Annls Soc. r. zool. Belg. — T. 114 (1984) — fasc. 1 — pp. 83-88 — Bruxelles 1984

(*Manuscript received on 16 October 1982*)

THE MAXILLARY OUTER LOBE, AN IMPORTANT SYSTEMATIC TOOL IN ISOTOMIDAE (COLLEMBOLA)

by

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SUMMARY

The morphology of the maxillary outer lobe is described. It consists of a palp which is either simple, bifurcate or trifurcate, and a sublobal plate which has from 0 to 4 hair-like processes. The differentiation of the lobe is examined in various isotomide genera. In Anurophorinae there is much intrageneric variation in the sublobal plate, in Isotominae the situation is more stabile except in the large genus *Isotoma* where the species fall in three groups based upon development of the palp. Sharp differences are often found among closely related species, which makes the character of prime importance in systematic work. The character is possibly adaptive, associated with food and feeding habits.

INTRODUCTION

During the last few years I have noticed that details of the maxillary outer lobe are often different in closely related species of the family Isotomidae. Other families offer less variation, but even here it is possible to delimit certain groups.

The function of the maxillary outer lobe is unclear, but the movable lobe probably acts together with labrum and labium during feeding. Goto (1972) points to some details of the anatomy that indicates a chemoreceptory function.

MATERIAL AND METHODS

The maxillary outer lobe is located on each side of the head near the base of the labrum (Fig. 1 : 1). To observe the fine anatomy of the lobe, it is necessary to decapitate the specimen and mount the head in a slide with a shallow cavity where it can be rotated and observed from all sides. An upright position, where the head can be observed obliquely from the front, is most convenient. Sometimes squeezed specimens are excellent, but squeezing gives an unpredictable result. With some training total mounts with specimens in lateral position may be adequate. Slides are prepared according to the method of Gisin (Gisin, 1960).

RESULTS

Anatomy of the maxillary outer lobe

The maxillary outer lobe forms an integrated part of the external « mouth », lying on either side of the labrum distal to the pleural folds (Fig. 1 : 1). The basal part of the lobe continues inside the head where it articulates with the basal shaft (stipes) of the maxilla. The external lobe (Fig. 1 : 2) terminates in a long hair-like structure set on the tip of a prominent papilla. The long « hair » differs from ordinary setae by absence of the basal socket. Probably it has a sensory function (GOTO, 1972). On the ventral side of the papilla a curved, hair-like process is often present. Above this a similar but shorter process may be present on the papilla in a dorso-lateral position. These processes are probably not homologous to ordinary setae as their bases are unmodified, without sockets. The papilla together with its terminal sensorial hair and one or two processes, is here called the palp. The palp is either simple (only terminal hair present, Fig. 1 : 4), bifurcate (ventral process present) or trifurcate (both ventral and dorso-lateral processes present, Fig. 1 : 2 and 5). Near the base of the palp an ordinary seta, the basal seta, is always present. Ventrally to the palp a curved, plate-like structure is present. It is here called the sublobal plate. The sublobal plate may have 0, 1, 2, 3 or 4 hair-like processes, called sublobal hairs. They are probably homologous with the processes of the papilla. The sublobal hairs are usually set equally spaced along a curved line. Sometimes the inner hair is smaller than the others. Rarely all hairs are set in a single group (*Archisotoma*, Fig. 1 : 3). The apical edge of the sublobal plate is smooth, membraneous, without granulation.

In order to test the constancy of the characters, 30-40 specimens of *Anurophorus laricis*, *septentrionalis* and *atlanticus* from different Scandinavian localities were examined. No intraspecific variation was found. However, some variation in the number of sublobal hairs (often asymmetric) is seen in *Uzelia* and *Pseudisotoma*.

Anurophorinae

Most genera of this subfamily have a simple palp and a variable number of sublobal hairs.

