

# Cladistic analysis of the genus *Dichaetophora* Duda (Diptera: Drosophilidae) and a revised classification

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Phylogenetic relationships among the genus *Dichaetophora*, the genus *Nesiodrosophila* and the *Lordiphosa tenuicauda* species-group and some possibly related genera of Drosophilinae were analyzed in this study using 30 morphological characters derived from 34 species. It is concluded that the three taxa constitute a monophyletic group, within which three monophyletic groups are recognized: *Dichaetophora* + *Nesiodrosophila* comprise a monophyletic group, while the *L. tenuicauda* group is divided into two monophyletic groups. This clade is revised as the genus *Dichaetophora*, with its three constituent monophyletic groups treated as new species-groups: the *agbo*, the *tenuicauda* and the *acutissima* groups. *Nesiodrosophila* becomes a junior synonym. A key to the species-groups is provided.

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## Introduction

*Dichaetophora* was established as a subgenus of *Drosophila* Fallén by Duda (1940), based on the single species, *Drosophila aberrans* Lamb, from the Seychelles. The original diagnostic characters for this subgenus were the anterior dorsocentral setae minute or absent, as in *Mycodrosophila* Oldenberg, but the portion of costal vein proximal to the subcostal break neither thickened nor dark. However, when Burla (1954) described two new and one informally named species, *Drosophila agbo*, *Drosophila suruku* and *Drosophila* sp. n., aff. *aberrans*, of this subgenus from Africa, he invalidated the above characters. Instead, he used the eyes very oblique to the body axis and ocellar setae inserted outside the triangle made by ocelli (this is different from the ocellar triangle sensu McAlpine 1981) as the subgeneric diagnosis.

Wheeler & Takada (1964) established the genus *Nesiodrosophila* for the single species, *Nesiodrosophila lindae* Wheeler & Takada, from Palau, Caroline Islands, with the following characters: 'Small species; arista plumose; anterior reclinate orbital large, beside proclinate; ocellars outside ocellar triangle; face flat; second oral bristle developed; acrostichal hairs irregular, in four to six

rows; no prescutellars; anal vein weak.' Although these characters in combination can be used to discriminate this genus from others, any single character is not diagnostic for this genus. However, Wheeler & Takada (1964) did not refer to any differences between *Dichaetophora* and *Nesiodrosophila*. Some Asian species which had previously been included in the subgenus *Dichaetophora* were transferred to *Nesiodrosophila*, but without explicit reasoning (Okada 1976, 1977, 1984; Nishiharu 1981). One new species from Zaire was added to *Dichaetophora* by Graber (1957) and many new species to *Nesiodrosophila* (Lin & Ting 1971; Nishiharu 1981; Bock 1982, 1984; McEvey & Bock 1982; Okada 1984, 1988; Toda et al. 1987; Toda 1989; Gupta & De 1996). Consequently, the four known named and one unnamed species of *Dichaetophora* are all from the Ethiopian Region, and 42 species of *Nesiodrosophila* are distributed in Asia (26), New Guinea (10), Australia (7), Micronesia and Madagascar (one species each): *N. lindae* is distributed over the first four of these areas.

The relationships between *Dichaetophora* in Africa and *Nesiodrosophila* in other regions have never been studied, other than by Grimaldi (1990).

He included both genera, each represented by a single species (*Dichaetophora aberrans* and *Nesiodrosophila rotundicornis* Okada) in his very extensive cladistic analysis of almost all Drosophilidae. Grimaldi concluded that these two genera were rather distantly related to each other, and regarded *Dichaetophora* as an independent genus in the infratribe Drosophilini, while including *Nesiodrosophila* in the *Scaptomyza* genus group of the *Drosophila* genus complex of the Drosophilini.

In a recent phylogenetic study focusing on the genus *Lordiphosa* Basdan, Hu & Toda (2001) concluded that *Lordiphosa* is polyphyletic: i.e. the *L. tenuicauda* species-group is a lineage independent from the other members of *Lordiphosa*. Furthermore, the *L. tenuicauda* group was placed as the sister group to *Nesiodrosophila*, and this clade of the *L. tenuicauda* group + *Nesiodrosophila* was suggested to be more or less related to the sub-

genus *Drosophila* and the genera *Hirtodrosophila* Duda and *Scaptomyza* Hardy. These were supported also by molecular data (Katoh et al. 2000).

Thus, *Dichaetophora*, *Nesiodrosophila* and the *L. tenuicauda* group seem to be closely related to each other, but their phylogenetic relationships have not yet been revealed. Furthermore, to reveal the relationships between these and possibly related taxa may be informative to resolve some major issues in the phylogeny of Drosophilidae, such as the monophyly of the subgenus *Drosophila* and the origin of Hawaiian drosophilids. This study aims to solve this problem, by including all species of the *L. tenuicauda* group that were taxonomically reviewed by Hu et al. (1999), and some representatives of *Dichaetophora* and *Nesiodrosophila*, in a cladistic analysis of morphological characters.

Table 1. Taxa examined for cladistic analysis.

| Genus                  | Subgenus                  | Species-group        | Species                                     |
|------------------------|---------------------------|----------------------|---|
| <i>Drosophila</i>      | ( <i>Sophophora</i> )     | <i>obscura</i>       | <i>obscura</i> Fallén 1823                  |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>tenuicauda</i> (Okada 1956)              |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>emeishanensis</i> Hu & Toda 1999         |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>chaoi</i> Hu & Toda 1999                 |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>pseudotenuicauda</i> (Toda 1983)         |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>flexicauda</i> (Okada 1966)              |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>alticola</i> Hu, Watabe & Toda 1999      |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>presuturalis</i> Hu & Toda 1999          |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>shennongjiana</i> Hu & Toda 1999         |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>yeren</i> Hu & Toda 1999                 |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>acutissima</i> (Okada 1956)              |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>harpophallata</i> Hu, Watabe & Toda 1999 |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>cyanea</i> (Okada 1988)                  |
| <i>Lordiphosa</i>      |                           | <i>tenuicauda</i>    | <i>pseudocyanea</i> Hu & Toda 1999          |
| <i>Dichaetophora</i>   |                           |                      | sp. n., aff. <i>aberrans</i> (Burla 1954)   |
| <i>Dichaetophora</i>   |                           |                      | <i>agbo</i> (Burla 1954)                    |
| <i>Dichaetophora</i>   |                           |                      | <i>suruku</i> (Burla 1954)                  |
| <i>Nesiodrosophila</i> |                           |                      | <i>sakagamii</i> Toda 1989                  |
| <i>Nesiodrosophila</i> |                           |                      | <i>raridentata</i> (Okada & Chung 1960)     |
| <i>Nesiodrosophila</i> |                           |                      | <i>delicata</i> Wheeler & Takada 1981       |
| <i>Nesiodrosophila</i> |                           |                      | <i>ogasawarensis</i> Toda 1987              |
| <i>Nesiodrosophila</i> |                           |                      | <i>surukella</i> (Okada 1965)               |
| <i>Nesiodrosophila</i> |                           |                      | <i>okadai</i> Nishiharu 1981                |
| <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 1961              |
| <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 1832)               |
| <i>Hirtodrosophila</i> |                           | <i>hirticornis</i>   | <i>nokogiri</i> (Okada 1956)                |
| <i>Hirtodrosophila</i> |                           | <i>quadrivittata</i> | <i>quadrivittata</i> (Okada 1956)           |

