



HOKKAIDO UNIVERSITY

Title	A New Species Group in the Genus <i>Dichaetophora</i> Duda (Diptera: Drosophilidae) Based on a Phylogenetic Analysis, with Descriptions of Four New Species from China
Author(s)	Hu, Yao-guang; Toda, Masanori J.
Citation	Zoological Science, 22(11), 1265-1276 https://doi.org/10.2108/zsj.22.1265
Issue Date	2005-11
Doc URL	https://hdl.handle.net/2115/32969
Rights	(c) 日本動物学会 / 本文献の公開は著者の意思に基づくものである
Type	journal article
File Information	i0289-0003-22-11-1265.pdf



A New Species Group in the Genus *Dichaetophora* Duda (Diptera: Drosophilidae) Based on a Phylogenetic Analysis, with Descriptions of Four New Species from China

Yao-guang Hu* and Masanori J. Toda

*Institute of Low Temperature Science, Hokkaido University, Nishi 8, Kita 19,
Kita-ku, Sapporo 060-0819, Japan*

ABSTRACT—A new species group, the *sinensis* group, is established within the genus *Dichaetophora*, based on a phylogenetic analysis of 37 adult morphological characters from 26 drosophilid species, including ten known species of *Dichaetophora*; four newly described species (*Di. abnormis*, *Di. hainanensis*, *Di. bicornis*, and *Di. sinensis* spp. nov. from China); and some representatives of related genera (*Drosophila*, *Hirtodrosophila*, and *Scaptomyza*).

Key words: *Dichaetophora*, Drosophilidae, new species group, phylogenetic tree, taxonomy, China

INTRODUCTION

Dichaetophora was established as a subgenus of the genus *Drosophila* Fallén by Duda (1940). Grimaldi (1990) regarded this taxon as an independent genus in the new infratribe Drosophilini based on his very extensive cladistic analysis. Hu and Toda (2002) examined relationships among *Dichaetophora*, the *Lordiphosa tenuicauda* species group, and the genus *Nesiodrosophila* Wheeler & Takada by a cladistic analysis of 30 morphological characters, and revealed that these three taxa constitute a monophyletic group. Based on this result, they revised the genus *Dichaetophora*, including the above three groups, and established three species groups within it: the *agbo*, *tenuicauda*, and *acutissima* groups. Accordingly, a total of 60 species of the genus have been reported worldwide (Hu and Toda, 2002).

Recently, four new species were brought from China; their external morphology implies a close relationship to the genus *Dichaetophora*. This study examines phylogenetic positions of these new species within the subfamily Drosophilinae, especially focusing on relationships to the genus *Dichaetophora*, by a cladistic analysis of 37 adult morphological characters from a total of 26 selected species. Based on the result, we establish a new species group within the genus *Dichaetophora* comprising the four new species described herein.

MATERIALS AND METHODS

Species studied

We selected the four new and 10 known species of *Dichaetophora* as the main target taxa (Table 1). In addition, some representatives of possibly related drosophiline genera, *Scaptomyza* Hardy, *Hirtodrosophila* Duda, and *Drosophila*, were included as ingroup species, because the relationships of these genera to the target taxa remained uncertain (Hu and Toda, 2001, 2002). As an outgroup species, we chose *Drosophila* (*Sophophora*) *obscura* Fallén, 1935, based on the results of our previous studies (Hu and Toda, 2001, 2002): the sophophoran clade (the subgenus *Sophophora* Sturtevant + the genus *Lordiphosa* Basden) was the sister group to the clade including the present ingroup taxa, and furthermore *Dr. obscura* occupied the most ancestral position in the sophophoran clade.

Observations

The specimens studied were either preserved in 70% ethanol, or dried and pinned. External morphology was observed under a stereoscopic microscope, and metric characters were measured with an ocular micrometer. To observe the detailed structures of the head, thorax, legs, and male and female terminalia, respective organs were detached from the body, cleared by warming in a 10% KOH solution to around 100°C for several minutes, and observed in a droplet of glycerol under a compound light microscope. Dry, pinned specimens were softened by warming in 70% ethanol for several minutes before dissection. Drawings were made on the basis of photomicrographs taken by a digital camera connected to a computer. Scanning electron photomicrographs were taken for some characters.

Cladistic analyses

The original data matrix, 26 species × 37 characters, is given in Table 2. Analyses were performed with PAUP version 4.0b10 (Swofford, 2002). Due to memory and processor limitations, we employed an approximate (heuristic) search strategy using the ran-

* Corresponding author. Phone: +81-11-706-5499;
Fax : +81-11-706-7142;
E-mail: hu@pop.lowtem.hokudai.ac.jp

Table 1. Taxa included in the cladistic analysis.

Genus	Subgenus	Species group	Species
<i>Drosophila</i>	(<i>Sophophora</i>)	<i>obscura</i>	<i>obscura</i> Fallén, 1823
<i>Dichaetophora</i>		<i>sinensis</i>	<i>abnormis</i> sp. nov.
<i>Dichaetophora</i>		<i>sinensis</i>	<i>hainanensis</i> sp. nov.
<i>Dichaetophora</i>		<i>sinensis</i>	<i>bicornis</i> sp. nov.
<i>Dichaetophora</i>		<i>sinensis</i>	<i>sinensis</i> sp. nov.
<i>Dichaetophora</i>		<i>tenuicauda</i>	<i>tenuicauda</i> (Okada, 1956)
<i>Dichaetophora</i>		<i>tenuicauda</i>	<i>alticola</i> (Hu <i>et al.</i> , 1999)
<i>Dichaetophora</i>		<i>tenuicauda</i>	<i>yeren</i> (Hu & Toda, 1999)
<i>Dichaetophora</i>		<i>acutissima</i>	<i>acutissima</i> (Okada, 1956)
<i>Dichaetophora</i>		<i>acutissima</i>	<i>cyanea</i> (Okada, 1988)
<i>Dichaetophora</i>		<i>agbo</i>	<i>agbo</i> (Burla, 1954)
<i>Dichaetophora</i>		<i>agbo</i>	<i>suruku</i> (Burla, 1954)
<i>Dichaetophora</i>		<i>agbo</i>	<i>sakagamii</i> (Toda, 1989)
<i>Dichaetophora</i>		<i>agbo</i>	<i>raridentata</i> (Okada & Chung, 1960)
<i>Dichaetophora</i>		<i>agbo</i>	<i>surukella</i> (Okada, 1965)
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>testacea</i>	<i>testacea</i> von Roser, 1840
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>immigrans</i>	<i>immigrans</i> Sturtevant, 1921
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>quinaria</i>	<i>transversa</i> Fallén, 1823
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>funnebris</i>	<i>funnebris</i> (Fabricius, 1787)
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>repleta</i>	<i>hydei</i> Sturtevant, 1921
<i>Drosophila</i>	(<i>Drosophila</i>)	<i>virilis</i>	<i>virilis</i> Sturtevant, 1916
<i>Drosophila</i>	(<i>Dorsilopha</i>)		<i>busckii</i> Coquillett, 1901
<i>Scaptomyza</i>	(<i>Parascaptomyza</i>)		<i>pallida</i> (Zetterstedt, 1847)
<i>Scaptomyza</i>	(<i>Scaptomyza</i>)		<i>graminum</i> (Fallén, 1823)
<i>Hirtodrosophila</i>		<i>hirticornis</i>	<i>nokogiri</i> (Okada, 1956)
<i>Hirtodrosophila</i>		<i>quadrivittata</i>	<i>quadrivittata</i> (Okada, 1956)

