COMPARATIVE MORPHOLOGY OF THE DROSOPHILID FLIES. II

Phallic organs of the subgenus *Drosophila*

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I. Introduction

The phallic organs of the subgenus *Sophophora* of the genus *Drosophila*, especially the *willistoni*,[4,10,22] *obscura*[2,3,7,12,13] and *melanogaster*[21,25,26,27,28] groups, have recently been investigated by several workers, while the knowledge of the organs of the subgenus *Drosophila* s. str. seems to be rather scanty. Malogolowkin[23,24] compared 16 groups of the subgenus, taking one species from each group, and evaluated relative relationships using 50 characters of genitalia. The result he obtained nearly corresponds to the earlier classification of the subgenus. Burla and Pavan[20] proved intimate relationships of the *calloptera*, *tripunctata*, *quinaria*, and *guarani* groups, which are common in having strongly sclerotinized "distal bow", or an organ identical with the present author's "structure like posterior paramere." In the present paper the results of comparison of the organs of 16 Japanese and 4 American species of the subgenus will be reported.

The author wishes to acknowledge his indebtedness to Prof. D. Moriwaki, who has given him kind direction and every facility in carrying out the present work. He also wishes to thank to Dr. J. C. Dan for reading the manuscript, and Messrs. H. Kurokawa, S. Ohba, E. Ohnishi, H. Takada, Y. Yoshida and various other persons who have cooperated in collecting valuable materials of the drosophilid flies. The author desires to acknowledge the aid given this investigation in the form of a grant for Fundamental Science Research of Japan.

II. Descriptions

In order to simplify description for each species and to facilitate comparisons of species or groups, the "phallic formula (p.f.)", "divergency type (d.t.)", "divergency index (d.i)" and "difference value (d.v.)", which were established by the author[26], have been applied here also. Additional to the originally given ten items[26] of the morphological characters of the organs, three more items (11-13) have been chosen; i.e.

11. Aedeagus laterally (L), or horizontally flattened (1).
12. Aedeagus without (M), or with a prominent basal vertical rod on its ventral surface (m).
13. Basal apodeme of the aedeagus as long as or longer than aedeagus (N), or less than half length of aedeagus (n).

Therefore the phallic formula of each species of the *melanogaster* group[26] should be revised by adding alphabetical signs corresponding to these three items,

while the d.t. and d.v. will remain unchanged. The phallic formula, d.t. and d.v. of each species of the subgenus are shown in Table 1.

Table 1. The phallic formula (p.f.), divergency type (d.t.) and divergency index (d.i.) of each species of the subgenus *Drosophila* s. str.

Species	p.f.	d.t.	d.i.	Place of origin of materials examined
virilis section				
D. subtilis Kikkawa & Peng	ABCDEf'g_0HIKlMN	f'g_0l	3.5	Tokyo
D. melanissima K. & P. (nec Sturtevant)	ABCdEf$_0$g$_0$HIklMN	df$_0$g$_0$kl	7.0	Tokyo
D. americana Spencer	a'Bc'dEf$_0$g$_0$HIklm'n'	a'c'df$_0$g$_0$klm'n'	9.0	Texas
D. novamexicana Patterson	a'Bc'dEf$_0$g$_0$HIklm'n'	a'c'df$_0$g$_0$klm'n'	9.0	Texas
D. virilis Sturtevant	a'Bd'cEf$_0$g$_0$HIklm'n'	a'c'df$_0$g$_0$klm'n'	9.0	Otaru, Pasadena
D. robusta gr. I*	a'b'CdEf$_0$g$_0$HIklmn	a'b'df$_0$g$_0$klmn	10.0	Abashiri, Morioka, Tokyo, etc.
D. sordidula K. & P.	a'BCdEf$_0$g$_0$Hiklmn	a'df$_0$g$_0$iklmn	10.5	Morioka, Tokyo, Kiso
D. repleta gr. I	a'BCdEfg$_0$HIkLmn	a'dfg$_0$kmn	7.5	Tokyo
D. hydei Sturtevant	a'BCdEfg$_0$HIkLmn	a'dfg$_0$kmn	7.5	Tokyo
D. gibberosa Patterson & Mainland	aBCdEfg$_0$HIklmn	adfg$_0$klmn	9.0	Mexico
quinaria section				
D. transversa Fallén Type I.	aBCdEfgHIkLMN	adfgk	5.0	Tokyo
D. nigromaculata K. & P.	aBcdEfg'HIkLMN	acdfg'k	5.5	Tokyo
D. testacea van Roser	ab'CdEfgHIkLMN	ab'dfgk	5.5	Hakkoda
D. bizonata K. & P.	ab'CdEfgHIkLMN	ab'dfgk	5.5	Tokyo
D. macrospina Stalk.	abPCdEfg$_0$HIkLMN	ab'dfg$_0$k	6.5	Texas
D. funebris Fabricius	aBCdEfg$_0$HIkl'mn	adfg$_0$kl'mn	8.5	Otaru
D. histrio Meigen	aBcdEfg$_0$HIkLmn	acdfg$_0$kmn	9.0	Towada, Kumotoriyama
D. virgata Tan, Hsu & Sheng	aBCdEfg$_0$HIkLmn	adfg$_0$kmn	8.0	Tokyo
D. immigrans gr. I	aBCdEfgHIkLmn	adfgkmn	7.0	Tokyo
D. immigrans Sturtevant	aBCdEfgHIkLmn	adfgkmn	7.0	Tokyo

