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Systematic and biogeographical analyses of the *denticeps* group, with description of two new species (Diptera, Drosophilidae)

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The *denticeps* group OKADA (1967:3) of the subgenus *Hirtodrosophila* DUDA is an extraordinary group among the genus *Drosophila* FALLÉN. Two species are hitherto known of this group and in this paper two new species are to be added. These four species are put into taxometric, especially numerical phyletic, and chorological analyses, which should be necessary, not to say enough, for evaluating systematic relationships of closely related species.

My hearty thanks are due to Dr. H. KUROKAWA and Mr. F. HIHARA, Tokyo Metropolitan University, and Dr. T. SHIROZU, Kyushu University, for their kindness of affording me with precious material. Acknowledgement is also made of partial financial support from the grant of the Japan Society for the Promotion of Science as part of the Japan-U.S. Cooperative Science program.

✓ *Drosophila* (*Hirtodrosophila*) *kurokawai* sp. n.

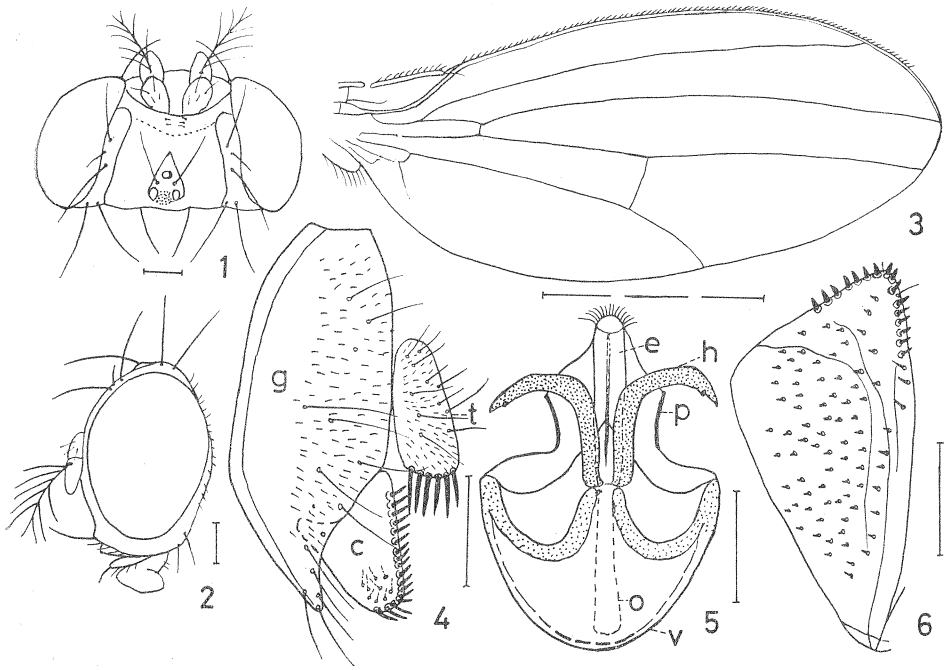
(Figs. 1–6)

♂, ♀. Body about 2.0–2.5 mm in length, dark orange yellow. Eyes oval, pilose. Antenna with second joint dark yellowish brown, third greyish brown. Arista with five upper and two lower long branches beside a moderate fork. Palpi yellowish brown, with a long terminal seta and a few ventral fine setae. Ocellar triangle yellowish brown, caudally black. Periorbits greyish brown. Front dark yellowish brown, anteriorly orange and broader than length down middle, posteriorly broader than half head width. Face flat, greyish brown; carina very short and narrow. Clypeus yellowish brown. Cheek yellowish grey, one-eighth as broad as the greatest diameter of eye. Anterior reclinate orbital one-fourth as long as

Taxometric and chorological analyses of the *denticeps* group, with description of two new species and deduction of key from dendrogram.

