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Systematic Relationships Among Ten Species of Subgenus *Drosophila* (Diptera: Drosophilidae) in Korea

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ABSTRACT

This study sought to observe systematic relationships through taximetrical analyses by morphological characters among the 10 species, on three species in the *virilis* section (*D. virilis*, *D. tsigana* and *D. lacertosa*) and seven species in the *quinaria* section (*D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai* and *D. unispina*) of the subgenus *Drosophila*. In the cluster and the cladistic analysis among the members of subgenus *Drosophila*, 10 species was divided into the 1st group of *D. virilis*, *D. tsigana*, and *D. lacertosa* and the 2nd group of *D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai*, and *D. unispina*. In cluster analysis, the 2nd group had three sister groups; one sister group that clusted *D. angularis* and *D. brachynephros* then *D. unispina* was clusted to them, another sister group clusted *D. curvispina* and *D. takadai* then *D. kuntzei* was clusted to them and the other sister group of *D. nigromaculata*. In the 10 species, *D. virilis* and *D. lacertosa* were the first to be divided and then *D. tsigana*. Although 1st group which *D. virilis* was belonged can be determined as more primitive than the 2nd group, it seemed that this group was not the direct ancestor of the 2nd group, rather there should be another ancestor. Among the *quinaria* species group, *D. nigromaculata* was the first to be divided and *D. kuntzei* was the most recent species to be divided.

Key words: subgenus *Drosophila*, systematic relationship, Korea

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INTRODUCTION

Drosophilidae are divided in multi-levels distributed worldwide. Any study on the relationship considering their ecogeological characters can be pivotal in speciation studies. For phylogenetic study on Drosophilidae, there are morphological characters, ecological, reproductive isolation, and molecular biology studies.

Genus *Drosophila* includes a vast number of species and various specialized species that are distributed in different regions. Subgenus *Drosophila* of Genus *Drosophila* includes 22 species groups and there are approximately 800 known species in the world (Wheeler, 1986). There are 23 species of 12 species groups in Korea and they are about 20% of 117 species of Korean Drosophilidae (Lee and Kim, 1987; Kim and Joo, 2002).

Analysis of the description in systematic study can present a problem in discussing interspecific relationship. Numerical analysis is used as one of its solutions (Okada, 1984, 1986; Lee et al., 1993).

For morphological studies on subgenus *Drosophila*, Hsu (1949) compared the morphological characters of genitalia to divide the subgenus *Drosophila* into *quinaria* section and *virilis* section. Furthermore, Okada (1956) performed a morphological description on subgenus *Drosophila* in Japan. As for studies on the genus *Drosophila* in Korea, Chung and Rho (1960) reported on the variation of genitalia of three species (*D. angularis*, *D. brachynephros* and *D. unispina*). Lee and Choi (1985) elaborated on the morphological analysis of genitalia, length and index of wings, and color of body on four species of *quinaria* species group. Adding *D. nigromaculata* to the previous three species formed this group; they determined that *D. nigromaculata* had the furthest relationship and *D. angularis* and *D. brachynephros* were more closely related than *D. unispina*. Moreover, Lee and Joo (1987) reported that based on soluble protein analysis results on five species in the *quinaria* species group including the previous four with *D. curvispina*, *D. angularis* and *D. brachynephros* were most closely related and *D. nigromaculata* was the furthest from the other four species. Regarding the reports on the relationships of Drosophilidae through numerical analysis of morphology, a study on genus *Scaptomyza* by Kim and Hong (1997) and others existed. However, there was no taximetrical study on subgenus *Drosophila*.

This study sought to observe interspecific systematic relationships through taximetrical analysis by morphological characters on three species in the *virilis* section (*D. virilis*, *D. tsigana* and *D. lacertosa*) and seven species in the *quinaria* section (*D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai* and *D. unispina*) of the subgenus *Drosophila*.

MATERIALS AND METHODS

Ten species of subgenus *Drosophila* used in this study were collected in Inchon (*D. virilis*), Mt. Chonma (*D. tsigana*), Mt. Sori (*D. lacertosa*, *D. angularis*, *D. brachynephros* and *D. unispina*), Mt. Chiri (*D. curvispina*), Mt. Chiak (*D. kuntzei* and *D. nigromaculata*) and Daegwallyeong (*D.*

Table 1. Diagnostic characters for taximetrical analysis on the 10 species of the subgenus *Drosophila*.