* *Drosophila* sp. belonging to the *robusta* group.

III. General characteristics of the phallic organs of the subgenus *Drosophila*

Aedeagus usually not entirely bifid (A=90% of the examined species), non-pectinated (B=90%) and bare (C=75%). Anterior paremeres usually minute (d=95%), connected to the aedeagus (E=100%) and sometimes without sensilla (f_0=30%). Posterior parameres absent in many cases (g_0=70%). Novasternum usually with a pair of prominent spines (I=95%) and a deep median notch (k=95%). Ventral fragma usually easily separable from the novasternum (80%).

The subgenus *Drosophila* may be distinguished from the allied subgenus *Sophophora*, of which a score of species having been examined by the author,[26] as shown below.

Key to two subgenera of the genus *Drosophila*

1. Aedeagus without prominent vertical rod (m=100%) and more or less laterally flattened (L=100%). Anterior parameres usually large (D=87%) and with sensilla apical or mesal (f+F=95%). Posterior parameres never absent (g_0=0%) and articulated to the aedeagus (100%). Basal apodeme as long as or longer than aedeagus (N=100%). d.i. range 0.0-6.0 ..... Subgenus *Sophophora*

— Aedeagus often with prominent vertical rod (M=42.5%) and not always laterally flattened (L=57.5%). Anterior parameres usually minute (d=95%) and sometimes without (f_0=32.5%) sensilla. Posterior parameres usually absent (g_0=72.5%). Basal apodeme often shorter than aedeagus (n=57.5%). d.i. range 3.0-10.5..... Subgenus *Drosophila* s. str.....2

IV. Comparison of the two sections of the subgenus *Drosophila*

The subgenus *Drosophila* s. str. has been divided by Hsu ('49) into two sections, *quinaria* and *virilis*, chiefly according to whether the genital arch (novatergum) is separated from or contiguous to the anal lobe (decatergum) in males. These two sections may be distinguished by the features of the phallic organs as below.

Key to sections of the subgenus *Drosophila*

2. Aedeagus laterally flattened at least apically and apparently bilobed at least partially..... *virilis* section.....3

— Aedeagus horizontally flattened at least apically and apparently fused to large extent ..... *quinaria* section ...11

V. Comparisons of groups aud species

Thus far more than a score of groups are known of the subgenus *Drosophila*, of which 10 were available for examination: 5 of the *virilis*, and 5 of the *quinaria* section. Several ungrouped species were also examined. These groups may be distinguishable as shown in the following key, with which is combined a key to species.

