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COMPARATIVE MORPHOLOGY OF THE MOUTHPARTS OF THE FAMILY DOLICHOPODIDAE (DIPTERA)*

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Abstract

SATÔ, M. 1991. Comparative morphology of the mouthparts of the family Dolichopodidae (Diptera). *Ins. matsum. n. s.* 45: 49-75, 4 tables, 16 figs.

Adult mouthparts of 51 dolichopodid species are examined. Contrary to Cregan's (1941) results, a closer observation of the mouthparts shows that groups based on morphologies of the mouthparts are consistent with Robinson's (1970) classification of subfamilies based on other body parts.

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Contents.

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INTRODUCTION

The family Dolichopodidae is widely distributed in the world, and contains more than 150 genera and approximately 6000 described species, most of which are small and slender flies with long legs. Both larvae and adults are almost exclusively predacious (Dyar and Knab, 1912), though detailed feeding behavior remains unknown except in some species (e.g., Bishop and Hart, 1947 ; Smith, 1959 ; Williams, 1938).

Some work has been made on morphologies of the mouthparts of this family (e. g., Langhoffer, 1901 ; Snodgrass, 1922 ; Cregan, 1941 ; Negrobov, 1976). Cregan (1941), among others, examined 50 species belonging to 32 genera and divided the genera into 12 groups on the basis of the "complexity" of the mouthparts (Table 2). She pointed out that Becker's (1922) classification of subfamilies is inconsistent with her groups, because several subfamilies contain groups of different complexity levels of the mouthparts. Later, Hardy (1964), following the results of Cregan, discussed the evolution of dolichopodid mouthparts, and Negrobov (1976) studied sexual dimorphism and interspecific differences. Cregan's grouping, however, has not been re-examined. In this study the mouthparts of 51 dolichopodid species belonging to 24 genera are examined and Cregan's grouping is criticized. The feeding mechanism of adults is also discussed.

MATERIAL AND METHODS

The species examined, collected from Japan unless otherwise stated, are given in Table 1. Many of them were not identified, while some others are undoubtedly new to science.

The head of a dried specimen was removed from the body and heated in 10% KOH at 70°C for one hour. Then it was transferred into lactic acid containing acid fuchsine and heated at 70°C for two hours. After dipped in a mixture of glacial acetic acid (1 part) and methyl salicylate (1 part) for 30 minutes, it was placed in α-terpineol on a slide and dissected. The mouthparts thus dissected were mounted in Canada balsam, and observed under a microscope, often with an oil-immersion objective. The superficial structures of the epipharynx, hypoglossa and pseudotrachea were observed with a SEM (HITACHI S-2100A).

Sexual dimorphism was also found in this study. Measurement of *Dolichopus nitidus* (unpublished data), in which sexual dimorphism is not remarkable in comparison with other dolichopodids, shows that the head and mouthparts are significantly larger in the female and that the hypopharynx is acuter at the tip in the male. A more remarkable sexual dimorphism is found in *Conchopus borealis*, but even in this case dimorphism does not influence the grouping.

NOTES ON SYSTEMATICS AND BIOLOGY

The Dolichopodidae are closely related to the family Empididae and particularly to the subfamily Microphorinae (Chvāla, 1981). Colless (1964) pointed out that the structure of mouthparts in *Microphorella* (Empididae) is remarkably similar to that of *Sympycnus* (Dolichopodidae). Most Empididae are predators. Some species are

Table 1. A list of the species examined.

Diaphorinae
- *Argyra diaphana* Fabricius, ♂, the Netherlands
- *Chrysotus* sp. A, ♂, ♀
- *C.* sp. B, ♀
- *Diaphorus* sp. A, ♀

Dolichopodinae
- **Dolichopus gubernator* Mik, ♂
- *D.* sp. A, ♂, ♀
- *D.* sp. B, ♂
- *D.* sp. C, ♀
- *D. nitidus* (Fallén), ♂, ♀
- *D. ptenopedilus* Meuffels, ♂
- *Gymnopternus* sp. A, ♂
- *G.* sp. B, ♂
- *Hercostomus nigripennis* (Fallén), ♂, the Netherlands
- *H.* sp. A, ♂
- *H.* sp. B, ♂
- *H.* sp. C, ♂, ♀
- *Poecilobothrus nobilitatus* Linné, ♂, ♀, the Netherlands
- *Tachytrechus* sp. A, ♂, ♀

Hydrophorinae
- *Acymatopus minor* Takagi, ♂, ♀
- *Conchopus abdominalis* Takagi, ♂, ♀
- *C. borealis* Takagi, ♂, ♀
- *Diostracus fasciatus* Takagi, ♂, ♀
- *D. miyagii* Takagi, ♀
- *D. punctatus* Takagi, ♂
- *D. tarsalis* Takagi, ♂, ♀
- *Hydrophorus celestialis* Takagi, ♂, ♀, Nepal
- *H. praecox* Lehmann ♂, ♀
- **Liancalus zhenzhuristi* Negrobov, ♂, ♀
- *Thambemyia pagdeni* Oldroyd, ♂, Malaysia
- *Thinophilus flavipalpis* (Zetterstedt), ♀

Medeterinae
- *Medetera borealis* Thuneberg, ♂
- *M. japonica* Negrobov, ♀
- *M. takagii* Negrobov, ♀
- *M.* sp. A, ♀

Neurigoninae
- *Neurigona* sp. A, ♀
- *N.* sp. B, ♀
- *N.* sp. C, ♀

Rhaphiinae
- *Rhaphium* sp. A, ♂
- *R.* sp. B, ♀
- *R.* sp. C, ♀

Sciapodinae
- *Condylostylus japonicus* Kasagi, ♀
- *C. nebulosus* (Matsumura), ♂, ♀
- *Mesorhaga* sp. A, ♂
- *Sciapus* sp. A, ♂, ♀
- *S.* sp. B, ♂
- *S.* sp. C, ♀

Sympycninae
- *Campsicnemus pectinulatus* Loew, ♀, the Netherlands
- *C. scambus* Fallên, ♀, the Netherlands
- *Sympycnus* sp. A, ♂, ♀
- *Syntormon* sp. A, ♂
- *S.* sp. B, ♂

* New to Japan.

Table 2. Cregan's grouping and Becker's subfamilies.

Group	Neurigoninae	Medeterinae	Sciapodinae	Diaphorinae	Rhaphiinae	Dolichopodinae	Plagioneurinae	Campsicneminae	Hydrophorinae	Aphrosylinae	*
(Primitive) I ↑				*Diaphorus* *Chrysotus*							
II	*Neurigona*								*Scellus*	*Aphrosylus*	*Millardia*
III									*Diostracus*		
IV		*Medeterus* *Thrypticus*			*Rhaphium*			*Xanthochlorus*			
V			*Condylostylus*								
VI			*Sciapus* *Mesorhaga*								*Laxina*
VII									*Thinophilus*		
VIII									*Hypocharassus*		
IX											*Melanderia*
X				*Argyra*	*Peloropeodes*			*Campsicnemus* *Teuchophorus*	*Hydrophorus* *Liancalus*		
XI						*Gymnopternus*					
XII ↓ (Complex)					*Syntormon*	*Dolichopus* *Hygroceleuthus* *Pelastoneurus* *Tachytrechus*	*Plagioneurus*	*Sympycnus*			

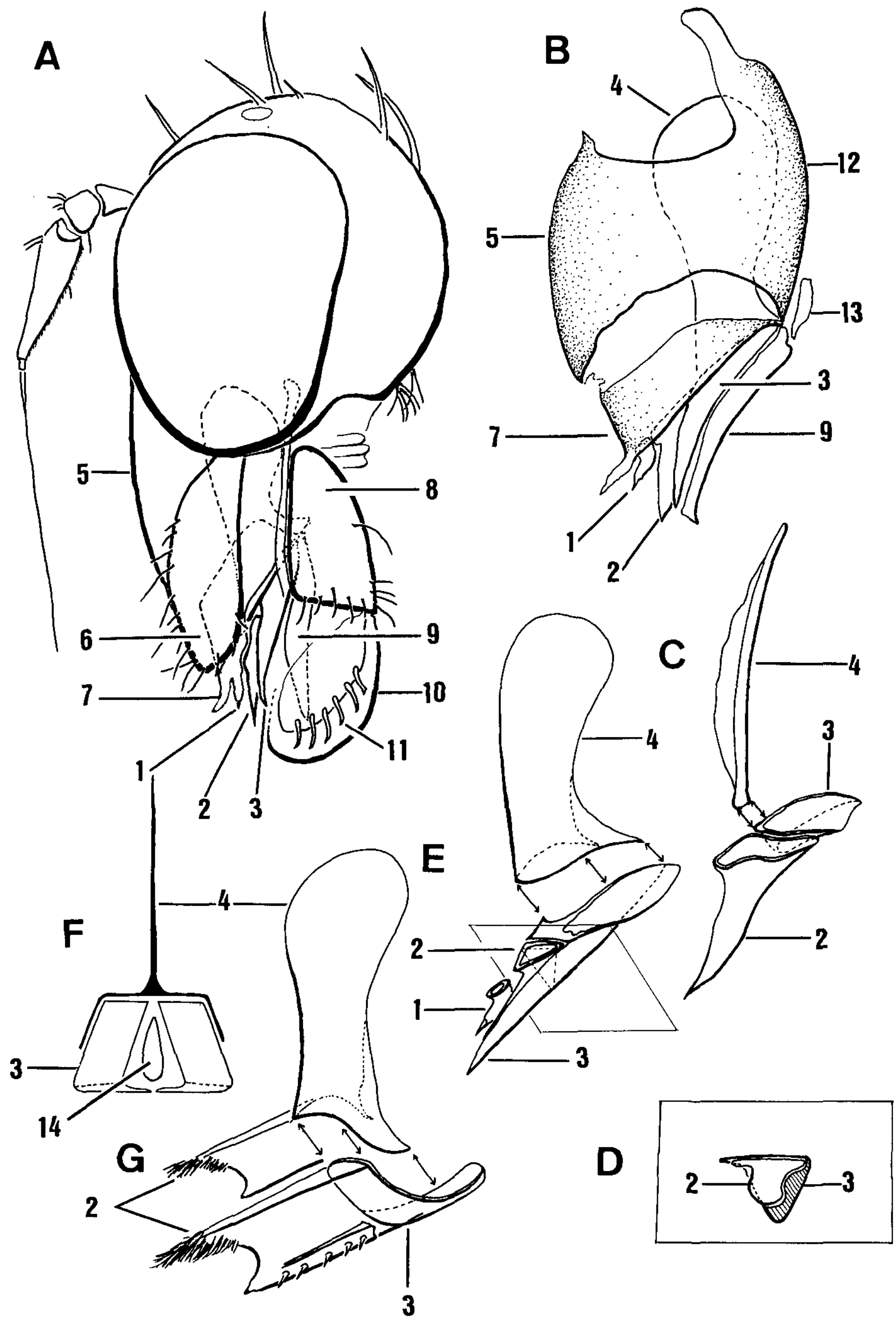
* Unplaced genera by Becker (1922).