No.	Character	Cluster analysis	Cladistic analysis
1	Aedeagus	bifid (A), fused (a)	bifid (0), fused (1)
2	Aedeagus	non-pectinated (B), pectinated (b)	non-pectinated (0), pectinated (1)
3	Aedeagus	bare (−), pubescent (+)	bare (0), pubescent (1)
4	Aedeagus	laterally (C), horizontally flattened (c)	laterally (0), horizontally flattened (1)
5	Basal vertical rod on its ventral surface of aedeagus	present (+), absent (−)	absent (0), present (1),
6	Basal apodeme of aedeagus	longer than aedeagus (D), less than half length of aedeagus (d)	longer than aedeagus (0), less than half length of aedeagus (1)
7	Sensilla at anterior paramere	present (+), absent (−)	present (0), absent (1)
8	Posterior paramere	contiguous (E), non-contiguous (e)	contiguous (0), non-contiguous (1)
9	Phallosomal index	average index	less than 1.3 (0), more than its (1)
10	Anal plate and genital arch	contiguous (F), separated (f)	contiguous (0), separated (1)
11	Small hairs on anal plate	present (+), absent (−)	present (0), absent (1)
12	Black teeth on clasper	more than 10 (G), less than its (g)	more than 10 (0), less than its (1)
13	Secondary teeth on clasper	present (+), absent (−)	present (0), absent (1)
14	Bristle of upper of genital arch	present (+), absent (−)	present (0), absent (1)
15	Lobe of egg guide	round (H), triangular (h)	round (0), triangular (1)
16	Body color	black (I), yellow (i)	black (0), yellow (1)
17	Abdominal tergites	interrupted cross band (J), spots (j)	interrupted cross band (0), spots (1)
18	Numbers of upper branch of arista	less than 6 (K), more than its (k)	less than 6 (0), more than its (1)
19	Numbers of apical setae at palpus	one (L), several (l)	one (0), several (1)
20	Ratio of greatest width of cheek and diameter of eye	average ratio	less than 0.3 (0), more than its (1)
21	Ratio of Orb1 and Orb2	average ratio	less than 0.3 (0), more than its (1)
22	Ratio of Or1 and Or2	average ratio	less than 0.3 (0), more than its (1)
23	Wing crossvein	clouded (M), or clear (m)	clouded (0), clear (1)
24	C-index	average index	less than 3.5 (0), more than its (1)
25	4V-index	average index	less than 1.3 (0), more than its (1)
26	4C-index	average index	more than 0.8 (0), less than its (1)
27	3cf-index	average ratio	less than 0.5 (0), more than its (1)
28	5X-index	average index	less than 1.3 (0), more than its (1)
29	Sterno-index	average index	more than 0.65 (0), less than its (1)
30	Acrostichal hair	8 rows (N), 6 rows (n)	8 rows (0), 6 rows (1)

takadai), respectively.

In order to ascertain morphological relationships of the 10 species, 30 morphologic characters from abdomen, wing index, and others with its primary focus on genitalia that were considered as significant standard for classification were selected and performed cluster and cladistic analysis (Table 1).

RESULTS AND DISCUSSION

The character of subgenus *Drosophila* is that there are 3-4 egg filaments, the coronal fertilized spermatheca is twisted longitudinally, and finally the testis is long screwed shape. The black band on the back of the abdomen is narrow or interrupted in the middle. The 10 species used in this

Table 2. Data matrix on the 10 species of the subgenus *Drosophila* comprising thirty diagnostic characters, each of which is coded in quantitative characters.