proclinate, nearer to proclinate than to posterior reclinate, which is slightly longer than proclinate. Vibrissa strong, other orals fine (Figs. 1, 2). Mesonotum and scutellum mat dark orange yellow, thoracic pleura paler. Humerals two, lower longer. Acrostichal hairs in six rows. Anterior dorsocentrals two-thirds as long as posteriors, distance between anterior and posterior pairs half distance between anterior pair. Anterior scutellars divergent, longer than posteriors, which are nearer to each other than to anteriors. Sterno-index 0.5. Legs yellow, metatarsi slightly shorter than the lest of tarsal joints in fore and mid legs, slightly longer than the rest of trarsal joints in hind legs. Preapicals on all tibiae, apicals prominent on mid tibia. WINGS (Fig. 3) relatively long, somewhat fuscous. R_{2+3} very weakly curved to costa at tip; R_{4+5} and M parallel; crossveins clear. C-index 4.0; 4V-index 1.7; 4C-index 0.7; 5x-index 1.7; Ac-index 2.3. C3-fringe on basal two-fifths. Halteres orange brown. Abdominal tergites dark yellow, with narrow irregularly demarcated caudal dark bands.

Periphallic organs (Fig. 4) pale yellowish brown. Genital arch setigerous and pubescent, dorsally somewhat narrowing, ventrally sharply pointed. Anal plate oblong, pubescent and hairy, ventral margin broadly truncate and with about six large bristles in a row. Clasper trianglular, with about fifteen small pointed black teeth in a straight row. Phallic organs (Fig. 5): Aedeagus pale brown, rod-shaped,



Figs. 1–6. *Drosophila* (*Hirtodrosophila*) *kurokawai* sp. n. 1, 2. Head; 3. Wing; 4. Periphallic organs; 5. Phallic organs, ventral aspect; 6. Egg-guide. c. clasper; e. aedeagus; g. genital arch; h. hypandrial process; o. apodeme of aedeagus; p. posteior parameres; t. anal plate; v. ventral fragma. Scale 1.0 mm for Fig. 3; 0.1 mm for others.

apically with hair crown. A pair of hypandrial processes large, long, black, twice curved ventrally. Posterior parameres fused to become a large flap and seemingly fused with aedeagus. Ventral fragma semicircular. Ejaculatory apodeme with stalk weakly dilated distally, plate two-thirds as long as stalk. Egg-guide (Fig. 6) pale orange, dorsally much convexed, apically triangular, with about twenty-five black marginal teeth and about fifty-five small paler teeth scattered on the lobe; basal isthmus very short.

Testis bright yellow, with three outer and two inner thick coils. Vasa deferentia slender, with short common duct. Paragonia hyaline, thick, once folded. Spermatheca conical, black, duct intromittent less than half way of the theca. Parovaria as long as spermathecal duct, knob weakly swollen. Ventral receptacle slender, with about two loose folds. Mid-intestine with three coils. Malpighian tubules with short common ducts, posterior branches completely looped. Rectal papillae four, pointed, two-fifths as broad as long.

Holotype. ♂, Asakawa, Tokyo, 29 XI 1970 (KUROKAWA).

Allotype. ♀, Dôryusan, Kanagawa Pref., 28 XI 1966 (OKADA).