Table 3. Some genera studied by Cregan (1941) and their positions in authors.

genera	Becker (1922)	Robinson (1970)	Ulrich (1980)
Argyra	Diaphorinae	Diaphorinae	Rhaphiinae
Aphrosylus	Aphrosylinae	Hydrophorinae	Hydrophorinae
Campsicnemus	Campsicneminae	Sympicninae	Sympicninae
Sympycnus	Campsicneminae	Sympicninae	Sympicninae
Syntormon	Rhaphiinae	Sympicninae	Sympicninae
Teuchophorus	Campsicneminae	Sympicninae	Sympicninae
Peloropeodes	Rhaphiinae	Peloropeodinae	Sympicninae
Plagioneurus	Plagioneurinae	Plagioneurinae	Rhaphiinae
Xanthochlorus	Campsicneminae	Xanthochlorinae	Sympicninae

Table 4. Feeding habits of Dolichopodidae.

Species	Food	Reference
Scellus virago	Agromyzids	Doane (1907)
Sciapus sp.	Thrips	Malloch (1917)
Dolichopus renidescens	Mosquito larvae	Bishop and Hart (1931)
D. nigricauda	〃	
D. walkeri	〃	〃
Campsicnemus funipennis Par.	Collembola	Williams (1938)
Hydrphorus sp.	Larva of *Chironomus hawaiiensis* Grims	〃
Dolichopus ramifer Lw.	Tiny annelids	Cregan (1941)
Sciapus maritimus Beck.	Tiny psychodid fly	Colyer and Laurence (1951)
Medetera jacula Fall.	Collembola, Diptera, Hemiptera, Psocoptera and Thysanoptera [marked preference]	
M. truncorum Mg.	〃	〃
M. dendrobaena Kow.	〃	〃
M. ambigua Zett.	〃	〃
Neurigona sp.	Typhlocibidae (Homoptera)	Fonseca (1955)
Poecilobothrus nobilitatus L.	Larvae of Culex	Smith and Empson (1955)
Neurigona suturalis Fall.	Female psyllids	Smith (1959)
Dolichopus ungulatus L.	Aphid exuviae and excretions	White (1976)
D. trivialis Hal.	〃	〃
D. griseipennis Stann.	〃	〃
Chrysotus gramineus Fall.	Collembola	〃
Poecilobothrus nobilitatus L.	Water fleas, other tiny aquatic animals	Fonseca (1978)
Medetera petulca Wheeler	Spiders, mites, small centipedes, Collembola, Diptera (Sciaridae, Psychodidae, Cecidomyiidae), Homoptera (including Aphididae), lepidopterous larvae	Bickel (1985)
Medetera spp.	Aphids and eriophyid mites on apple	Rathman and Brunner (1988)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known to feed on nectar and pollen and others on dead insects trapped in spiders' webs (Downes and Smith, 1969).

In classifying dolichopodid subfamilies Robinson (1970) and Ulrich (1980) introduced a few modifications to Becker's scheme (Table 3). As regards the relationship of the subfamilies, however, no deatiled analysis has yet been made. Morphological analysis of the mouthparts may be one of effective means for phylogenetic reconstruction in this family.

The published feeding habits of Dolichopodidae are summarized in Table 4. Most species of this family occur near moist habitats, because their preys, small insects belonging to diverse groups, abound in such habitats. Information as to the biology of the Dolichopodidae is, however, still too insufficient to explain the morphological diversity of mouthparts.

Observations

1. Hypopharynx

The hypopharynx is sharp at the tip ; its anterior part is inserted between the ventral lobes of the hypoglossa.

It varies in shape in a gradual transition from a long, slender lanceolate type to a broader triangular type (Fig. 3). In this part no distinct groups can be recognized except for three genera, *Hydrophorus, Sympycnus* and *Medetera*, which show their own types. *Hydrophorus* has a pentagonal hypopharynx, thus obviously differing from the other genera examined. *Hydrophorus celestialis* is an unusual micropterous alpine fly, but it also has a pentagonal hypopharynx. In *Medetera* the hypopharynx, when viewed laterally, is bent apically. In *Sympycnus* it is much broadened basally and has a short basal projection ventrally.

2. Hypoglossa

The family Dolichopodidae is provided with a unique hypoglossa (Fig. 2. A-3), which is especially remarkable in having dense microspines on the dorsal surface (Fig. 12. D). The hypoglossa consists of the following three parts : central plate (Fig. 2. B-6, C-6), microspine areas (Fig. 2. B-5, C-5) and ventral lobes (Fig. 2. B-7, C-7). The central plate is placed underneath the hypopharynx, and variable in shape. Usually it is a triangular or rectangular plate with ventral projections on both sides. *Medetera* is unique in having an X-shaped central plate. Two mountain stream genera, *Diostracus* and *Liancalus*, have a square, very strongly sclerotized one. The central plate is absent in some genera (*Acymatopus, Campsicnemus, Conchopus, Hydrophorus, Neurigona, Tachytrechus* and *Thambemyia*).

Fig. 1. Head and mouthparts of Dolichopodidae. A, lateral view of head of *Conchopus borealis* ; B, lateral view of mouthparts of *C. borealis* ; C, lateral view of mouthparts of *Medetera* ; D, transverse section at the position indicated by a square in E ; E, lateral view of mouthparts of *Conchopus* ; F, frontal view of basal epipharygeal sclerites and epipharyngeal endoskeleton of *Dolichopus* ; G, lateral view of mouthparts of *Dolichopus*. 1, "anterior projection" of apical epipharyngeal sclerite ; 2, apical epipharyngeal sclerite with main posterior projection ; 3, basal epipharyngeal sclerite ; 4, epipharyngeal endoskeleton ; 5, clypeus ; 6, palpus ; 7. labrum ; 8, theca ; 9, hypopharynx ; 10, labella ; 11, pseudotrachea ; 12, cibarial pump ; 13, salivary bulb ; 14, median epipharyngeal sclerite.

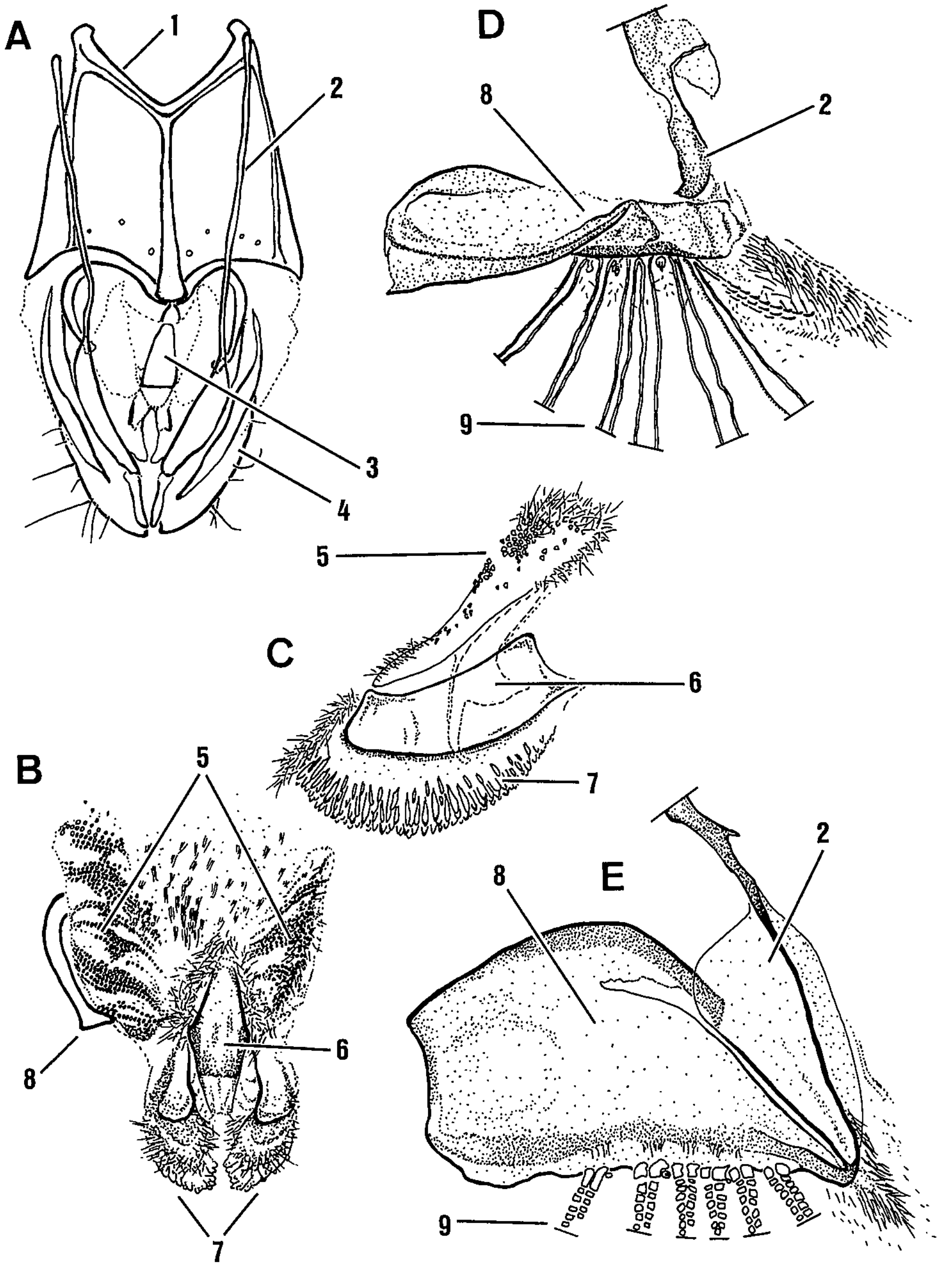


Fig. 2. Mouthparts of Dolichopodidae. A, anterior view of labium parts of *Dolichopus nitidus* ; B, anterior view of hypoglossa of *D. nitidus* ; C. lateral view of hypoglossa of *D. nitidus* ; D, discal sclerite of *Condylostylus neblosus* : E, discal sclerite of *Dolichopus nitidus*. 1, theca ; 2, paraphyses ; 3, hypoglossa ; 4, labella ; 5, microspine area ; 6, central plate ; 7, ventral lobe ; 8, discal sclerite ; 9, pseudotrachea.