## Materials and methods

*Species studied.* – All the thirteen known species of the *L. tenuicauda* group (Hu et al. 1999), three species of *Dichaetophora* and six species of *Nesiodrosophila* were selected for this study (Tab. 1). In addition, representatives of the drosophiline genera, *Scaptomyza*, *Hirtodrosophila* and *Drosophila*, were included because the relationships of these genera to the focal taxa remain uncertain (Hu & Toda 2001). We followed the generic classification revised by Grimaldi (1990), where some subgenera such as *Hirtodrosophila* and *Lordiphosa* of *Drosophila* were elevated to the generic rank in light of the cladistic analysis. As outgroup, we chose *Drosophila (Sophophora) obscura* Fallén, based on the results of Hu & Toda (2001): the clade of *Sophophora* + the major *Lordiphosa* was placed as the sister group to the clade of above taxa, and *D. obscura* was placed at the most ancestral position in the former clade.

*Observation.* – The specimens studied were preserved in 70% ethanol or dried and pinned. The dry, pinned specimens were softened by warming in 70% ethanol for several minutes before dissection. Mouthparts and male and female terminalia were removed and cleared in a 10% KOH solution at 100°C for several minutes before being examined in a droplet of glycerol under a compound light microscope. Drawings were made on the basis of microscope photographs taken by a digital camera that was connected with a computer. Ordinary and scanning electron microscope photographs were taken of some characters.

*Phylogenetic analyses.* – The data analysis was performed using PAUP version 3.1.1 (Swofford 1993). Memory and processor limitations required us to use an approximate (heuristic) searching strategy. The applied strategy used random taxon-addition sequence and tree bisection-reconnection (TBR) branch-swapping methods. Such a 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 optimization was performed using DELTRAN (delayed transformation) and ACCTRAN (accelerated transformation). Branch support was quantified in two ways: bootstrap analysis with 1000 replicates and Bremer analysis (Bremer 1994). A heuristic search method with 'simple' addition

sequence and the TBR procedure was applied to the bootstrap analysis. Bremer support was calculated, using PAUP version 3.1.1 (Swofford 1993) 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 most parsimonious cladogram.

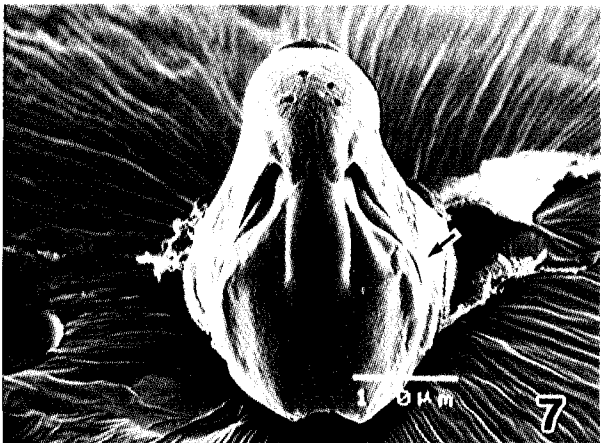
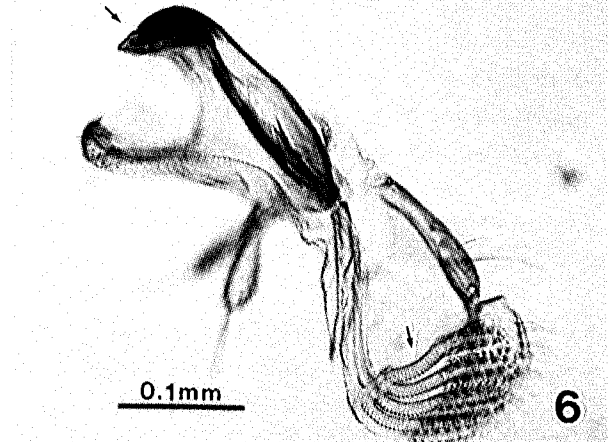
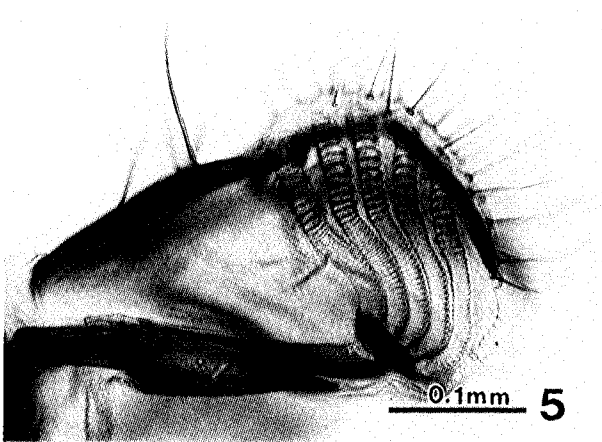
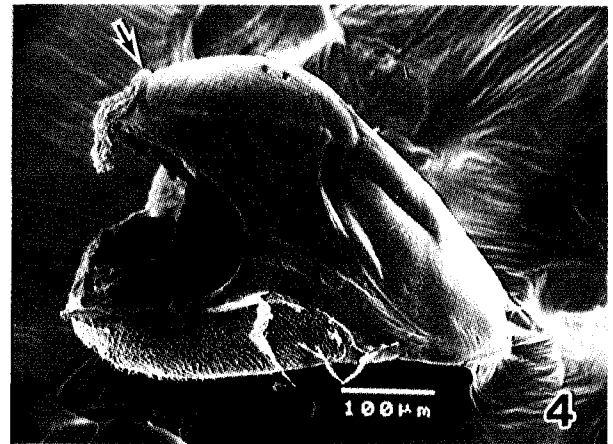
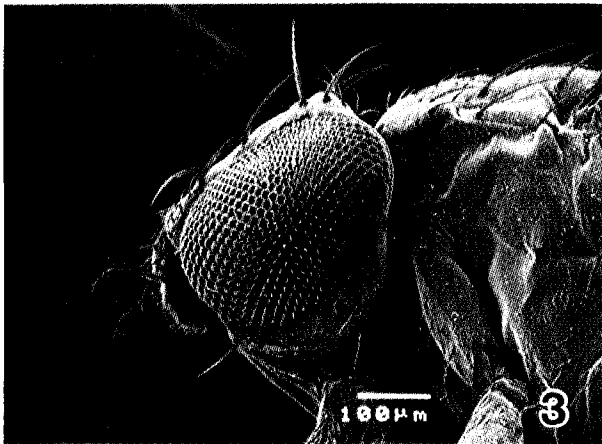
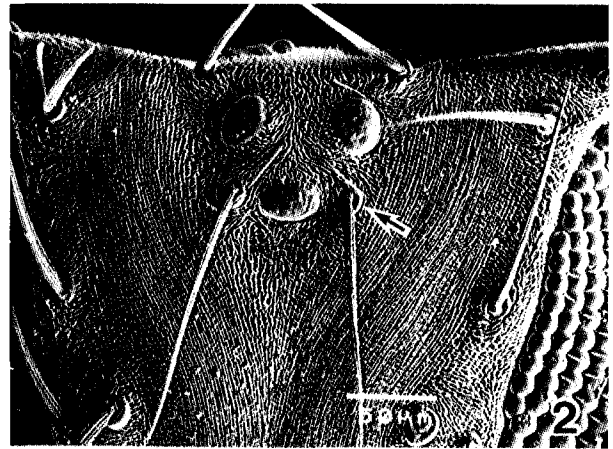
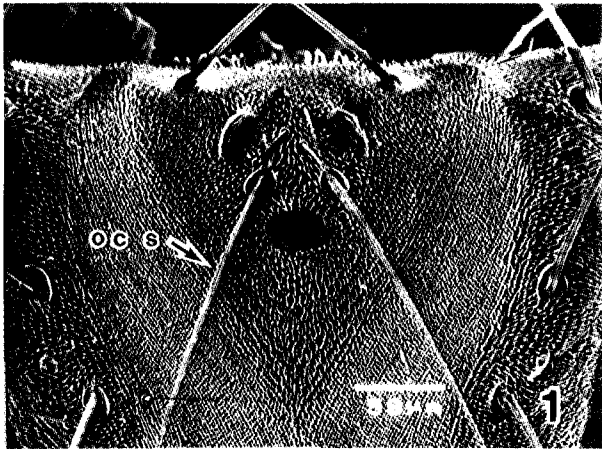
*Characters.* – Characters used for this study were selected from Hu & Toda (2001), with the addition of several new characters. A total of 30 characters of male and female adult morphology were analysed. Character polarity was determined by the outgroup comparison method (Watrous & Wheeler 1981) that all characters of the outgroup species, *Drosophila obscura*, were coded as 0. All transformation series were assumed to be 'unordered'. Many characters correspond to those of Hu & Toda (2001), in which case the character number in Hu & Toda (2001) is given in parentheses as 'HT#'.