Table 2. Matrix of 37 morphological characters from 26 drosophilid species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	
<i>Dr. obscura</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Di. abnormis</i>	1	0	0	1	1	1	1	0	1	1	2	0	0	1	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	1	1
<i>Di. bicornis</i>	1	0	0	1	1	1	1	0	1	1	2	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1
<i>Di. hainanensis</i>	1	0	0	1	1	1	1	0	1	1	2	0	0	1	0	0	?	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1
<i>Di. sinensis</i>	1	0	0	1	1	1	1	0	1	1	2	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	1	1
<i>Di. tenuicauda</i>	0	0	0	0	1	1	0	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Di. alticola</i>	0	0	0	0	1	1	0	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1
<i>Di. yeren</i>	0	0	0	0	1	1	0	0	1	1	2	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	?
<i>Di. acutissima</i>	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1
<i>Di. cyanea</i>	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	
<i>Di. agbo</i>	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1
<i>Di. suruku</i>	0	1	1	0	1	1	0	1	1	1	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	1	0	0	1
<i>Di. sakagamii</i>	0	1	1	0	1	1	0	1	1	1	2	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	1
<i>Di. raridentata</i>	0	1	1	0	1	1	0	1	1	1	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	0	1
<i>Di. surukella</i>	0	1	1	0	1	1	0	1	1	1	2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2	0	1	1	1	0	1
<i>Dr. testacea</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	2	1	0	1	1	0	0	0	0
<i>Dr. immigrans</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	1	1	0	0	0
<i>Dr. transversa</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	1	1	1	1	0	0	0
<i>Dr. funebris</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	2	1	0	1	1	0	0	0
<i>Dr. hydei</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0
<i>Dr. virilis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0
<i>Dr. busckii</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	2	0	0	1	1	0	0	0	0
<i>Sc. pallida</i>	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0
<i>Sc. graminum</i>	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	2	1	1	1	0	0	0	0
<i>Hi. nokogiri</i>	0	0	0	0	1	1	0	2	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0
<i>Hi. quadrivittata</i>	0	0	0	0	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0

dom taxon-addition sequence and tree bisection-reconnection (TBR) branch-swapping options. The heuristic search was repeated 100 times, which decreased the possibility of missing islands of more parsimonious cladograms. For the consensus tree of resulting maximum-parsimony cladograms, character optimizations were performed using both DELTRAN (delayed transformation) and ACCTRAN (accelerated transformation). Branch support was evaluated in two ways: bootstrap analysis with 1000 replicates and Bremer analysis (Bremer, 1994). A heuristic search with 'simple' addition sequence and TBR branch-swapping was performed for the bootstrap analysis. Bremer support was calculated with PAUP version 4.0b10 and TreeRot version 2 (Sorenson, 1999). The total support index, ti , was calculated as the sum of all Bremer support values over the resulting tree divided by s , the length of the most parsimonious cladogram.

Type depositories

The type specimens were deposited in the following institutions: College of Life Science, Peking University, Beijing, China (PKU); Systematic Entomology, the Hokkaido University Museum, Hokkaido University, Sapporo, Japan (SEHU).

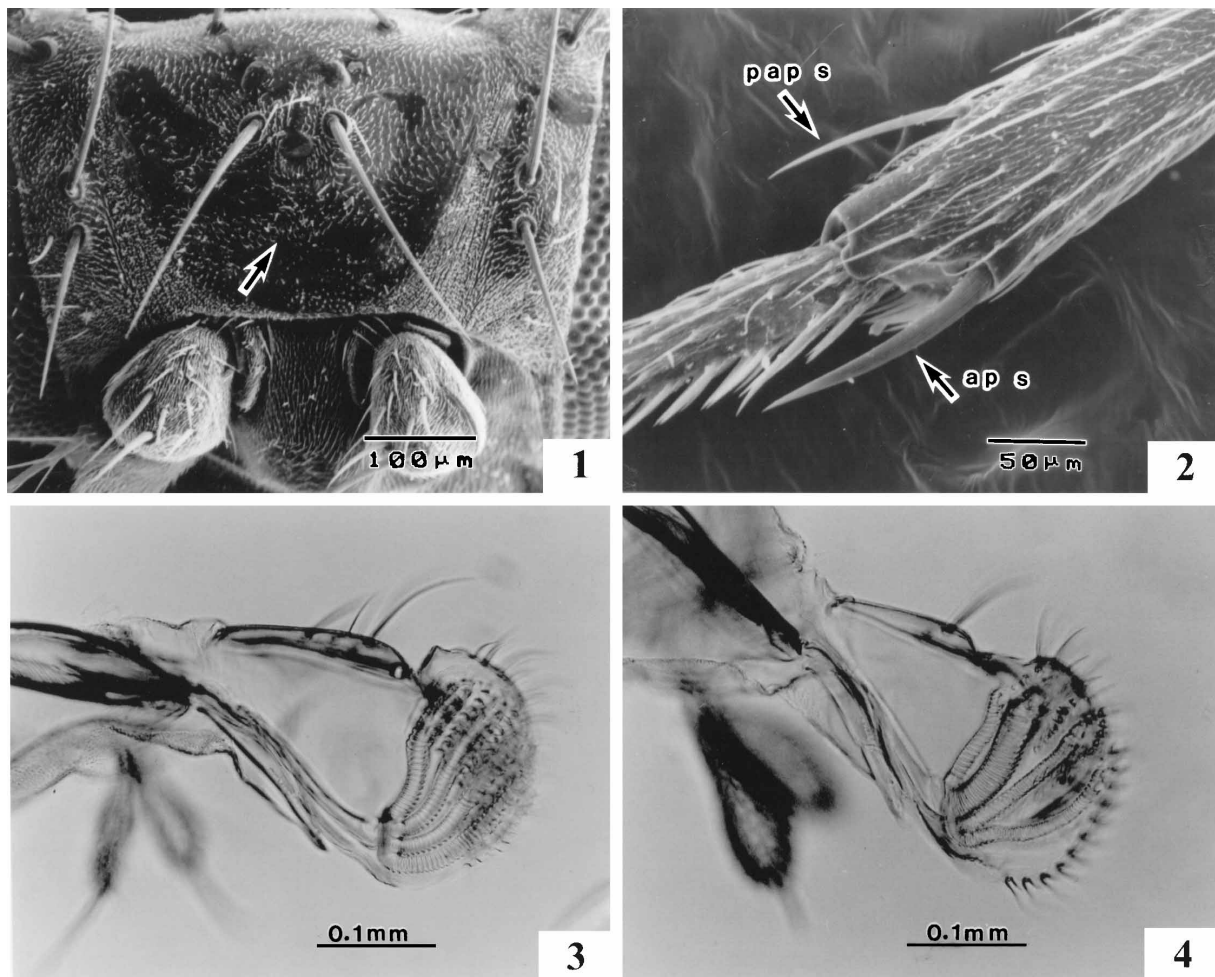
Characters

In character selection and coding, we endeavored to include as

many characters as possible in the analysis, as long as these could be assumed to be homologous and be defined objectively; characters that varied continuously, without any gaps among the taxa examined were excluded from the analysis. We selected a number of characters from Hu and Toda (2002), with the character number from this reference given in parentheses as (HT#) in the following list, and added several new characters. In all, a total of 37 characters of male and female adult morphology were analysed. Character polarity was determined by the outgroup comparison method (Watrous and Wheeler, 1981): all characters of the outgroup species, *Dr. obscura*, were coded as 0. All transformation series were assumed to be unordered.

Head

1. Ocellar triangle; (0) neither very large nor glossy, (1) very large and glossy (Fig. 1).
2. (HT2). Eye, longest axis; (0) nearly orthogonal to body axis, (1) distinctly oblique.
3. (HT3). Frons, profile line from base to ptilinal fissure; (0) convex, (1) nearly straight.
4. Interfrontal setulae on frontal vitta; (0) a few present, (1) absent (Fig. 1).
5. (HT5). Setulae on basal lobe of palpus; (0) a few present, (1) absent.
6. (HT6). Cibarium, anterior margin; (0) thickened, (1) not thick-



Figs. 1–4. Some characters used in the phylogenetic analysis: 1. Frons of *Dichaetophora abnormis* sp. nov.; 2. Tibia and 1st tarsomere (apical and basal parts, respectively) of foreleg of *Dichaetophora abnormis* sp. nov.; 3. Labellum (lateral view) of *Dichaetophora tenuicauda* (Okada, 1956); 4. Labellum (lateral view) of *Dichaetophora sakagamii* (Toda, 1989). pap s=preapical seta, ap s=apical seta.

ened.

7. Cibarium, number of medial sensilla per side; (0) 12 to 26 (Fig. 5), (1) 40 or more (Fig. 6).
8. (HT8). Cibarium, dorsal wall; (0) pear-shaped, with posterior portion oval (Fig. 6), (1) medially constricted, with posterior portion parallel-sided (Fig. 5), (2) oval or oblong, medially without constriction.
9. (HT9). Cibarium, anterior end; (0) not dilated laterally, (1) more or less dilated.
10. (HT10). Cibarium, anterolateral corners; (0) distinctly protruded, (1) only slightly protruded.
11. (HT11). Labellum, number of pseudotracheae per side; (0) 6 or more, (1) 5, (2) 4 (Figs. 3,4).
12. Labellum, widths of pseudotracheae; (0) nearly the same (Fig. 3), (1) distinctly varied (Fig. 4).
13. (HT12). Arista, number of ventral branches excluding terminal fork; (0) 2 or more, (1) only 1.
14. Prementum, ventral surface; (0) nearly flat or slightly swollen at distal end, (1) forming discrete bump (Figs. 8–11A).
15. (HT13). Subvibrissal seta, length; (0) distinctly shorter than vibrissa, (1) nearly subequal to vibrissa and prominently longer than other orals.