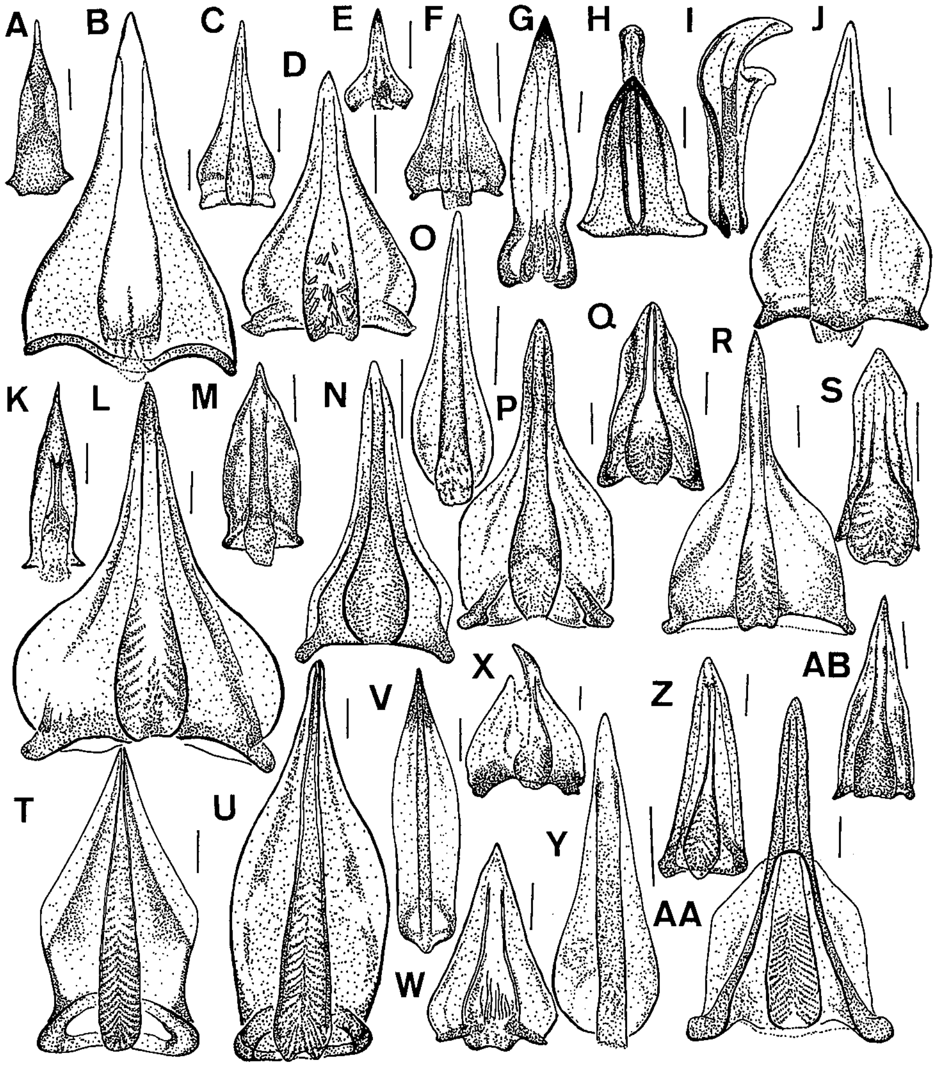


Fig. 3. Hypopharynx. A, *Sciapus* sp. A ; B, *Dolichopus ptenopedilus ;* C, *Hercostomus* sp. ; D, *Gymnopternus* sp. A ; E, *Sympycnus* sp. A ; *F, Syntormon* sp. A ; G, *Neurigona* sp. C ; H, *Medetera* sp. A ; I, lateral aspect of H ; J. *Poecilobothrus nobilitatus* ; K, *Condylostylus nebulosus* ; L, *Argyra* sp. ; M, *Mesorhaga* sp. A ; N, *Chrysotus* sp. A ; O, *Rhaphium* sp. ; P, *Thinophilus flavipalpis* ; Q, *Hydrophorus celestialis* ; R, *Liancalus zhenzhuristi* ; S, *Hydrophorus praecox* ; T, *Conchopus borealis* (female) ; U, *Conchopus borealis* (male) ; V, *Thambemyia pagdeni* ; W, *Campsicnemus pectinulatus* ; X, *Diaphorus* sp. A ; Y, *Rhaphium* sp. B ; Z, *Acymatopus minor* ; AA, *Diostracus fasciatus* ; AB, *Tachytrechus* sp. A. Scale, 0.05 mm.

The microspine areas are found laterally to the hypopharynx, and are connected to the paraphyses (Fig. 6. C and Fig. 12. D). The function of the microspines, which may be peculiar to this family, is unknown. The ventral lobes are membranous ventral parts of hypoglossa and receive the tip of the hypopharynx. The hypoglossa has numerous minute processes on the surface in many genera (Fig. 6. D). In *Diostracus* and *Liancalus* it is very strongly sclerotized, and is equipped apically with sclerotized plates, in which the hypopharynx is wrapped.

3. Discal sclerite

Although the "discal sclerite" may not be homologous throughout the dipterous families, this term is applied in this study to the sclerotized part to which the pseudotracheae are attached (Fig. 2. D-8 and E-8).

The discal sclerite is, in most dolichopodid genera examined, triangular in shape, with a dorsal projection which is connected with the side of the hypoglossa. An exception is found in three sciapodine genera, in which it is rectangular in shape, with no projection. The head of the paraphysis is connected apically to the ventral tip of the discal sclerite in most genera examined.

In the flies of the lick-and-suck type liquid food passes through the pseudotracheae and collecting channel and is collected in the oral aperture which is surrounded by the discal sclerites. Then it is conveyed to the tubular structure framed by the epipharynx and hypopharynx. Dolichopodidae may take food in another way for the following reasons: 1) absence of collecting channel, 2) absence of tubular structure, and 3) strong sclerotization of pseudotracheae.

4. Epipharynx

In most families of Diptera, the epipharynx is fused with the labrum. In Dolichopodidae, however, it is separated from the labrum and consists of four parts: apical epipharyngeal sclerites, basal epipharyngeal sclerites, median epipharyngeal sclerite and epipharyngeal endoskeleton (Fig. 1. A-1, -2, B-2, -3). These parts show very characteristic forms peculiar to this family. The epipharyngeal endoskeleton (Fig. 1. C-4, E-4, F-4, G-4) projects into the cibarial pump (Fig. 1. B-12). It is placed on a pair of sclerites, the basal epipharyngeal sclerites (Fig. 1. C-3, E-3, F-3, G-3), which are in turn connected with the apical epipharyngeal sclerites (Fig. 1. C-2, E-2, G-2) on the front. The median epipharyngeal sclerite (Fig. 1. F-14) is connected to the "dorsal plate" (Graham-Smith, 1930) of the cibarial pump by a thinner membrane and sandwiched in between the basal epipharyngeal sclerites. The tip of the median epipharyngeal sclerite is attached to the ventral tip of the epipharyngeal endoskeleton.

Many minute spines are found on the surface of the apical and basal epipharyngeal sclerites in many genera (Fig. 4, 5 and 6-A, B), and are peculiar to this family.

4-1. Epipharyngeal endoskeleton

The epipharyngeal endoskeleton shows four types. In many genera it is platelike, and apically roundish and membranous (Fig. 1. E-4 and G-4). In *Neurigona, Rhaphium* and *Syntormon* it is very small as compared with the apical and basal epipharyngeal sclerites and labrum, completely connected with the basal epipharyngeal sclerites, and not round but angular apically. A third type is only found in