Key to groups and species of the *virilis* section

3. Anterior parameres large and basally with sensilla (f'); median notch of novasternum absent; submedian spines about 3 pairs.....
..... *Drosophila subtilis* Kikkawa & Peng

— Anterior parameres minute; sensilla apical or absent; novasternum deeply notched; submedian spines at most 1 pair.....4

4. Aedeagus broad in lateral aspect; anterior parameres without sensilla, ending before the level of insertion of submedian spines 5

— Aedeagus narrow in lateral aspect; anterior parameres with sensilla apical ...9

5. Aedeagus apparently entirely bifid.....
.....*melanica* group: *D. melanissima* Kikkawa & Peng (nec Sturtevant)

— Aedeagus partially bifid 6

6. Ventral fragma round at base; basal apodeme about 1/2 as long as aedeagus ..... *virilis* group.....7

— Ventral fragma quadrate at base; basal apodeme about 1/4 as long as aedeagus ..... *robusta* group.....8

7. Aedeagus S-shaped in lateral aspect .....
.....*D. novamexicana* Patterson and *D. americana* Spencer

— Aedeagus fusiform in lateral aspect.....*D. virilis* Sturtevant

8. Aedeagus suddenly narrowing at base, subapically with minute teeth .....
..... *D.* sp. *robusta* group I

— Aedeagus tapering to base, subapically without minute teeth.....
..... *D. sordidula* Kikkawa & Peng

9. Tip of anterior paramere not reaching the level of insertion of submedian spines ..... *annulimana* group: *D. gibberosa* Patterson & Mainland

— Tip of anterior paramere extending beyond the level of insertion of submedian spines .....*repleta* group.....10

10. Aedeagus with a pair of broad, dorsally curved apical lobes, basal to which are present cone-like processes .....*D.* sp. *repleta* group I

— Aedeagus with a pair of narrow, ventrally recurved subapical spurs; cone-like processes absent ..... *D. hydei* Sturtevant

Key to groups and species of the *quinaria* section

11. Posterior paramere-like structures present, contiguous to novasternum and separated from aedeagus 12

— Posterior paramere-like structures absent, or if present, they are separated from novasternum and contiguous to aedeagus 15

12. Aedeagus slightly broadened at apex; posterior paramere-like structures contiguous with each other by means of a narrow linear bar...*quinaria* group.....13

— Aedeagus exceedingly broad at apex; posterior paramere-like structures contiguous with each other by means of a broad quadrate plate.....14

13. Aedeagus non-pubescent and apically without teeth .....
..... *D. transversa* Sturtevant, Type I

— Aedeagus pubescent and apically with 4 teeth .....
.....*D. nigromaculata* Kikkawa & Peng

14. Aedeagus subapically toothed but subbasally smooth .....
..... *testacea* group: *D. testacea* van Roser

— Aedeagus subapically smooth but subbasally toothed .....
.....*bizonata* group: *D. bizonata* Kikkawa & Peng

15. Anterior parameres articulated to novasternum and with apical sensilla; aedeagus pubescent .....*D. histrio* Meigen

— Anterior parameres confluent with novasternum.....16

16. Aedeagus apically or subapically bifid.....*funebris* group.....17

— Aedeagus apically or subapically not bifid ..... *immigrans* group.....18

17. Paired posterior paramere-like structures present, articulated to the tip of aedeagus; vertical rod absent; basal apodeme as long as aedeagus.....
.....*D. macrospina* Stalker & Spencer

— No posterior paramere-like structures; vertical rod developed; basal apodeme short, less than 1/3 length of aedeagus ..... *D. funebris* Fabricius

18. Posterior paramere-like structures absent ····· *D. virgata* Tan, Hsu & Sheng
— Posterior paramere-like structures present ····· 19
19. Posterior paramere-like structure 1-jointed····· *D.* sp. *immigrans* group I
— Posterior paramere-like structure 2-jointed ····· *D. immigrans* Sturtevant

VI. Discussion

A negatively correlated development of vertical rod and basal apodeme is observed; the longer the basal apodemes, the shorter the vertical rods. These changes from MN to mn occur in a parallel fashion in the 2 sections; those species thought to be primitive, such as *D. subtilis* and *D. melanissima* of the *virilis* section and *D. transversa, D. nigromaculata, D. testacea* and *D. bizonata* of the *quinaria* section showing MN, the 3 examined species of the *virilis* group, m′n′ and the remaining ones, mn; while in the subgenus *Sophophora,* all the members of the *obscura* and *melanogaster* groups examined show MN, and *D. willistoni,* m′n′. The ventral fragma varies greatly in shape from one species to another even within a group, being elongate triangular, hemispherical or short quadrate, roughly according to whether the ventral apodeme of the corresponding species is long, intermediate or short, respectively. A similar relation is also recognized in the subgenus *Sophophora* (Table 2).