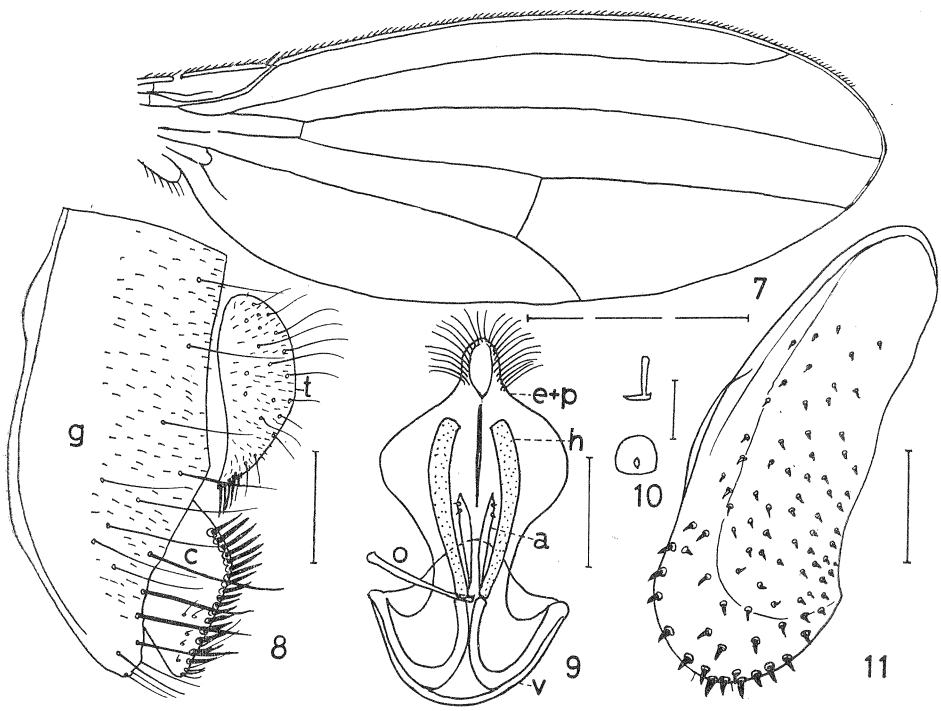
Paratypes. 1♂, Asakawa, Tokyo, 24 X 1957 (KUROKAWA); 2♀, Taishakukyo, Hiroshima Pref., 25 X 1958 (OKADA); 1♂, Chichibu, Saitama Pref., 1 XI 1970 (HIHARA).

Relationships. Closely allied to *D. denticeps* OKADA and SASAKAWA in having relatively long wings, bristly anal plate, numerous discal teeth of egg-guide, and large elongate hypandrial processes. It differs from *denticeps*, however, in having two ventral branches of arista (single in *denticeps*), ventrally truncate anal plate (pointed in *d.*), thick and apically not forked hypandrial processes (slender and apically forked in *d.*), ventrally more sharply pointed genital arch, more numerous discal teeth of egg-guide, and much fewer coils of ventral receptacles.

Drosophila (*Hirtodrosophila*) *paradenticeps* sp. n.
(Figs. 7–11)

♂, ♀. Body about 2.5–3.0 mm in length, greyish yellow. Eye dark reddish brown, with thick piles. Antenna orange, Arista with four upper and one lower branches beside a large fork. Palpi orange yellow, slender, with an apical stout seta. Ocellar triangle and clypeus orange brown. Periorbits yellowish grey, short. Postverticals very long. Front mat orange grey, anteriorly slightly broader than length down middle, posteriorly two-thirds as broad as head width. Face yellowish grey, flat. Carina narrow and short. Cheek orange yellow, one-fifth as broad as the greatest diameter of eye. Anterior reclinate orbitals fine, slightly nearer to proclinate than to posterior reclinate. Vibrissa strong, second oral four-fifths as long as vibrissa, succeeding orals smaller. Mesonotum mat dark orange, caudomedially darker. Scutellum mat yellowish orange, triangularly pointed. Thoracic pleura orange brown. Humerals two, lower longer. Acrostichal hairs in six rows. Anterior dorsocentrals two-thirds as long as posteriors, distance between anterior and posterior pairs four-sevenths distance between anterior pair. Anterior scutellars divergent, longer than posteriors, which are also divergent and

nearer to each other than to anteriors. Sterno-index 0.7. Legs yellowish orange; metatarsi longer than the rest of tarsal joints. Preapicals on all tibiae. Wings relatively long, slightly fuscous. R_{2+3} apically curved to costa; R_{4+5} and M distally nearly parallel. C-index 3.5; 4V-index 1.2; 4C-index 0.6; 5x-index 1.5; Ac-index 2.7. C1-bristles two, unequal; 3C-fringe on basal four-ninths. Halteres orange yellow. Abdominal tergites yellowish brown, with narrow caudal black bands which are interrupted medially.