### Head:

- Ocellar setae; (0) inside triangle made by ocelli (Fig. 1), (1) outside (Fig. 2).
- Eye, longest axis; (0) nearly rectangular to body axis, (1) distinctly oblique (Fig. 3).
- Frons, profile line from base to ptilinal fissure; (0) convex, (1) nearly straight (Fig. 3).
- Palpus, number of prominent long setae; (0) only one, (1) 2 or more.
- Setulae on basal lobe of palpus; (0) a few present, (1) absent. (HT5).
- Cibarium, anterior margin; (0) thickened, somewhat triangularly protruded in lateral view (Fig. 4), (1) not thickened (Fig. 6).
- Hypopharynx, apodeme; (0) absent or almost flat, (1) expanded in anterior portion. (HT7).
- Cibarium, dorsal wall; (0) pear-shaped, with posterior portion oval (Fig. 7), (1) medially constricted, with posterior portion parallel-sided (Fig. 8), (2) oval or oblong, medially without constriction (Fig. 9).
- Cibarium, anterior end; (0) not dilated laterad (Fig. 9), (1) more or less dilated (Fig. 10).
- Cibarium, anterolateral corners; (0) distinctly protruded (Fig. 9), (1) only slightly protruded (Fig. 10).
- Labellum, number of pseudotracheae; (0) 6 or more, (1) 5 (Fig. 5), (2) 4 (Fig. 6).
- Arista, number of ventral branches excluding terminal fork; (0) 2 or more, (1) only one. (HT16).
- Subvibrissal seta, length; (0) distinctly shorter than vibrissa, (1) nearly subequal to vibrissa and prominently longer than other orals.

### Thorax:

- Acrostichal setulae, number of rows; (0) 6 or more, (1) 4 or less. (HT20).



15. Mid katapisternal seta, length; (0) present, distinctly longer than other setulae below it, (1) absent or indistinguishable from others. (HT22).

#### Legs:

16. Fore tibia, preapical dorsal seta; (0) present (Fig. 11, 12), (1) absent.  
 17. Fore tibia, apical seta; (0) as thin as preapical dorsal or neighboring setae (Fig. 11), (1) distinctly stout (Fig. 12).  
 18. Mid tibia, preapical dorsal seta; (0) present, (1) absent.

#### Male terminalia:

19. Epandrium, setae; (0) present not only on ventral portion but also on other portions, (1) only on ventral portion. (HT28).  
 20. Surstylus, fusion to epandrium; (0) fused, (1) separated but articulated. (HT29).  
 21. Surstylus, stout or peg-like setae on outer mesal surface; (0) absent, (1) present (Fig. 13).  
 22. Surstylus, pubescence; (0) absent, (1) covering nearly entirely or partly (Fig. 13).  
 23. Cercus, fusion to epandrium; (0) separated, (1) fused. (HT33).  
 24. Hypandrium, paramedian setae; (0) present, (1) absent. (HT37).  
 25. Paramere, fusion to hypandrium; (0) separated, (1) fused. (HT39).  
 26. Paramere, fusion to aedeagus; (0) articulated with aedeagus (Fig. 17, 18), (1) fused to aedeagus, (2) fused to aedeagal guide. (HT41).  
 27. Paramere, shape; (0) elongated, more or less sclerotized (Fig. 17), (1) plate-like (Fig. 18), (2) small, somewhat conical or hemispherical.  
 28. Paramere, pubescence; (0) absent (Fig. 17), (1) partly covering (Fig. 18).  
 29. Aedeagus, basal processes; (0) present (Fig. 17), (1) absent (Fig. 18).

#### Female terminalia:

30. Oviscapt, apical ovisensillum; (0) neither so robust nor the largest among marginal ones (Fig. 14), (1) robust and the largest, distinguishable from the others (Fig. 15, 16).