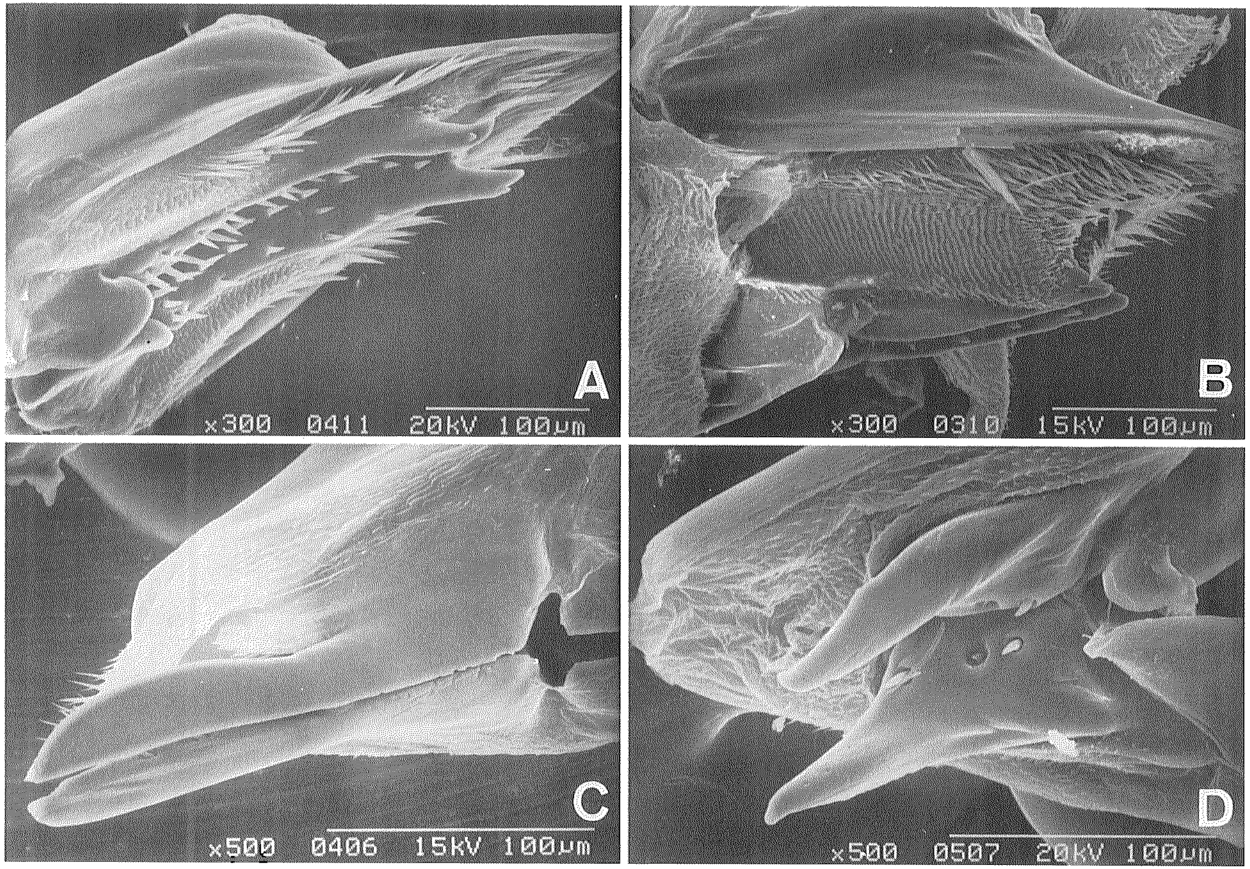


Fig. 4. Epipharynx. A, *Rhaphium* sp. C ; B, *Gymnopternus* sp. B ; C, *Neurigona* sp. C ; D, *Medetera japonica*.

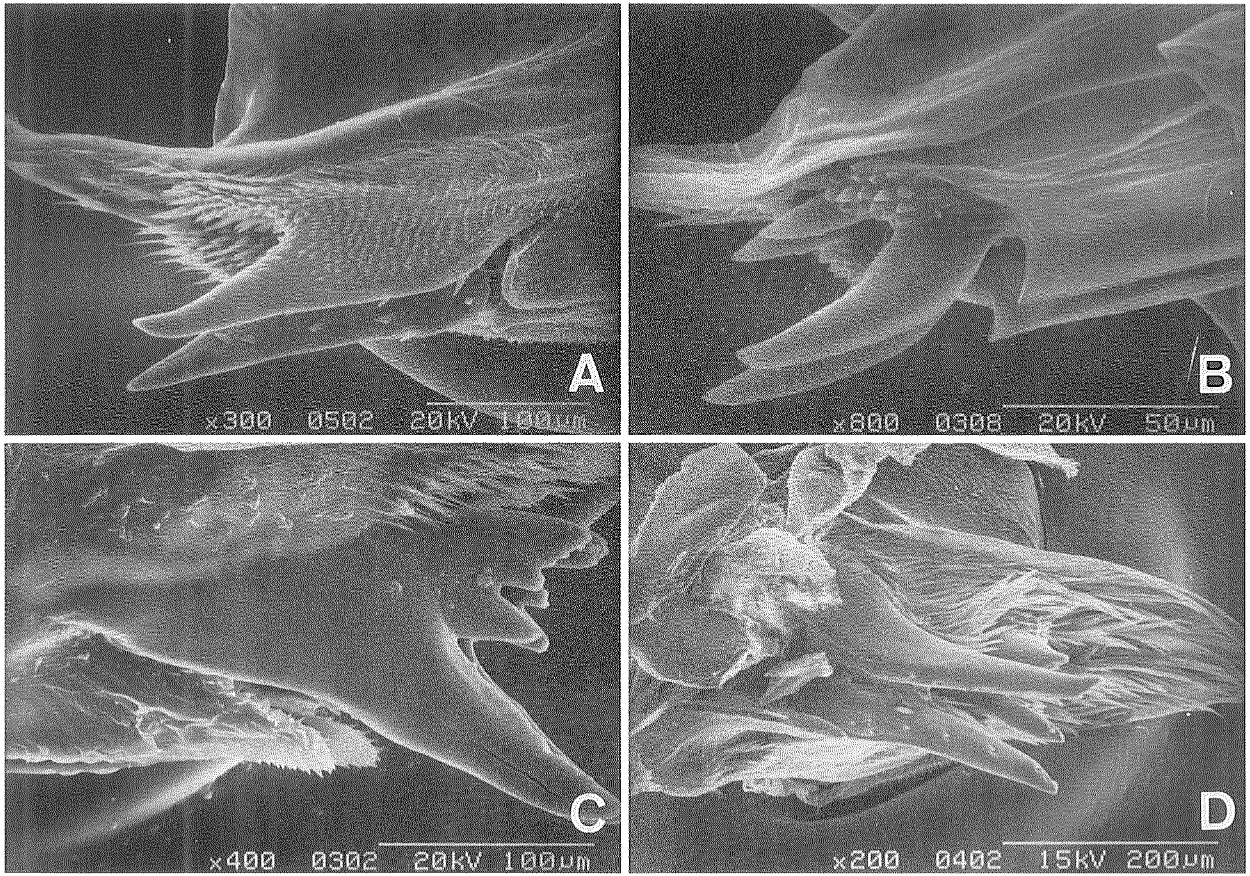


Fig. 5. Epipharynx. A, *Tachytrechus* sp. A ; B, *Mesorhaga* sp. A ; C, *Thinophilus flavipalpis* ; D, *Diostracus fasciatus*.

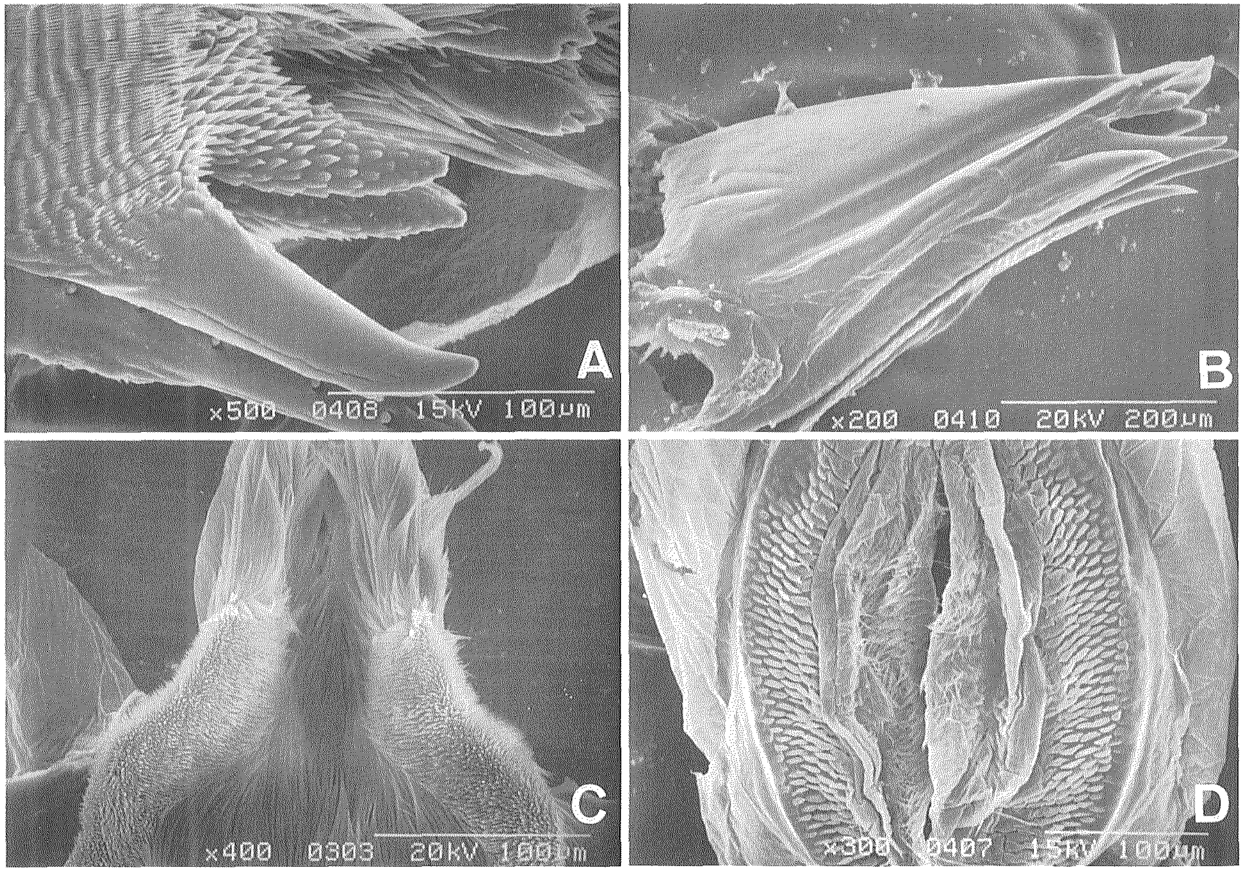


Fig. 6. Epipharynx. A, *Liancalus zhenzhuristi* ; B, *Conchopus abdominalis*. C, dorsal face of hypoglossa of *Dolichopus* sp. C ; D, ventral face of hypoglossa of *Liancalus zhenzhuristi*.