Tetracanthella. Palp simple, sublobal hairs either 1 (*strenzkei* GISIN, *pseudomontana* CASSAGNAU), 2 (*afurcata* HANDSCHIN), 3 (*arctica* CASSAGNAU, *wahlgreni* LINNANIEMI, *pyrenaica* CASSAGNAU, *ethelae* WRAY) or 4 (*sylvatica* YOSII, *elevata* CASSAGNAU).

Uzelia. Palp simple, sublobal hairs 1 (*kuehnelti* CASSAGNAU) or 3 (*setifera* ABSOLON). A few specimens of *setifera* with 2 on one side and 3 on the other are seen.

Anurophorus. Palp simple, sublobal hairs 1 (*laricis* NICOLET), 2 (*septentrionalis* PALISSA [Fig. 1, 4], *racovitzai* DENIS, *cuspidatus* STACH) or 3 (*atlanticus* FJELLBERG and one unidentified species from Colorado). Species with 4 sublobal hairs are not observed.

Pseudanurophorus. Palp simple or bifurcate (only *binoculatus* KSENEMAN), sublobal hairs 3 (*binoculatus*, *arcticus* CHRISTIANSEN) or 4 (*inoculatus* BØDVARSSON).

Paranurophorus simplex DENIS. Palp simple, 4 sublobal hairs.

Weberacantha octa CHRISTIANSEN. Palp bifurcate, 4 sublobal hairs.

The other « spined » Anurophorinae (*Tuvia*, *Martynovella*, *Pentacanthella*, *Pseudofolsomia*, *Yosiiella*, *Gressitacantha*) are not examined, except a peculiar form from N-E Siberia having 8 anal spines (« *Octodontophora* » Martynova in lit.) which has bifurcate palpe and 4 sublobal hairs.

Proisotominae

The genera of this subfamily have either simple or bifurcate palp. Number of sublobal hairs usually 4, but species with 0, 1 or 3 are also seen.

Folsomia. All species examined so far have bifurcate palp and 4 sublobal hairs.