## Results and discussion

The heuristic analysis of the data matrix (Tab. 2) resulted in 12 equally most parsimonious cladograms of length 76 steps with the following statistics: CI (consistency index) = 0.447, RI (character retention index) = 0.825 and *ti* (total support

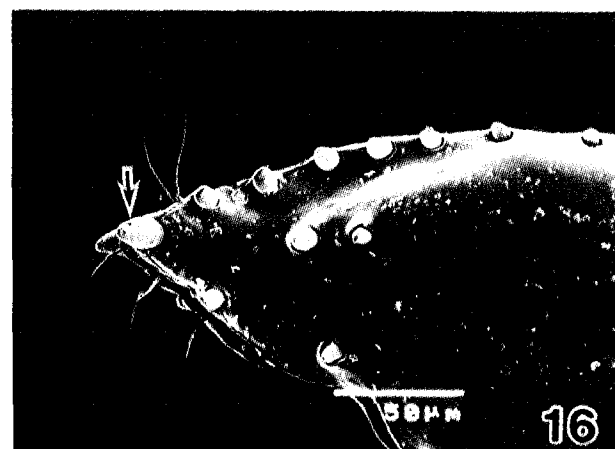
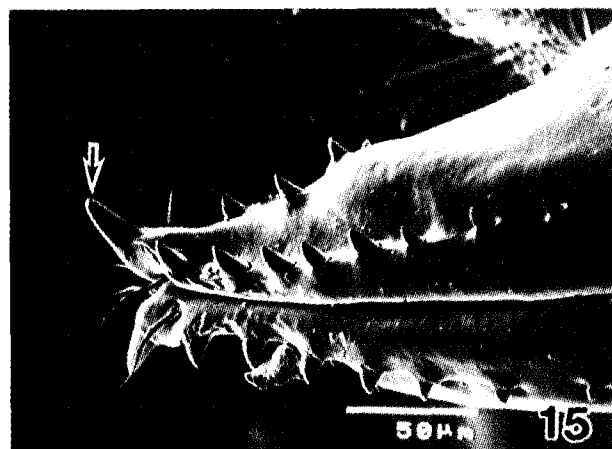
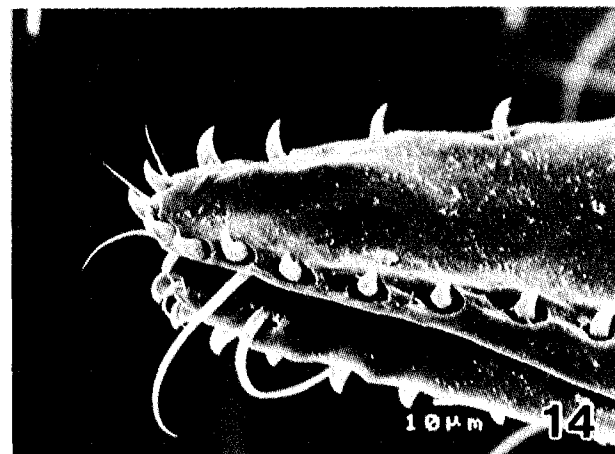
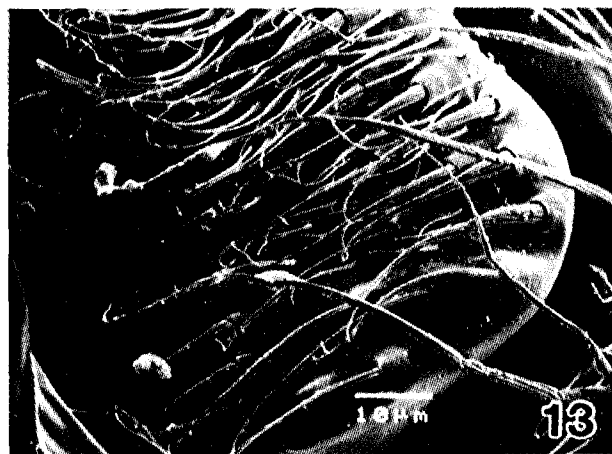
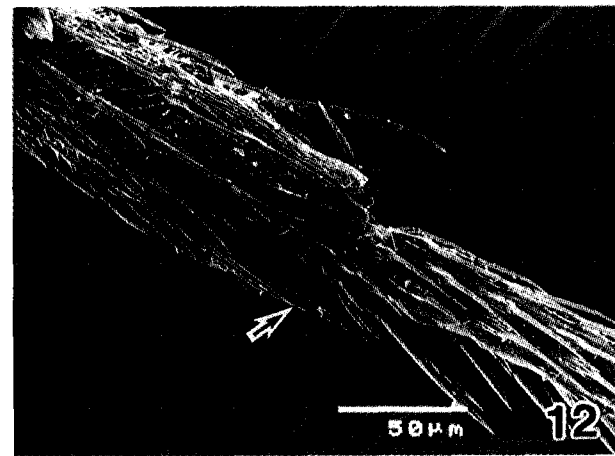
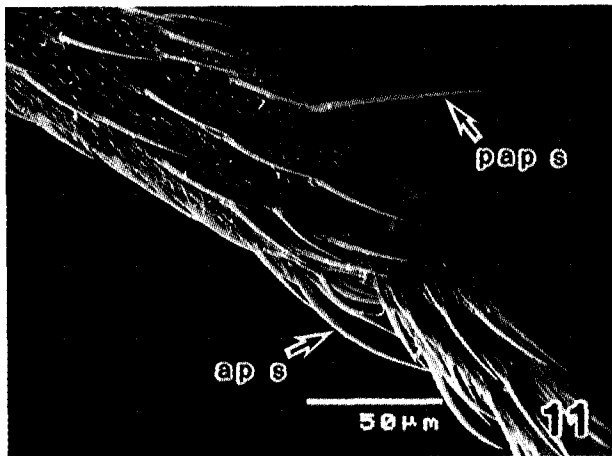
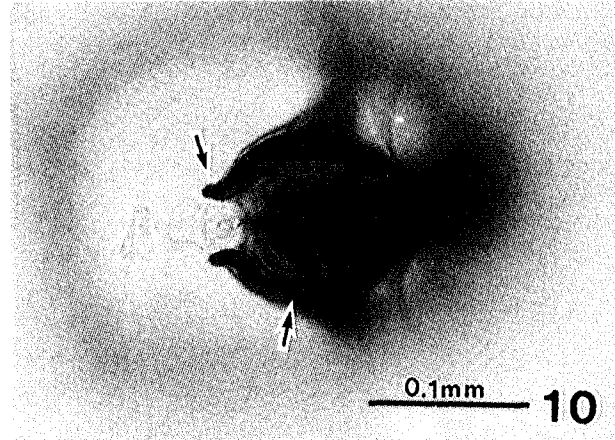
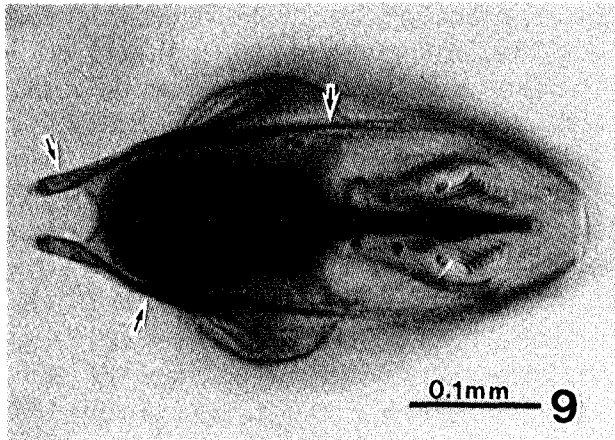
index) = 0.37. Figure 19 shows the strict consensus tree. Apomorphies are indicated on each branch of this cladogram, based on the results of character optimization. Although DELTRAN and ACCTTRAN yielded the same result for most transformation series, different hypotheses for character evolution were produced for transformation series 4, 15, 26 and 27. Synapomorphies not identified by both DELTRAN and ACCTTRAN are excluded from the following discussion. Bootstrap frequency and Bremer support value are indicated above and below within a circle at each branch, respectively.