Figs. 7–11. *Drosophila* (*Hirtodrosophila*) *paradenticeps* sp. n. 7. Wing; 8. Periphallic organs; 9. Phallic organs, ventral aspect; 10. Ejaculatory apodeme; 11. Egg-guide. a. anterior paramere; other signs as in Figs. 1–6. Scale 1.0 mm for Fig. 7; 0.1 mm for others.

Periphallic organs (Fig. 8) yellow. Genital arch setigerous and pubescent, ventrally triangular. Anal plate setigerous and pubescent, ventrally narrowly pointed, with an apical tuft of several stout black bristles. Clasper broad, distally with a convexed row of about twenty large pointed teeth. Phallic organs (Fig. 9): Aedeagus completely fused to posterior parameres, orange brown, apically with a crown of long hairs. Anterior parameres pale yellow, small but slender, subapically with a few sensilla. Apodeme of aedeagus very short. A pair of hypandrial processes dark brown, thick, long, and gently looped. Posterior parameres fused to compose a roof-like flap. Ventral fragma hemispherical. Ejaculatory apodeme as in Fig. 10. Egg-guide (Fig. 11) orange brown, elliptical, broadly rounded at

tip, with about twelve black marginal teeth and about sixty minute yellowish discal scattered teeth.

Holotype ♂, allotype ♀, and paratypes 6♂, 1♀, Alishan, Taiwan, swept among vegetation at swanpy places, 14 VIII 1967 (OKADA).

Relationships. Resembles *D. tripartita* OKADA from Nepal in having ventrally pointed anal plate, ventrally gently narrowing genital arch, small apodeme of aedeagus, and thick and long hypandrial processes. It differs from *tripartita*, however, in having aedeagus fused to posterior parameres (separated in *t.*), anterior parameres well developed (absent in *t.*), and egg-guide apically rounded (triangular in *t.*)

Drosophila (*Hirtodrosophila*) *denticeps* OKADA and SASAKAWA

Drosophila (*Hirtodrosophila*) *denticeps* OKADA and SASAKAWA, 1956. Akitsu, 5: 26 (Japan).

Previously recorded from Tohoku, Kanto, and Chubu Districts of Honshu, additional data being Kinki District, 2♀, Kibune, Kyoto Pref., 17X 1967 (OKADA) and Kyushu District, 1♂, Mt. Kuju, between Karaike and Makimoto, Ooita Pref., 17 VI 1968 (SHIROZU).

Drosophila (*Hirtodrosophila*) *tripartita* OKADA

Drosophila (*Hirtodrosophila*) *tripartita* OKADA, 1966, Bull. Brit. Mus. (NH), Entom. Suppl. 6: 78 (Nepal).

The organs identified by me (op. cit.: 78) as anterior parameres are found to be "hypandrial processes" through the finding of true anterior parameres in *D. paradenticeps*.

Taxometric analysis

To find the systematic relationships of the four species of the *denticeps* group, ten major diagnostic characters, each coded fundamentally in two states, are put in analyses. Proximity analysis (CARMICHAEL and SNEATH, 1969) by means of MCD (mean character distance of Cain and Harrison) and of S_{RR} (coefficient of Russel and Rao) and cluster analysis by UPGA (unweighted pair-group analysis using average linkage) are adopted. The dendrogram resulted from MCD and UPGA is shown in Fig. 12. It shows that *D. denticeps* and *D. tripartita* are compactly clustered together and *D. kurokawai* and *D. paradenticeps* are connected to them successively. The dendrogram obtained from S_{RR} and UPGA is similar as in that from MCD and UPGA, merely different from the latter in the relative levels of branching, which are indicated by numerical figures in parentheses in Fig. 12. The CPCC (cophenetic correlation coefficient) between the original $n \times n$ table and the matrix derived from dendrogram is higher in S_{RR} (0.89) than in MCD (0.85) analysis. Furthermore, the S_{RR} coefficient, in which negative matches are excluded from numerator ($S_{RR}=n_{JK}/n$), coincides with the simple concrodance of derived states (Throckmorton, 1968), and they eventually conform to synapomorphy principle of Hennig (1966). Consequently, at least for constructing a "phyletic" dendrogram it can

Table 1. Data table of four *denticeps*-group species compared over ten diagnostic characters, each of which is coded in two states, 0 and 1, after making adjustment. For further explanation see in the text.