Thorax

16. (HT14). Acrostichal setulae, number of rows; (0) 6 or more, (1) 4 or less.
17. (TH15). Mid katapisternal seta, length; (0) present, distinctly longer than other setulae below it, (1) absent or indistinguishable from others.

Legs

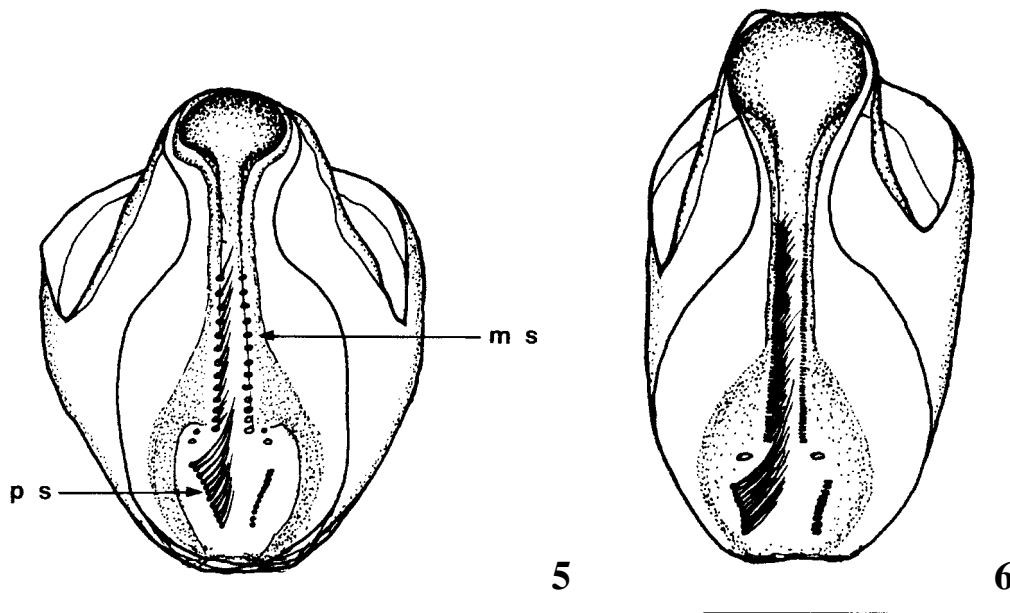
18. (HT16). Foreleg tibia, preapical dorsal seta; (0) present, (1) absent.
19. Foreleg tibia, apical seta; (0) as thin as preapical dorsal or neighboring setae; (1) distinctly stout (Fig. 2).
20. (HT18). Midleg tibia, preapical dorsal seta; (0) present, (1) absent.

Male terminalia

21. (HT19). Epandrium, setae; (0) present not only on ventral portion but also on other portions (Figs. 8–11B), (1) only on ventral

portion.

22. Surstylus, fusion to epandrium; (0) fused (Figs. 9–11B), (1) separated but articulate (Fig. 8C).
 23. Surstylus, comb(s) of peg-like prensisetae; (0) one set arranged linearly (Fig. 9B), (1) arranged irregularly (Figs. 8C, 10–11B).
 24. (HT21). Surstylus, stout or peg-like setae on outer mesal surface; (0) absent (Figs. 8C, 9–11B), (1) present.
 25. (HT22). Surstylus, pubescence; (0) absent, (1) covering nearly entirely or partly.
 26. (HT23). Cercus, fusion to epandrium; (0) separated (Figs. 8–11B), (1) fused.
 27. Cercus, caudoventral sclerotization; (0) less sclerotized, (1) strongly sclerotized (Figs. 9–11B).
 28. (HT24). Hypandrium, paramedian setae; (0) present (Figs. 8F,G, 9–11D,E), (1) absent.
 29. (HT25). Paramere, fusion to hypandrium; (0) separated, (1) fused (Figs. 8G, 9–11E).
 30. (HT26). Paramere, fusion to aedeagus; (0) articulated with aedeagus (Figs. 8G, 9–11E), (1) fused to aedeagus, (2) fused to aedeagal guide.
 31. (HT27). Paramere, shape; (0) elongated, more or less sclerotized (Figs. 9–11D,E), (1) plate-like (Fig. 8F,G), (2) small, somewhat conical or hemispherical.
 32. (HT28). Paramere, pubescence; (0) absent (Figs. 8F,G, 9–11D,E), (1) partly covering.
 33. (HT29). Aedeagus, basal processes; (0) present, (1) absent.
 34. Aedeagal guide; (0) almost absent (Fig. 8G), (1) present (Figs. 9–11E).
 35. Hypandrium, fusion to aedeagal guide (nested to ch. 34–1); (0) separated, (1) fused (Figs. 9–11E).
 36. Aedeagus, apical membranous dilation like trumpet; (0) absent; (1) present (Figs. 8F,G, 9–11D,E).
- Female terminalia
37. (HT30). Oviscapt, apical ovisensillum; (0) neither so robust nor the largest among marginal ones, (1) robust and the largest, distinctly distinguishable from the others (Figs. 8H, 9–10F).



Figs. 5–6. Cibarium (dorsal view): 5. *Dichaetophora raridentata* (Okada & Chung, 1960); 6. *Dichaetophora sinensis* sp. nov. m s=medial sensilla, p s=posterior sensilla. (Scale line=0.1 mm).