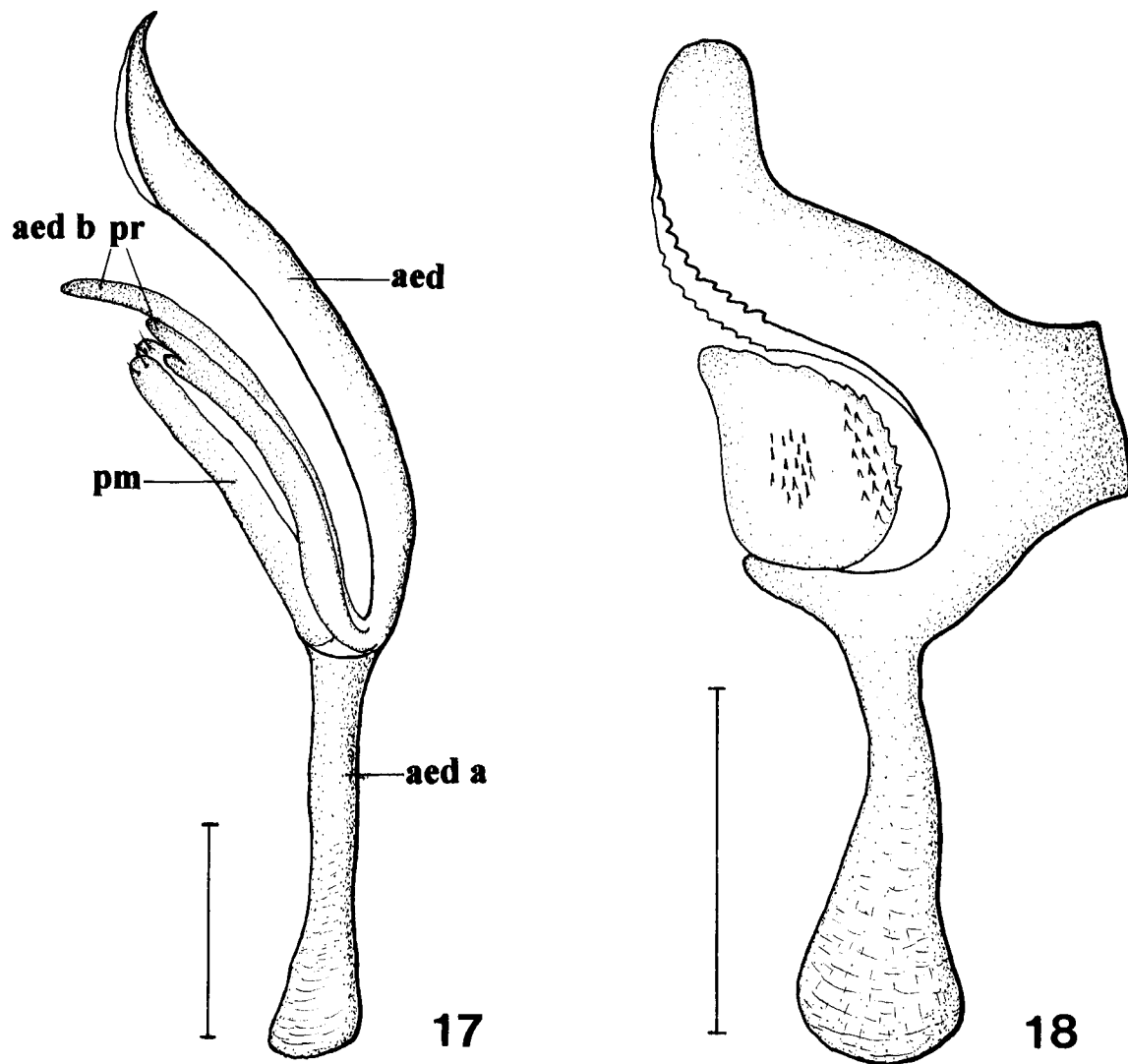
The cladogram shows that *Dichaetophora*, *Nesiodrosophila* and the *L. tenuicauda* group constitute a monophyletic group strongly supported (bootstrap value = 85.6%, Bremer support = 4 steps) by the following synapomorphies: the cibarium only slightly protruded at anterolateral corners (ch.10-1) and the oviscapt with apical ovisensillum robust and the largest among the marginals (ch.30-1) as autapomorphies, and the ocellar setae outside triangle made by ocelli (ch.1-1; homoplasies seen in *Drosophila transversa* Fallén and *Scaptomyza graminum* (Fallén); but the ocellar setae arising inside triangle made by ocelli, ch.1-0, in *Lordiphosa harpophallata* Hu, Watabe & Toda regarded as a secondary reversal), the absence of setulae on the basal lobe of palpus (ch.5-1; a homoplasy seen in the genus *Hirtodrosophila*), the anteriorly expanded hypopharyngeal apodeme (ch.7-1; a homoplasy seen in the subgenus *Drosophila*), and the less than six pseudotracheae in labellum (ch.11-1,2; the five pseudotracheae regarded as having evolved independently also in *Hirtodrosophila nokogiri* (Okada)).

