ground color with tergites 3-5 dark brown; setae brown and setulæ yellow brown; wing length 4.7
mm and thorax length 2.0 mm. Male head (Fig. 22) yellow brown except dark brown ocellar triangle; frons brown, sparsely covered with fine yellow brown setulae, deeply concave with highly modified frontal setae; anterior 2 frontal setae greatly enlarged and flattened with 2nd seta slightly shorter than and about 0.7x as thick as 1st seta; posterior 2 frontal setae much thinner with 3rd seta twice as thick as 4th one, both setae about 0.7x as long as 1st seta; fronto-orbital plate associated with enlarged setae sharply elevated; frontal-head ratio 0.40, eye ratio 0.70 and genal-eye ratio 0.10; inner vertical seta 0.8x longest diameter of eye; outer vertical seta 0.6-0.8x as long as inner vertical seta; postocellar seta 0.4x as long as inner vertical seta; paravertical seta 0.5x as long as postocellar seta; ocellar triangle dark brown; ocellar seta 1.3-1.7x as long as ocellar triangle; antenna with aristal-antennal ratio 1.7; scape and pedicel with yellow brown setulae; arista short pubescent, dark brown except yellow brown base; parafacial narrow, about 0.3x as wide as flagellomere 1; facial ridge with short fine pale setulae; genal seta yellow brown; postgena moderately swollen with long yellow brown setulae; postocular setae extended 0.6x distance from upper eye margin to lower eye margin; supracervical setulae yellow brown; maxillary palp with brown apical and subapical setulae. Thorax predominantly yellow brown with dark brown to brown setae and yellow brown setulae; scutum heavily pruinose with large triangular dark brown speck behind postpronotal lobe (the paratype male from Sichuan has a small additional dark speck just behind transverse sutures); dorsocentral seta about 0.4x distance from level of intra-alar seta to poststatural supra-alar seta; scutellum slightly convex, almost bare with few tiny marginal setulae, basal seta 2.4-2.6x as long as scutellum and apical seta 1.7x as long as scutellum; proepisternum densely covered with long yellow brown setulae; anepisternum with lower seta 0.7-0.9x as long as upper seta; lower half of katepisternum dark brown; mediotergite shiny brown. Legs yellow brown with brown to yellow brown setae and setulae; fore femur strongly swollen with 5 posterior ventral setae; midtibial spur 1.3-1.5x as long as midtibia width. Wing (Fig. 16) hyaline with brown to yellow brown pattern; typical Anomoia-type pattern with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R₅₆; crossvein DM-Cu strongly oblique forming apically pointed cell dm; basal area enclosed by pterostigma, crossvein
R-M, and basal half of cell DM-Cu almost entirely dark brown except for hyaline spot covering middle 1/3 of cell c and small postero-medial hyaline spot in cell br; wing-thorax ratio 2.3, vein R4+5 ratio 2.6-2.8, vein M ratio 0.48-0.55 and subcostal-costal ratio 0.50-0.56; R4+5, with 11 tiny setae between node and crossovisen R-M.

Male abdomen (Fig. 6) about as long as wide; syntergite 1+2 yellow brown; tergites 3-5 dark brown; sternites 1-4 yellow brown; sternite 5 brown; epandrium (Fig. 28) brown and sur stylius yellow brown; lateral sur stylius with both anterior and posterior lobes angular, truncate apically in lateral view; glans (Fig. 33) with distinct subapical lobe; acro phallus abruptly narrowed near apex, directed downward at about 75 degree angle; dorsal sclerite without extensive sculpture pattern found in most other genera of the subtribe Chetostomiatina; vesica relatively large, about 0.7x as long as sclerotized portion of glans.

Female unknown.

**DISTRIBUTION**

China (Sichuan, Yunnan).

**ETYMOLOGY**

The specific epithet is a noun derived from the Latin ‘niger’, meaning black, and ‘humerus’, meaning shoulder, referring to the dark area behind postpronotal lobe.

*Paramyiolia yunnana* (Wang, 1998) **Comb. Nov.** (Figs. 7, 17, 18, 23, 24, 29, 34–38).


**TYPE MATERIAL**

**HOLOTYPE:** ♂., CHINA: Yunnan: Xiaomengyang, 850 m, 28-III-1957, F.J. Pu; **PARATYPE:** 1 ♀, same locality as holotype, 810 m, 26-III-1957, D.H. Liu.

**DIAGNOSIS**

*Paramyiolia yunnana* can be distinguished from its congeners by the following combination of characteristics: 1) wing narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; 2) scutum almost completely yellow brown; 3) male abdominal tergites 1-3 (Fig. 7) and female tergites 1-4 yellow brown; 4) male abdominal tergite 4 and female abdominal tergite 5 with a pair of large dark brown specks; 5) male abdominal tergite 5 and female tergite 6 dark brown; 6) female head with 2 pairs of frontal setae. This species is very similar to Japanese *P. cornuta*, but can be separated by the above characters 3-5 (see Figs. 7 vs. 8).