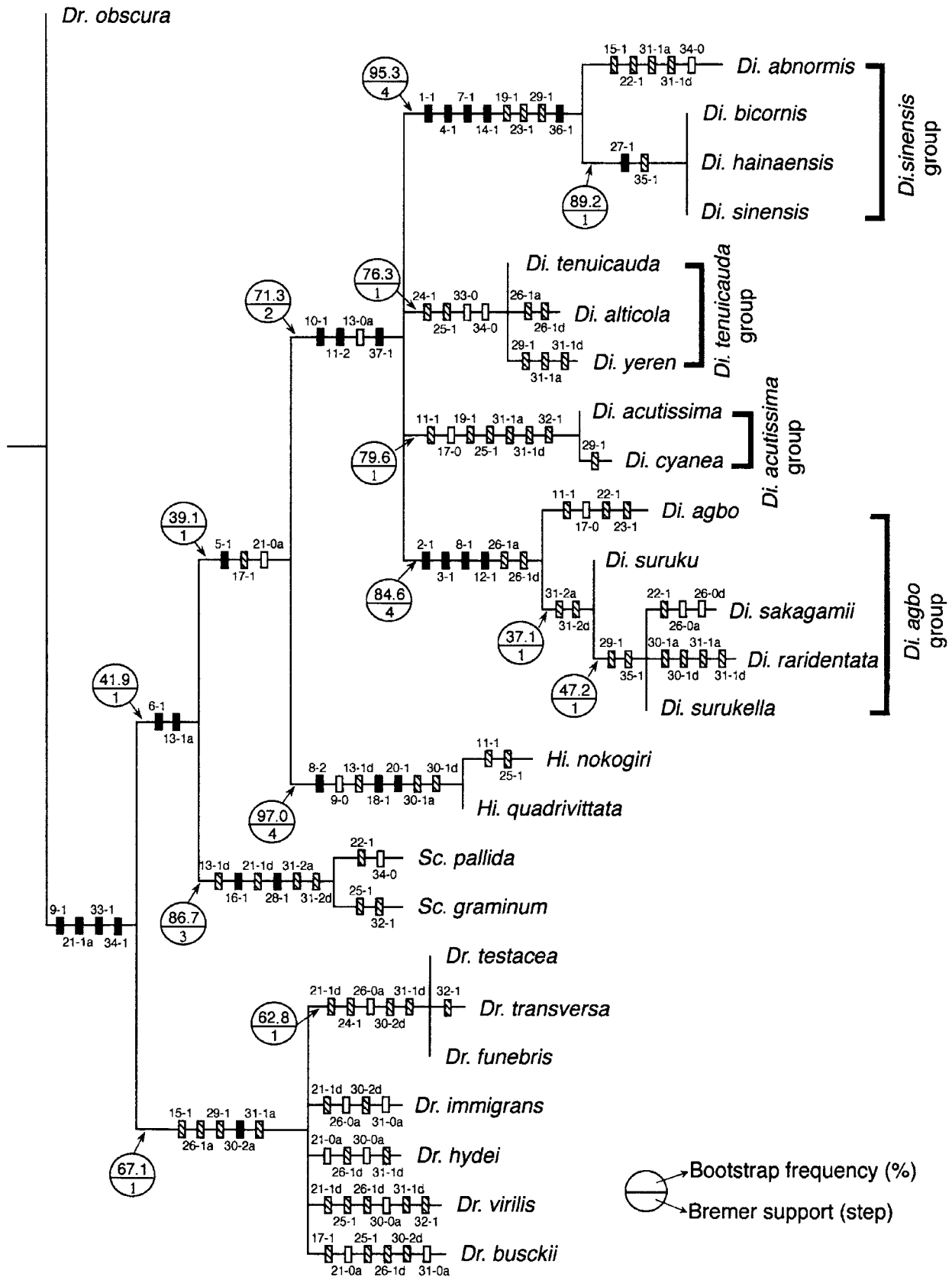


Fig. 7. The strict consensus of 100 most parsimonious cladograms obtained using PAUP (length=91, CI=0.451, RI=0.742, $ti=0.334$), with indication of apomorphies (solid hashmarks indicate non-homoplasious changes, stripe marks homoplasious changes, and open marks reversals; different results from ACCTRAN and DELTRAN are marked with 'a' and 'd', respectively).

RESULTS AND DISCUSSION

Cladogram and phylogeny

The heuristic analysis of the data matrix (Table 2) resulted in 100 equally most parsimonious cladograms with the following statistics: length=91 steps, CI (consistency index)=0.451, RI (character retention index)=0.742, and *ti* (total support index)=0.334. The strict consensus tree was rooted by the outgroup (Fig. 7). Apomorphies are indicated on each branch of this cladogram, based on the results of character optimization. Although DELTRAN and ACCTRAN yielded the same result for most transformation series, different hypotheses for character evolution were produced for transformation series 13, 21, 26, 30 and 31. Synapomorphies not identified by both DELTRAN and ACCTRAN have been excluded from the following discussion. The support values are indicated in a circle at each branch, with the bootstrap frequency given above the Bremer value.

The four new species formed a clade strongly supported (bootstrap value=95.3%, Bremer support=4 steps) by the following synapomorphies: ocellar triangle very large and glossy (ch. 1-1); frontal vitta without interfrontal setulae (ch. 4-1); number of medial, cibarial sensilla 40 or more per side (ch. 7-1); ventral surface of prementum forming discrete bump (ch. 14-1); aedeagus apically with pale, membranous trumpet-like dilation (ch. 36-1). This clade was placed in a comparable position to the three known species groups, the *tenuicauda*, *acutissima* and *agbo* groups, within the genus *Dichaetophora*. The monophyly of the genus *Dichaetophora*, including the clade comprising the four new species, was reconfirmed (bootstrap value=71.3%, Bremer support=2 steps) by the same synapomorphies as in Hu and Toda (2002): cibarium only slightly protruded at anterolateral corners (ch. 10-1); apical ovisensillum on oviscapt robust and the largest among marginals (ch. 37-1); pseudotracheae in labellum less than six per side (ch. 11-1,2; the occurrence of five pseudotracheae is regarded as having evolved independently in *Hirtodrosophila nokogiri* (Okada, 1956)). Among the four new species, *Di. bicornis*, *Di. hainanensis*, and *Di. sinensis* spp. nov. were regarded as monophyletic (bootstrap=89.2%, Bremer=1 step) based on the following synapomorphies: caudoventrally strongly sclerotized cercus (ch. 27-1); aedeagus fused to aedeagal guide (ch. 35-1; a homoplasy is seen in the lineage leading to the clade of *Di. sakagamii* (Toda, 1989) + *Di. raridentata* (Okada & Chung, 1960) + *Di. surukella* (Okada, 1965)).

In addition, this study reconfirmed the results of our previous study (Hu and Toda, 2002), *i.e.*, the monophyly of the *tenuicauda*, *acutissima*, and *agbo* species groups of the genus *Dichaetophora*, the subgenera *Drosophila* + *Dorsilopha* Sturtevant (though the genus *Drosophila* is paraphyletic; *cf.* Throckmorton, 1975; Hu and Toda, 2001; Tarrio *et al.*, 2001), and the genera *Scaptomyza* and *Hirtodrosophila*. However, the relationship among the three known species groups and the new clade within the genus *Dichaetophora* was not resolved in the present study. Hu and Toda (2002)

suggested the monophyly of the *tenuicauda* + *acutissima* group, although both bootstrap and Bremer supports were low. We attribute the difference from our previous study to exclusion of one character, HT4 (the number of prominent, long setae on the palpus), from the present analysis, because the four new species show an intermediate state of this character (palpus bearing 1 prominent, terminal seta and another subprominent, lateromedian seta). Furthermore, the relationships among genera were not so highly resolved in the present study.

DESCRIPTIONS

Since the four new species comprised a clade within the genus *Dichaetophora*, we hereby establish a new species group, the *sinensis* group, in this genus; descriptions of the four component species are given below. The synapomorphies supporting this clade are listed as the diagnostic characters for the species group.

Dichaetophora sinensis species group

Diagnosis. Ocellar triangle very large, reaching to ptilinal fissure, glossy dark brown (Fig. 1). Frontal vitta without interfrontal setulae (Fig. 1). Cibarium with 40 or more medial sensilla per side (Fig. 6). Prementum discretely swollen at ventral portion (Figs. 8–11A). Aedeagus apically with pale, membranous trumpet-like dilation (Figs. 8F, 9–11D). Foreleg with distinctly stout, apical seta on tibia (Fig. 2). Cercus caudoventrally strongly sclerotized (Figs. 9–11B), except for *Di. abnormis* sp. nov.

Description. Head: Supracervical setae tapered, thin, apically curved and sharp. Eye brownish red. Face brown or dark brown, somewhat glossy. Frontal vitta narrow. Gena, occiput, and postgena brown or dark brown. Carina broad and high. Pedicel brown to dark brown; 1st flagellomere grayish brown, pubescent; arista with terminal bifurcation. Clypeus dark brown to black. Palpus grayish brown, club-shaped, with 1 prominent, terminal seta and another subprominent, lateromedian seta. Cibarium not thickened on anterior margin, slightly protruded at anterolateral corners; dorsal wall of cibarium pear-shaped, anteriorly strongly convex in lateral view; anterior portion of hypopharynx shorter than posterior tubular portion. Labellum with 4 pseudotracheae nearly the same in width per side.

Thorax entirely brown or dark brown. Acrostichal setulae in 6 irregular rows. Mid katepisternal seta minute, indistinguishable from other setulae below. Basal, scutellar setae nearly parallel; apicals cruciate. Prescutellar setae absent.

Wing: Veins grayish brown; R_{2+3} slightly curved to costa at tip; R_{4+5} and M parallel. C_1 setae 2; dorsal one stout. Basal medial-cubital (bm-cu) crossvein absent. Halter pale gray; stem darker.

Legs: Apical, ventral setae on fore- and midleg tibiae; preapical, dorsal setae on tibiae of all legs. Male foreleg without sex combs.

Abdominal tergites entirely brown or blackish brown,

without caudal band. Sternites pale gray or grayish brown.

Male terminalia: Epandrium nearly entirely pubescent, with a few setae caudodorsally and many longer ones ventrally; apodeme narrow. Surstylus nearly semicircular, lacking pubescence, with irregular rows of peg-like prensisetae on outer surface, dorsoproximally fused to epandrium (except for *Di. abnormis* sp. nov.). Cercus nearly entirely pubescent, separated from epandrium. Hypandrium with 1 pair of paramedian setae (except for *Di. bicornis* sp. nov.). Paramere lacking pubescence, elongated and club-shaped, with 2–3 small sensilla apically (except for *Di. abnormis* sp. nov.), ventrally fused to hypandrium. Gonopods absent. Aedeagus without basal processes; aedeagal guide fused to hypandrium (except for *Di. abnormis* sp. nov.); apodeme rod-like, fused to aedeagus.