Within the above clade three monophyletic groups were recognized: *L. tenuicauda* group A (*tenuicauda* (Okada) + *emeishanensis* Hu & Toda + *chaoi* Hu & Toda + *pseudotenuicauda* (Toda) + *alticola* Hu, Watabe & Toda + *flexicauda* (Okada) + *presuturalis* Hu & Toda + *shennongjiana* Hu & Toda + *yeren* Hu & Toda), *L. tenuicauda* group B (*acutissima* (Okada) + *harpophallata* + *cyanea* (Okada) + *pseudocyanea* Hu & Toda) and *Dichae-*

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Figures 1-8. Some characters used in the phylogenetic analysis: (1) Frons of *Hirtodrosophila quadrivittata*; (2) ditto of *Nesiodrosophila ogasawarensis*; (3) head and thorax (lateral view) of *N. ogasawarensis*; (4) cibarium (lateral view) of *Drosophila virilis*; (5) labellum (lateral view) of *Lordiphosa cyanea*; (6) cibarium and labellum (lateral view) of *Lordiphosa tenuicauda*; (7) cibarium (dorsal view) of *D. virilis*; (8) ditto of *Nesiodrosophila raridentata*. oc s = ocellar seta.





Figures 17, 18. Paramere, aedeagus and aedeagal apodeme (lateral view): (17) *Lordiphosa emeishanensis*; (18) *Lordiphosa pseudocyanea*. Scale-line = 0.1 mm. aed b pr = aedeagal basal process, aed = aedeagus, pm = paramere, aed a = aedeagal apodeme.

*tophora* + *Nesiodrosophila*. The monophyly of *L. tenuicauda* group A was supported (bootstrap value = 77.6%, Bremer support = 2 steps) by the stout setae on the outer mesal surface of surstylus (ch.21-1; a homoplasy seen in a lineage within the subgenus *Drosophila*) and the presence of a pair of processes at the base of aedeagus (ch.29-0; regarded as having secondarily been regained). The monophyly of *L. tenuicauda* group B was justified

(bootstrap value = 77.0%, Bremer support = 2 steps) by the distinctly stout apical seta on the tibia of foreleg (ch.17-1) as an autapomorphy, and the five pseudotracheae in the labellum (ch.11-1; homoplasies seen in a lineage of the genus *Dichaetophora* and *H. nokogiri*) and the partly pubescent paramere (ch.28-1; homoplasies seen in *D. transversa*, *Drosophila virilis* Sturtevant and *S. graminum*). Although these two groups were

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Figures 9-16. Some characters used in the phylogenetic analysis: (9) Cibarium (dorsal view) of *Hirtodrosophila nokogiri*; (10) anterior part of cibarium (dorsal view) of *Lordiphosa tenuicauda*; (11) tibia and 1st tarsomere (apical and basal parts, respectively) of foreleg of *L. tenuicauda*; (12) ditto of *Lordiphosa pseudocyanea*; (13) surstylus (lateral view) of *L. tenuicauda*; (14) oviscapt of *Drosophila immigrans*; (15) ditto of *L. tenuicauda*; (16) ditto of *Lordiphosa acutissima*. pap s = preapical seta, ap s = apical seta.

Table 2. Data matrix for 34 drosophilid species and 30 morphological characters.

|   | 1 |   |   |   |   | 1 1 1 1 1 |   |   |   |   | 1 1 1 1 2 |   |   |   |   | 2 2 2 2 2 |   |   |   |   | 2 2 2 2 3 |   |   |   |   |   |   |   |   |   |   |   |
|---|---|---|---|---|---|-----------|---|---|---|---|-----------|---|---|---|---|-----------|---|---|---|---|-----------|---|---|---|---|---|---|---|---|---|---|---|
|   | 1 | 2 | 3 | 4 | 5 | 6         | 7 | 8 | 9 | 0 | 1         | 2 | 3 | 4 | 5 | 6         | 7 | 8 | 9 | 0 | 1         | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 |   |   |
| <i>D. (Sophophora) 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 |   |   |   |
| <i>Lordiphosa tenuicauda</i>                      | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. emeishanensis</i>                           | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. chaoi</i>                                   | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. pseudotenuicauda</i>                        | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. flexicauda</i>                              | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | ?         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | ? | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. alticola</i>                                | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. presuturalis</i>                            | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. shennongjiana</i>                           | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |   |   |
| <i>L. yeren</i>                                   | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 1         | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | ? |   |   |
| <i>L. acutissima</i>                              | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |   |   |
| <i>L. harpophallata</i>                           | 0 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |   |   |
| <i>L. cyanea</i>                                  | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |   |   |
| <i>L. pseudocyanea</i>                            | 1 | 0 | 0 | 1 | 1 | 1         | 1 | 0 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0         | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |   |   |
| <i>Dichaetophora</i> sp. n., aff. <i>aberrans</i> | 1 | 1 | 1 | 1 | 1 | 1         | 1 | 1 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 0 | 0 | 0 | 1 | 0         | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |   |   |
| <i>D. agbo</i>                                    | 1 | 1 | 1 | 1 | 1 | 1         | 1 | 1 | 1 | 1 | 1         | 0 | 0 | 0 | 0 | 0         | 0 | 0 | 0 | 1 | 0         | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 |   |   |
| <i>D. suruku</i>                                  | 1 | 1 | 1 | 1 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 |   |
| <i>Nesiodrosophila sakagamii</i>                  | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 |   |   |
| <i>N. raridentata</i>                             | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |   |   |
| <i>N. delicata</i>                                | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |   |   |
| <i>N. ogasawarenensis</i>                         | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |   |   |
| <i>N. surukella</i>                               | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 |   |
| <i>N. okadai</i>                                  | 1 | 1 | 1 | 0 | 1 | 1         | 1 | 1 | 1 | 1 | 2         | 0 | 0 | 1 | 1 | 0         | 0 | 0 | 0 | 1 | 0         | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 |   |   |
| <i>D. (Drosophila) testacea</i>                   | 0 | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 0 | 1 | 0 | 0         | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |   |
| <i>D. immigrans</i>                               | 0 | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |   |
| <i>D. transversa</i>                              | 1 | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 1 | 0 | 0 | 1         | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |   |
| <i>D. funebris</i>                                | 0 | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 1 | 0 | 0 | 1         | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 |   |
| <i>D. hydei</i>                                   | 0 | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |   |
| <i>D. virilis</i>                                 | 0 | 0 | 0 | 0 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | 0         | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |   |
| <i>D. (Dorsilopha) busckii</i>                    | 0 | 0 | 0 | 1 | 0 | 0         | 0 | 1 | 0 | 0 | 0         | 0 | 1 | 0 | 1 | ?         | 0 | 0 | 0 | 0 | 0         | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 0 | 1 | 0 |   |
| <i>S. (Parascaptomyza) pallida</i>                | 0 | 0 | 0 | 0 | 0 | 1         | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 0 | 1 | 1 | 0         | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 1 |   |
| <i>S. (Scaptomyza) graminum</i>                   | 1 | 0 | 0 | 1 | 0 | 1         | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0         | 0 | 0 | 1 | 0 | 0         | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 |   |
| <i>Hirtodrosophila nokogiri</i>                   | 0 | 0 | 0 | 0 | 1 | 1         | 0 | 2 | 0 | 0 | 1         | 1 | 0 | 0 | 1 | 1         | 0 | 1 | 0 | 0 | 0         | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| <i>H. quadrivittata</i>                           | 0 | 0 | 0 | 1 | 1 | 1         | 0 | 2 | 0 | 0 | 0         | 1 | 0 | 0 | 1 | 1         | 0 | 1 | 0 | 0 | 0         | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |

