New Characters Observed on Isolated Jaws and Basal Plates of the Family Gnathostomulidae (Gnathostomulida)

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Summary. 1. The jaws of the family Gnathostomulidae have four major parts (fig. 80): articularium, involucrum, dentarium, and suspensorium.

2. The articularium is highly specialized and fully freed from functions other than articulation of the jaws and the prevention of twisting motions. It consists of a symphysis lamella, joined by a symphysis in vertical position.

3. The involucrum is a specialization in the higher families of the Scleroperalia and the Austrognathiidae. In Gnathostomulidae it is of medium length with a well-defined caudal end, surrounding an apertura caudalis. From there a much thinner tectum lateralis continues. It is formed by a dorsal extension of the lamella interna which bends-as lamella externa-laterally and then ventrally, leaving only a fissure-like opening medioventrally: the incisura ventralis.

4. The dentarium consists of a thin lamella interna, which is always thickened in three portions, forming the arcus dorsalis, medialis, and ventralis. These arcs form the bases of the teeth. The arcus medialis also bears the strong dens terminalis. The dentation is more complicated and minute than the light microscope can resolve. An incisura dorsalis is found in few cases, cutting into the lamella interna from the caudal end.

5. The suspensorium is specialized into two portions: an anchorage part at the more fixed end, and an apophysis part nearer the moving ends of the jaw system.

a) The cuticularized parts of the cauda system are always paired, but can be symmetrically or asymmetrically developed. In the first case the cuticularized caudae are tube- or cushion-like; in the latter case they are tubeshaped again, but a cauda dorsalis and a cauda ventralis can be distinguished.

b) The apophyses are wing-shaped only distally, proximally they are differentiated (fibularized) into two fibulae functioning as cuticularized sinews: the fibula medialis originates at the ventrocaudal end of the lamella interna, the fibula lateralis at the ventral margin of the lamella externa. Together they form the fenestra ventralis, varying in dimension.

c) In addition a fibula radialis is developed, strengthening the apertura caudalis of the involucrum. This fibula originates at the connecting point of the ventrocaudal end of the lamella externa and the fibula lateralis and it inserts in the caudal portion of the lamella interna either ventrally or dorsally. In the latter case it seems to be replaced by a sinew. Corresponding to its position it may bisect the fenestra ventralis into a fenester ventrocaudalis and ventrofrontalis and/or the apertura caudalis into a apertura caudolateralis and caudomedialis.

6. The basal plate is composed of three major parts: pars centralis, pars alaris, and the serrula.

7. The pars centralis forms a roof-like structure originating on the basis denticis, on top of the transverse axis, or the dorsum alae, of the wing system. A strong dens medialis forms the ridge of the roof, while groups of teeth form the margins.

8. The pars alaris consists of a dorsum alae —the stronger middle part, stretched in transverse direction. On both ends it bifurcates, thus forming five separate areas within the pars alaris: two are paired—the alae frontales and the alae laterales— and the unpaired mediocaudal portion, the tectum caudalis, which is much thinner. These portions seem to correspond to the widely representative five-partition of the alae in basal plates of Gnathostomulida.

9. The distal portion of the frontomedial margin of the alae frontales always bears a flat, scale-like dentation: the serrulae. Only in the genus *Gnathostomula* does the proximal portion of this margin not end freely; it bends medially underneath the pars centralis. There the two sides meet and form an infundibulum. In this construction the originally paired serrulae continue proximally and fuse medially on the infundibulum.

Contents

A. Introduction

In two recent papers the genus *Semaeognathia* (Riedl, 1970) was described, and, based on several new species, the genus *Gnathostomula* was newly studied (Riedl, 1971). Both genera, representing the most derived types of the largest suborder, Scleroperalia, now form the family Gnathostomulidae (Sterrer, 1971).

In accord with this systematic position, the structure of the cuticularized parts of the pharynx system are fairly complex and rather small. In particular the dentation of the central part of the basal plate and of the ridges of the jaws is minute and at the very limits of the possibilities of light microscopy. Though investigation on the ultrastructure level yields additional information (Riedl, 1970) one may hesitate recommending this technique for taxonomic investigations in being too time consuming. Since these cuticularized parts are useful for the taxonomy of the group, new methods should first be tried which may be employed at the generally less sophisticated facilities of the marine station.

In addition to this it becomes obvious that some parts of these cuticularized pieces are hidden in the tissues of the pharynx system and appear or don't appear with differing pressure in the squeeze preparation.

All these facts make it desirable to isolate the jaws as well as the basal plate and to restudy them thus freed under optimal optical conditions.

The very aim of this paper is to demonstrate the rich information obtainable from the isolated cuticularized parts, to demonstrate the volume of trends observable even in a single family, and to encourage those students of gnathostomulids not to give up in the face of the impossible smallness of these parts, but to extract the minute characters of the jaws and basal plates for the benefit of a better understanding of the natural relationship of this group.

B. Material and Methods

Living animals extracted from sediments of lenitic beaches at Onslow Bay, North Carolina, have been used. About 25 specimens of four genera, Filospermoidea as well as Bursovaginoidea, were treated and investigated. In this paper the results within the Gnathostomulidae are described, based on the species *Semaeognathia sterreri* Riedl, *Gnathostomula brunidens* Riedl, *G. jenneri* Riedl, and *G. microstyla* Riedl. An outline of the groups of Gnathostomulida and the species of Gnathostomulidae known today is given at the beginning of Chapter D.

The methods involved are divided into extraction, documentation, and description.
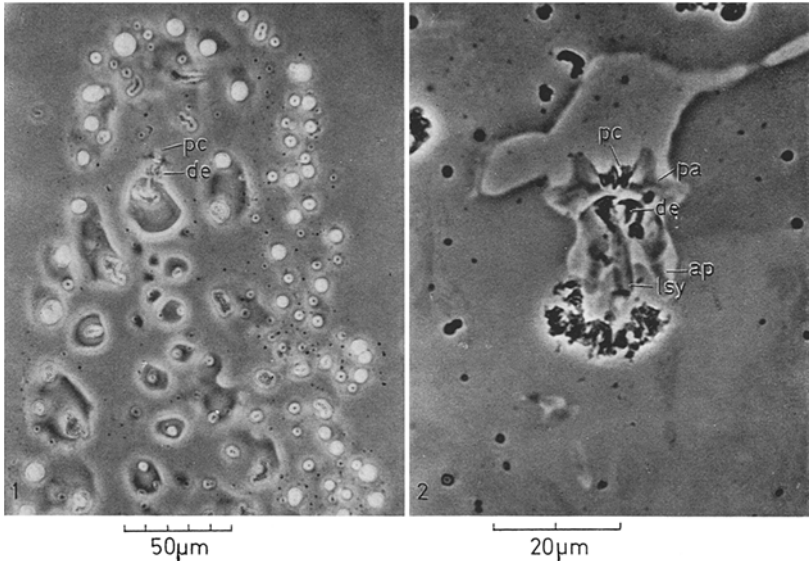
Figs. 1 and 2. Process of isolating the cuticularized parts under coverslip, with phase contrast; Fig. 1. In the middle of the bleaching process (body outline still imaginable). Fig. 2. Towards the end of bleaching but before rinsing

