Prof. Toyohi Okada
with best regards
Walter Hackman

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The relation between the genera Scaptomyza and Drosophila (Diptera, Drosophilidae)

WALTER HACKMAN

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Various characters used for separation of the two genera are discussed. The *Drosophila* subgenus *Lordiphosa* is compared with taxa within *Scaptomyza*. *Elmomyza* subg. n. is described. It includes all the Hawaiian species hitherto included in subg. *Trogloscaptomyza* Frey. The question whether *Scaptomyza* is a monophyletic genus or not is discussed. A more probable alternative is that it is paraphyletic.

Walter Hackman, Department of Entomology, Zoological Museum, University of Helsinki, N. Järnvägsg. 13, SF-00100 Helsinki, Finland.

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The separating characters

The external morphological characters generally used for separating the genus *Scaptomyza* Hardy from *Drosophila* Fallén are the following:

The head nearly square in profile and the greatest eye dimension more or less oblique in *Scaptomyza*. In *Drosophila* the head is usually higher than long and the greatest eye dimension is more or less vertical.

Arista with one or no ventral branch in addition to the end fork in *Scaptomyza* and with two or more ventral branches in *Drosophila*. Mesonotum usually dull in *Scaptomyza*, usually shiny in *Drosophila*.

Acrostichal rows of hairs 2—4 in *Scaptomyza*, 6—8 in *Drosophila*.

The *Scaptomyza* subgenera often have characteristic features in the male terminalia, but no key characters have been found for separating the entire genus from *Drosophila*.

Prominent dentate egg-guides occur in the *Scaptomyza* species with leaf-mining larvae. Leaf-miners are rare in *Drosophila*. On the other hand, sclerotized egg-guides with dense marginal dentation often occur in both genera and these structures have a function in copulation (NATER 1953). Some *Scaptomyza* subgenera tend to have very weakly sclerotized egg-guides (cf. HACKMAN 1959).

Inner anatomical characters, such as the shape of the spermathecae, testes, vasa deferentia, paragonia, ejaculatory apodemes, and Malphigian tubules, have been used as important characters by THROCKMORTON (1962, 1966) in studies of the phylogeny in the entire *Drosophila* complex (including related genera) and for separation of endemic Hawaiian Drosophilas and Scaptomyzas. The inner anatomy of *Scaptomyza* species from other parts of the world is poorly known (see further p. 100).

Characters of the eggs, larvae and puparia have also been used to some extent in the taxonomy of the *Drosophila* complex (THROCKMORTON 1962). The egg-filaments are usually short in *Scaptomyza* and long in *Drosophila*. OKADA (1968b) gives much information about the developmental stages of *Drosophila*, but too little is known about *Scaptomyza*.

Anomalies in occurrence of key characters

In his excellent analysis of the phylogeny of the *Drosophila* complex THROCKMORTON (1962) has shown that almost every subgenus or species group has one or more species possessing a character used as key character for another genus, subgenus or species group of the complex. He discussed the phenomenon in detail and suggested an explanation (see also THROCKMORTON 1968). Thus none of the external morphological key characters mentioned above can be used alone for complete separation of *Scaptomyza* and *Drosophila:*

The shape of the head and the degree of obliqueness of the eyes is not a particularly reliable character. An arista with only one ventral ray in addition to the end fork occurs in *Drosophila* also: in many *Hirtodrosophila* species, *Dichaetophora clypeonigra* Okada, *Drosophila* (s. str.) *cameraria* Haliday. On the other hand, several *Scaptomyza* species (subgenus *Bunostoma, Scaptomyza* (s. str.) *sinica* Lin & Ting, the *Euscaptomyza* species and two unplaced species from New Zealand) have two ventral rays (cf. HARDY 1965, HARRISON 1959, LIN & TING 1971, TSACAS 1972).

The degree of mesonotal pollinosity (dull versus shiny) is also a character of minor value. For example, in *Scaptomyza* the *Bunostoma* species generally have a shiny mesonotum.