	Species	*denticeps*	*tripartita*	*kurokawai*	*paradenticeps*
1.	Ventral branches of arista two (0) or one (1)	1	0	0	1
2.	Preapicals of fore tibia distinct (0) or obscure (1)	1	0	0	0
3.	Lower tip of genital arch triangular (0) or pointed (1)	0	0	1	0
4.	Clasper teeth row straight (0) or convexed (1)	0	0	0	1
5.	Lower tip of anal plate truncate (0) or pointed (1)	0.5	1	0	1
6.	Hair crown of aedeagus large (0) or small (1)	1	1	0	0
7.	Aedeagus and posterior parameres fused (0) or separated (1)	1	1	0	0
8.	Anterior parameres present (0) or absent (1)	1	1	1	0
9.	Apodeme of aedeagus longer (0) or shorter (1) than aedeagus	0	1	0	1
10.	Egg-guide apically rounded (0) or triangular (1)	1	1	1	0
	Divergency Index (d.i.)	6.5	6.0	3.0	4.0

be said that S_{RR} analysis is superior to MCD analysis.

In preparing $n \times t$ data table, each character (t) was coded in two states, 0 and 1, except for the charcter 5, for which an intermediate step, 0.5, was inserted. The order of character states for each character was primarily determined either randomly or, if possible, in accordance with presumed phylogenetic evidence, and secondarily adjusted so as to match the irreversibility and parsimony principles of evolution (CAMIN and SOKAL, 1965; SOKAL, 1966). Adjusting coding order might be the procedures to gain the most parsimonious dendrogram, and this is accomplished after provisional clustering on the basis of primary determination of the order of states is made. The adjusted orders of coding are given in Table 1. In general, the adjusted orders are such as acceptable in view of presumed phylogeny except for the characters 4 and 6, for which no trends of pseudophylogenetic differentiation can be assumed. The coding for character 4 can be reverted without affecting parsimony principle, while that for character 6 would require one more step if reverted. The dendrogram requires only one step for each character, except for characters 1, 5, and 9, which require two steps each. These three characters are shown to have the derived state, 1, common to two major clusters (Fig. 12), and therefore, can be ascribed to "Operational Primitives" of THROCKMORTON (1968: 373), which are deletable from the taxonomic structure.

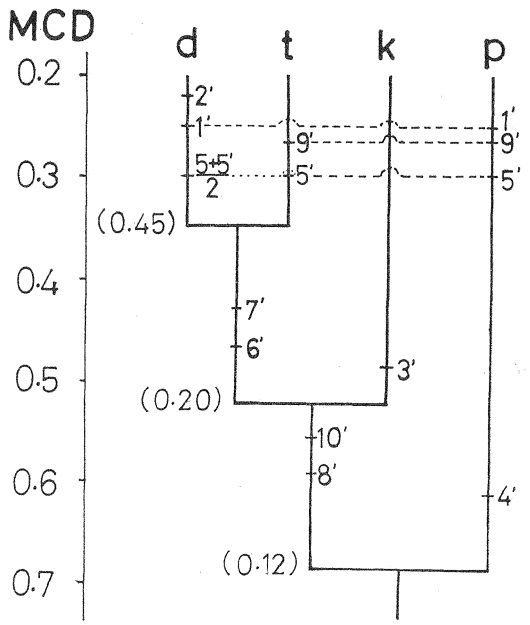


Fig. 12. A dendrogram showing relationships of the four species of the *denticeps* group, based on MCD proximity analysis and UPGA cluster analysis. d. *denticeps*; k. *kurokawai*; p. *paradenticeps*; t. *tripartita*. A short cross bar with dashed numerical figure indicates a step at which the corresponding character might change from state 0 to state 1. The numerical figures in parentheses indicate the branching levels in the case of S_{RR} analysis.