I. Extraction

To free the cuticularized parts from the tissue, sodium hypochlorite has been added to the living animals, as used for rotifers (Myers, 1938; Koehler and Hayes, 1969). The specimen is kept under coverslip in seawater in a fairly squeezed preparation. Sodium hypochlorite is sucked in. A concentration of 4% dissolves the tissues in minutes; a concentration of 1% and less is preferred though the process takes about one day. Tapping the coverslip allows freeing (under permanent optical control) the cuticularized parts from the remaining droplets of dissolved tissue (Figs. 1, 2).

The basal plate and the teeth of the jaws are strongly resistant, and bleaching even over several days does not show any change in their structure. However other parts, such as the apophyses or the symphysis appendices, become transparent and finally collapse if the bleach acts for too long. Consequently the bleaching process has to be stopped and the isolated parts have to be rinsed in distilled water.

Although the isolated parts are only a few microns wide, the change of losing them in the washing process can be overcome by allowing only strictly horizontal or vertical rinsing currents at one time, and by doing it on the movable stage of the microscope, always under the coverslip. One hundred times magnification and good phase contrast allow following the straight path of the specimen during the rinsing process. After bleach and tissue debris is removed, glycerin (30% in distilled water) is added; the nonius positions of the stage are noted and the water is removed by use of a desiccator. The remaining glycerin film (under the coverslip) which holds the specimen should preferably be about 10 to 15 μm thick.
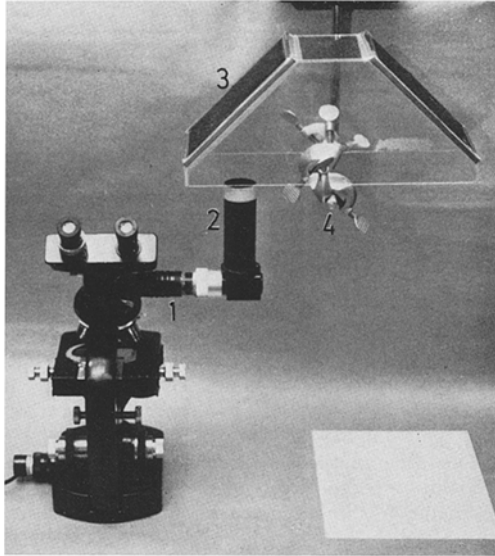
Fig. 3. Double mirror developed to extend the linear magnification in respect
to the drawing board,; *1* wild drawing tube *2* optical funnel, *3* double mirror,
4 parts of chemical stand (position adjusted for 5000 × magnification)

In this connection it might be worth mentioning that we found, besides those
of gnathostomulids and rotifers, the cuticularized parts and the cuticula of marine
tardigrades as well to be equally resistent to sodium hypochlorite. The cuticula
of kinorhynchs and the scales and hooks of gastrotrichs (e.g. *Tetranchiroderma*)
dissolve much more quickly; the cuticula of nematodes soaks, swells, and disap-
pears the quickest. Stylets of nemertines (e.g. *Ototyphlonemertes*) are also resistant
and disintegrate slowly, showing conical layers before fully dissolving. On the
contrary, stylets and hooks of the proboscis of turbellarians dissolve quickly
(e.g. in *Macrostomum* and in Gnathorhynchidae).—Such differences may allow
more extensive application of the method for comparative investigations.

II. Documentation

In the high viscosity of glycerin the specimens can be rolled into different
positions by moving the coverslip. They can be kept still in each position for
drawing or photography. To keep them longer in stable positions, a cold-stage
might be recommended. In addition the microscope should be allowed to warm
up for a few hours to expand the stage holder and optics to a definite position,
otherwise a permanent relative translocation of the specimen, though slow, will
impair documentation.

For drawings, the Wild drawing tube, combined with the Wild M20 microscope
was used, allowing a linear magnification of 1500 times (using the Fluotar Hi
100 Ph 1.30 objective and the level of the table as projection screen). Yet higher
magnification, between 3000 and 10000 times, was preferable.

The most convenient way to meet this requirement is to rotate the drawing tube 180° around its longitudinal axis (which its design allows) and to reflect the image of the drawing board over a variably longer distance back into the eyepiece. For this purpose a double mirror is required (Fig. 3) in order to guarantee orthogonal projection as well as to keep the right edge of the image up and not reverse the sides. To adjust the desired additional magnification the mirror system might be moved vertically (e.g. on a chemical stand). To avoid projecting more than the desired drawing area onto the visual field, a tubeshaped and blackened optical funnel might be glued (to the filterholder) on the drawing tube.

Most of the drawings shown in this paper have been made at 5000 times linear magnification. This allows separation of visible characters with sufficient precision.

III. Description

After the first publication on Gnathostomulida in German, and later almost entirely in German, publication shifted, in 1969, to almost entirely in English and then fully in English. However, due to the growing interest in this group, one can foresee that the monolingual condition will not persist for long.

Additionally, since the method of isolation of the cuticularized parts in Gnathostomulida yields remarkable amounts of very special characters, care is required to ensure unambiguous terminology.

Consequently we made the attempt to employ Latin nomenclature for the more important homolog parts. This method has proved very beneficial for interlanguage communication, and for the advancement in vertebrate anatomy; it may be hoped then that comparative anatomy of gnathostomulids will also benefit if this step is made early enough (compare "list of abbreviations" and Fig. 80).

In order to keep the contribution short, photographic documentation is reduced to examples only. This is all the more adviseable since even just one position of a specimen requires several photographs in different optical levels. The combination of such documents is, however, shown in the drawings.

C. Results

Among the cuticularized parts of Gnathostomulidae, the jugum, bursa mouthpiece, and stylet disappear fairly quickly in the bleaching process. Only jaws and basal plate, with most of their parts, are remaining longer. So we will confine the discription to the two latter. A general description of each of the two organs shall be given first and the systematic application and relationship will be outlined at the end.