**DESCRIPTION**

Body (Figs. 7, 17, 18) predominantly yellow brown with tergites 4-5 in male and tergites 5-7 in female largely dark brown; setae brown to dark brown and setulae yellow brown; wing length 4.7-4.9 mm and thorax length 2.0-2.2 mm. Male head (Fig. 23) yellow brown except dark brown ocellar triangle; frons brown, sparsely covered with fine yellow brown setulae, deeply concave with highly modified frontal setae; anterior 3 frontal setae greatly enlarged and flattened with only 4th seta of normal size; 2nd frontal seta about 0.7x, 3rd seta 0.4x, and 4th seta 0.3x as thick as 1st seta; lengths of frontal setae in series decreasing from anterior to posterior (as 1.0 - 0.9 - 0.8 - 0.7x); fronto-orbital plate associated with enlarged setae sharply elevated; frontal-head ratio 0.40, eye ratio 0.73-0.74 and genal-eye ratio 0.12-0.14; inner vertical seta 0.7-0.8x longest diameter of eye; outer vertical seta 0.6x as long as inner vertical seta; postocellar seta 0.4x as long as inner vertical seta; paravertical seta 0.5x as long as postocellar seta; ocellar triangle dark brown; ocellar seta 1.3-1.6x as long as ocellar triangle; antenna with aristal-antennal ratio 1.7-1.8; scape and pedicel with yellow brown setulae; arista short pubescent, yellow brown; parafacial narrow, about 0.2-0.3x as wide as flagellomere 1; facial ridge with short fine pale setulae; genal seta yellow brown; postgena moderately swollen with long yellow brown setulae; postocular setae extended 0.6x distance from upper eye margin to lower eye margin; supracervical setae yellow brown; maxillary palp with brown apical and subapical setulae. Female head similar to that of male without frontal modification (Fig. 24); frontal-head ratio 0.37, eye ratio 0.76 and genal-eye ratio 0.12; with only 2 pairs of frontal setae. Thorax predominantly yellow brown with dark brown to brown setae and yellow brown setulae; scutum heavily pruinose yellow brown; dorsocentral seta about 0.4x distance from level of intra-alar seta to poststural supra-alar seta; scutellum slightly convex, almost bare with few tiny marginal setulae, basal seta 2.1-2.6x as long as scutellum and apical seta 1.4-1.8x as long as scutellum; proepisternum densely covered with long yellow brown setulae; anepisternum with lower seta slightly shorter than upper seta; lower half of katepisternum dark brown; mediosternum shiny yellow brown. Legs yellow brown with yellow brown setae and setulae; fore femur strongly swollen with 6-7 posteroventral setae; midtibial spur 1.2-1.5x as long as midtibia width. Wing (Figs. 17, 18) hyaline with brown to yellow brown pattern; typical *Anomoia*-type pattern with narrow, medially-interrupted C-band extending from DM-Cu to anterior apical wing margin and then along margin to slightly beyond apex of vein R4+5; crossvein DM-Cu strongly oblique forming apically pointed cell dm; basal area enclosed by pterostigma, crossovisen R-M, and basal half of cell DM-Cu almost entirely dark brown except for hyaline spot covering middle 1/3 of cell c; wing-thorax ratio 2.2-2.3, vein R4+5 ratio 2.6-2.7, vein M ratio 0.55-0.59 and subcostal-costal ratio 0.42; R4+5 with 8-15 tiny setulae between node and crossovisen R-M.

Male abdomen (Fig. 7) about as long as wide; tergites 1-3 yellow brown; tergite 4 with pair of large dark brown specks; tergite 5 dark brown; sternites 1-4 yellow brown; sternite 5 brown; epandrium (Fig. 29) dark brown and sur stylius yellow brown; lateral sur stylius with both anterior and posterior lobes angular, truncate apically in lateral view; glans (Fig. 34) with distinct subapical lobe; acrophallus abruptly narrowed near apex, directed downward at about 75 degree angle; dorsal sclerite without extensive sculpture pattern found in most other genera of the subtribe Chetostomiatina; vesica relatively large, about 0.4x as long as sclerotized portion of glans.

Female abdomen with tergites 1-4 yellow brown; tergite 5 dark brown except narrow yellow brown mid-stripe; tergite 6 dark brown; sternites 1-5 yellow brown; sternite 6 brown; oviscape (Figs. 35 and 37) dark brown with 2 long ventral marginal and 2 long dorsal marginal setae; eversible membrane (Fig. 37) cylindrical, without any strong teeth; dorsal and ventral taeniae extending almost entire length of eversible membrane; aculeus (Fig. 36) long, slender, with apex laterally flattened with serrated apical; 3 spherical spermathecae with transverse spinules (Fig. 38); apical portion of spermathecal duct not swollen.

**DISTRIBUTION**

China (Yunnan).

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