Species / Character	*vir.*	*tsi.*	*lac.*	*ang.*	*bra.*	*cur.*	*kun.*	*nig.*	*tak.*	*uni.*
1	A	A	A	a	a	a	a	a	a	a
2	B	B	b	B	B	B	B	B	B	B
3	+	−	−	−	−	−	−	+	−	−
4	c	c	c	C	C	C	C	C	C	C
5	+	−	+	−	−	−	−	−	−	−
6	d	D	d	D	D	D	D	D	D	D
7	−	−	+	+	+	+	+	+	+	+
8	E	E	E	e	e	E	E	E	E	E
9	1.28	1.10	1.41	1.71	1.27	1.22	1.42	1.14	2.14	1.32
10	F	F	F	f	f	f	f	f	f	f
11	+	+	+	−	−	−	−	−	−	−
12	g	G	G	G	G	G	G	g	G	G
13	−	−	−	+	+	+	+	+	+	+
14	+	−	+	−	−	−	−	−	−	+
15	h	H	H	H	H	H	H	H	H	H
16	I	I	I	i	i	i	i	i	i	i
17	J	J	J	j	j	j	j	j	j	j
18	K	K	k	k	k	K	k	K	k	k
19	L	l	l	l	l	l	l	L	l	L
20	0.33	0.25	0.33	0.17	0.17	0.14	0.29	0.25	0.25	0.14
21	0.33	0.33	0.25	0.25	0.20	0.20	0.20	0.25	0.20	0.17
22	0.50	0.50	0.67	0.50	0.50	0.50	0.25	0.75	0.80	0.40
23	m	m	m	m	m	m	M	M	M	m
24	2.73	2.45	4.19	3.01	2.77	3.09	3.75	3.24	3.10	3.13
25	1.75	1.71	1.61	1.60	1.68	1.62	1.89	1.53	1.53	1.48
26	0.99	1.05	1.45	0.97	1.31	0.79	0.81	0.74	0.82	0.91
27	0.65	0.33	0.64	0.42	0.40	0.39	0.38	0.52	0.43	0.45
28	1.31	1.23	1.33	1.38	1.26	1.18	1.05	1.07	1.09	1.35
29	0.90	0.90	0.70	0.60	0.60	0.60	0.60	0.70	0.50	0.60
30	n	n	n	N	n	n	n	n	n	n

Abbreviations of species names are as follows: *vir.* = *D. virilis*; *tsi.* = *D. tsigana*; *lac.* = *D. lacertosa.*; *ang.* = *D. angularis*; *bra.* = *D. brachynephros*; *cur.* = *D. curvispina*; *kun.* = *D. kuntzei*; *nig.* = *D. nigromaculata*; *tak.* = *D. takadai*; *uni.* = *D. unispina*.

Table 3. Similarity coefficient (Gower's) based on thirty quantitative characters.

Species	*vir.*	*tsi.*	*lac.*	*ang.*	*bra.*	*cur.*	*kun.*	*nig.*	*tak.*
D. tsigana	0.673								
D. lacertosa	0.665	0.594							
D. angularis	0.317	0.561	0.470						
D. brachynephros	0.331	0.531	0.464	0.941					
D. curvispina	0.401	0.630	0.582	0.872	0.877				
D. kuntzei	0.291	0.526	0.448	0.798	0.810	0.834			
D. nigromaculata	0.417	0.532	0.336	0.671	0.660	0.767	0.737		
D. takadai	0.271	0.512	0.439	0.822	0.841	0.885	0.853	0.758	
D. unispina	0.367	0.502	0.453	0.871	0.843	0.836	0.804	0.745	0.810

The abbreviations of species names are the same as in Table 2.

study can be divided into *virilis* and *quinaria* sections. The *quinaria* species group belong in *quinaria* section is derived from immigrans-Hirtodrosophila radiation (Throckmorton, 1975). From seven *quinaria* species group used this study, *D. angularis*, *D. brachynephros* and *D. unispina* populate the same habitat. However, *D. angularis* and *D. brachynephros* were collected from lower altitudes while *D. unispina* live in comparatively high altitudes. Moreover *D. nigromaculata* is a semidomestic species and *D. curvispina* dwell in the high altitude area. *D. kuntzei* and *D. takadai* inhabit in lower altitude area than *D. curvispina* independently from one another for their ecological differences. In the *virilis* section, *D. virilis* is a domestic species and *D. tsigana* and *D. lacertosa* live in lower altitude area. Especially, *D. tsigana's* main feed is tree sap. Likewise each species has its own unique ecological character.

Data matrix compiled pursuant to the standard of Table 1 to ascertain morphological relationships through cluster analysis on the 10 species of Korean subgenus *Drosophila* is as shown in Table 2. The species with small sensilla on aedeagus are *D. virilis* and *D. nigromaculata*, and the rest do not have such features (3). *D. takadai* show the largest phallosomal index value of 2.14, and *D. tsigana* show the lowest value of 1.10. As for the crossvein in the wing, *D. kuntzei*, *D. nigromaculata* and *D. takadai* are black and the remaining four species have clear crossveins (23). *D. nigromaculata* show the lowest 4-index value (26).