I. The Jaws

The organization of the jaws in Gnathostomulidae can be derived from types of lesser differentiation, particularly with regard to lamellarization, dentation, and the formation of the suspension in the pharynx musculature. The following four major parts show specialization with different trends.
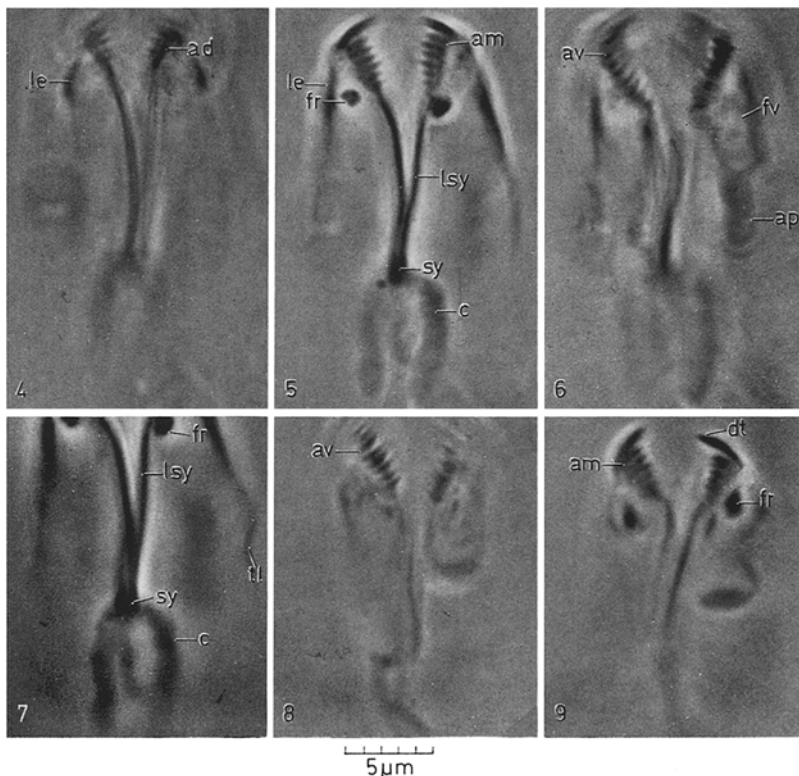
Figs. 4–9. *Gnathostomula brunidens* jaws. Figs. 4–6. Medium bleaching seen from dorsal, focus changing from dorsal to medial to ventral. Fig. 7. Short bleaching, seen from dorsal, focus medial. Figs. 8 and 9. Strongly bleached, seen from ventral, focus changing from ventral to medial

a) Articularium

The forceps-like basic pattern of the gnathostomulid jaws, as represented in Filospermoidea and some of the lower Bursovaginoidea, consists of a pair of elements with increasing differentiation on both ends and partly on their external side: dentation, symphysis-cauda complex, and apophyses. The lamellarization varies in filospermoids but is established in bursovaginoids, and in the former the cauda is not differentiated. The apophyses are not visible and the anterior lamella, which is dentated, is not so clearly separated in the lower families. The cauda formation emerges in Onychognathiidae and Gnathostomulidae, and only in the latter is the anterior part fully distinguished.

This remaining middle part shall be called articularium (ar), which is specialized to the simple function of articulation. The articularium

is the result of differentiating specialization. In Gnathostomulidae it is fully freed from other functions: terminally a simple structure. We shall distinguish only two substructures.

1. The Symphysis (sy) in Gnathostomulidae is a simple thickening surrounding the sharply bent end of the symphysis lamella. It is produced within the tissue, has the more amorphous consistancy of a "suspensorium" (see below), seems only to connect the symphysis lamella with the structure of the cauda, and fully repeats the shape of the end of the lamella. Seen from dorsal or ventral it generally looks knob-like (Figs. 11, 29, 34). From the side it shows less sharp boundaries with the cauda and irregular ones with the lamella (Figs. 13, 31, 36). In *Gnathostomula jenneri* it is more poorly developed, but the principle is the same (Figs. 16, 18).

2. Lamellae symphysis (lsy) in the family are very much separated from the rest of the differentiations—spanning almost two-thirds of the length of the jaw system. Produced at the surface of epithelium of the mouth cavity, the lamellae are equally thick (0.2 µm) over their entire length, and fairly equal in height, like the base of dissecting forceps.

This is particularly true in *Gnathostomula microstyla* (Fig. 31). In *G. jenneri* (Fig. 18) they widen proximally—which is unusual—, and in *G. brunidens* (Fig. 13) the distal part is broader. In *Semaeognathia sterreri* only the proximal end becomes narrow (Fig. 35), which seems to be a more conservative feature. An index such as maximum height/symphysis height shows *Gnathostomula* spp. around 1 (0.9–1.2) and *Semaeognathia* with 3.7. Anteriorly the lamellae symphysis extends into the lamellae of the involucrum and ends here: knobs, ridges, and ledges complicate the structures.

b) Involucrum

One of the trends in jaw development in Bursovaginoidea is the formation of hollow and cone-shaped tips which wrap around the ends of the musculature. This gives more protection and stability, and more surface for muscle attachment without further material. Several attempts in this direction are found in the Scleroperalia, but the Gnathostomulidae are the most advanced. While originating close to the Gnathostomulidae, which is the highest branch of Scleroperalia, the Austrognathiidae (the only family of the Conophoralia today) have reached the same goal, but in a somewhat different way.

The development of the involucrum (in) can be understood as an extension and solidification of that cuticularized and prelamellarized part which is dentated: the lamella interna (li).
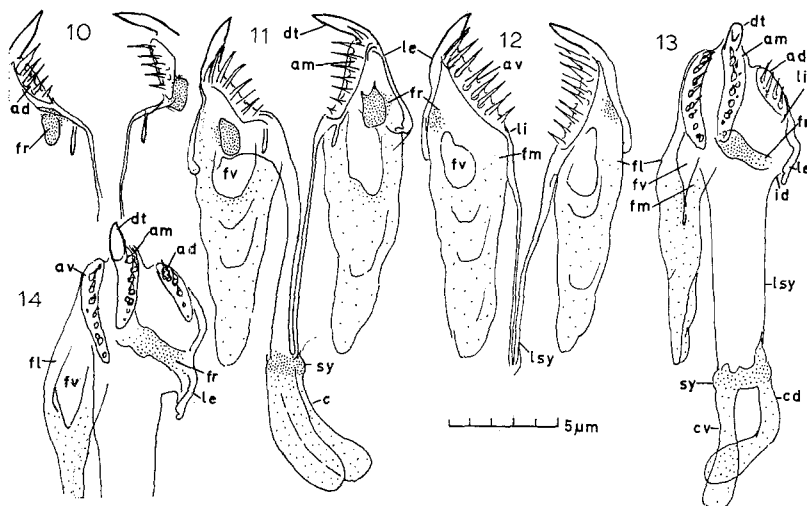
Figs. 10–14. *Gnathostomula brunidens* jaws. Figs. 10–12. Seen from dorsal, focus changes from dorsal to medial to ventral. Figs. 13 and 14. Seen from lateral. Fig. 13. Right side seen from left. Fig. 14. Left side seen from left

1. The Lamella externa (le) extends from the lamella interna first dorsolaterally, then it bends ventrally and ventromedially where it reaches or almost reaches the ventral end of the lamella interna. It forms a cone-shaped wrapping which is elliptical in cross section. In a horizontal section the cone is about 50° in Gnathostomula and 35° in *Semaeognathia*; in a frontal section the cone is very obtuse on its tip and is about as long as it is wide in both genera (comp. Figs. 11, 16, 29, 34 with 13, 18, 31, 35).