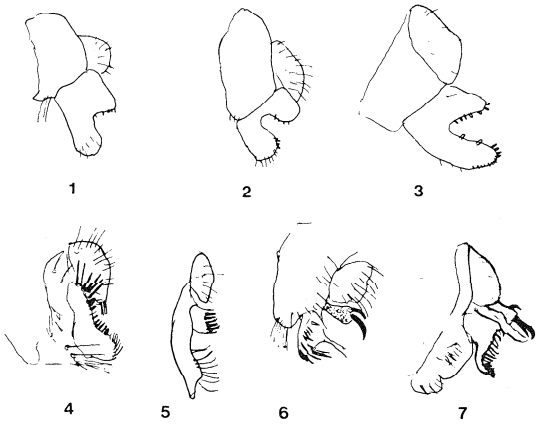
The number of acrostichal hairs has been considered the most important separating character. However, in *Drosophila* the *Lordiphosa* species usually have only four rows (between the dorsocentral bristles). Four rows also occur in *Drosophila (Dichaetophora) clypeonigra* and, less constantly, in some *Hirtodrosophila* species (OKADA 1968a, BÄCHLI 1973). Among the Hawaiian Scaptomyzas more than 60 have six rows as in *Drosophila.* Species with only two rows have always been placed in *Scaptomyza* and not in *Drosophila,* and species with eight rows have never been assigned to *Scaptomyza.*

The subgenera of Scaptomyza

Sixteen subgenera have been distinguished in *Scaptomyza* (HACKMAN 1959, OKADA 1973, TSACAS 1972, TSACAS & COGAN 1976) and one more is added in this paper. The subgenera are comparatively distinct and separated by combinations of about 10 characters of external morphology. Two endemic species from New Zealand (described by HARRISON 1959) and some African species are still unplaced. Most of the subgenera are comparatively distinct from *Drosophila* and a general *Scaptomyza* type can be recognized, but there is considerable overlap of characters between the Hawaiian "Drosophiloids" and "Scaptomyzoids" (THROCKMORTON 1966, CARSON et al. 1970). Before the borderline between *Scaptomyza* and *Drosophila* can be discussed further, however, there is a taxonomic and nomenclatorial matter to be cleared up.

History of the subgenus Trogloscaptomyza

The *Scaptomyza* subgenus *Trogloscaptomyza* was created by FREY (1954, as a subgenus of *Parascaptomyza)* for a single species, *S. (T.) brevilamellata* Frey from Tristan da Cunha. In my classification of *Scaptomyza* species (HACKMAN 1959) I included in the same subgenus a number of Hawaiian species which agreed in certain external characters with the type species from Tristan da Cunha. Later (HACKMAN 1962), I transferred five of the Hawaiian species to the subgenus *Rosenwaldia* Malloch. The remaining Hawaiian species form a small and less typical fraction of the Hawaiian *Trogloscaptomyza,* in which HARDY (1965, 1966) included more than 80 endemic Hawaiian species. No other species of this



Figs. 1—7. Male genitalia of *Scaptomyza* and *Drosophila* species. Side view, ventral parts omitted. 1. *Scaptomyza (Rosenwaldia) mitchelli* Hackman, 2. *S. (Elmomyza) recava* Hardy, 3. *S. (Trogloscaptomyza) brevilamellata* Frey, 4. *Drosophila (Lordiphosa) nigricolor* Strobl, 5. *Scaptomyza (Bunostoma) bryanti* Hackman, 6. *Drosophila (Sophophora) kikkawai* Burla, 7. *Scaptomyza (Parascaptomyza) frustulifera* (Frey). Redrawn figures: 1 and 5 from HACKMAN 1959, 2 from HARDY 1965, 3 and 7 from FREY 1954, 6 from OLROYD 1958.

taxon has been found elsewhere in the Pacific or on any continent, and the single species from Tristan da Cunha in the Southern Atlantic has thus become a zoogeographical enigma (cf. CARSON et al. 1970), demanding reexamination. A comparison of *Rosenwaldia, Trogloscaptomyza brevilamellata* and the Hawaiian "*Trogloscaptomyza*" (in the table *Elmomyza* subg. n.) is made in Table 1.