Table 2. Interrelations between basal apodeme, vertical rod and ventral fragma.

Basal apodeme	Vertical rod	Ventral fragma	Subgenus *Drosophila*		Subgenus *Sophophora*
			virilis section	*quinaria* section	
long (M)	absent or short (N)	long, triangular		*transversa* *macrospina*	*nipponica* *bipectinata*
		hemispherical	*subtilis* *melanissima*	*nigromaculata* *testacea* *bizonata* *funebris*	*obscura* group *melanogaster* group (excl. *nipponica* subgr., *bipectinata*)
intermediate (m′)	intermediate (n′)	hemispherical	*americana* *novamexicana* *virilis*		*willistoni*
short (m)	long (n)	hemispherical	*hydei*	*virgata*	
		(short) quadrate	*repleta* gr. I *gibberosa* *sordidula* *robusta* gr. I	*histrio* *immigrans* gr. I *immigrans*	

There are some other structural elements, which appear in groups or species rather at random, such as pubescency of the aedeagus as seen in *D. histrio, D. nigromaculata* and, though slightly, in the 3 species of the *virilis* group; disappearance of sensilla on the anterior parameres as seen in *D. melanissima, D. virilis, D. sordidula, D. robusta* group I, *D. funebris;* more than 1 pair of submedian spines in *D. subtilis* and *D. hayashii;* very long spines in *D.* sp. *repleta* group I, *D. testacea, D. transversa, D. funebris* and *D. immigrans.*

Table 3. Difference values (d.v.) between each two species of the subgenus *Drosophila*.

		quinaria section								*virilis* section						
		immigrans gr. I & *immigrans*	*virgata*	*histrio*	*funebris*	*macrospina*	*testacea* & *bizonata*	*nigromaculata*	*transversa*, Type I	*gibberosa*	*repleta* group (2 spp.)**	*sordidula*	*robusta* gr. I	*virilis* group (3 spp.)*	*melanissima*	*subtilis*
virilis section	*subtilis*	7.5	6.5	8.5	6.0	5.0	6.0	7.0	5.5	5.5	6.0	7.0	6.5	5.5	3.5	0.0
	melanissima	6.0	5.0	6.0	4.5	3.5	4.5	5.5	4.0	4.0	4.5	3.5	3.0	2.0	0.0	
	virilis group (3 spp.)*	5.0	4.0	4.0	3.5	4.5	5.5	5.5	5.0	3.0	3.5	2.5	2.0	0.0		
	robusta gr. I	4.0	3.0	4.0	2.5	4.5	5.5	7.5	6.0	2.0	2.0	1.5	0.0			
	sordidula	4.5	3.5	4.5	3.0	6.0	7.0	8.0	6.5	2.5	3.0	0.0				
	repleta group (2 spp.)**	1.5	0.5	1.5	1.0	3.0	4.0	5.0	3.5	1.5	0.0					
	gibberosa	2.0	1.0	2.0	0.5	3.5	4.5	5.5	4.0	0.0						
quinaria section	*transversa*, Type I	2.0	3.0	4.0	3.5	1.5	0.5	3.5	0.0							
	nigromaculata	3.5	4.5	3.5	5.0	3.0	2.0	0.0								
	testacea & *bizonata*	2.5	3.5	4.5	4.0	1.0	0.0									
	macrospina	3.5	2.5	3.5	3.0	0.0										
	funebris	1.5	0.5	1.5	0.0											
	histrio	2.0	1.0	0.0												
	virgata	1.0	0.0													
	immigrans gr. I & *immigrans*	0.0														

* *virilis*, *americana* and *novamexicana*.