placed as the sister groups, the monophyly of the *L. tenuicauda* group as a whole was not strongly supported (bootstrap value = 36.6%, Bremer support = 1 step). The third monophyletic group, *Dichaetophora* + *Nesiodrosophila*, was supported (bootstrap value = 83.7%, Bremer support = 3 steps) by the following three auto- and two synapomorphies: eye with the longest axis distinctly oblique to the body axis (ch.2-1), very flat frons (ch.3-1), the cibarial dorsal wall with posterior portion parallel-sided (ch.8-1), the cercus fused to the epandrium (ch.23-1; homoplasies seen

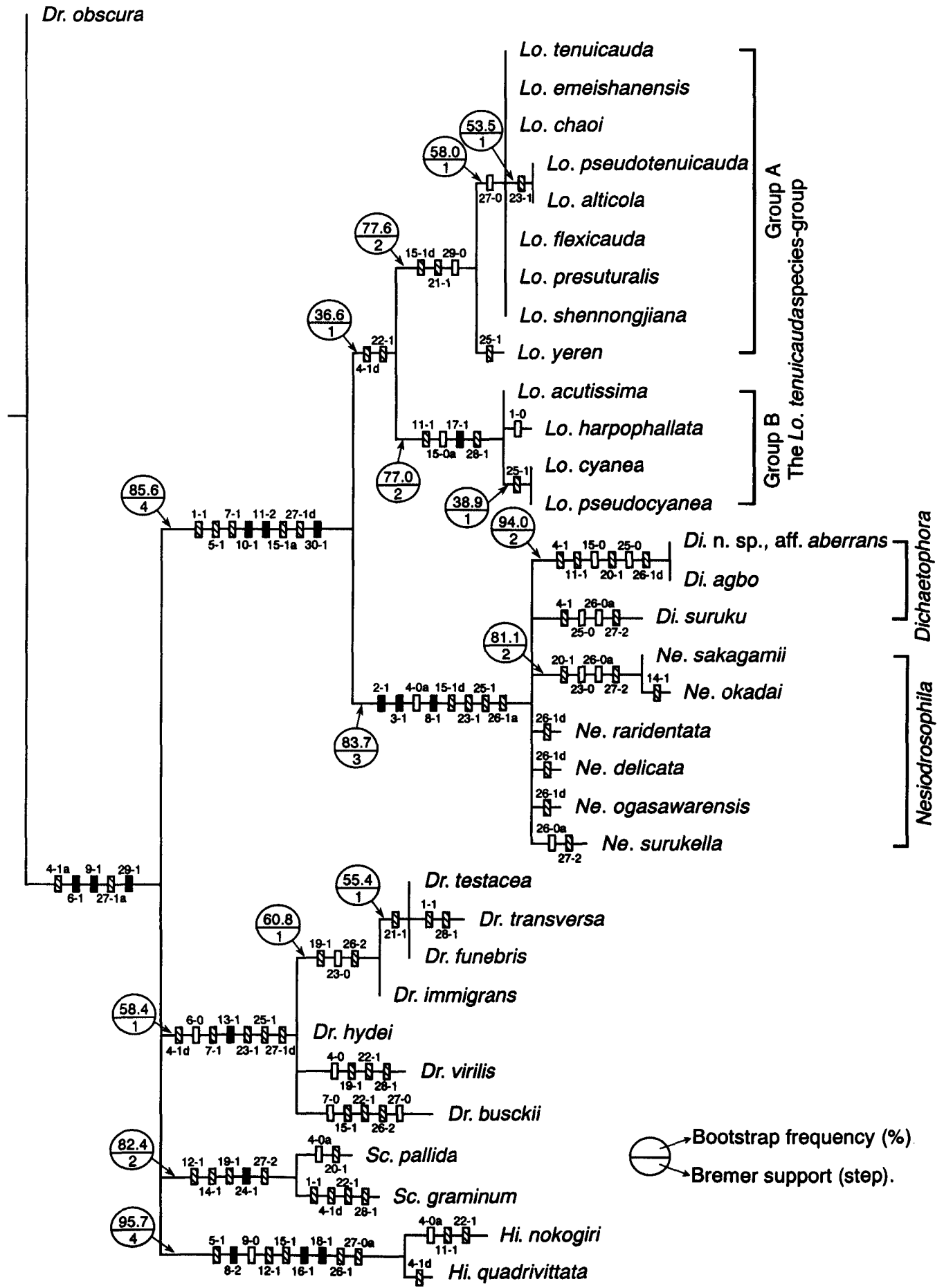
in a lineage of *L. tenuicauda* group A and the subgenus *Drosophila*; but a secondary reversal to the plesiomorphic state, ch.23-0, seen in *Nesiodrosophila sakagamii* Toda + *Nesiodrosophila okadai* Nishiharu) and the paramere fused to the hypandrium (ch.25-1; homoplasies seen in *L. yeren*, a lineage of *L. tenuicauda* group B and the subgenus *Drosophila*; but a secondary reversal to ch.25-0 seen in the genus *Dichaetophora*).

In addition, the genus *Scaptomyza* and *Hirtodrosophila* were each recognized as monophyletic (bootstrap value = 82.4% and 95.7%, Bremer sup-

→

Figure 19. The strict consensus of 12 most parsimonious cladograms obtained using PAUP (length = 76, CI = 0.447, RI = 0.825, *ti* = 0.37), with indication of apomorphies (solid hashmark indicates non-homoplasious change, stripe mark homoplasious change, and open mark reversal; different results from ACCTRAN and DELTRAN are marked with 'a' and 'd', respectively).





port = 2 and 4 steps, respectively), reconfirming the results of Hu & Toda (2001).