Female terminalia: Oviscap yellow, with 10–12 marginal and 4 lateral, more or less robust, peg-like ovisensilla; apical one very robust, distinguishable from others. Hypoproct nearly entirely pubescent. Sterntie VII deeply notched caudomedially, V-shaped, nearly entirely pubescent. Spermathecal capsule broader than long; introvert broad, finely wrinkled on basal half, ca. 2/3 as deep as capsule (Figs. 8I, 9–10G).

***Dichaetophora abnormis* sp. nov.**

(Fig. 8)

Diagnosis. Paramere large, plate-like in ventral view, medially with 2 sensilla (Fig. 8F,G). Hypandrium with 1 pair of very stout, paramedian spines on densely pubescent lobes (Fig. 8F,G). Surstylus separated from epandrium; main lobe semicircular, with ca. 30 peg-like prensisetae scattered dorsally to caudoventrally and thin setae medially to ventrally; a pair of very peculiar arms elongated from inner margin of main lobe, with comb of 3 peg-like teeth basally and S-shaped appendage at tip of outer arm; S-shaped appendage with 2 peg-like teeth at one end and 1 sharp tooth at the other (Fig. 8C,D).

Description. Male and female: Head with ca. 18 supracervical and 25–27 postocular setae per side. Face dark brown. Gena, occiput, and postgena dark brown. Pedicel usually dark brown. Clypeus brownish black.

Wing slightly fuscous.

Legs dark grayish brown. Fore- and hindleg 1st tarsomeres as long as 3 and 4 succeeding tarsomeres combined, respectively; midleg 1st tarsomere slightly longer than remaining tarsomeres combined.

Abdominal tergites entirely glossy black. Sternites grayish brown.

Male terminalia: Epandrium ventrally broad, dorsally narrow, with ca. 40 long setae per side (Fig. 8B). Tenth sternite posteromedially notched (Fig. 8E). Cercus narrow, caudoventrally not sclerotized, pubescent except for ventral margin, with ca. 23 setae (Fig. 8B). Hypandrium slightly wider than long (Fig. 8F). Aedeagus very broad in lateral view, especially basally, dorso-apically with slightly curved, acute process; apodeme as long as aedeagus (Fig. 8G).

Female terminalia: Oviscap yellowish brown, somewhat narrow, apically pointed; with 4 lateral and 12 marginal pegs, and 1 ventrosubapical and 3 dorsosubapical, trichoid ovisensilla; anteroventral bridge narrow, ca. 1/3 as long as oviscap, posteromedially with small, triangular expansion (Fig. 8H).

Measurements: BL (body length)=2.71 mm in holotype (paratypes: 2.65–2.89 in 3♂, 2.86–3.30 in 3♀); ThL (thorax length)=1.22 mm (1.30–1.34 in ♂, 1.51–1.76 in ♀); WL (wing length)=2.84 mm (2.83–2.84 in ♂, 2.71–3.01 in ♀); WW (wing width)=1.20 mm (1.23–1.31 in ♂, 1.20–1.51 in ♀).

Indices: arb (dorsal branches of arista/ventral branches of arista)=4.5/2, FW/HW (frontal width/head width)=0.54 (0.52–0.55), ch/o (maximum width of gena/maximum diameter of eye)=0.26 (0.22–0.28), prorb (proclinate orbital/posterior reclinate orbital in length)=0.50 (0.55–0.71), rcorb (anterior reclinate orbital/posterior reclinate orbital in length)=0.21 (0.22–0.25), vb (subvibrissa/vibrissa in length)=0.75 (0.76–0.85), dcl (anterior dorsocentral/posterior dorsocentral in length)=0.65 (0.64–0.71), sctl (basal scutellar/apical scutellar in length)=0.94 (0.90–0.96), sterno (anterior katepisternal/posterior katepisternal in length)=damaged (0.54–0.59), orbito (distance between proclinate and posterior reclinate orbitals/distance between inner vertical and posterior reclinate orbital)=0.47 (0.48–0.56), dcp (length distance between ipsilateral dorsocentrals/cross distance between anterior dorsocentrals)=0.65 (0.64–0.71), sctlp (distance between ipsilateral scutellars/cross distance between apical scutellars)=0.90 (0.90–1.05), C (a/b; a: 2nd costal section between subcostal break and R_{2+3} , b: 3rd costal section between R_{2+3} and R_{4+5})=1.61 (1.59–1.75), 4c (b/d; d: M_1 between r-m and dm-cu)=1.51 (1.56–1.65), 4v (c/d; c: M_1 between dm-cu and wing margin)=2.45 (2.40–2.68), 5x (e/f; e: CuA_1 between dm-cu and wing margin, f: dm-cu between M_1 and CuA_1)=2.18 (1.78–2.57), ac (b/i; i: distance between distal ends of R_{4+5} and M_1)=2.96 (3.01–3.19), M (e/d)=0.81 (0.82–0.97), C3F (g/(g+h); g: length of heavy setation on 3rd costal section, h: length of light setation on 3rd costal section)=0.72 (0.71–0.76).

Holotype: ♂, China: Mt. Emei, Sichuan, 17.VII.1992, by sweeping, H. Watabe leg. (PKU).

Paratypes: China: 1♀, same data as for holotype; 1♂, 1♀, same data as for holotype, except collected 19.VII.1992; Babaoshan, Guangdong: 1♂, 11.IX.1989, 1♂, 1♀, 12.IX.1989, by sweeping, H. Watabe and M. J. Toda leg. (PKU, SEHU).

Distribution. China (Sichuan, Guangdong).

Relationship. This species resembles *Dichaetophora acutissima* (Okada) in having the apical seta on foreleg tibia only slightly stouter than the preapical, dorsal seta; in having the aedeagus large, broad and plate-like in lateral view; and in body color pattern, but can be clearly distinguished from the latter by having 4 pseudotracheae per side on labellum and by the unique morphology of hypandrium and surstylus.