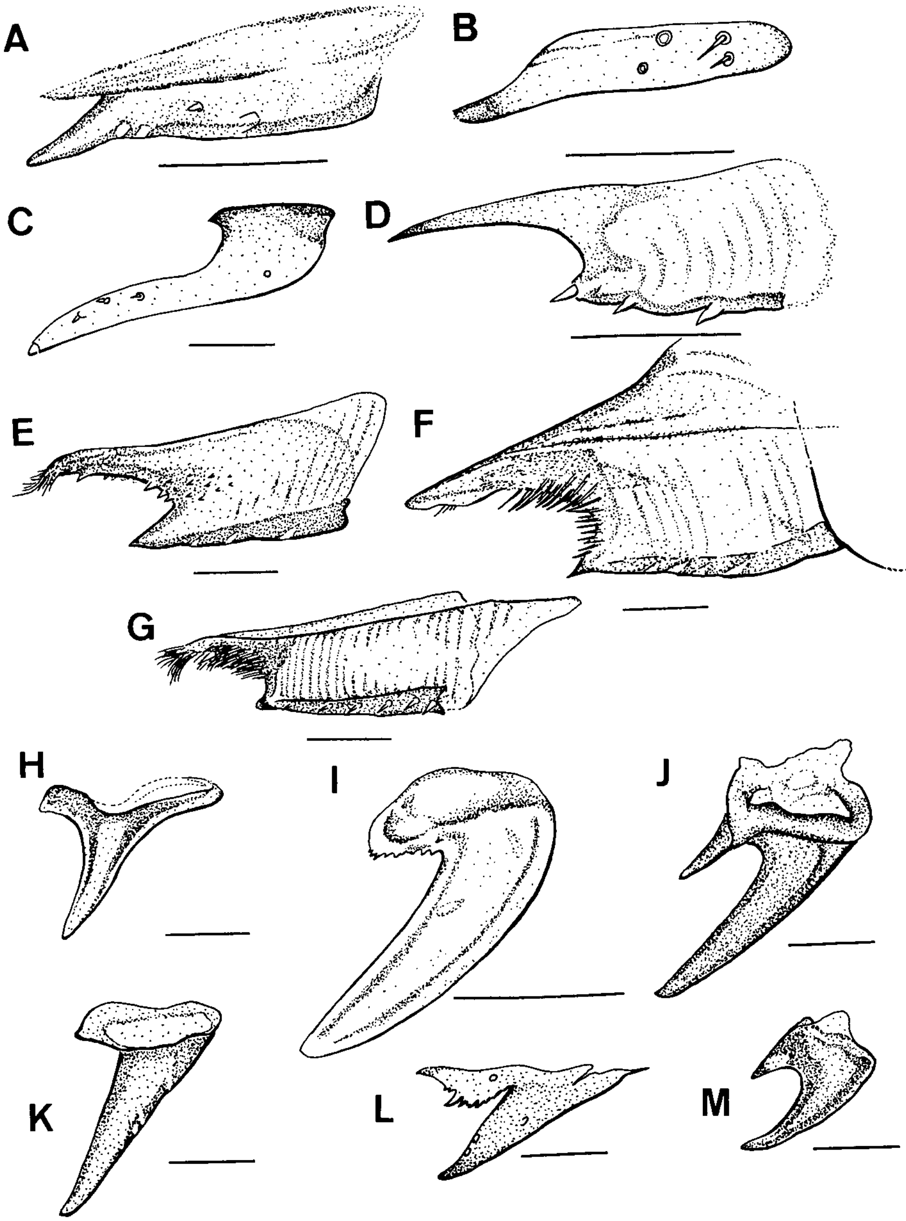


Fig. 7. Apical epipharyngeal sclerite. A, *Rhaphium* sp.; B, *Rhaphium* sp. C; C, *Neurigona* sp.A; D, *Syntormon* sp. A; E, *Hercostomus* sp. A; F, *Gymnopternus* sp. B; G, *Dolichopus nitidus*; H, *Medetera borealis*; I, *Acymatopus minor*; J, *Condylostylus japonicus*; K, *Hydrophorus* sp. A; L, *Chrysotus* sp. A; M, *Sciapus* sp. A. Scale, 0.05 mm.

Medetera. This genus has a very slender, sticklike endoskeleton, which projects into the cibarial pump (Fig. 1. C–4) and is membranous anteriorly. The fourth type is a triangular fin-like endoskeleton and is found in *Conchopus abdominalis* and *Thambemyia pagdeni*.

In one species of *Neurigona*, which has a long and convex labrum as in hoverflies, it is not the cibarial pump but the labrum that receives the epipharyngeal endoskeleton. The state in this species may be comparatively primitive.

4-2. Basal epipharyngeal sclerites and median epipharyngeal sclerite

The basal epipharyngeal sclerites are uniform in the genera examined except in the two marine-shore genera *Conchopus* and *Thambemyia*. In these genera, each of the basal epipharyngeal sclerites has a very long projection which surpasses the apical epipharyngeal sclerite (Fig. 1. D and E).

The median epipharyngeal sclerite is also little variable in shape, being a slender leaf-like plate in most genera examined.

4-3. Apical epipharyngeal sclerites

The apical epipharyngeal sclerites show the greatest variety in the mouthparts of this family. They are divided into two types. In one of them they have a simple projection. This type is further divided into four subtypes as follows. Subtype 1 (Fig. 7. A & B): long and slender, with a short projection (*Rhaphium*). Subtype 2 (Fig. 7. D, F and G): wedgelike (as seen in *Dolichopus, Gymnopternus, Poecilobothrus, Sympycnus* and *Syntormon*); in this subtype, the bases of apical epipharyngeal sclerites are membranous, connecting to the tips of the basal epipharyngeal sclerites. Subtype 3 (Fig. 7. C): with a very long projection extending forward (*Neurigona*). Subtype 4 (Fig. 7. H and K): with a strongly sclerotized projection on the underside (*Hydrophorus* and *Medetera*). (In Subtypes 1, 2 and 3 the projection runs in parallel with the ventral margin of the labrum). This type (especially Subtypes 1, 2 and 3) may be primitive in this family, the epipharynx having some resemblance to the normal type seen in other dipterous families (Peterson, 1916). In several species of the family Empididae the epipharynx is elongate and has many small spines at the tip, but no distinct projection is found (Bletchly, 1954).

The other type has two or more strongly sclerotized projections with ornamentation, and is found in the fifteen genera other than the nine mentioned above. This type is further divided into six subtypes as defined below, which become successively more complex in structure in the mentioned order. Subtype 1 (Fig. 7. E, I, L and Fig. 8. A), to which *Acymatopus, Argyra, Campsicnemus, Chrysotus, Diaphorus, Hercostomus*, and *Tachytrechus* belong, has many spines anteriorly to the projection. Subtype 2 (Fig. 7. J and M), with a simple projection and with another much smaller one anteriorly, is found in *Condylostylus, Mesorhaga* and *Sciapus*. In the remaining four subtypes, the projection is enormously developed and variously shaped. Subtype 3 (Fig. 8. B) has a toothed lobe on the anterior base of the projection and is found in *Thinophilus*. Subtype 4 (Fig. 8. C) has been observed in *Diostracus*, in which the anterior part also projects downwards. Subtype 5 (Fig. 8. D) has one anterior and two posterior projections. This subtype is found in *Liancalus*. In Subtype 6 (Fig. 8. E and F), each apical epipharyngeal sclerite is divided into two parts: the anterior part may be called "apical armature", which lies under the labrum, and the

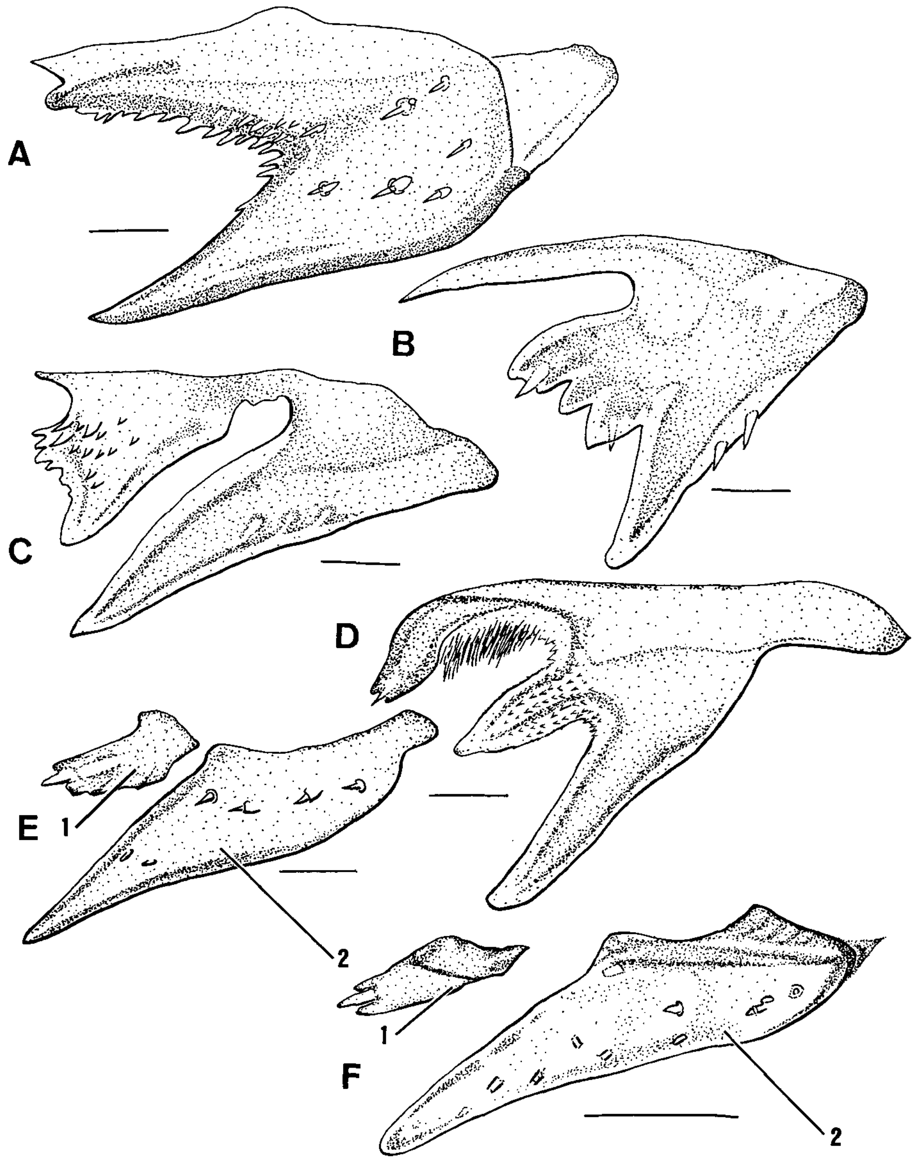


Fig. 8. Apical epipharyngeal sclerite. A, *Argyra* sp. B; B, *Thinophilus flavipalpis*; C, *Diostracus fasciatus*; D, *Liancalus zhenzhuristi*; E, *Conchopus borealis*; F, *Thambemyia pagdeni*. 1, apical armature; 2, main projection. Scale, 0.05 mm.

posterior part is the main projection; these parts appear to be connected by membrane. This subtype is represented by *Conchopus* and *Thambemyia*.