The results of similarity index according to Gower's (1971) from Table 2 were shown in Table 3. On the results of analysis, *D. angularis* and *D. brachynephros* were most similar to one another with 0.941 and the next in line in similarity was between *D. takadai* and *D. curvispina* (0.885). *D. virilis* and *D. takadai* showed the furthest relationship (0.271). The seven species in *quinaria* species group of *quinaria* section (*D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai* and *D. unispina*) revealed close relationships with over 0.7 index value.

The results of UPGMA (Sneath and Sokal, 1973) based on Table 3 were as shown in Fig. 1. *D. virilis*, *D. tsigana* and *D. lacertosa* form one group and the remaining seven species form another group. In the seven species of *qunaria* section, *D. angularis*, *D. brachynephros*, *D. unispina* and

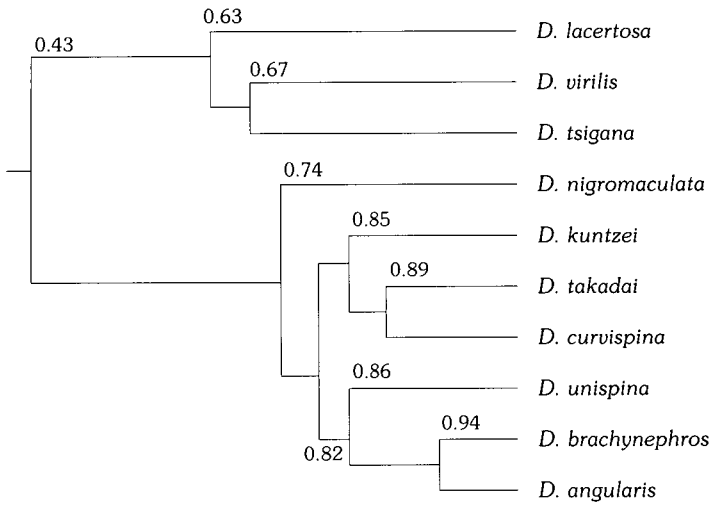

Fig. 1. A dendrogram on the 10 species of the subgenus *Drosophila* based on similarity coefficient. The numbers are branch length.

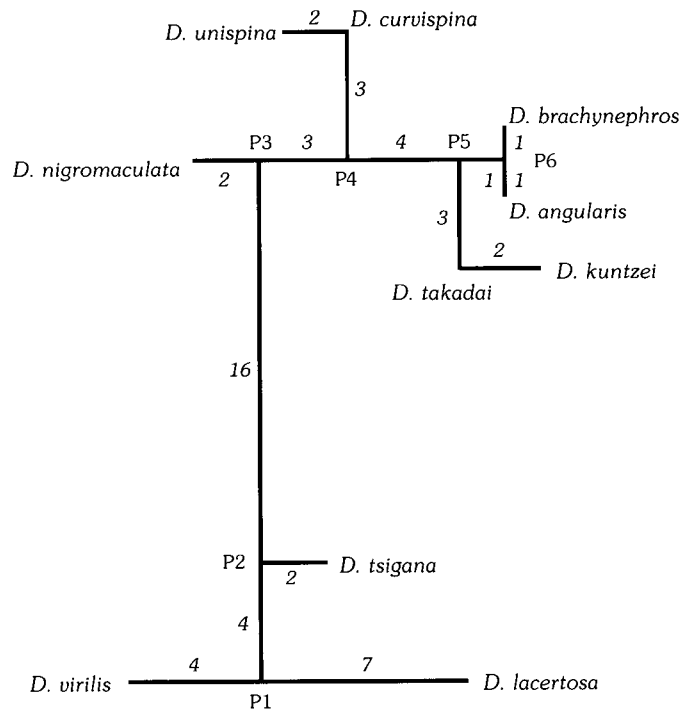

Fig. 2. A cladogram on the 10 species of the subgenus *Drosophila* by Wagner algorithm.

D. curvispina form one sister group and *D. kuntzei* and *D. takadai* form another sister group. *D. nigromaculata* forms a different sister group from them. On the other hand, among the three

Table 4. Data matrix on the 10 species of the subgenus *Drosophila* comprising thirty diagnostic characters as in Table 1, each of which is coded in binary characters.