Etymology. In reference to complicated shape of abnor-

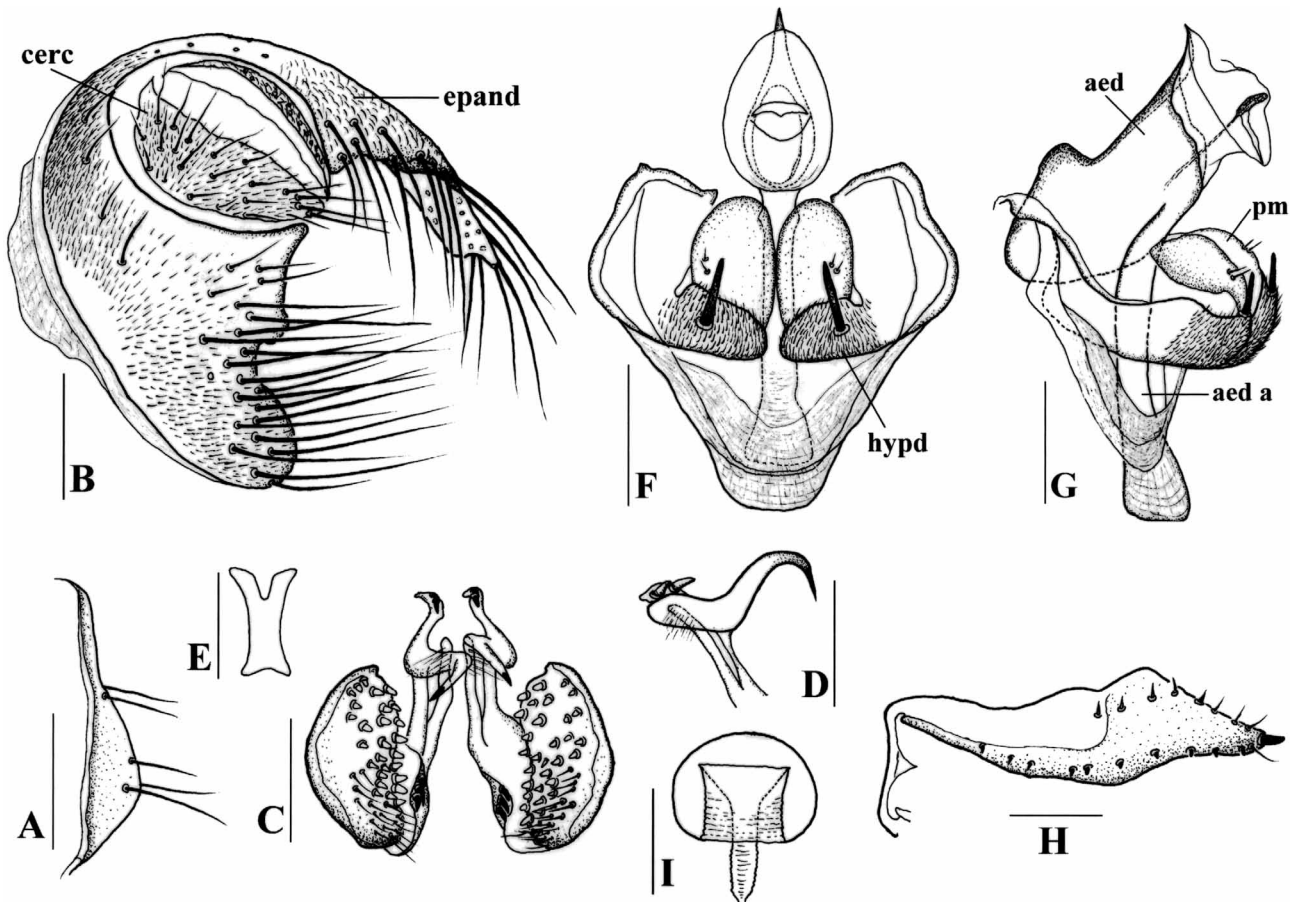


Fig. 8. *Dichaetophora abnormis* sp. nov. A, prementum; B, epandrium (epand) and cercus (cerc); C, surstylus (ventral view); D, dorsal appendage of surstylus (lateral view); E, 10th sternite (ventral view); F, hypandrium (hypd), parameres, aedeagus, and aedeagal apodeme (ventral view); G, hypandrium, parameres (pm), aedeagus (aed), and aedeagal apodeme (aed a) (lateral view); H, oviscapt; I, spermatheca. (Scale-line=0.1 mm).

mal surstylus.

***Dichaetophora bicornis* sp. nov.**

(Fig. 9)

Diagnosis. Cercus caudoventrally with outwardly protruded, very strongly sclerotized, black, plate-like process (Fig. 9B). Hypandrium partly pubescent around 2 pairs of small, paramedian spines (Fig. 9D,E). Aedeagus apically with 1 pair of elongated, horn-like processes (Fig. 9D,E).

Description. Male and female: Head with 21–22 supracervical and ca. 25 postocular setae per side.

Legs dark grayish brown. Foreleg 1st tarsomere as long as 3 succeeding tarsomeres combined; mid- and hindleg 1st tarsomeres as long as remaining tarsomeres combined.

Male terminalia: Epandrium tapering below but apically rounded, with ca. 12 setae per side (Fig. 9B). Surstylus with 11 apically sharp, black, peg-like prenisetae arranged in somewhat curved row (Fig. 9B). Tenth sternite dorsally extended, ventrolaterally semicircular (Fig. 9C). Cercus with ca. 35 setae (Fig. 9B). Hypandrium as wide as long. Paramere half as long as aedeagal, apical process, with 2 small sensilla apically (Fig. 9D,E). Aedeagus narrow and

long, slightly curved ventrally; apodeme slightly shorter than aedeagus (Fig. 9E).

Female terminalia: Oviscapt yellowish brown, somewhat narrow, apically pointed, with 4 lateral and ca. 13 marginal peg-like, and 1 subterminal, trichoid ovisensilla; anteroventral bridge narrow, ca. 1/3 as long as oviscapt, posteromedially with large, triangular expansion (Fig. 9F). Spermathecal capsule apically shallowly indented (Fig. 9G).

Measurements: BL=2.45 mm (2.71–2.84 in 5♂, 2.77–2.84 in 3♀); ThL=1.16 mm (1.18–1.26 in ♂, 1.20–1.32 in ♀); WL=2.60 mm (2.38–2.73 in ♂, 2.56–2.75 in ♀); WW=1.13 mm (1.13–1.15 in ♂, 1.10–1.19 in ♀).

Indices: arb=4.5/2, FW/HW=0.57 (0.55–0.58), ch/o=0.34 (0.30–0.36), prorb=0.68 (0.62–0.67), rcorb=0.28 (0.25–0.28), vb=0.31 (0.26–0.32), dcl=0.69 (0.70–0.75), sclt=0.97 (0.95–0.99), sterno=0.54 (0.47–0.54), orbito=0.46 (0.45–0.49), dcp=0.62 (0.63–0.66), scltp=0.86 (0.83–0.96), C=1.84 (1.71–2.00), 4c=1.62 (1.38–1.69), 4v=2.71 (2.62–2.79), 5x=1.94 (1.88–2.04), ac=3.01 (2.90–3.40), M=0.86 (0.77–0.89), C3F=0.98 (0.95–0.98).

Holotype: ♂, China: Mt. Emei, Sichuan, 17.VII.1992, H. Watabe leg. (PKU).

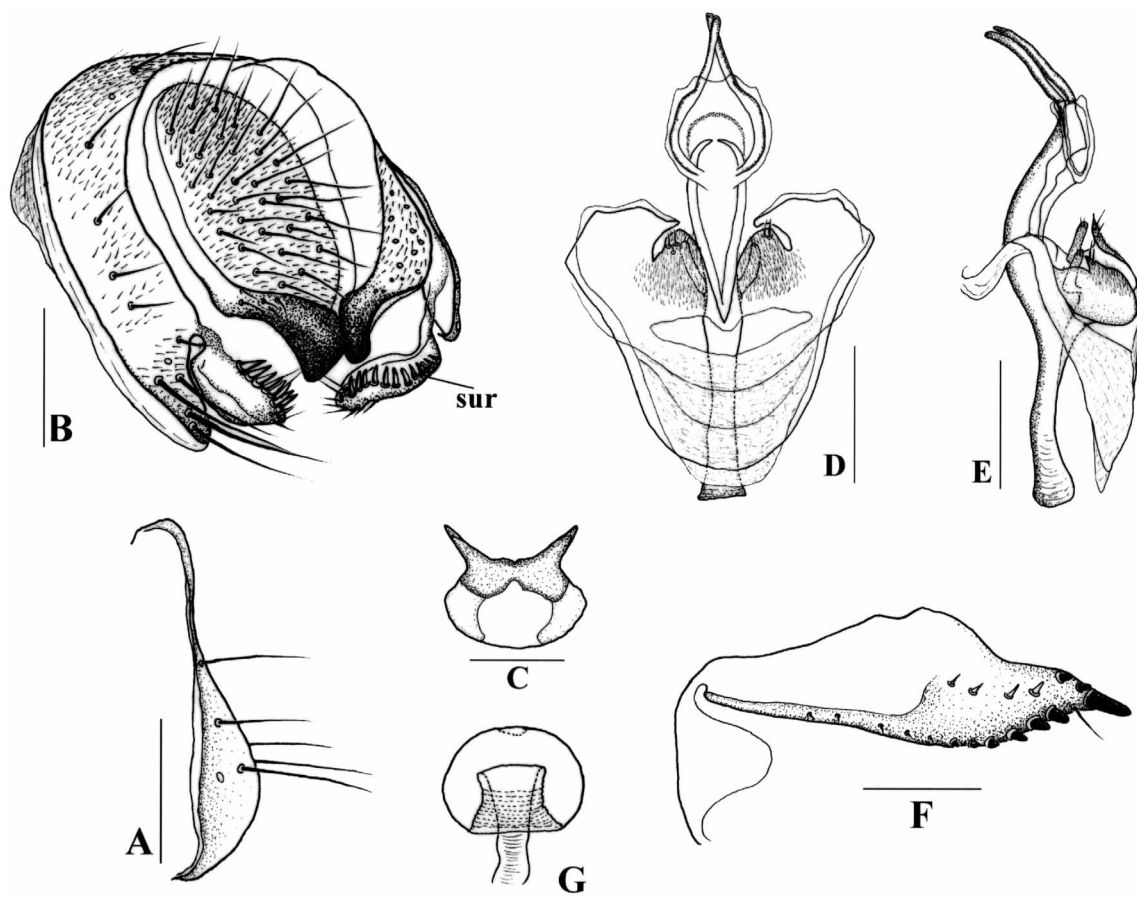


Fig. 9. *Dichaetophora bicornis* sp. nov. A, prementum; B, epandrium, cercus and surstylus (sur); C, 10th sternite (ventral view); D, hypandrium, parameres, aedeagus and aedeagal apodeme (ventral view); E, hypandrium, parameres, aedeagus and aedeagal apodeme (lateral view); F, oviscapt; G, spermatheca. (Scale line=0.1 mm).