The thickness of the lamella externa varies more than does that of the lamella symphysis and reaches 0.3 μm in *Semaeognathia* and 0.4 μm in all the *Gnathostomula* investigated. It is generally thinner at the tip of the cone and thickens caudally and many reach 0.5 to 0.6 μm at the nodus lateralis (nl) where the fibula radialis (fr) ends (as will be described in "suspensorium").

2. Incisura ventralis (iv). The bottom of the cone is formed not so much by the lamella externa but rather by a structure of the suspensorium, namely the frontal end of the apophyses (ap). The two elements fuse in a ventrolateral position of the involucrum (Figs. 12, 16, 28, 37) but the apophysis has a ventral window (fv), which may or may not be closed by a very thin layer of the lamella externa. But whether or not the epithelium within the incisura ventralis would show a very thin cuticularization would not be much of a morphological difference.

The Gnathostomulidae have "fused lamella jaws" in the sense that the incisura ventralis of the lamella externa fuses with the frontolateral margin of the apophysis, regardless whether the fenester ventralis extends all the way to the tip of the cone (Figs. 16, 37), and regardless whether the window has a thin cover. The term must be seen as a functional principle.

3. *Apertura caudalis* (ac) and *tectum lateralis* (tl). The cone of the involucrum has a caudal opening (ac) whose dimensions are defined mainly by the form and the length of the lamella externa. Generally the length of the lamella is 3 to 5 μm und about equal from dorsal to ventrolateral. In *G. microstyla* however, it shortens from its dorsal and lateral length of 5 μm (Figs. 31, 30, 29) to 2.5 μm where it ventro-laterally fuses with the apophysis (Fig. 28).

This apertura caudalis is elliptical and usually 6 μm high and 3 μm (*Semaeognathia* and *G. microstyla*) or 4 μm broad (*G. brunidens* and *G. jenneri*). With the sole exception of the fibula radialis which to an extent crosses the apertura caudalis, it allows musculature and other tissue to pass unrestricted to the caudal and caudolateral directions.

From the caudal margin of the lamella externa a much thinner (0.1 to maximum 0.2 μm) and translucent cuticularized product of the jaw epithelium may extend further caudolaterally: the tectum lateralis (tl). Traces of this membrane may exist in all the species investigated, but they are particularly evident in *G. jenneri* (Figs. 16, 19). Nothing definite can be said about the length of this tectum lateralis since it becomes so thin after a distance of 2–3 μm from the apertura caudalis that light microscopy generally does not even show it in a direct side view; but it might very well be 5 to 10 μm long, covering the entire side of the inner pharynx musculature as long as it stays in the caudo-lateral direction.

The boundary between lamella externa and tectum lateralis is not visible in jaws before isolation. The two had to be described together (as "shoulder lamella": Riedl, 1971, shl).

c) Dentarium

The median part of the terminal cone whose outer part has been described as involucrum bears the dentation and a set of other differentiations, together termed the dentarium (de).

This dentarium, formerly not more than the tooth-bearing distal part of the forceps, becomes a well-defined unit within the jaw's organization of the derived family Gnathostomulidae. Its formation is partially initiated by the arc-shaped arrangement of the teeth which may have developed independently in Filospermoids (Pterognathiidae) and Burso-vaginoids (Mesognathariidae and more clearly in Onychognathiidae)

Onychognathiidae in addition initiate two further steps: an enlargement of the tooth-bearing field (compared to the height of the lamella symphysis) in *Onychognathia* and the separation of a terminal tooth within the row in *Nanognathia*.

1. The Lamella interna (li) reaches from the media lmargin of the proximal part of the apophysis (Figs. 12, 28) or from the fenestra ventralis (if the latter is wide; Figs. 16, 37) up to the dorsal tooth-bearing ridge. Its length spans from the terminal tooth to the start of the lamella symphysis, whose boundary is differentiated by a reduction of height from the distal to the proximal lamella. Height of lamella interna/lamella symphisis ranges between 2 and 3 (5 μm/2.5 μm, 5.5/2, 6/2, 5/2.5).

The lamella interna is differentiated into three arcs, thickened ledges or ridges, bearing the dentation and thin fields in between. In these fields the lamella is very thin, probably not more than 0.1 μm (its side view, the only one permitting more precise measurement, is always obstructed by the tooth ridges).

2. Three Arcs are always well developed. Each is slightly crescent-shaped. The arcus dorsalis (ad) is convex (to the dorsal) and the shortest in the three species of *Gnathostomula*. The arcus ventralis (av) is always concave and the longest. The anterior tip of both of them is pointed toward the dens terminalis. The latter (dt) sits on the tip of the arcus medialis (am). This arcus has a medium length in *Gnathostomula*, but is the shortest of all three in *Semaeognathia*, which could be interpreted as a conservative character. It also seems to be the straightest. The bending of the arcus medialis in the Fig. 13, 14, 18, 31 and 35 not only varies but also shows the dens terminalis pointing toward the concave side, indicating that the slightly convex side points rather laterally.

The derivation of these three arcs will gain phylogenetic interest with regard to the relationship between Gnathostomulidae and the next lower Scleroperalians, such as Onychognathiidae, but also with regard to the origin of the Austrognathiidae. It might very well be that the arcus dorsalis and arcus ventralis are homologous to the dentation of the more conservative Scleroperalia (Sterrer, 1971) and that the isolation of the dens terminalis gave rise to the intermediate arc. We know analogous additions in two genera of the Mesognathariidae.