Species / Character	*vir.*	*tsi.*	*lac.*	*ang.*	*bra.*	*cur.*	*kun.*	*nig.*	*tak.*	*uni.*	P1	P2	P3	P4	P5	P6
1	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
4	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
5	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
6	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
7	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
8	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
9	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1
10	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
11	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
12	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
13	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
14	0	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1
15	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1	1
17	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0
18	0	0	1	1	1	1	1	0	1	1	0	0	0	0	1	1
19	0	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0
20	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
21	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
22	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0
23	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1
24	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0
27	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0
28	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1
29	0	0	0	1	1	1	1	0	1	1	0	0	0	1	1	1
30	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

The abbreviations of species names are the same as in Table 2. The letter P including number means the nodes as in Fig. 2.

species in *D. virilis* section, *D. virilis* and *D. tsigana* were clusted first and then *D. lacertosa* was clusted to them.

The compilation of 30 characters from Table 2 into binary characters such as primitive (0) and derived character (1) is shown in Table 4. The result of their cladistic analysis is shown in Fig. 2.

According to the cladistic analysis, the tree has six ancestors. In the 10 species, *D. virilis* and *D.*

lacertosa were first divided from ancestor P1 and *D. tsigana* was divided from P2. It was shown that among 10 species, *D. kuntzei* was divided from *D. takadai* last.

Results of cluster and cladistic analysis, 10 species of subgenus *Drosophila* can be divided into the 1st group of *D. virilis*, *D. tsigana*, and *D. lacertosa* and the 2nd group of *D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai* and *D. unispina*. The 2nd group had three sister groups; one sister group that clusted *D. angularis* and *D. brachynephros* then *D. unispina* was clusted to them, another sister group clusted *D. curvispina* and *D. takadai* then *D. kuntzei* was clusted to them and the other sister group of *D. nigromaculata*. In the 10 species, *D. virilis* and *D. lacertosa* were the first to be divided and then *D. tsigana*. Although 1st group where *D. virilis* belonged can be determined as more primitive than the 2nd group, it seemed that the 1st group was not the direct ancestor of the 2nd group, rather there should be another ancestor. Species in the 2nd group were divided from ancestor P3. Among the 2nd group, *D. nigromaculata* was the first to be divided and *D. kuntzei* was the most recent species to be divided. Okada (1988) determined that *virilis* section was more primitive than the *quinaria* section based on overall analysis of morphological characters, genitalia, reproductive organ, and others for all species of Drosophilidae. The results of this study coincide with the reports by Okada (1988) and *D. virilis* was considered to be the species with the most primitive characters among the 10 species analyzed. Watabe et al. (1990) stated that *D. pengi* (Okada and Kurokawa, 1957) and Nesiodrosophila septentriata (Takada and Maekawa, 1984) were synonyms for *D. tsigana*. *D. tsigana* showed some similarities in its morphological characters with genus Nesiodrosophila, another genus. In view of these morphological characters, *D. tsigana* in the *melanica* species group of *virilis* section currently can be separated into a new species group.

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요 약

한국산 초파리아속에 속하는 *quinaria* section 7종(*D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai*, *D. unispina*)과 virilis section 3종(*D. virilis*, *D. tsigana*, *D. lacertosa*)을 대상으로 형태적 수리분석을 실시하여 종간 계통학적 유연관계를 알아보았다. 집괴분석과 분지분석을 실시한 결과 초파리아속 10종은 *D. virilis*, *D. tsigana*, *D. lacertosa*의 제1군과 *D. angularis*, *D. brachynephros*, *D. curvispina*, *D. kuntzei*, *D. nigromaculata*, *D. takadai*, *D. unispina* 제2군으로 나눌 수 있다. 집괴분석 결과 제2군은 3개의 아군 즉, *D. angularis*와 *D. brachynephros*가 집괴된 후에 *D. unispina*가 집괴되는 아군과, *D. curvispina*와 *D. takadai*가 집괴된 후에 *D. kuntzei*가 집괴되는 아군, 그리고 *D. nigromaculata* 아군으로 나눌 수 있다. 그리고 *D. virilis*와 *D. lacertosa*가 가장 먼저 분지된 종이었으며, *D. tsigana*가 그 다음이었다. *D. virilis*가 속한 제1군은 제2군보다 더 먼저 파생되었다고 할 수 있으나, 제1군이 제2군의 직접적인 조상형은 아니고 다른 조상형이 있었을 것이며, 제2군에서는 *D. nigromaculata*가 가장 먼저 파생되었고, *D. kuntzei*가 가장 늦게 파생되었다고 생각된다.