** *repleta* gr. I and *hydei*.

The differences between each 2 species are shown in Table 3 in the form of "difference value" (d.v.) (Okada '53), which is calculated from comparison of the phallic formulae of the 2 species, in determining, for example, the differences between A (=0) and a (=1), A and a′ (=0.5), and a and a′, as 1.0, 0.5 and 0.5 respectively. The intrasectional ranges of d.v. are 0–5.0 and 0–7.0 in the *quinaria* and *virilis* sections respectively, while the intersectional d.v. values range from 0.5 to 8.5, the largest d.v. (8.5) being found between *D. subtilis* and *D. histrio*, the smallest (0.5) between *repleta* group and *D. virgata*, and also between *D. funebris* and *D. gibberosa*. The smallest intrasectional d.v. (0) are observed between each 2 species of the *virilis* group, between *D. hydei* and *D.* sp. *repleta* group I, between *D.* sp. *immigrans* group I and *D. immigrans*, and also between *D. testacea* and *D. bizonata*, all being intragroup cases except the last one which is a unique intergroup case.

Hsu's suggestion ('49), that the *immigrans* group might have come from the *robusta* group by the separation of the anal plate and some other changes, cannot, however, be agreed to by the author, because of the fact that the separation occurs

in *Gitona, Amiota, Leucophenga, Mycodrosophila* and subgenera *Hirtodrosophila, Sophophora, Pholadoris, Siphlodora,* and the *quinaria* section of the subgenus *Drosophila,* and that the fusion occurs in the subgenera *Dorsilopha, Phloridosa* and the *virilis* section of the subgenus *Drosophila.*[17] In general the separation occurs in the simpler, or so-called more primitive, members of the family, while the fusion occurs in the forms of opposite characters. Thus the separation should be preceded by the fusion and not vice versa.

In the *virilis* section, *D. subtilis* shows the smallest value of d.i. (3.5), somewhat resembling the subgenus *Pholadoris* in the general features of the phallic organs. The *melanica* group seems to be related to the *willistoni* group of the subgenus *Sophophora,* and also to the *virilis* and *robusta* groups. The *repleta* group is allied in some features to the *quinaria* section more closely than is any other group of the *virilis* section. The differentiation of the organs in the species of this section is clearcut, except in the case of the *virilis* group.

In the *quinaria* section, the *testacea* and *bizonata* groups show a close resemblance to each other (d.v.=0.0), and are also similar to the *calloptera* group and its allies[20] in having a prominent quadrate plate, or "distal bow" of Burla and Pavan.[20] This plate, having lateral arms continuous with the lateral processes of the novasternum, seems to be a deformed structure of the posterior parameres, with the musculature degenerated. The similar but less pronounced structures are perceptible in the *quinaria* group, and also, though the homology is doubtful, in *D. immigrans, D. virgata* and *D. macrospina.*

The posterior parameres are well developed in all the members of the subgenus *Sophophora* — 16 species of the *melanogaster* group,[26] 8 species of the *obscura* group and 1 species of the *willistoni* group, — so far as the author examined, in which the each paramere is contiguous with the aedeagus by means of one arm, and with the novasternum by another or outer arm; sometimes two parameres are contiguous with each other (*nipponica* subgroup and most of the species of the *montium* subgroup[26]), resulting in the structure found in *D. testacea, D. bizonata* and *D. transversa* Type I (g). If the posterior parameres are thought to have lost connection with the novasternum, the paired structures seen in *D. macrospina* (Fig. 29, p′) would be derived. If on the other hand, the connection with the novasternum be lost and the mutual connection be pronounced, the posterior paramere would take the features possessed by *D. immigrans* and *D.* sp. *immigrans* group I (Figs. 37–40, p′). The fact that the most of Japanese species of the genus *Leucophenga* have the similar structures, connected to the basal portion of the aedeagus, seems to throw light upon the homology of the structure to the true posterior parameres.

Summary

1. The phallic organs of 20 species of the subgenus *Drosophila* were examined in detail and studied comparatively.
2. The taxonomic systems established for the subgenus *Drosophila* by several authorities, based on various morphological characters, including the periphallic organs, were proved generally applicable also for a classification using the phallic organs.