As regards a number of external characters, *Trogloscaptomyza brevilamellata* takes an intermediate position between *Rosenwaldia* and the Hawaiian "*Trogloscaptomyza*". It may be mentioned that the general shape of the male clasper (Figs. 1—3) is rather similar in the three taxa compared, but this is evidently a symplesiomorphic character. I have therefore considered it necessary to separate the Hawaiian species in the new subgenus *Elmomyza* subg. n., named in honour of Prof. D. Elmo Hardy, Honolulu. The description follows below.

Subgenus Elmomyza subg. n.

Trogloscaptomyza, HACKMAN 1959 pro partim, non FREY 1954.

Trogloscaptomyza, HARDY 1965, Hawaiian species, non FREY 1954.

Type species: *Scaptomyza (Trogloscaptomyza) acronastes* HARDY 1965.

One humeral bristle, head usually nearly square in profile, eyes not strongly oblique. Male genitalia without a secondary clasper. Arista usually with two dorsal and no ventral rays basad to end fork, which is sometimes lacking. Acrostichal hairs usually in six rows, in one species group in four rows, but never in two rows. The clasper (substylus) stout, distally concave or bilobate with denticles along at least some part of the marginal egg-guides weakly sclerotized. For comparison with other taxa, see Table 1. Distribution: Hawaiian Islands.

The borderline between Scaptomyza and Drosophila

Several cases of adaptive radiation can be traced in the evolution of the *Drosophila* complex (THROCKMORTON 1975), but the most impressive and unique example is provided by the Hawaiian Drosophilidae, in which nearly 500 endemic species have been described. The majority of them have been placed in *Drosophila* or in new endemic

Table 1. Comparison of characters of the *Scaptomyza* subgenera *Rosenwaldia, Trogloscaptomyza* and *Elmomyza* subg. n.

	Rosenwaldia	*Trogloscaptomyza*	*Elmomyza* subg. n.
Head in profile	flattened	flattened	usually nearly square, rarely flattened or higher than long
Greatest dimension of eye	strongly oblique	strongly oblique	± oblique rarely vertical
Arista rays basad to end fork	2 dorsal, no or 1 short ventral	2 dorsal, no ventral	usually 2 dorsal, no ventral, end fork sometimes reduced
Acrostichal rows of hair	2—4 rows	2 rows	4—6 rows, usually 6
Dorsocentral bristles (presutural and postsutural)	1+2	0+2	usually 0+2 (in one species 1+2)
Male genitalia	clasper stout, bilobate or ± concave distal margin, usually with denticles (Fig. 1)	clasper stout, bilobate, with denticles (Fig. 3)	clasper stout ± bilobate or of other shape, with denticles (Fig. 2)
Female egg-guide	weakly sclerotized	(female unknown)	weakly sclerotized
Distribution	Hawaii (6 species) Marquesas (type species)	Tristan da Cunha (1 species)	Hawaii (87 species)

genera derived from *Drosophila* and these are all called "Drosophiloids" by THROCKMORTON (1966). The rest are the "Scaptomyzoids", which comprise the *Scaptomyza* species and the species of the derived genus *Titanochaeta* Knab, in all 131 described species. A detailed investigation made by THROCKMORTON (1966), including extensive study of internal organs, showed that there is considerable overlap of characters between the Scaptomyzoids and the Drosophiloids. There are species groups, and even a subgenus, which are more or less intermediate between the genera. Throckmorton observes that "the simplest and most parsimonious conclusion" is that the Scaptomyzoids originated in Hawaii from the same stock as the Drosophiloids. According to him the alternative conclusion that founder Drosophilids were introduced twice into Hawaii is less likely in view of the improbable parallelism that this would involve. As a corollary of the first alternative, he puts forward the theory that the entire genus *Scaptomyza* had its origin in Hawaii, from which it spread out all over the world, undergoing adaptive radiation as it did so. Though not incompatible with the age of the Hawaiian Islands (see further CARSON et al. 1970), the theory is rather hard to believe. Let us therefore consider the question whether *Scaptomyza* is a monophyletic taxon or not.