3. The Dentation in its detail remains beyond the reach of light microscopy. The suggestions made that the number of teeth so clearly seen (compare Figs. 5, 8, 23) are optical minimum distances of an actually more complex dentation (Riedl, 1971) is becoming very likely. The drawings repeat the optical patterns and a regular comb-like structure appears in lateral views.
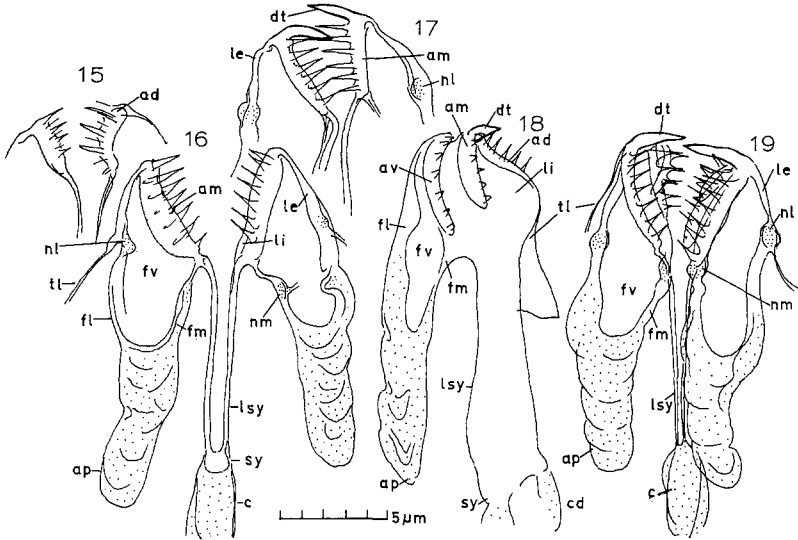
Figs. 15–19. *Gnathostomula jenneri* jaws. Figs. 15–17. Seen from dorsal, focus changing from dorsal to medial to ventral. Fig. 18. Right side seen from left. Fig. 19. Combination of all focus levels, seen from the ventral

But if the structure unfolds by bending (Figs. 15, 16), new patterns emerge between those initially visible. Lateral views also show a higher complexity (Figs. 13, 14). The structures are undoubtedly teeth, sometimes flattened in dens position, most likely greater in number than are visible, more irregular than they appear, most probably in more than one single row arrangement.

This must especially be considered for the dentation of the arcus ventralis in *Semaeognathia* (Figs. 35, 37, 38) as well as for most of the "umbrella-like" dentation of the three lower families of the Scleroperalia. The apparently combined tooth structures may be caused by umbrella-like lamellae connecting the single teeth as well as by broad lamellar teeth slightly overlapping one another. The latter is indicated by the structure of the serrulae (s) on the ala frontalis (af) of the basal plate—as will be described in a later chapter.

4. *An incisura dorsalis* (id) occurs if the caudal extension of the lamella interna, dorsal to the connection with the lamella symphysis and medial to the lamella externa, is reduced. This is partially so in *Gnathostomula brunidens,* more so in *G. microstyla* (Fig. 13, 31), but a deep incisura dorsalis is represented in *Semaeognathia* (Fig. 35). In this case the caudal part of the arcus dorsalis seems to be free from a medioventral connection. It is further supported by the lamella externa, and

the dorsal margin of the lamella symphysis can be traced deep into the region of the involucrum.

Also this feature of *Semaeognathia* may be considered conservative within the Gnathostomulidae whereas the complete lack of an incisura dorsalis in *G. jenneri* (Fig. 18) probably shows the most derived condition.

d) Suspensorium

The suspension of the jaws within the muscle system of the pharynx generally shows two areas of special differentiation: an anchorage structure near the symphysis and a paired handle-like structure on the lateral sides on the branches of the forceps. Both demonstrate independent trends within the Gnathostomulida and even different trends within orders and families. The anchor parts were called symphyses (in a larger sense) and caudae; the handles were uniformly termed apophyses.

1. Anchors. In the Filospermoidea the material of the symphysis can be extensively enlarged laterally to a pair of crescent-shaped horizontal structures, which by function, structure and specificity would merit the term "ancora". In Bursovaginoidea no such structure is known. Only lowest genera (IV and V in Sterrer, 1971), not yet described, may show a thickening of the symphysis in comparable position. But Mesognathariidae and Gnathostomariidae have very simple symphyses, at least as non-isolated jaws would indicate. The three higher families, on the other hand, develop an—assumably—new character, called "cauda". This is a caudal appendix to the symphysis, which often consists of an unpaired hyaline sack, and of a pair of cuticularized fingers in Gnathostomulidae, and which is always correlated with a centralization of the caudal and unpaired muscle sack not originating on the side walls of the forceps branches but on the symphysis itself (see Sterrer, 1971).

2. Caudae. The portions of the cauda which remain after the bleaching process are, in the four species investigated, the two cuticularized fingers—the pars sclerosa of this organ, for simplicity called caudae (c) (and not cauda sclerosa) here.

Among the nine species which I recently described in the family Gnathostomulidae, only *Gnathostomula arabica*, *G. armata*, *G. karlingi*, *G. microstyla*, and *Semaeognathia sterreri* (Riedl, 1970, 1970) have clearly shown the paired component in unisolated jaws and, in dorsal or ventral views, maybe *G. mediocristata* too, but this is less certain. In *Gnathostomula jenneri* and *G. brunidens* this feature was indicated, but not clearly. The isolated preparations show this portion definitely and justify the assumption made that they occur in all Gnathostomulidae.

Position and shape however, show a surprising diversity within the family and indicate that the organ is still in a flexible or inventive, in other words an experimental and possibly young evolutionary stage.

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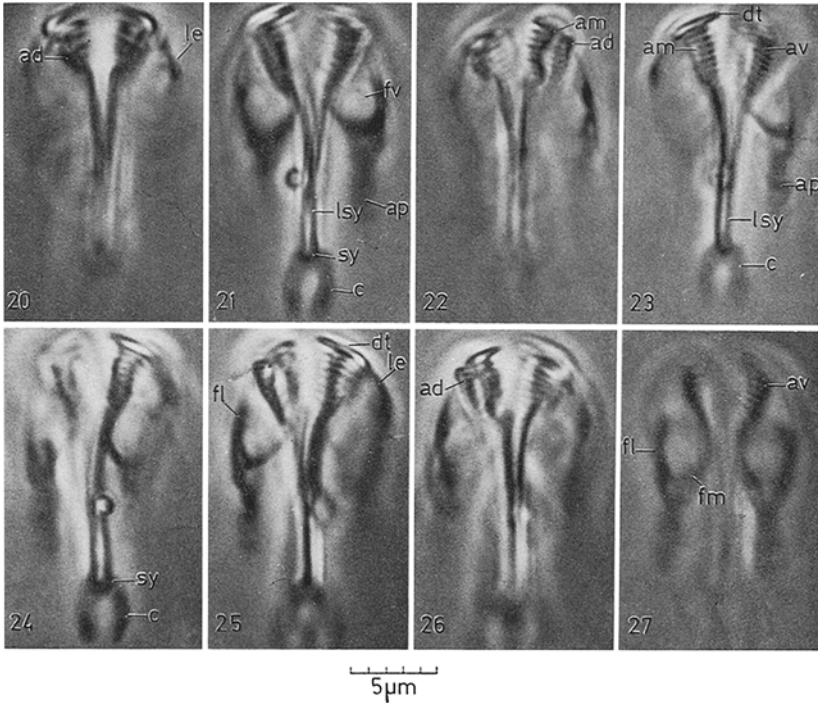
Figs. 20–27. *Gnathostomula microstyla* jaws. Figs. 20 and 21. Seen from dorsal, focus from dorsal to ventral. Figs. 22 and 23. seen from dorsolateral, focus from dorsal to ventral. Figs. 24–26. Seen from ventrolateral, focus changes from ventral to medial to dorsal. Fig. 27. Seen from ventral with focus at ventral level

In *Semaeognathia*, assumably again the most conservative stage within the family, the origin of the cauda dexter and cauda sinister (c [d], c [s]) is side by side, corresponding to the comparably small symphysis (Figs. 34, 38), and they both bend slightly downwards (Figs. 35, 36).