Chorological analysis

The *denticeps* group is assumed to have originated in the Southeast Asiatic Continent. One of the evidences of this assumption is the occurrence of closely related species in Nepal (*tripartita*) and in Japan (*denticeps*). Judging from the divergency index (d. i.; Table 1), which coincides with the sum of code values or steps of total characters for an OTU (OKADA, 1954), *D. kurokawai* (d.i.=3.0) is more primitive than *D. denticeps* (d.i.=6.5). The sequence is proved also by the much simpler ventral receptacle of the former species than that of the latter. Consequently, *D. kurokawai* might not have been derived from *D. denticeps*, and they should have invaded Japan from the Continent independently or allochronically (Fig. 13).

D. denticeps is larger in body size than *D. kurokawai* and the former is distributed in the higher lands and more northward in Japan than the latter is. The sequence of body size differences in relation to distribution ranges between the two species would match Asahina's rule, which refers to that the insect species or groups supposed to have the center of distritution in the southern areas (in the case of Northern Hemisphere) are apt to become larger in body size northward (ASAHINA, 1950).

In this context another evidence is given to the southern origin of the *denticeps* group.

The members of this group have features somewhat intermediate between those of the genera *Drosophila* FALLÉN and *Scaptomyza* HARDY. Comparatively long wings, paired long hypandrial processes, scattered teeth of egg-guide lobes, and leaf-mining larvae are the features sometimes found in common among this group and *Scaptomyza*. While, six rows of acrostichal hairs, two ventral branches of arista, and not much slender bodies, which are found in the most of this group, better fit in *Drosophila*.

Beside the *denticeps* group, there are several drosophilid groups which are thought to be intermediate between the genera *Drosophila* and *Scaptomyza*: e.g., subgenus *Trogloscaptomyza* FREY of the genus *Scaptomyza* (see HARDY, 1965: 573) and subgenus *Engiscaptomyza* KANESHIRO of the genus *Drosophila* (see KANESHIRO, 1969: 80), both occurring in Hawaii Islands and assorted to the "Scaptoids" sens. THROCKMORTON (1966). Some of the *Engiscaptomyza* species have a pair of elongate hypandrial processes resembling that of *denticeps* group. Consequently, it is plausible that the Hawaiian endemic Scaptoid species have had a common ancestor to the Asiatic *denticeps* group. Furthermore, the discovery in Japan of *D. kurokawai*, which is the most primitive species among this group and has two ventral branches of arista and well defined preapicals on fore tibiae, seems to give