3. Some morphological elements of the phallic organs appear to have penetrated repeatedly or in an anastomosing fashion into the different sections of groups of the subgenus.
4. Some pairs of elements, for examples basal apodeme and vertical rod, show correlate changes in the degree of development from species to species.

Literature cited (*cited indirectly)

1)-19) same as listed in the previous paper.[26] 20) Burla, H. and Pavan, C. '53 Rev. Brasil. Biol., 13: 291–314. 21) Burla, H. '54 ibid. 14: 41–54. 22)*Malogolowkin, C. '52 ibid. 12: 79–96. 23)-'52 DIS, 26: 110. 24)*-'53 Rev. Brasil. Biol., 13: 245–264. 25) Moriwaki, D., Okada, T. and Kurokawa, H. '52 DIS, 26: 112. 26) Okada, T. '54 Kontyû, 22: 36–46. 27)* Salles, H. '48 Summ. Brasil. Biol., 1: 348. 28) Takada, H. and Makino, S. '52 DIS, 26: 123.

Explanation of Plates

Plate 17

Phallic organs of the drosophilid flies belonging to the *virilis* section. Figures with odd numbers show the ventral aspects (on the left half) and the dorsal aspects (on the right half); figures with even numbers are the lateral aspects of the organs detached of novasternum and ventral fragma.

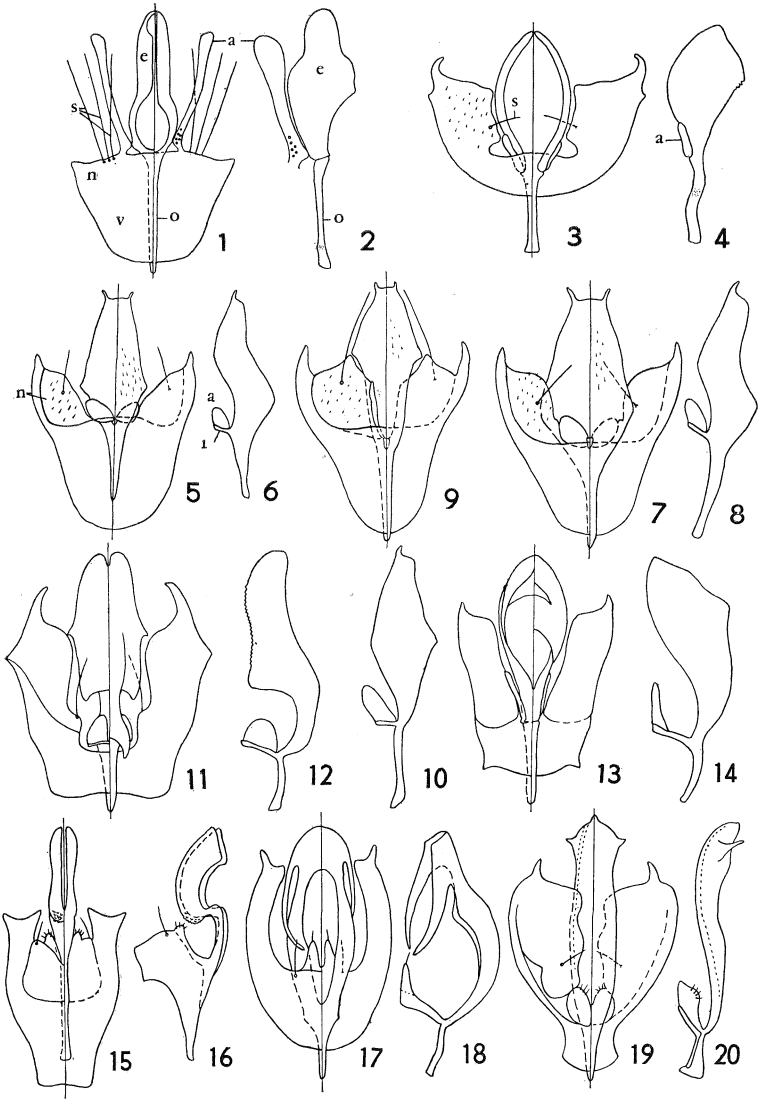
Figs. 1-2. *Drosophila subtilis*. Figs. 3-4. *D. melanissima*. Figs. 5-6. *D. americana*. Figs. 7-8. *D. novamexicana*. Figs. 9-10. *D. virilis*. Figs. 11-12. *D.* sp. of the *robusta* group I. Figs. 13-14. *D. sordidula*. Figs. 15-16. *D.* sp. of *repleta* group I. Figs. 17-18. *D. hydei*. Figs. 19-20. *D. gibberosa*.