In *Gnathostomula microstyla*, which in many respects forms a type of its own ("microstyla" type: Riedl, 1971), the caudae are also unique. Though there are still caudae dexter and sinister in symmetrical position, both caudae originate somewhere along the full width of the symphysis (Fig. 31). They form flat cushions 2 μm high but 1 μm thick: at their origin only 0.3 to 0.6 μm thick.

In *Gnathostomula brunidens* and *G. jenneri*, which are very related in many respects ("jenneri" type: Riedl, 1971), the two caudae are placed one above the other, forming a cauda dorsalis and a cauda ventralis

(cd, cv). This is also the explanation for the paired organization which is almost invisible in squeeze preparations. The cuticularized caudae cover each other (Figs. 11, 16, 19); only if seen from the lateral (Figs. 13, 18) do they appear well-separated: each resting on one end of the 2–3 μm high symphysis.

Since the "cauda dexter-sinister" probably is the more conservative type, the intermediate stage of the "cauda dorsalis-ventralis" type would be of interest. Is the cushion form of *G. microstyla* intermediate? And is the cauda dorsalis the former cauda dexter or sinister? Or are the dorsoventral caudae independently developed? The investigation of more species may clarify these questions.

The angle between the cuticularized pairs is wider in living conditions; it grows with increasing pressure in squeeze preparations and shrinks considerably during the isolation process. This again indicates the existence of a central flexible cell or cushion of tissue which expands under pressure and disintegrates in the bleaching process, and it also indicates flexibility and forceps-like tension of the cuticularized parts of the caudae.

3. The Apophyses (ap). As mentioned before, the term apophysis has been used in a more functional sense for all paired and lateral appendices of the bars of the jaws-forcep system, which most obviously function as bases for the lateral or ventrolateral muscles. Sterrer (1971), who introduced the term, is using it with the same care. So whether or not the apophyses occurring in the two orders are homologous remains an open question.

The existence of apophyses in the three lower families of Scleroperalia is unclear. They may have hidden in the tissues; they may be not cuticularized, or not yet be developed. In *Onychognathia* (Riedl, 1971) however, apophyses are well distinguished and seem to be characteristically small, simple and in a very distal position: originating at the lamella interna itself. If they exist in conophoralians (Austrognathiidae), and they may, their position must also differ from the family described here.

All Gnathostomulidae possess large apophyses. They were first clearly seen in *Semaeognathia* (Riedl, 1970) and provided the name for this genus. They were later (Riedl, 1971) seen in the tissue of *Gnathostomula armata* and *G. karlingi*, seen in traces in *G. brunidens*, *G. nigrostoma*, and *G. arabica*, not seen in *G. jenneri*, *G. mediocristata*, and *G. microstyla*. Yet, since they clearly show in isolated jaws of *G. jenneri* and *G. microstyla*, there remains little doubt about all Gnathostomulidae having them.

These apophyses consist generally of a pair of wing-shaped plates, kept in a frontal position and on a level 1–2 μm below that of the arcus ventrales. The wings originate medially at the ventral edge of the
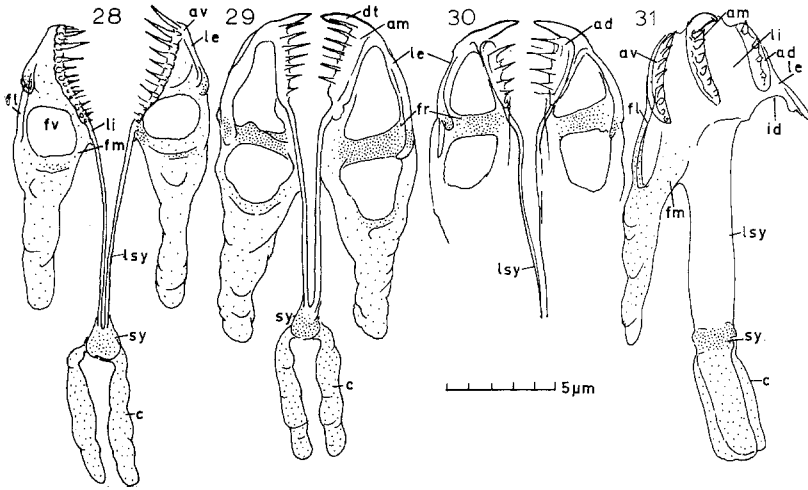
Figs. 28–31. *Gnathostomula microstyla* jaws. Figs. 28–30. Seen from ventral, focus changing from ventral to medial to dorsal. Fig. 31. Right side seen from left

lamella interna and laterally along the ventral border of the lamella externa—in the incisura ventralis.

The structure of the apophyses differs quite a bit from all the lamella types and has more similarity to the cuticularized parts of the cauda; like the latter the apophyses seem to be formed within the tissues of the mouth cavity rather than on their surface. The surface is rough; the material seems rather porous, and the outlines are much less clear or defined than are the lamellae.

The maximum breadth (anteriorly) is 3–4 μm; the maximum thickness varies between 1–1.5 μm. The length is 14–15 μm in *Gnathostomula* spp. and 11–12 μm in *Semaeognathia* (measured from the distal end of the incisura ventralis). The main axis points caudally or slightly latero-caudally and both breadth and thickness diminish caudally to form wavy sides and an obtuse end. Most characteristically the surface and/or the density of the material shows a ripple-like pattern. Each ripple has a crescent-shape with its convex side pointing caudally and its bending also increases towards the caudal end. Wherever the apophyses were still clearly seen within the tissues, the outline looked smoother, more defined and regular (Riedl, 1970, 1971), showing a shoulder-like extension on the inner margin (*Gnathostomula karlingi*), on the outer one (*Semaeognathia sterreri*) or on both of them, the latter very pronounced like an additional caudolateral subwing (*Gnathostomula armata*). What remains of the apophyses after bleaching is probably not more than the more cuticularized axis of the organ.