Cryptopygus. All species examined so far have bifurcate palp. Number of sublobal

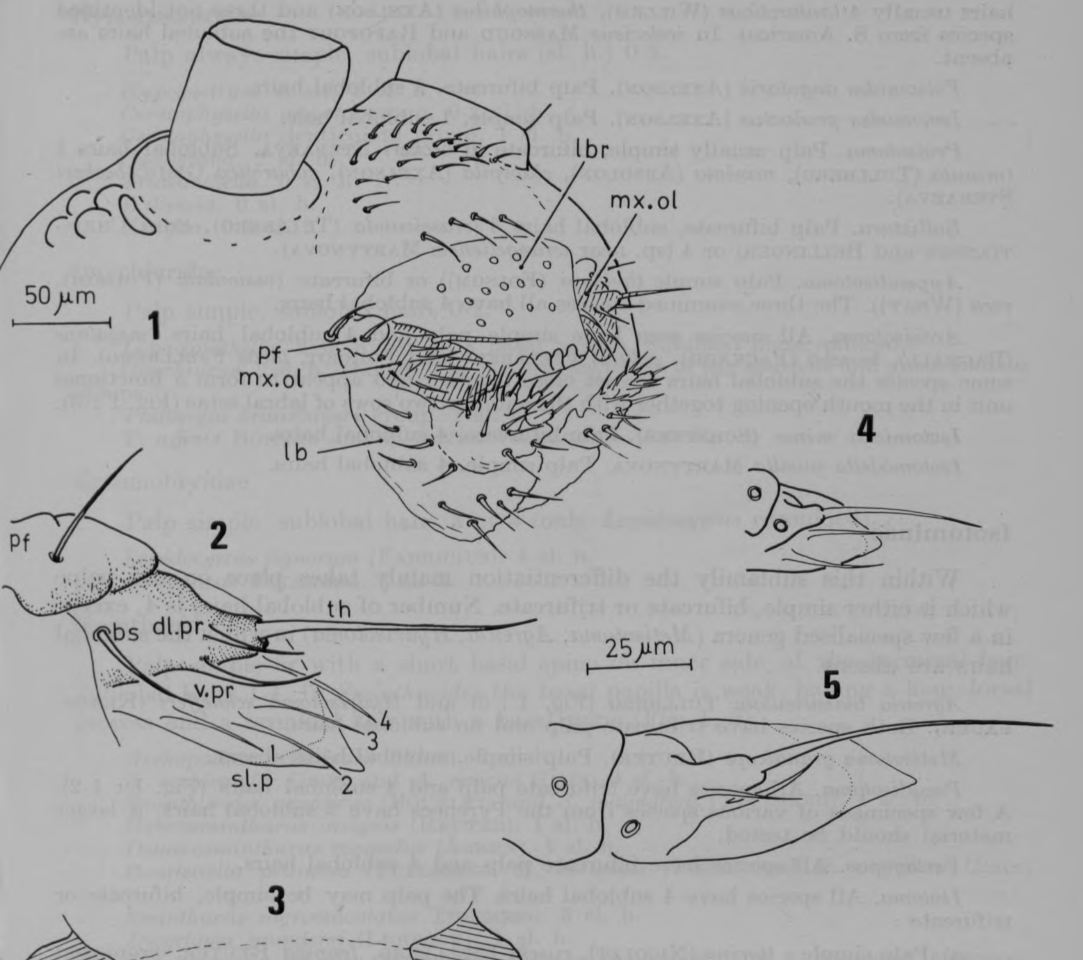

Fig. 1. — 1 : *Pseudisotoma sensibilis*. Mouth region showing position of maxillary outer lobe (mx. ol), labrum (lbr), labium (lb) and pleural fold (pf); 2 : *Pseudisotoma sensibilis*. Maxillary outer lobe with basal seta (bs), dorso-lateral process (dl. pr), sublobal plate (sl. p), terminal hair of palp (th), ventral process (v. pr) and sublobal hairs (1-4); 3 : *Archisotoma polaris*. Labrum and maxillary outer lobe (hatched); 4 : *Anurophorus septentrionalis*. Simple palp and two sublobal hairs; 5 : *Agrenia bidenticulata*. Trifurcate palp, sublobal hairs absent; 6 : *Sminthurides aquaticus*. Modified palp with dorsal process (d. pr) and basal spine (b. sp). 1-4 : Sublobal hairs.

hairs usually 4 (*antarcticus* (Willem), *thermophilus* (Axelson) and three not identified species from S. America). In *indecisus* Massoud and Rapoport the sublobal hairs are absent.

Folsomides angularis (Axelson). Palp bifurcate, 3 sublobal hairs.

Isotomodes productus (Axelson). Palp simple, 1 sublobal hair.

Proisotoma. Palp usually simple, bifurcate in *beckeri* Stebaeva. Sublobal hairs 1 (*minuta* (Tullberg), *minima* (Absolon), *clavipila* (Axelson), *subarctica* Gisin, *beckeri* Stebaeva).

Ballistura. Palp bifurcate, sublobal hairs 3 (*crassicauda* (Tullberg), *extra* Christiansen and Bellinger) or 4 (sp. near *wrangeliensis* Martynova).

Appendisotoma. Palp simple (*bulbosa* (Folsom)) or bifurcate (*vesiculata* (Folsom), *veca* (Wray)). The three examined species all have 4 sublobal hairs.

Archisotoma. All species seen have simple palp and 4 sublobal hairs (*megalops* (Bagnall), *besselsi* (Packard), *polaris* Fjellberg and Poinsot, *theae* Fjellberg). In some species the sublobal hairs are set close together and appear to form a functional unit in the mouth opening together with the anterior two rows of labral setae (Fig. 1 : 3).

Isotomiella minor (Schäffer). Palp bifurcate, 4 sublobal hairs.

Isotomodella pusilla Martynova. Palp simple, 4 sublobal hairs.

Isotominae

Within this subfamily the differentiation mainly takes place on the palpe which is either simple, bifurcate or trifurcate. Number of sublobal hairs is 4, except in a few specialised genera (*Metisotoma*, *Agrenia*, *Hydrisotoma*) in which the sublobal hairs are absent.