The phylogeny of Scaptomyza

Among the Hawaiian species of *Drosophila* and *Scaptomyza* the most obvious overlapping of characters is found in the subgenus *Engioscaptomyza* Kaneshiro. For practical reasons this subgenus was retained in *Drosophila,* but its internal characters suggest that it belongs to the Scaptomyzoids (HARDY 1966, KANESHIRO 1969). The "white-tip-scutellum group" among the Drosophiloids also show several Scaptomyzoid characters (THROCKMORTON, 1966). It seems most probable that the same ancestral stock in Hawaii has given rise to the Drosophiloids and at least the Scaptomyzoids belonging to the big subgenus *Elmomyza,* subg. *Rosenwaldia,* subg. *Alloscaptomyza,* subg. *Tantalia* and the genus *Titanochaeta.* OKADA (1973) places the endemic Hawaiian *Scaptomyza* subgenus *Exalloscaptomyza* Hardy on the same branch of a phenogram as *Hemiscaptomyza* and *Scaptomyza* (s. str.) keeping it quite separate from the other Hawaiian *Scaptomyza* subgenera. Okada's phenogram is based on a dozen external characters, including the seven used in my old hypothetical system of the *Scaptomyza* subgenera (HACKMAN 1959). No *Exalloscaptomyza* species has been found outside Hawaii and the similarity with *Hemiscaptomyza,* a subgenus not found in the Pacific area, is probably due to parallelism. *Exalloscaptomyza* Hardy may be a strongly differentiated off-shoot of the Scaptomyzoid branch. The spermathecae (Fig. 21) depicted for several species by THROCKMORTON (1966) are of a rather aberrant type, but the same type is also found in *Titanochaeta contestata* Hardy from Hawaii.

It seems more difficult to clarify the origin of the subgenus *Bunostoma,* described by MALLOCH (1932) as a genus and with endemic species in Hawaii, other island groups in the Pacific and in Australia. Though not typical Scaptomyzas in general appearance, the *Bunostoma* species have been included in *Scaptomyza* because of some key characters (see Table 2 and HACKMAN 1959). The spermathecae of the Hawaiian species are of the same general type as in several *Scaptomyza* species (see Figs. 8—14). In OKADA's phenogram (1973) *Bunostoma* is a sister group of the other Hawaiian subgenera excluding *Exalloscaptomyza.* The male genitalia differ distinctly in type from those in *Elmomyza* and the Drosophiloids near the branching-off point of the Scaptomyzoids. It therefore seems uncertain that *Bunostoma* has its origin in Hawaii and the possibility exists that it was introduced separately from some other part of the Pacific, where the subgenus is widely distributed (Bonin Is., Marquesas, Samoa).

The *Bunostoma* species show some external similarity to the *Drosophila* subgenus *Lordiphosa* Basden, which has not been considered in THROCKMORTON's (1962, 1966) studies on the Drosophila complex. LASTOVKA & MACA (1978), who revised the European species of *Lordiphosa,* insert this small but widely distributed subgenus as an isolated branch near *Sophophora* and *Chymomyza.* A comparison of *Bunosoma* and *Lor-*