4. *Fenestra ventralis* (fv). Each of the specimens of the four species investigated shows a window-like structure in the proximal part of the apophyses. It very much looks like a free passage (as the name indicates), yet the possibility can't be excluded that it is only an optically very transparent area. Clearly, though, this fenestra ventralis is always found in a mechanically logical position — at the region in construction where surface area can be spared and gained eleasticity might be advantageous.

The fenestra ventralis is always longer than wide if it is reasonably developed, but it is variable in size from species to species. It is 1.5 to 3 μm in *Gnathostomula brunidens*, 2 μm in *G. microstyla*, but 2 to 5 μm in *Semaeognathia* and 3 to 7 μm in *G. jenneri*, and in these two latter it reaches proximally to the end of the incisura ventralis.

5. *The Fibulae* (f). A consequence of the fenestra ventralis are two ledges on both sides of the fenestra which become the more pronounced the more sizeable the window gets.

The inner one or fibula medialis (fm) is the most compact in *Gnathostomula brunidens*, as broad as long, barely a fibula to speak of (Fig. 12). In *G. microstyla* and *Semaeognathia* the fibula interna is short, but very slender (Fig. 28, 34, 37). In *G. jenneri* it is however slender as well as long (Figs. 16, 18, 19): about 0.4 to 3 μm. The fibula medialis always originates at the ventrocaudal edge of the lamella interna (the clearest seen from the lateral: Figs. 13, 18, 31, 35).

The outer ledge or fibula lateralis (fl) is, in principle, like the fibula medialis, compact in *G. brunidens* (Fig. 12) but thin and long at the same time in the three other species: 2–4 μm long and 0.3–0.5 μm thick (Figs. 16, 28, 37). It seems to originate not only from the ventrocaudal edge of the lamella externa, but from its entire ventral margin (Figs. 14, 18, 31, 35).

The fibulae mediales and laterales, remember, are by their position cuticularized sinews and may very well function as sinews or their prolongations. The solid wing of the apophyses most probably functions as a sinew plate, providing more space for muscle attachment. But this might be very different in the third ledge of the Gnathostomlidae jaws which is described next.

6. *Fibula radialis* (fr). The third ledge proceeds in a radial direction, generally from the ventrocaudal portion of the lamella interna to the corresponding part of the lamella externa. So it forms a clasp which bridges the widest span of the involucrum and it may at the same time cross the fenestra ventralis and the apertura caudalis. It most obviously functions as a prop or strut at the weakest point of the involucrum, thus preventing the cone from collapsing if muscle tension pulls both of its margins backwards.
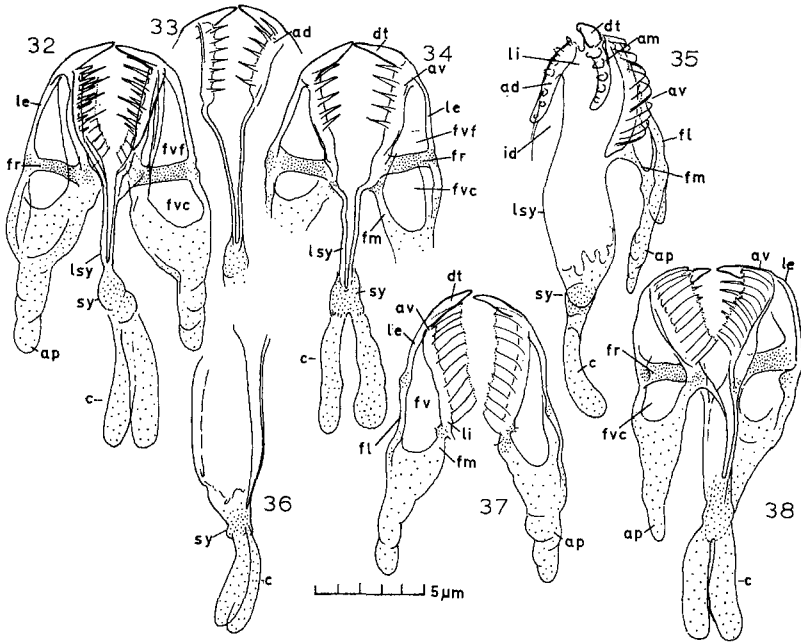
Figs. 32–38. *Semaeognathia sterreri* jaws. Figs. 32–34. Seen from dorsal. Fig. 32. Combination of all focuses. Figs. 33 and 34. Focus changing from dorsal to medial. Fig. 35. Left side seen from right. Fig. 36. All focuses, seen from left and slightly dorsal. Fig. 37.Seen from ventral, focus ventral, Fig. 38. Combination of all focuses, seen from ventral and slightly from right

This, at least, is the obvious case in the probably more conservative organization represented again by *Semaeognathia* and *Gnathostomula microstyla*.

In *Semaeognathia* the fibula radialis originates medially somewhat above the fibula medialis and between the caudal ends of the arcus medialis and ventralis (Figs. 32, 34, 38). From here it spans radially and slightly towards the ventral to meet the caudoventral end of the lamella externa at the point where the latter is reached first by the fibula externa. If seen from the caudal end of the jaws, the two fibulae radiales would appear as a pair of roof-trees pointing slightly upwards medially to the ridge. This construction crosses the apertura caudalis only in its ventralmost position, but (if seen dorsally) it crosses the wide fenestra ventralis in the middle, dividing it into a smaller fenestra ventrocaudalis (fvc) and a larger fenestra ventrofrontalis (fvf) under the cover of the involucrum.

In *Gnathostomula microstyla* the origin of the fibula radialis is more ventral, namely together with the fibula medialis at the caudal tip of the arcus ventralis. From here it spans radially to reach the caudolateral portion of the lamella externa slightly above the fibula lateralis (Figs. 29, 30). In this arrangement the fibulae radiales are in an almost horizontal position. The apertura caudalis is, as in the former genus, crossed only in its ventralmost portion and the fenestra ventralis is not divided; the fibula radialis runs above its anterior margin.

In *Gnathostomula brunidens* the position of the fibula radialis is seemingly all different. It stands almost vertical, and seen from dorsal (Figs. 5, 7) or ventral (Fig. 9) its optical cross section is very apparent. The correlation with the former species can be understood if one assumes that the origin of this fibula has migrated dorsally along the caudal portion of the lamella interna until it is finally located in a position caudal to the arcus dorsalis (Figs. 10, 13, 14). From this position it must now radiate ventrolaterally (Fig. 11) to meet the place where the lamella externa fuses with the fibula lateralis (Fig. 12). No division of the fenestra ventralis is the consequence, but the apertura caudalis becomes fully divided almost in the middle by the "beams" of a steep roof construction, forming an apertura caudolateralis (acl) and caudomedialis (acm).