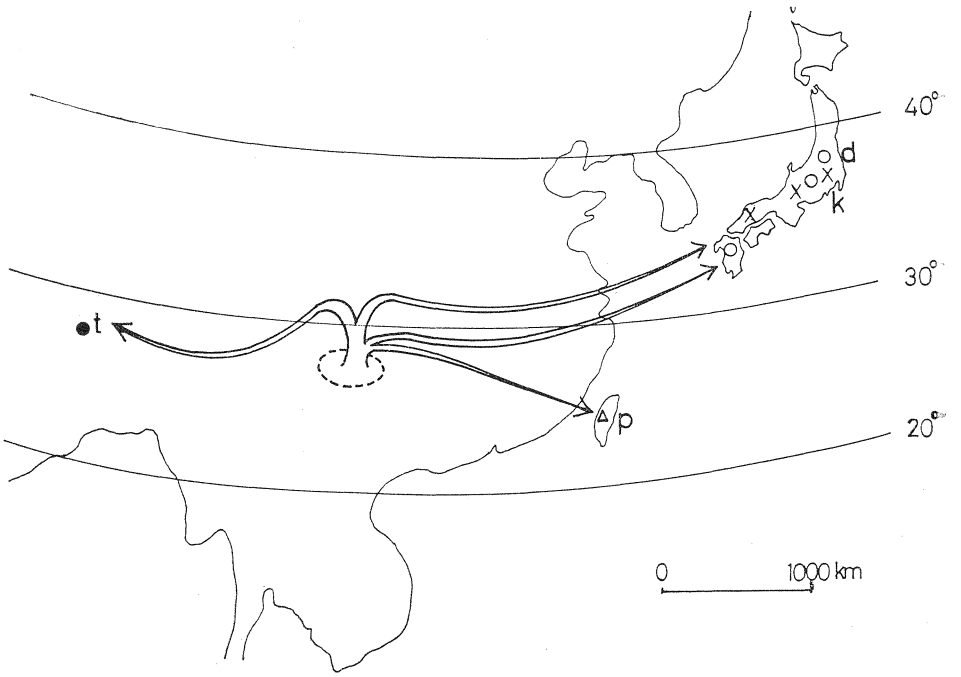


Fig. 13. Distribution, its real states and presumed courses, of the four species of the *denticeps* group. d. *denticeps* (open circle); k. *kurokawai* (cross); p. *paradenicetps* (open triangle); t. *tripartita* (solid circle).

the more concrete evidence for the close connection between the Hawaiian and Japanese endemic species of Drosophilidae than was suggested before (OKADA, 1967: 33).

Construction of a diagnostic key from the dendrogram

The attempts of constructing a diagnostic key from the dendrogram resulted from proximity and cluster analyses have been made by SOKAL and SNEATH (1963: 275) and several microbe taxonomists. The procedures they adopted are 1) to eliminate all those characters which are unsuitable for identification, 2) to select the smallest number of characters required in order to differentiate every taxon from every other one, 3) to make each stage in the key to have only two alternatives, and 4) to find unique combinations of two or more character states.

The following key to species of the *denticeps* group is directly deduced from the informations given in the dendrogram, which are branching sequences of species and adjusted order or steps of character states (Fig. 12). The key would satisfy the above mentioned procedures. The selection of the diagnostic key characters would itself match the procedures 1 and 2, adoption of pair-group method the procedure 4, and citing parsimonious steps of character states the procedures 4. The numerical figures in parentheses appearing in the key indicate the character states, e.g., (8) is state 0 of character 8, and (8′) is state 1 of the same character.

1. Anterior parameres present (8); clasper teeth in a convexed row (4′); egg-guide apically rounded (10) ..... *paradenticeps*
   Anterior parameres absent (8′); clasper teeth in a straight row (4); egg-guide apically triangular (10′) 2
2. Lower tip of genital arch pointed (3′); aedeagus with a large hair crown (6); aedeagus and posterior parameres fused (7)..... *kurokawai*
   Lower tip of genital arch triangular (3); aedeagus with a small hair crown (6′); aedeagus and posterior parameres separated (7′)..... 3
3. Arista with a single ventral branch beside a terminal fork (1′); preapicals on fore tibiae obscure (2′); lower tip of anal plate weakly pointed ((5+5′)/2); apodeme of aedeagus longer than aedeagus (9) ..... *denticeps*
   Arista with two ventral branches beside a terminal fork (1); preapicals on fore tibiae distinct (2); lower tip of anal plate pointed (5′); apodeme of aedeagus shorter than aedeagus (9′)..... *tripartita*

Summary

Analyses were made for the systematic and biogeographical relationships of four species of *denticeps* group of *Drosophila* (*Hirtodrosophila*) including two newly described species, *kurokawai* from Japan and *paradenticeps* from Taiwan. A numerical phyletic analysis resulted in finding the closest relationships of Japanese *denticeps* and Nepalese *tripartita* and the highest primitiveness of *kurokawai*. It was suggested in view of chorology that the *denticeps*-group species had originated in the Southeast Asiatic Continent and that *denticeps* and *kurokawai* had invaded Japan independently or allochronically. Discussion was made on the close rela-

tionships of *denticeps* group and the Hawaiian endemic Scaptoid Drosophilidae. Attempts were made to draw the most parsimonious dendrogram through adjusting coding order of character states and to deduce a diagnostic key directly from the dendrogram. Superiority of S_{RR} to MCD was suggested as a procedure of numerical phyletics.

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