Agrenia bidenticulata Tullberg (Fig. 1 : 5) and *Hydrisotoma schaefferi* (Krausbauer). Both species have trifurcate palp and no sublobal hairs.

Metisotoma grandiceps (Reuter). Palp simple, sublobal hairs absent.

Pseudisotoma. All species have trifurcate palp and 4 sublobal hairs (Fig. 1 : 1-2). A few specimens of various species from the Pyrenees have 3 sublobal hairs. A larger material should be tested.

Vertagopus. All species have bifurcate palp and 4 sublobal hairs.

Isotoma. All species have 4 sublobal hairs. The palp may be simple, bifurcate or trifurcate :

a) Palp simple : *tigrina* (Nicolet), *ruseki* Fjellberg, *fennica* Reuter, *propinqua* Axelson, *divergens* Axelson, *germanica* Hüther and Winter, *bicolor* (Cassagnau), *randiella* Fjellberg, *christianseni* Fjellberg, *taigicola* Fjellberg, *creli* Fjellberg, *manitobae* Fjellberg, *quadra* Christiansen and Bellinger.

b) Palp bifurcate : *viridis* Bourlet, *multisetis* group, *nivalis* Carl, *albella* Packard, *nivea* Schäffer, *hiemalis* Schött, *violacea* Tullberg, *tshernovi* Martynova, *infuscata* Murphy, *neglecta* Schäffer, *blufusata* Fjellberg, *alaskensis* Fjellberg, *nigrifrons* Folsom, *gelida* Folsom, *inupikella* Fjellberg, *macleani* Fjellberg, *nixoni* Fjellberg.

c) Palp trifurcate : *tenuicornis* Axelson, *carpenteri* Börner, *subaequalis* Folsom, *olivacea* Tullberg, *nanseni* Fjellberg, *komarkovae* Fjellberg, *maritima* Tullberg, *blekeni* Leinaas, subgenus *Parisotoma* (*notabilis* Schäffer, *trispinata* MacGillivray, *agrelli* Delamare, *ekmani* Fjellberg and two other not yet identified species), subgenus *Sorensia* (two species from Kerguelen).

Isotomurus. All species/forms seen so far have bifurcate palp and 4 sublobal hairs.

Observations from other families

Poduridae

Podura aquatica Linnaeus. Palp simple, 1 sublobal hair.

Hypogastruridae

Palp always simple, sublobal hairs (sl. h.) 0-3.

Hypogastrura s. str. 2 sl. h.
Ceratophysella armata group. 0-2 sl. h.
Ceratophysella denticulata group. 1 sl. h.
Cyclograna. 2 sl. h.
Triacanthella. 0 sl. h.
Willemia. 0 sl. h.
Xenylla. 0-3 sl. h.

Onychiuridae

Palp simple, sublobal hairs 0-2.

Lophognathella. 2 sl. h. set on a basal papilla. Sublobal plate reduced.
Onychiurus. 2 sl. h., though 0 in two species/forms of the *sibiricus* and *groenlandicus* groups.
Tullbergia krausbaueri group. 1 sl. h.
T. affinis BÖRNER and *T. arctica* WAHLGREN. 0 sl. h.

Entomobryidae

Palp simple, sublobal hairs 3 or 4 (only *Lepidocyrtus* examined).

Lepidocyrtus lignorum (FABRICIUS). 4 sl. h.
L. cyaneus TULLBERG. 3 sl. h.

Sminthuridae

Palp simple or with a short basal spine on inner side of the terminal hair. Sublobal hairs 1-4. In *Sminthurides* the basal papilla is weak, having a long dorsal process and a terminal hair with a basal spine (Fig. 1, 6).