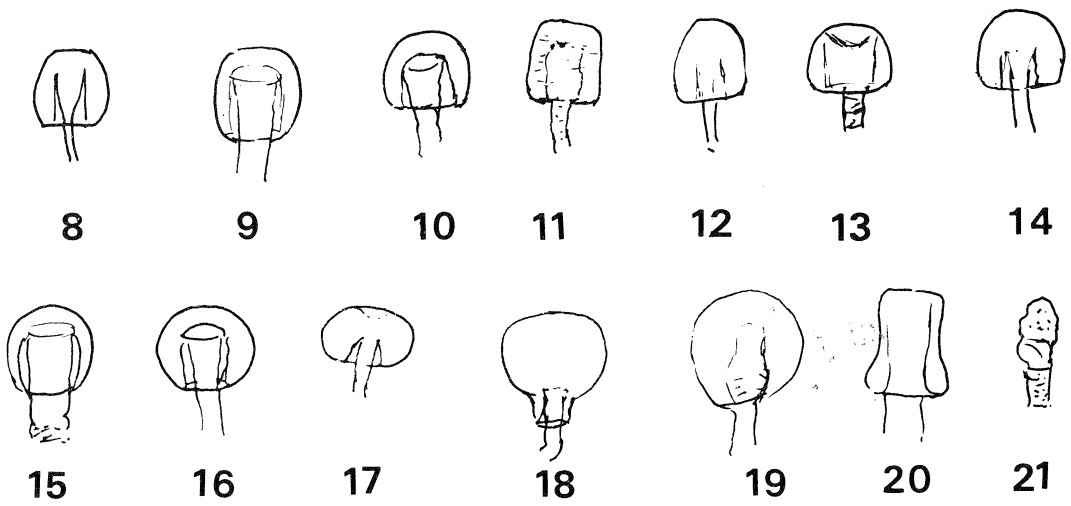
diphosa is made here in Table 2. I have also included in the table two unplaced endemic *Scaptomyza* species from New Zealand because they may have something to do with *Bunostoma* (data from HARRISON's (1959) descriptions of the species).

As shown in the table, *Bunostoma* differs from *Lordiphosa* in the number of humeral bristles and number of sternopleural bristles, and in having a small clasper (Fig. 5) of another type than in *Lordiphosa* (Fig. 4). On the other hand, there are certain similarities to the two New Zealand species.

The stout dentate clasper characteristic of most *Lordiphosa* species shows similarity to that of the less far evolved Hawaiian Drosophilidae (mentioned above) and of *Trogloscaptomyza* from Tristan da Cunha, and, as already suggested, this is probably a case of symplesiomorphism (Figs. 1—4). The internal reproductive organs are known for only 3 of the 13 *Lordiphosa* species: *D. (L.) andalusiaca* Strobl (BASDEN 1961), *D. (L.) collini* Lastovka & Maca (= *Scaptomyza apicalis*, sensu OKADA 1956, Fig. 39, misidentification) and *D. (L.) fenestrarum* Fallén (male organs drawn by Dr. Anssi Saura, unpubl.). The spermathecae are of the same type as in several *Scaptomyza* species (Figs. 8—14), whereas the testes and vasa deferentia (in *D. andalusiaca* and *D. fenestrarum)* are not of the same shape as in the few *Scaptomyza* species for which these organs are figured in the literature *(Parascaptomyza pallida, Scaptomyza* (s. str.) *consimilis* Hackman and *S.* (s. str.) *graminum* Fallén given by OKADA 1956; *Bunostoma* species, schematic figures given by THROCKMORTON 1966; cf. Figs. 22—25 in this paper). Testes and paragonia of the same type as in *D. fenestrarum* and *D. andalusiaca* occur in species of both *Hirtodrosophila* and *Sophophora* and *Chymomyza japonica* Okada; the testes are strongly coiled and the vas deferens thin. It is interesting to note in this connection that in the comparatively small genus *Chymomyza* (derived from the *Sophophora* branch by THROCK-

Table 2. Comparison of characters of *Drosophila* subg. *Lordiphosa, Scaptomyza* subg. *Bunostoma* and two unplaced *Scaptomyza* species from New Zealand.