Paratypes: China: 9 ♂, 5 ♀, same data as for holotype; 19 ♂, 18 ♀, same data as for holotype, except collected 19.VII.1992 (PKU, SEHU).

Distribution. China (Sichuan).

Relationship. This species resembles *Di. abnormis* sp. nov. in the partly pubescent hypandrium and in body color, but can be clearly distinguished from the latter by the cercus caudoventrally with very strongly sclerotized process; the elongated, club-shaped paramere; the surstylus fused to the epandrium; and the shape of aedeagus.

Etymology. In reference to the apical, horn-like processes on the aedeagus.

***Dichaetophora hainanensis* sp. nov.**

(Fig. 10)

Diagnosis. Cercus caudoventrally with yellowish brown, strongly sclerotized, outwardly protruded process (Fig. 10B). Aedeagus apically with small, triangular, slightly notched extension in lateral view (Fig. 10E).

Male and female (the specimens having almost lost color from long preservation in ethanol): Head with 19–20 supracervical and ca. 17 postocular setae per side.

Legs: Foreleg 1st tarsomere as long as 3 succeeding

tarsomeres combined; mid- and hindleg 1st tarsomeres slightly shorter than remaining tarsomeres combined.

Male terminalia: Epandrium ventrally rounded and slightly broader than dorsally, with ca. 28 setae per side (Fig. 10B). Surstylus with ca. 11 apically sharp, yellowish brown, peg-like prenisetae arranged in somewhat U-shaped row and ca. 10 spines on inner surface (Fig. 10B). Tenth sternite nearly rectangular, ventrolaterally with 1 pair of arms (Fig. 10C). Cercus with ca. 33 setae (Fig. 10B). Hypandrium lacking pubescence, with 1 pair of paramedian spines (Fig. 10D,E). Paramere ca. 1/3 as long as aedeagus, with 2 small sensilla apically (Fig. 10D,E). Aedeagus gently curved ventrally; apodeme shorter than 1/2 length of aedeagus (Fig. 10E).

Female terminalia: Oviscapt yellowish brown, somewhat narrow, apically pointed, with 4 lateral and ca. 9 marginal peg-like, and 1 subterminal, trichoid ovisensilla; anteroventral bridge narrow, ca. 1/3 as long as oviscapt, posteromedially slightly broadened (Fig. 10F).

Measurements (1 ♂ paratype was too heavily damaged for measuring): BL=1.92 mm (2.21–2.26 in 2 ♀); ThL=0.82 mm (0.91–0.94 in ♀); WL=1.85 mm (1.95–2.00 in ♀); WW=0.78 mm (0.86–0.87 in ♀).

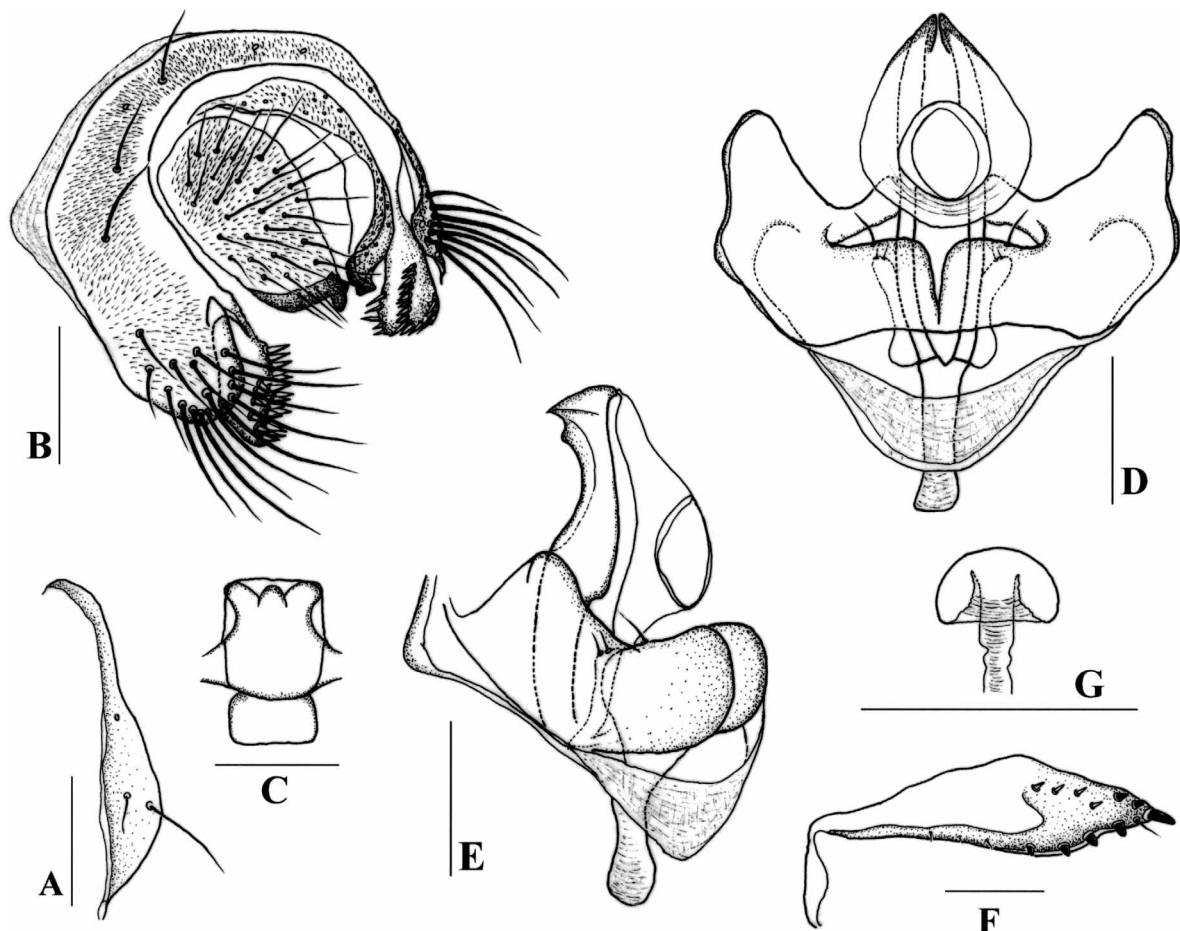


Fig. 10. *Dichaetophora hainanensis* sp. nov. A, prementum; B, epandrium, circus, and surstylus; C, 10th sternite (ventral view); D, hypandrium, parameres, aedeagus, and aedeagal apodeme (ventral view); E, hypandrium, parameres, aedeagus, and aedeagal apodeme (lateral view); F, oviscapit; G, spermatheca. (Scale line=0.1 mm).

Indices: arb=4-5/2, FW/HW=0.57 (0.60–0.62), ch/o=0.30 (0.28–0.30), prorb=0.76 (0.76), rcorb=0.22 (0.24–0.32), vb=damaged, dcl=0.66 (0.69–0.71), sctl=0.88 (0.92), sterno=damaged (0.43–0.44), orbito=0.35 (0.38–0.44), dcp=0.55 (0.56–0.60), sctlp=0.66 (0.67–0.69), C=1.82 (1.83–2.01), 4c=1.44 (1.50), 4v=2.84 (2.91), 5x=2.13 (2.15), ac=3.25 (3.27), M=0.90 (0.85), C3F=0.75 (0.71–0.72).

Holotype: ♂, China: Jianfengling, Ledong County, Hainan Is., 24.IX.1993, M. J. Toda leg. (PKU).

Paratypes: China: 1 ♂ (partly damaged), 4 ♀, same data as for holotype (PKU, SEHU).

Distribution. China (Hainan Is.).

Relationship. This species resembles *Di. bicornis* sp. nov. in having a caudoventral, strongly sclerotized, outwardly protruded process on the cercus, the surstylus fused to the epandrium, and the club-shaped paramere, but can be clearly distinguished from the latter by the lack of pubescence and 1 pair of paramedian spines on the hypandrium and by the shape of aedeagus, especially the lack of long, apical, horn-like processes.

Etymology. In reference to the type locality.

Dichaetophora sinensis sp. nov.