These epipharyngeal projections can be used in tearing food, and their development does not form a tubular structure of the epipharynx-hypopharynx, as generally seen in Diptera, by which liquid food is conveyed. If the function of the epipharyngeal projections is only to tear food, their development will be independent of the

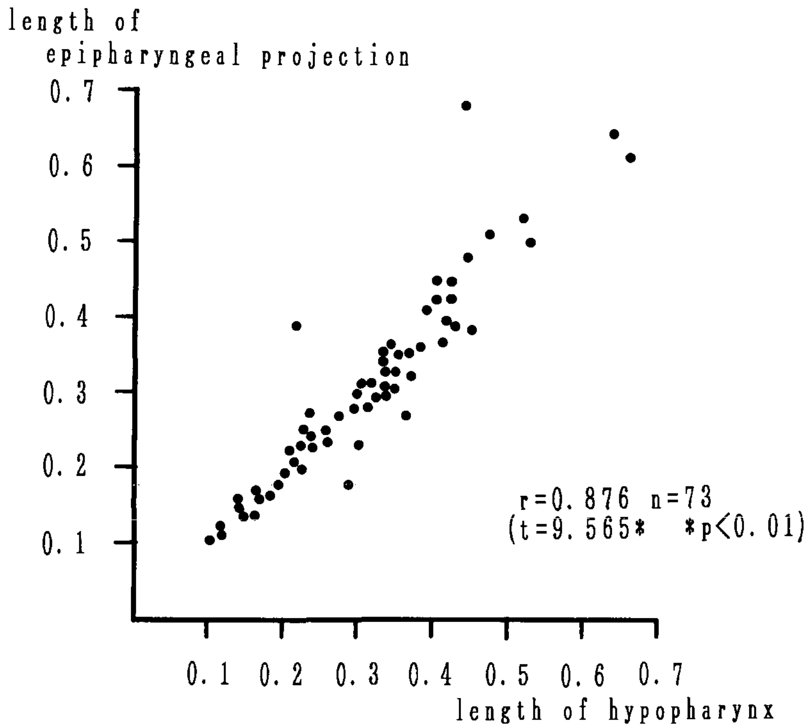


Fig. 9. Correlation between length of epipharyngeal projection and length of hypopharynx.

hypopharynx, the floor of the tubular structure. Nevertheless, there is a close correlation in size between the epipharyngeal projection and the hypopharynx (Fig. 9). Therefore it is probable that the epipharyngeal projection more or less retains the original function of the epipharynx, that is, conveyance of liquid food.

5. Pseudotracheae

In this family, there are always six pseudotracheae on the inner side of each labella. A pseudotrachea is constructed by two long opposed parts (Fig. 12. A and B). No "pseudotracheal ring" is seen in the dolichopodid pseudotrachea. In all dipterous families other than the Dolichopodidae, the pseudotrachea is not strongly sclerotized. On the basis of this fact, the most sclerous pseudotrachea may be regarded as representing the derived extreme in the Dolichopodidae. Six types are recognized, and may represent successive stages from the primitive (Type 1) to the derived extreme (Type 6) as follows.

In Type 1 (Fig. 10. A and B), each pseudotrachea is uniformly membranous, showing two opposed ribbon-like structures. This type is represented by *Condylostylus* and *Sciapus*, which have, in addition, a regressive pseudotrachea. Type 2 (Fig. 10. C) is found in *Mesorhaga* and *Medetera.* This type differs from Type 1 in having many small sclerotized specks on each ribbon. In some species of *Medetera*, the ribbon is wavelike on the side.

In Type 3 (Fig. 10. D and F), which is represented by *Rhaphium*, each pseudotra-

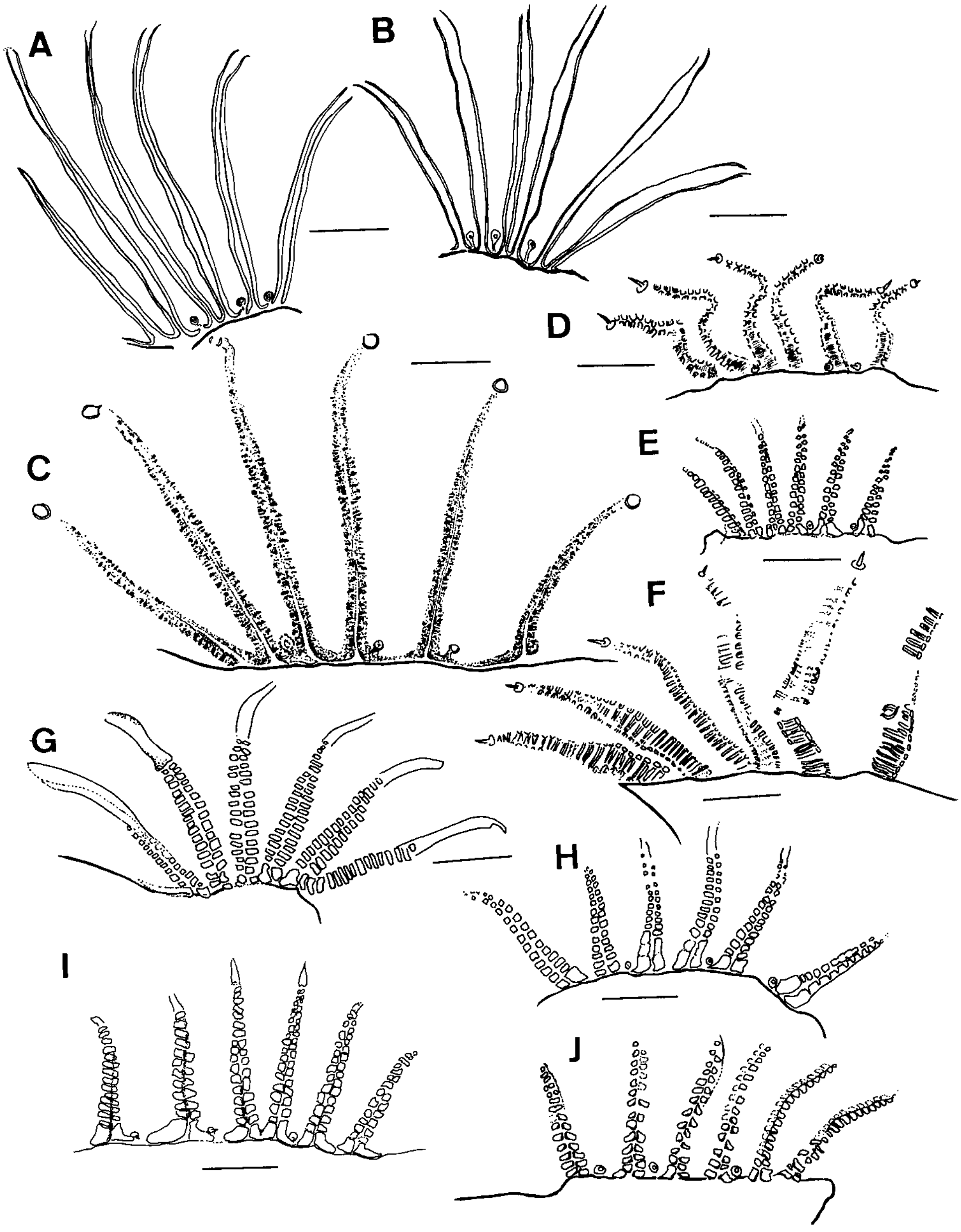
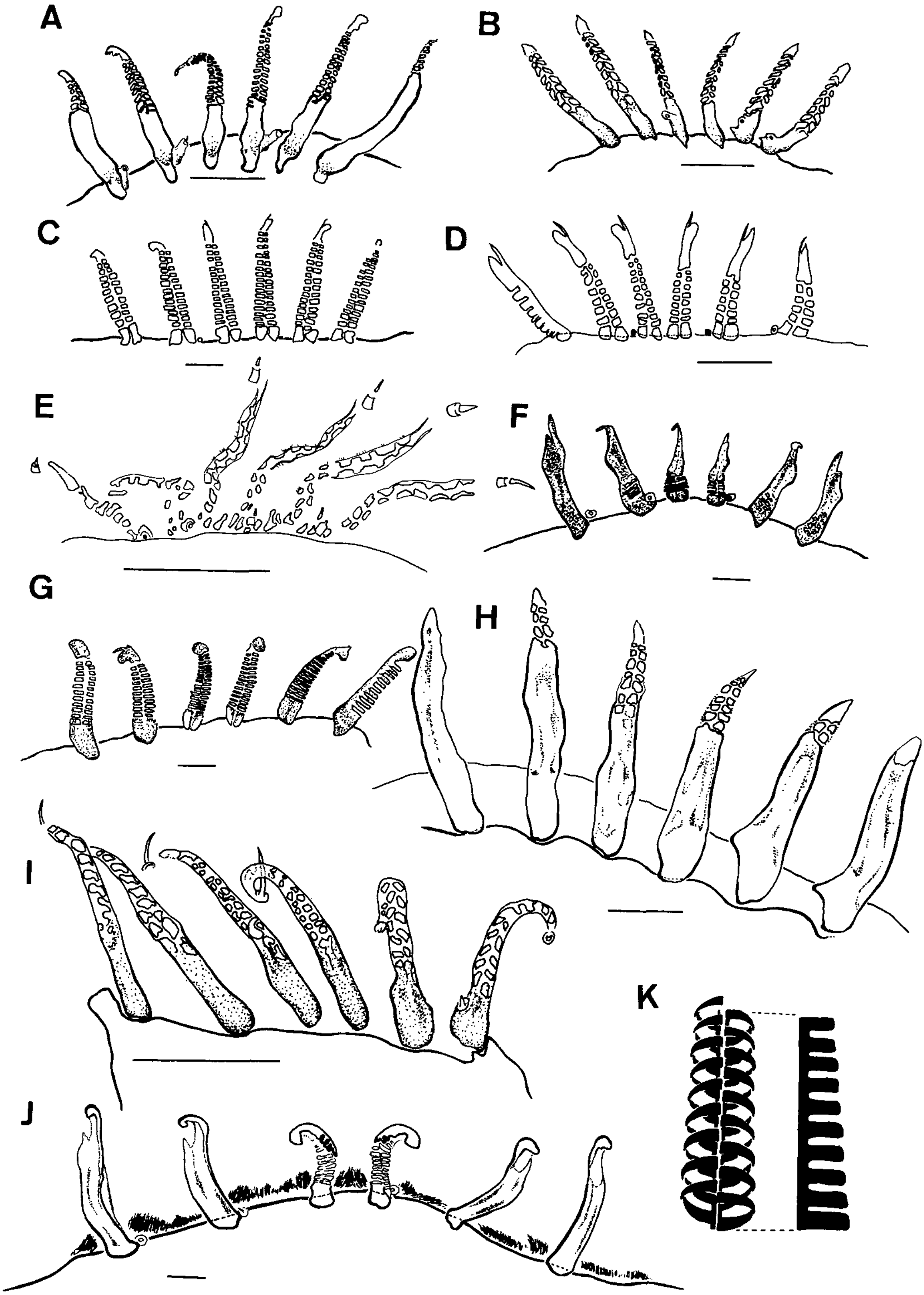