Plate 18

Phallic organs of the drosophilid flies belonging to the *quinaria* section. Aspects of figures as in Plate 17.

Figs. 21-22. *D. transversa*. Figs. 23-24. *D. nigromaculata* Figs. 25-26. *D. testacea*. Figs. 27-28. *D. bizonata* Figs. 29-30. *D. macrospina*. Figs. 31-32. *D. funebris*. Figs. 33-34. *D. histrio*. Figs. 35-36. *D. virgata*. Figs. 37-38. *D.* sp. of the *immigrans* group I. Figs. 39-40. *D. immigrans*.

e: aedeagus. a: anterior paramere. p: posterior paramere. p': structures like posterior paramere. o: ventral apodeme of the aedeagus. n: novasternum. v: ventral fragma. r: vertical rod of the aedeagus. s: submedian spine.



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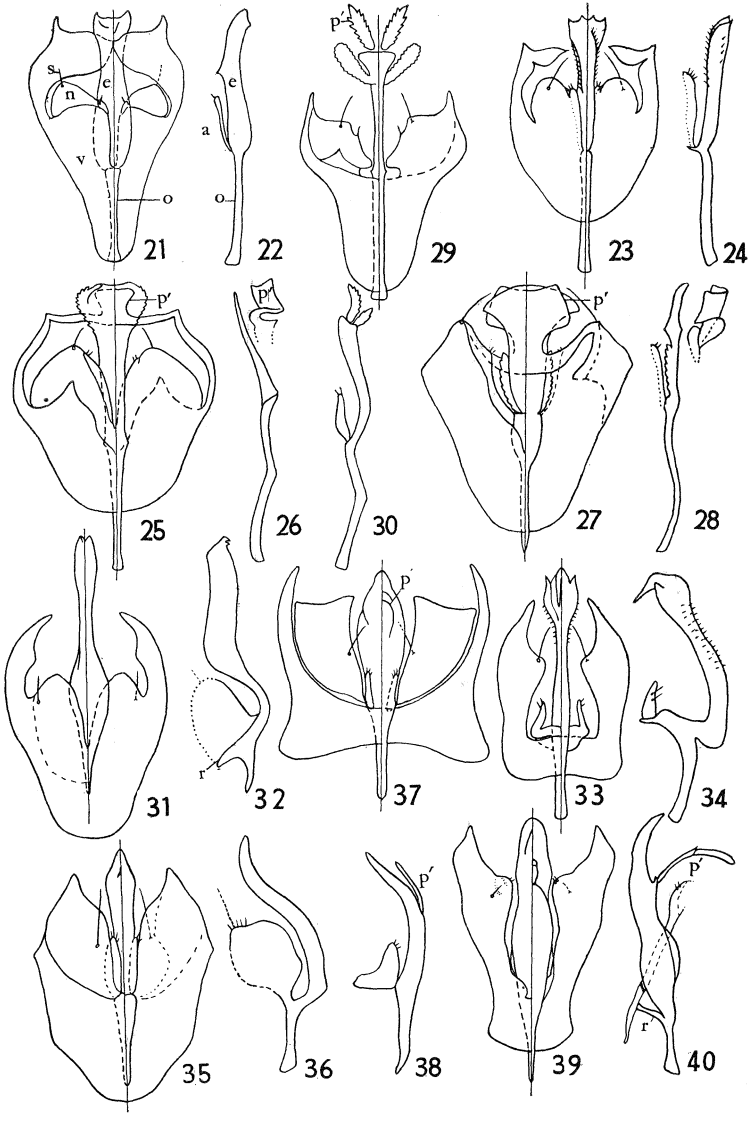

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