	Lordiphosa	*Bunostoma*	*S. flavella* and *S. fuscitarsis*
Head	not flattened	not flattened	not flattened
Eyes	± oblique	± oblique	
Facial carina	low and restricted to dorsal half of face	usually distinct in dorsal half of face (in the type species nose-like below)	prominent and nose-like below
Rays of arista	proximal to end fork: 2—3 ventral	2—3 ventral	1—2 ventral
Mesonotum	shiny without pattern brownish yellow or blackish	shiny, brownish black (1 species: yellow)	yellowish brown or purplish black
Humeral bristles	2	1 prominent	1 prominent
Acrostichal rows of hairs	4—6	2—4	2
Dorsocentrals	1+3	0+2 (1+3 in one species)	"two enlarged hairs anterior to dorsocentrals"
Sternopleurals	3 (posterior one longest)	2 (anterior one longer) 1+3 in one species	2 prominent
Male genitalia	no secondary clasper, clasper (surstylus) stout, dentate (usually as in Fig. 4)	no secondary clasper clasper rather small, usually dentate (cf. Fig. 5)	no secondary clasper clasper moderately stout *(S. flavella)* or small *(S. fuscitarsis)*, dentate
Egg-guides	heavily sclerotized, dentate	weakly sclerotized (except in type species)	not mentioned in description
Distribution	9 Palaearctic, 2 Oriental and 1 (2?) Nearctic species	Hawaii: 8 species Other Pacific Ils.: 4 species Australia: 1 species	New Zealand



Figs. 8—21. Spermathecae of *Scaptomyza* and *Drosophila* species. 8. *Drosophila (Lordiphosa) collini* Lastowka & Maca, 9. *Scaptomyza (Bunostoma) anomala* Hardy, 10. *S. (Parascaptomyza) pallida* (Zetterstedt), 11. *S. (Parascaptomyza) taiwanica* Lin & Ting, 12. *S.* (s. str.) *consimilis* Hackman, 13. *S.* (s. str.) *sinica* Lin & Ting, 14. *S.* (s. str.) *graminum* (Fallén), 15. *Drosophila (Engiscaptomyza) nasalis* Grimshaw, 16. *Scaptomyza (Hemiscaptomyza) hsui* Hackman, 17. *S. (Euscaptomyza) chylizosoma* (Segúy), 18. *S. (E.) kilemba* Tsacas, 19. *S. (E.) deemingi* Tsacas, 20. *S. (Lauxanomyza) horaeoptera* Tsacas & Cogan, 21. *S. (Exalloscaptomyza) mauiensis* (Grimshaw). All redrawn: 8, 12 and 14 after Okada 1956, 9, 10, 15, 16 and 21 after Throckmorton 1962 and 1966, 11 and 13 after Lin & Ting 1971, 17—19 after Tsacas 1972, 20 after Tsacas & Cogan 1976.

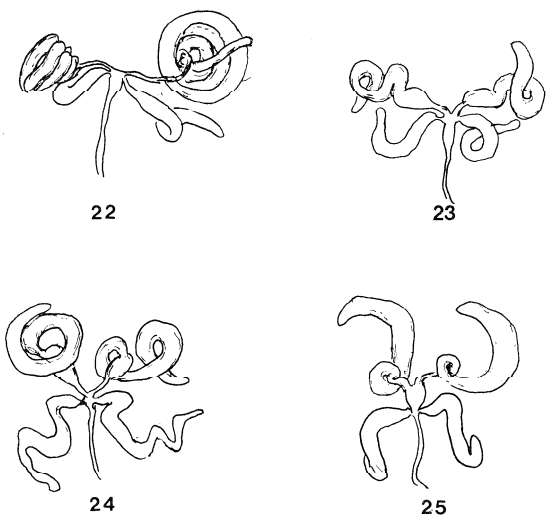
morton 1962) one species, *C. caudatula* (Zetterstedt), as shown in the figure by Okada (1956) with almost elliptic testes and a strongly enlarged vas deferens. When trying to derive the continental *Scaptomyza* species from the Hawaiian Scaptomyzoids Throckmorton (1966) was faced with the problem of the North American *Scaptomyza* (s. str.) *montana,* whose elliptical testes (cf. Wheeler 1952) are of a more primitive type than those in any of the Hawaiian Scaptomyzas. In the few other non-Hawaiian *Scaptomyza* species so far investigated, the testes are loosely coiled, being most elliptical in *S.* (s. str.) *graminum,* and the vas deferens is short and enlarged.