Fig. 10. Pseudotrachea. A, *Condylostylus japonicus* ; B, *Sciapus* sp. A ; C, *Medetera* sp. C ; D, *Rhaphium* sp. ; E, *Gymnopternus* sp. A ; F, *Rhaphium* sp. B ; G, *Neurigona* sp. B ; H, *Hercostomus* sp. A ; I, *Dolichopus ptenopedilus*. J, *Syntormon* sp. A. Scale, 0.05 mm.

Fig. 11. Pseudotrachea. A, *Hydrophorus* sp. A ; B, *Acymatopus mimor* ; C, *Argyra* sp. B ; D, *Chrysotus* sp. A (female) ; E, *Chrysotus* sp. A (male) ; F, *Thinophilus flavipalpis* ; G, *Liancalus zhenzhuristi* ; H, *Conchopus borealis* ; I, *Thambemyia pagdeni* ; J, *Diostracus fasciatus* ; K, schematic structure of a pseudotrachea. Scale, 0.05 mm.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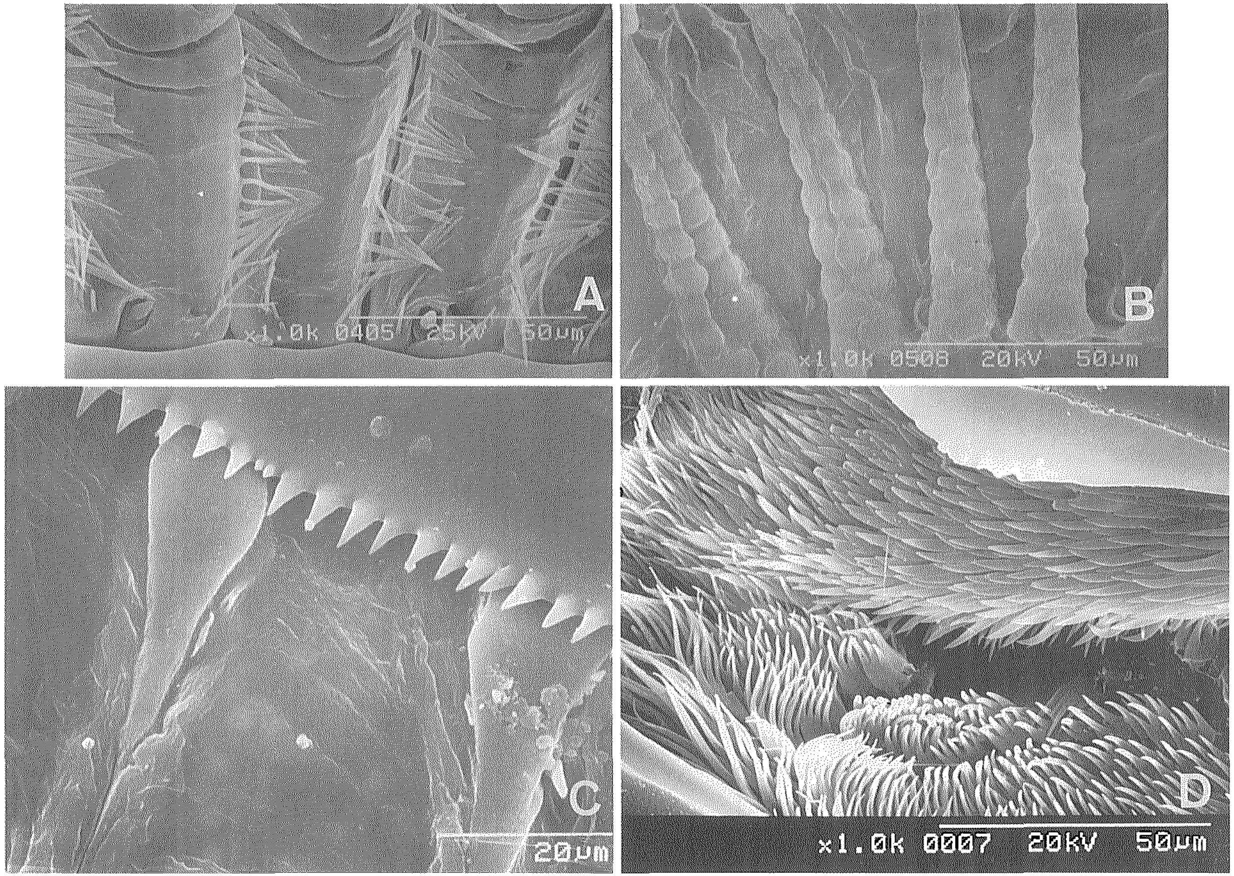

Fig. 12. Hypoglossa and Pseudotrachea. A, outerside of labella of *Dolichopus nitidus* ; B, innerside of labella of *Dolichopus nitidus* ; C, pseudotrachea of *Conchopus borealis* ; D, superficial structure of hypoglossa of *Hydrophorus praecox*.

cheal ribbon is sclerotized weakly and shows 20-25 distinct projections arranged like in a comb. Opposing projections of the ribbons are interposed like in a zipper on the bottom of the ditch between the ribbons. Interspaces between the pseudotracheae are very narrow at their basal ends. Type 4 (Fig. 10. E, G, H, I and J., Fig. 11. C, D, E and G) is represented by thirteen genera, *Argyra, Campsicnemus, Chrysotus, Diaphorus, Dolichopus, Gymnopternus, Hercostomus, Liancalus, Neurigona, Poecilobothrus, Sympycnus, Syntormon* and *Tachytrechus* ; the opposing projections (Fig. 11. K), 10-15 in number, are broad and strongly sclerotized. In Type 5 (Fig. 11. A, B, F and I), to which *Acymatopus, Thambemyia, Thinophilus* and *Hydrophorus* belong, the sclerotization of the pseudotracheae is stronger at the base ; the opposing projections are found only partly, usually towards the apex ; four pseudotracheae located on both lateral sides are more sclerotized as compared with the median two. Subtype 6 (Fig. 11. H and J) is shown by two genera, *Conchopus* and *Diostracus* ; the sclerotization is very strong (Fig. 12. C), so that the ditch between the paired ribbons is rudimentary or obsolete in lateral pseudotracheae ; the interspaces between pseudotracheae are very wide ; each pseudotrachea is short and curved outward.

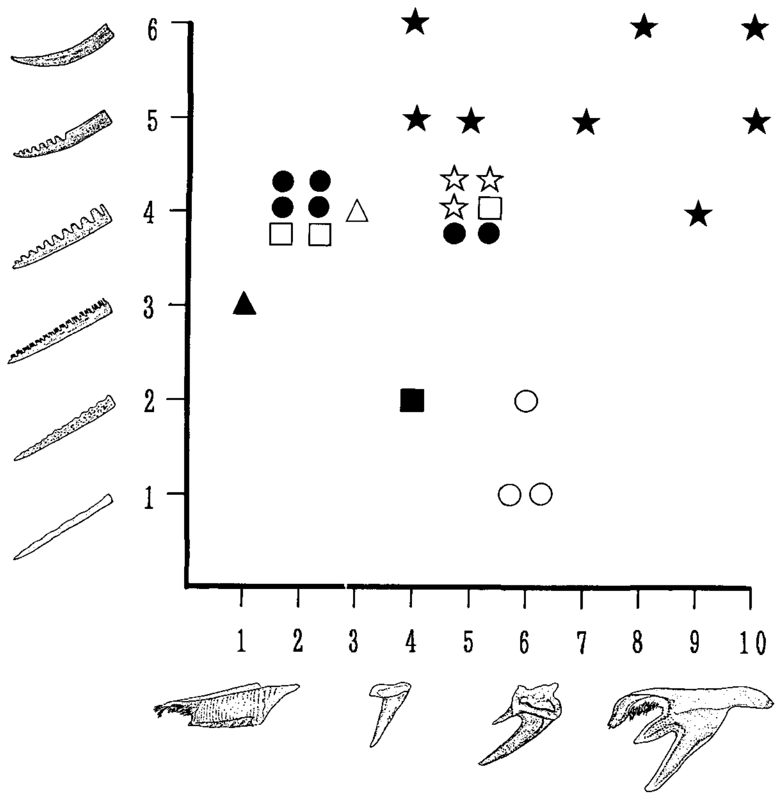

Fig. 13. Distribution of subfamilies in the correlation of the pseudotracheal and the epipharyngeal types. (○ = Sciapodinae, ● = Dolichopodinae, □ = Sympicninae, ■ = Medeterinae, △ = Neurigoninae, ▲ = Rhaphiinae, ☆ = Diaphorinae, ★ = Hydrophorinae.)