Arrhopalites principalis STACH. 2 sl. h.
A. cochlearifer GISIN and *A. sericus* GISIN. 3 sl. h.
Sminthurides aquaticus (BOURLET) and *S. malmgreni* (TULLBERG). 4 sl. h.
Heterosminthurus insignis (REUTER). 1 sl. h.
Deuterosminthurus repandus (ÅGREN). 1 sl. h.
Bourletiella pruinosa (TULLBERG), *B. hortensis* (FITCH) and *B. pistillum* GISIN. 1 sl. h.
Sminthurus nigromaculatus TULLBERG. 3 sl. h.
Dicyrtoma saundersi (LUBBOCK). 1 sl. h.
Sminthurinus concolor (MEINERT), *S. niger* (LUBBOCK) and *S. trinotatus* AXELSON. 1 sl. h.

DISCUSSION

Some generalisations could be drawn from the foregoing survey. In the subfamilies Anurophorinae and Proisotominae both the palp and the sublobal plate are highly variable. In some genera (*Anurophorus, Uzelia, Tetracanthella*) the palp is always simple, whereas the number of sublobal hairs varies from 1 to 4. This contrasts with the genera in the subfamily Isotominae which show much less variation with the notable exception of the genus *Isotoma* which has four sublobal hairs and a variable palp. Thus two different intrageneric strategies seem to be operating. Either the sublobal plate is variable or the palp is variable. In some heterogenous groups like *Proisotoma*, both strategies are seen.

As is evident from both *Anurophorus*, *Tetracanthella* and *Isotoma*, the differentiation of the maxillary outer lobe takes place at a rather low taxonomic level. Thus the character has considerable value in the practical identification of species. The bulky genus *Isotoma* will serve as a good example. The 45 examined species are grouped in three classes which clearly do not match with natural phylogenetic sections. Members of the *olivacea* complex (*olivacea, nanseni, komarkovae, infuscata, ruseki, tshernovi*) are found in all three classes. Similar conditions are found in the *viridis* and *violacea* groups.

It is probably of some significance that all *Isotoma* species with a simple palp also have a simple labral edge, at most with blunt, roundish folds or papillae. The species with bifurcate or trifurcate palp display a wide variety of labral structures, from simple to sharp folds, ridges, tubercles or spines.

It is of considerable interest to know the evolutionary sequence in development of the maxillary outer lobe. Because the differentiation operates within the lower taxonomic categories (species groups), such knowledge will give information about rather recent evolutionary steps and provide important markers during constructions of phylogenetic cladograms. Probably a simple palp and four sublobal hairs is the primitive (plesimorphic) condition in Isotomidae. If so, the development of the sublobal plate proceeds through reduction, whereas the palpe increases in complexity.

A simple, nonfurcate palp is the common condition throughout the collembole system. Within Hypogastruridae, generally held to be the most primitive of the families, it is the only condition found. Support for the idea of reduction of the sublobal plate may also be found in Hypogastruridae. *Hypogastrura* s. str., having two sublobal hairs, is considered to be more primitive than *Ceratophysella* (*denticulata* group) which has only one sublobal hair (CASSAGNAU, 1974). Species with four sublobal hairs are not yet seen in Hypogastruridae, but *Xenylla humicola* and *X. welchi* have three while more advanced species of that genus have two, one and finally none (FJELLBERG, 1984).

It is not at all evident why some genera (*Folsomia, Pseudisotoma, Vertagopus*) have a nonvariable maxillary outer lobe, whereas other genera (*Anurophorus, Tetracanthella, Isotoma*) are highly differentiated. The close proximity to the mouth (Fig. 1 : 3) may indicate that differentiation of the lobe is adaptive, related to food and feeding habits. However, *Isotoma* does not seem to be trophically more diverse than *Folsomia*, although these important aspects of collembolan life are still insufficiently known. If trophic adaptations are important in development of the maxillary outer lobe, then its cladogenetic information is oscured. Though it still ranks as a very useful systematic character.

ACKNOWLEDGEMENTS

Material for the present study has been provided by numerous colleagues from all over the world. During the last stage of the work, considerable improvements were initiated through discussions with Drs. Judith Najt and Louis Deharveng, Toulouse. Their rich collections were important sources of primary material.

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