(Fig. 11)

Diagnosis. Cercus caudoventrally with yellowish brown, strongly sclerotized, triangular flap (Fig. 11B). Aedeagus mediodorsally swollen, apically triangularly protruded but not notched in lateral view (Fig. 11E).

Description. Male: Head with ca. 15 supracervical and ca. 17 postocular setae per side. Fronto-orbital plate yellowish brown. Face brown. Gena, occiput, and postgena brown.

Thorax entirely glossy, yellowish brown.

Wing: Veins usually brown.

Legs yellowish brown. Foreleg 1st tarsomere as long as 3 succeeding tarsomeres combined; mid- and hindleg 1st tarsomeres slightly shorter than remaining tarsomeres combined.

Male terminalia: Epandrium broader ventrally than dorsally, with 13–16 setae per side (Fig. 11B). Surstylus with ca. 7 apically sharp, yellowish brown, peg-like prenisetae arranged in somewhat U-shaped row, and ca. 13 long spines from outer to inner, ventral margin. Tenth sternite nearly triangular, dorsolaterally with 1 pair of arms connected to surstyli, rounded on ventral margin (Fig. 11C).

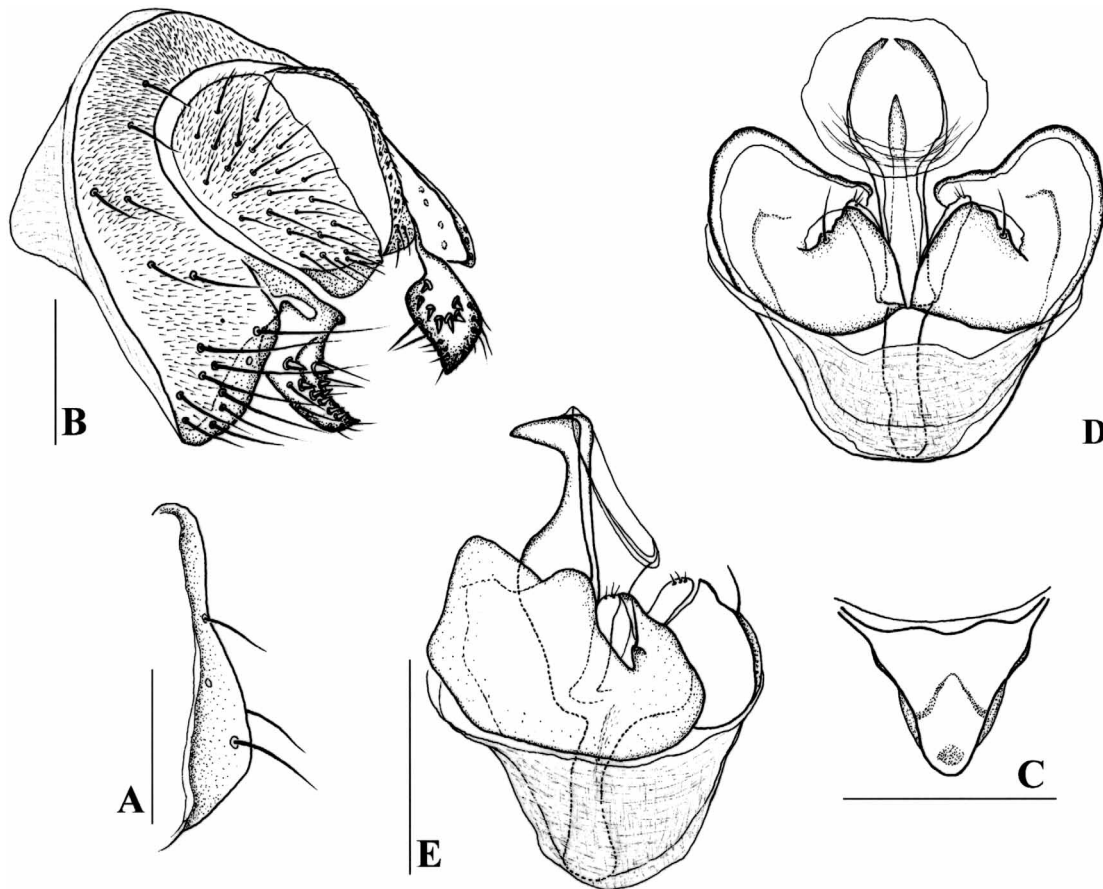


Fig. 11. *Dichaetophora sinensis* sp. nov. A, prementum; B, epandrium, circus, and surstylus; C, 10th sternite (ventral view); D, hypandrium, parameres, aedeagus, and aedeagal apodeme (ventral view); E, hypandrium, parameres, aedeagus, and aedeagal apodeme (lateral view). (Scale line=0.1 mm).

Cercus with ca. 26 setae (Fig. 11B). Hypandrium lacking pubescence, as wide as long, with 1 pair of paramedian spines (Fig. 11D,E). Paramere slightly shorter than half of aedeagus, with 3 small sensilla apically. Aedeagal apodeme shorter than aedeagus (Fig. 11D,E).

Measurements: BL=2.24 mm (2.42 in 1 ♂); ThL=0.95 mm (0.90 in ♂); WL=2.30 mm (2.28 in ♂); WW=0.97 mm (0.96 in ♂).

Indices: arb=4-5/2, FW/HW=0.59 (0.57), ch/o=0.31 (0.30), prorb=0.61 (damaged), rcorb=0.18 (damaged), vb=0.28 (0.27), dcl=damaged (0.66), sctl=damaged (0.98), sterno=0.48 (0.47), orbito=0.36 (0.31), dcp=0.63 (0.59), sctlp=0.89 (0.82), C=1.96 (1.70), 4c=1.59 (1.56), 4v=2.52 (2.48), 5x=damaged (2.10), ac=3.45 (3.32), M=damaged (0.91), C3F=0.74 (0.75).

Holotype: ♂, China: Mt. Emei, Sichuan, 19.VII.1992, H. Watabe leg. (PKU)

Paratype: China: 1 ♂, same data as for holotype (SEHU).

Distribution. China (Sichuan).

Relationship. This species resembles *Di. hinanensis* sp. nov. in the lack of pubescence on the hypandrium and the somewhat U-shaped row of prensisetae on the surstylus,

but can be distinguished from the latter by the cercal, caudoventral, strongly sclerotized portion not protruded but forming flap; the aedeagal, apical extension not notched; and the shape of 10th sternite.

Etymology. In reference to the type country.

ACKNOWLEDGMENTS

We thank L. Tsacas (Centre National de la Recherche Scientifique, France) and G. Bächli (Zoologisches Museum, Universität Zürich-Irchel, Switzerland), who permitted us to examine some invaluable specimens on loan; G. Takaku (Hokkaido University of Education) for his assistance in scanning electron microscopy; and H. Watabe (Hokkaido University of Education) for his help in collecting the specimens used in this study. This work was partly supported by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (Nos. 12375002 and 15255006) and from the Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 16-04184).

REFERENCES

- Bremer K (1994) Branch support and tree stability. *Cladistics* 10: 295–304
- Duda O (1940) Revision der afrikanischen Drosophiliden (Diptera).

- II. Annls hist-nat Mus natn hung 33: 19–53
- Grimaldi DA (1990) A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bull Am Mus Nat Hist 197: 1–139
- Hu Y-g, Toda MJ (2001) Polyphyly of *Lordiphosa* and its relationships in Drosophilinae (Diptera: Drosophilidae). Syst Entomol 26: 15–31
- Hu Y-g, Toda MJ (2002) Cladistic analysis of the genus *Dichaetophora* Duda (Diptera: Drosophilidae) and a revised classification. Insect Syst Evol 33: 91–102
- Sorenson MD (1999) TreeRot, version 2. Boston University, Boston
- Swofford DL (2002) PAUP: Phylogenetic analysis using parsimony, Version 4.0b10. Sinauer Associates, Sunderland
- Tarrio, R, Rodriguez-Trelles, F, Ayala, FJ (2001) Shared nucleotide composition biases among species and their impact on phylogenetic reconstructions of the Drosophilidae. Mol Biol Evol 18: 1464–1473
- Throckmorton, LH (1975) The phylogeny, ecology, and geography of *Drosophila*. In "Handbook of Genetics" Ed by RC King, Plenum Press, New York, pp 421–469
- Watrous LE, Wheeler QD (1981) The outgroup comparison method of character analysis. Syst Zool 30: 1–11

(Received July 7, 2005 / Accepted August 26, 2005)