As far as can be judged from the rather incomplete data available, *Lordiphosa* is distinctly separated from *Scaptomyza.*

The non-Hawaiian Scaptomyzas

If the unplaced subgenera are disregarded, the non-Hawaiian Scaptomyzas form two main branches (cf. Okada 1973). One of them contains the subgenera *Parascaptomyza* (no endemic species in Hawaii), *Macroscaptomyza, Boninoscaptomyza, Mesoscaptomyza* and *Metascaptomyza.* In this branch the males have a secondary clasper derived from the ventral part of the anal plate. The primary clasper (surstylus), at least in several *Parascaptomyza* species, is stout and dentate, approaching the plesiomorphic type mentioned earlier. A secondary clasper derived from the anal plate also occurs in *Drosophila* species of the subgenus *Sophophora,* and in the *D. kikkawai* species group it is strikingly similar to that in some *Parascaptomyza* species (Figs. 6 and 7). The *D. kikkawai* group has a wide distribution and is probably of Oriental origin (Tsacas & David 1977). This may of course be a further example of the irregular distribution of the key characters in Drosophilidae, already remarked on by Throckmorton.

The other branch of *Scaptomyza* is formed by *Dentiscaptomyza* Wheeler & Takada, *Hemiscaptomyza* Hackman, *Scaptomyza* (s. str.) and *Euscaptomyza* Séguy (in agreement with Okada's phenogram 1973). In the male genital characters the *Dentiscaptomyza* species are intermediate between the two branches. Most probably these branches have a common origin in the *"Hirtodroso-*



Figs. 22—25. Testes and paragonia of *Drosophila fenestrarum* and *Scaptomyza* species. 22. *Drosophila (Lordiphosa) fenestrarum* Fallén, 23. *Scaptomyza (Parascaptomyza) pallida* (Zetterstedt), 24. *S.* (s. str.) *consimilis* Hackman, 25. *S.* (s. str.) *graminum* (Fallén). Fig. 22 drawn after a sketch by A. Saura, 23—25 after Okada 1956.

phila radiation" (sensu Throckmorton 1975), being close to, but separate from the branch of the Hawaiian Drosophilidae. The less strong overlap of characters between the non-Hawaiian *Scaptomyza* branches and *Drosophila* may be explained by assuming that their separation was much earlier than that taking place in Hawaii between the Scaptomyzoids and Drosophiloids. If this hypothesis is correct, *Scaptomyza* is a paraphyletic taxon. In my opinion paraphyletic taxa can be retained for practical reasons. *Drosophila*, for example, is clearly paraphyletic, since several genera have been derived from different subgenera and species groups of *Drosophila*.

Unplaced subgenera

An unplaced subgenus is *Trogloscaptomyza* Frey, with the single species from Tristan da Cunha. It can hardly be derived from the endemic species groups (*Macroscaptomyza, Parascaptomyza* species) of Tristan da Cunha and Gough Island (for the species from Gough Island see Oldroyd 1958).

Another enigmatic subgenus is *Lauxanomyza* Tsacas & Cogan, from St. Helen Island. The single species, *S. (L.) horaeoptera* Tsacas & Cogan is a "Picture Wing" among the Scaptomyzas. The male clasper is stout and dentate, the egg-guides dentate and the spermathecae of unusual shape (Fig. 20; cf. Tsacas & Cogan 1976). The colour pattern on the wing (numerous coloured spots) is rare in *Scaptomyza*. Something of the kind exists in the subgenus *Euscaptomyza*, with three known species from the high mountains in Africa: one from the Mabilla Plateau in Nigeria, one from Ruwenzori and one from Kenya (Tsacas 1972). There is also some similarity in the male genitalia between *Lauxanomyza* and *Euscaptomyza*. The spermathecae of the three *Euscaptomyza* species are very different from each other (Figs. 17—19), but similar types occur in *Drosophila* species. *Euscaptomyza* and *Lauxanomyza* are possibly relicts of an old branch of *Scaptomyza*.

Concluding remarks

This study of the relationship between *Scaptomyza* and *Drosophila* has mainly been based on the literature, but also on investigation of dried specimens in the collection of the Zoological Museum of Helsinki University. It is obvious that much more information about the internal anatomy and biology of these flies is needed to give a more solid foundation for phylogenetic hypotheses.

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