However, the present study could not reveal the phylogenetic position of the clade comprising *L. tenuicauda* group A + *L. tenuicauda* group B + *Dichaetophora* / *Nesiodrosophila* within the in-group drosophiline taxa. In a molecular phylogenetic study with alcohol dehydrogenase gene by Katoh et al. (2000), also, the position of the *L. tenuicauda* species-group was uncertain: this group was placed as the sister group to the clade of *Hirtodrosophila* + *Mycodrosophila* in the minimum-evolution (Rzhetsky & Nei 1992) tree, but as sister taxa, not comprising a monophyletic group, to the clade of the *D. virilis* section + Hawaiian drosophilids in the most parsimonious tree, although bootstrap values were relatively low in both trees. Thus, to clarify the phylogeny at the suprageneric level more genera and genes, especially some evolving more slowly, are needed to be included in further studies.

### Classification

The clade composed of *L. tenuicauda* group A, *L. tenuicauda* group B and *Dichaetophora* + *Nesiodrosophila* was placed at a similar level to other genera, and should, therefore, be assigned to the generic rank. According to the nomenclatural priority, we apply *Dichaetophora* to the name of this revised genus, and *Nesiodrosophila* becomes a junior synonym. Furthermore, we assign species-groups to the three monophyletic groups within this expanded *Dichaetophora*. The revised classification is given below, with the generic diagnosis, a key to species-groups and details of the component species of each species-group.

#### Genus *Dichaetophora* Duda, 1940

*Dichaetophora* Duda 1940: 19 (also as *Dichaetophila*, error). Type species: *Drosophila aberrans* Lamb, 1914.

*Nesiodrosophila* Wheeler & Takada 1964: 238. Type species: *Nesiodrosophila lindae* Wheeler & Takada, 1964. **Syn. n.**

**Diagnosis.** – The cibarium only slightly protruded at anterolateral corners; the oviscapt with apical ovisensillum robust and the largest, distinguishable from the others (also seen as a synapomorphy, ap. 213 of Grimaldi 1990, in some drosophiline genera not included in the present study, such as *Jeannelopsis* Seguy, *Sphaerogastrella* Duda, *Mul-*

*gravea* Bock and *Liodrosophila* Duda); the basal lobe of palpus without setulae; the hypopharyngeal apodeme expanded anteriorly; the labellum with less than six pseudotracheae; the ocellar setae outside triangle made by ocelli (except for *L. harpophallata*).

The above diagnostic characters include some homoplasies seen also in other genera, but in combination clearly discriminate this genus from others. This genus includes the following three species-groups.

### Key to the species-groups

1. Longest axis of eye distinctly oblique to body axis; profile line of frons from base to ptilinal fissure nearly straight; posterior portion of cibarial dorsal wall parallel-sided; surstylus lacking pubescence ..... *agbo* species-group
- Longest axis of eye nearly rectangular to body axis; profile line of frons convex; posterior portion of cibarial dorsal wall oval; surstylus pubescent at least partly ..... 2
2. Scutum yellowish; dm-cu crossvein clear; mid katapisternal seta minute, indistinguishable from other setulae below it; apical seta on tibia of foreleg weak; surstylus with stout spines scattered on outer mesal surface; aedeagus with a pair of basal processes ..... *tenuicauda* species-group
- Scutum brownish to blackish; dm-cu crossvein clouded; apical seta on tibia of foreleg distinctly stout; mid katapisternal longer than other setulae below it; surstylus without stout spines on outer mesal surface; aedeagus without basal processes ..... *acutissima* species-group

### *Dichaetophora agbo* species-group

This species-group includes all the species having been assigned to *Drosophila* (*Dichaetophora*) or *Nesiodrosophila* (except for *N. facilis* Lin & Ting 1971, see below): *aberrans* (Lamb 1914), *agbo* (Burla 1954), *imitans* (Graber 1957), *suruku* (Burla 1954) and sp. n., aff. *aberrans* (Burla 1954) of previous *Drosophila* (*Dichaetophora*); *argentina* (McEvey & Bock 1982), *aristata* (Okada 1984), *brunnea* (Okada 1984), *burmana* (Okada 1984), *carinata* (Bock 1982), *cirricauda* (Okada 1988), *clypeonigra* (Okada 1968), *constricta* (Okada 1988), *delicata* (Nishiharu 1981), *fascifrons* (Okada 1988), *flava* (Nishiharu 1981), *heterodentata* (Okada 1984), *hexachaeta* (Okada 1984), *laeana* (Okada 1984), *lindae* (Wheeler & Takada 1964), *macalpinei* (Bock 1982), *madagascarensis* (Okada 1984), *magnidentata* (Lee 1964), *malayana* (Okada 1984), *mosana* (Bock 1984), *neo-*

*cirricauda* (Gupta & De 1996), *nigrifrons* (Okada 1988), *ogasawarensis* (Toda 1987), *okadai* (Nishiharu 1981), *papuana* (Okada 1984), *para-serrata* (Okada 1988), *pectinata* (McEvey & Bock 1982), *plana* (Bock 1982), *pleurostriata* (Singh & Gupta 1981), *quadrifrons* (Okada 1988), *quelparti-ensis* (Kang, Lee & Bahng 1967), *raridentata* (Okada & Chung 1960), *rotundicornis* (Okada 1966), *sakagamii* (Toda 1989), *sarawakana* (Okada 1984), *serrata* (Okada 1984), *spinipes* (Okada 1984), *sternopleuralis* (Okada 1984), *surukella* (Okada 1965), *tridens* (Okada 1984) and *wulaiensis* (Okada 1984) of previous *Nesiodrosophila*.

### ***Dichaetophora tenuicauda* species-group**

*Drosophila* (*Lordiphosa*) *tenuicauda* species-group: Toda 1983: 473.

*Lordiphosa tenuicauda* species-group: Hu et al. 1999: 105 (part).

This specis-group comprises the following nine species that have been assigned to the genus *Lordiphosa* as a part of the *tenuicauda* group: *alticola* (Hu, Watabe & Toda 1999), *chaoi* (Hu & Toda 1999), *emeishanensis* (Hu & Toda 1999), *flexicauda* (Okada 1966), *presuturalis* (Hu & Toda 1999), *pseudotenuicauda* (Toda 1983), *shen-nongjiana* (Hu & Toda 1999), *tenuicauda* (Okada 1956) and *yeren* (Hu & Toda 1999). In addition, *N. facilis* Lin & Ting 1971 undoubtedly belongs to this specis-group because of sharing all the diagnostic characters shown in the above key.

### ***Dichaetophora acutissima* species-group**

*Lordiphosa tenuicauda* species-group: Hu et al. 1999: 105 (part).

This specis-group comprises the four remaining species of the previous *L. tenuicauda* group: *acutissima* (Okada 1956), *cyanea* (Okada 1988), *harpophallata* (Hu, Toda & Watabe 1999) and *pseudocyanea* (Hu & Toda 1999).

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