Discussion

Fig. 13 gives a distribution of Robinson's (1970) subfamilies in the correlation of the pseudotracheal and epipharyngeal types. The accompanying figures show that Sciapodinae, Medeterinae, and Rhaphiinae are comparatively primitive in these features. The Hydrophorinae are a large group and comprise genera which show characteristic combinations of more or less derived types of the pseudotrachea and epipharynx. Moreover, a simple matching coefficient was calculated for similarity between genera in six features of the mouthparts (pseudotracheae, apical epipharyngeal sclerites, discal sclerites, epipharyngeal endoskeleton, hypoglossa and hypopharynx). The similarity is represented by cluster analysis and principal co-ordinates analysis (Fig. 14 and Fig. 15). These analyses show: 1) Mouthparts morphologies are rather well consistent with Robinson's (1970) classification of subfamilies; 2) Each of the subfamilies Sciapodinae, Dolichopodinae, Sympicninae and Diaphorinae

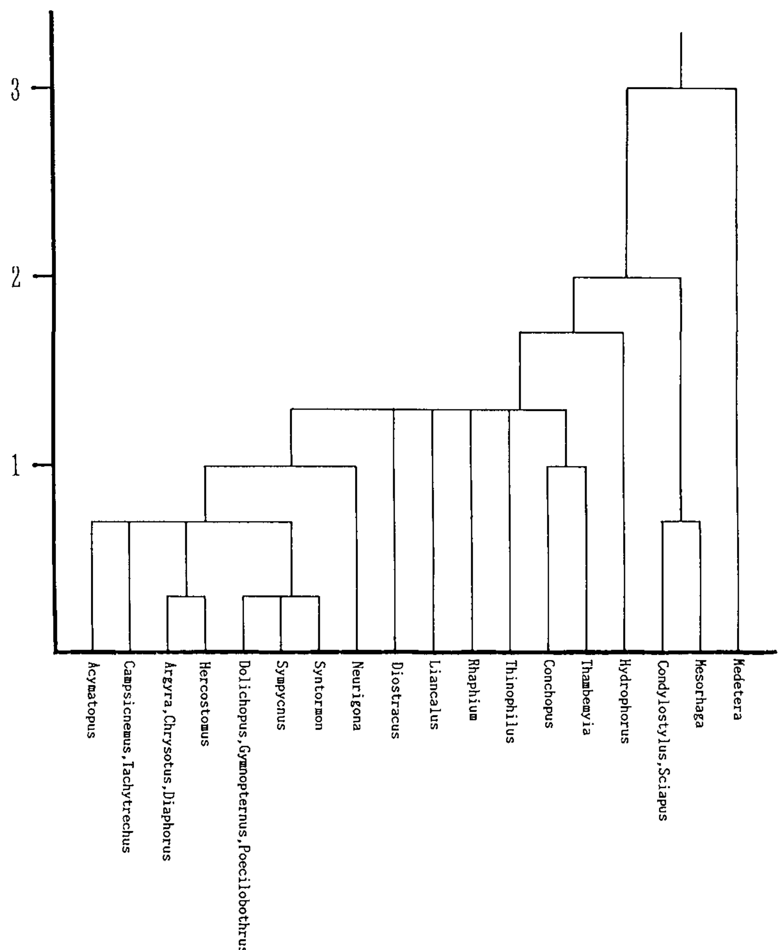

Fig. 14. Cluster analysis (nearest neighbor method) for dolichopodid mouthparts.

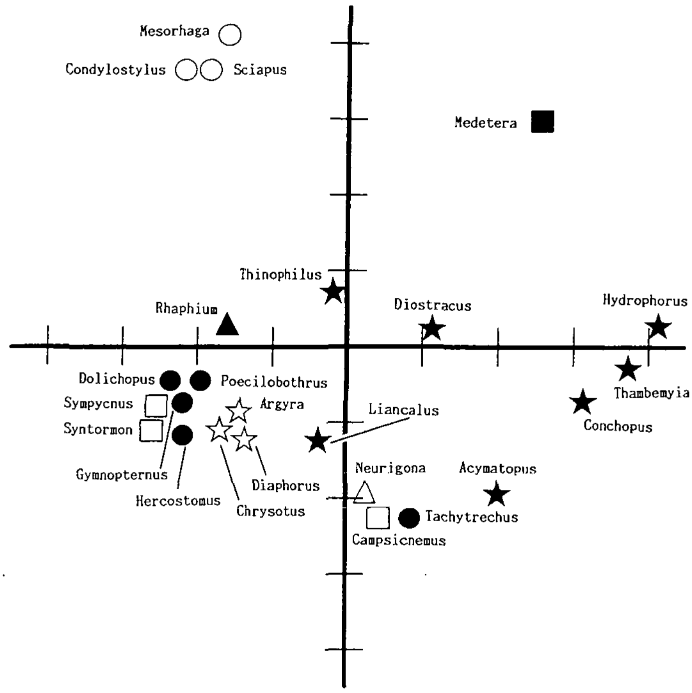

Fig. 15. Principal co-ordinates analysis for dolichopodid mouthparts. (○=Sciapodinae, ●=Dolichopodinae, □=Sympicninae, ■=Medeterinae, △=Neurigoninae, ▲=Rhaphiinae, ☆=Diaphorinae, ★=Hydrophorinae.)

is considerably uniform. (Two exceptional cases are recognized. In the subfamilies Dolichopodinae and Sympicninae, each of the genera *Tachytrechus* and *Campsicnemus* shows unique mouthparts morphologies.); 3) Sciapodinae and Medeterinae are quite different from others; 4) Dolichopodinae, Diaphorinae and Sympicninae are similar.

The present study does not support Cregan (1941), who pointed out inconsistencies of mouthparts with the classification of subfamilies. Actually, morphologies of the mouthparts of Dolichopodidae well agree with the current classification based on other external features. In this regard, the mouthparts of Dolichopodidae will give a useful source of information for phylogenetic reconstruction. The inconsistencies pointed out by Cregan may be due to the following facts. 1) She did not take into consideration the degree of sclerotization of the pseudotrachea and epiphryngeal endoskeleton. 2) Contrary to Cregan's examination, the number of pseudotracheal branches in the genus *Condylostylus* is not five but six, as revealed by this study; therefore, her Group V and VI should be placed in the same group. 3) Her arrangement of characters according to the degree of complexity is problematical; for instance, genera with the "geminately sclerotized" pseudotrachea were placed in groups of different complexity levels, from simple groups (Group I-III) through intermediate groups with the "ribbon-like" pseudotrachea (Group IV-VI) to complex groups (Group VII, VIII, X and XII). 4) She arranged all characters in only one series of morphological complexity in spite of the presence of divergence in the family. 5) Incompletion of Becker's classification of subfamilies.

APPENDIX

The dolichopodidae as compared with other Diptera are quite peculiar in the morphology of the pseudotrachea. What is, then, the function of the modified pseudotrachea in this family? Generally, feeding behavior of predacious flies is composed of the following three actions: (1) cathcing a prey, (2) holding it and (3) taking its body fluid. For example, asilids hold a prey by the fore legs, and inject venom into it with the blade-like mouthparts, then absorb its body fluid by thrusting the labrum-epipharynx and hypopharynx (Whitefield, 1925). Adult Dolichopodidae mainly prey on minute invertebrates. I observed adults of *Dolichopus* sp. pull a nematoceran larva (probably of the family Chironomidae) out of a puddle only by the use of the labella and take it in the oral cavity within a few seconds. A fly drawing a living prey into the oral cavity needs to hold the latter fast so that the prey cannot escape. It seems that the strongly sclerotized pseudotracheae of Dolichopodidae serve to keep a prey in the oral cavity. Judging from the morphologies of the epipharynx, dolichopodid flies absorb the prey's body fluid not by thrusting the epipharynx and hypopharynx into the prey as Asilidae do, but by tearing the prey with the epipharyngeal projections. These are supported by the characteristic development of the epipharyngeal endoskeleton, which is connected by muscle with the labrum. Movements caused by the muscle's contraction are transmitted to the apical epipharyngeal sclerite through the basal epipharyngeal sclerite, thus enabling the apical epipharyngeal sclerite to tear the prey by the projections. By the way, Snodgrass (1922) first considered the movements of the epipharynx.

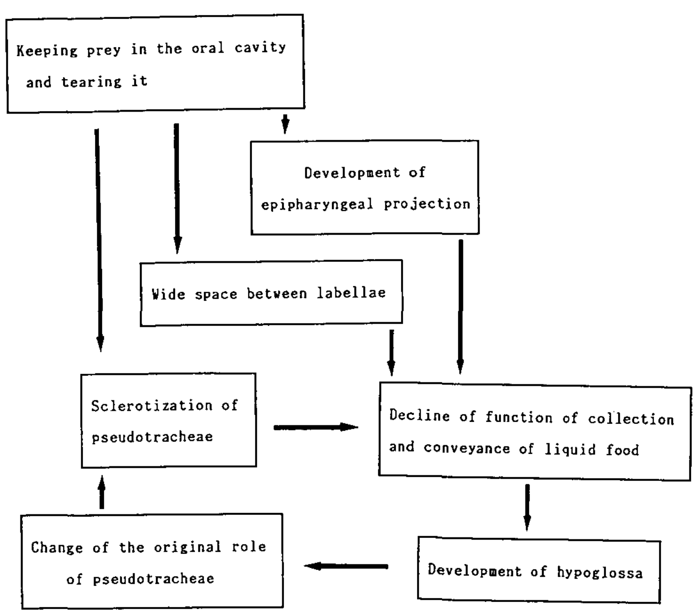

Fig. 16. Schematic diagram of factors in the evolution of dolichopodid mouthparts.

In conclusion, Fig. 16 shows the evolutionary development of the dolichopodid mouthparts on the basis of the supposition that liquid food is conveyed not by the pseudotracheae but by the hypoglossa to the hypopharynx. Ancestral dolichopodids as predators which capture prey in the labella developed the epipharyngeal projection and a wide space between the labella in accordance with the necessity of keeping the prey in the oral cavity and also of tearing it. This development may have required improvement in conveyance of liquid food. Development of the hypoglssa and the epipharynx with microspines has made up for the insufficiency. Then the pseudotracheae have become more and more sclerotized, because the original role of the pseudotracheae in conveying liquid food has now been filled by the hypoglossa. Thus, the sclerotized pseudotracheae have changed their role to holding the prey between the labella.

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