The support of the cone's margin remains the same although the strut has rotated its position almost 90°. But the pressure-tension the fibula radialis had to withstand in *Semaeognathia* and in *G. microstyla* must have changed to with-standing pulling-tension in *G. brunidens* if the rest of the jaw can be assumed to have remained essentially the same.

In *Gnathostomula jenneri* no fibula radialis is apparent. Yet there is a knob-like structure at the connection between fibula lateralis and lamella externa, exactly at the place where the outer end of the fibula radialis would be expected. This nodus lateralis (nl; Figs. 16, 17, 19) could very well be the ventrolateral remainder of a formerly solid fibula radialis.

This is the more likely, with regard to the close relationship with *G. brunidens*, since the function of the fibula radialis may have already changed from withstanding pressure-tension to withstanding pulling-tension; and such pulling-tension can be withstood by a sinew or tendon as well as by a bar or prop. Probably the fibula radialis has been substituted with a "ligamentum radialis" to save material, since saving material is a general feature in *G. jenneri*, as shown by the size of the fenester ventralis and the thin and long fibulae laterales and mediales.

Median knobs also appear (Figs. 16, 19). This nodus medialis (nm) occurs at the point where the fibula medialis joins the end of the lamella interna.

II. The Basal Plates

The principle of the organization of the basal plates, even in the more differentiated families, such as the Gnathostomulidae, is already widely understood (recent literature Riedl, 1970, 1971; Sterrer, 1971); to a certain extent the major trends in the basal plate's phylogeny are also anticipated.

From a simple disc-shaped plate caudal to the mouth opening, a wing-shaped structure is developed with more and more pronounced dentation in the center of its anterior margin. This is observable in both of the orders, but in Bursovaginoidea it becomes much more elaborate. Along with this tendency to move the supporting plate from caudal to lateral in the Gnathostomulidae it even moves further, differentiating in a radial pattern of which the most anterior part finally points anteriorly. It reaches more frontally than the area of dentation, and the dentation forms a well-defined field in the center.

For this reason the terms "wings" and "central part" were used and will be kept as "pars alaris" (pa) and "pars centralis" (pc) further on.

a) Pars Centralis

In all four species investigated, the pars centralis consists of a row of very tightly arranged teeth, 2–3 μm long. The number of these teeth is still not definitive. As in the dentation of the jaws, this has to do with the limitations of the light microscope. In isolated jaws 9, 11, or 13 teeth are generally apparent. But this difference is correlated with the breadth of the pars centralis and with the angle at which one observations them. In the most straight on view, (Figs. 48, 54, 64) specimens of *Gnathostomula* show additional patterns, bringing up the number of teeth from 11 to 15. In *G. microstyla* at least an indication was found (Fig. 64) that each of the marginal teeth might be double; this brings the number from 15 to 17. This may be close to the final number of the investigated species since the grouping of the dentation in the pars centralis is more regular than on the arcus of the jaws.

1. The Dens medialis, or central tooth (dm) is always the longest, is unpaired, inserts in the caudalmost position and reaches the furthest frontally. It is also thicker than the ones on its sides, with the possible exception of the lateralmost. It forms the ridge of the rooflike structure of the pars centralis.

It inserts almost vertically on the horizontal plane of the pars alaris. then bends gradually towards the dorsofrontal for the first half of its length. The bending then stretches more and more and its end points frontally and somewhat dorsally.
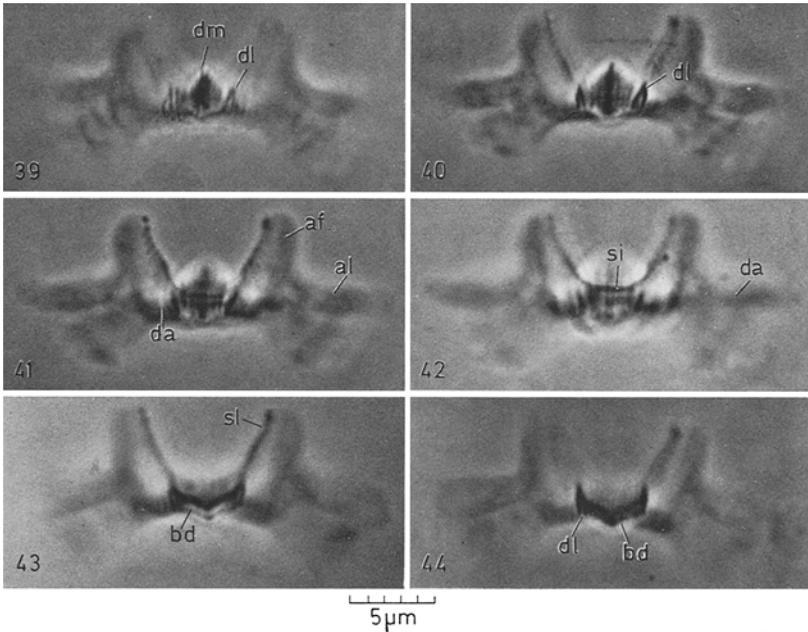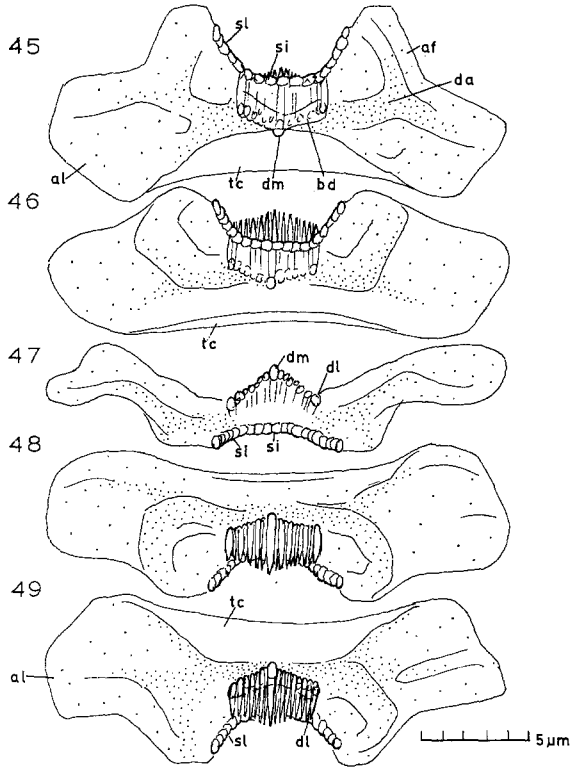
Figs. 39–44. *Gnathostomula brunidens*, basal plate. Figs. 39–42. Seen from dorsal focus changing from dorsal to medial and submedial to ventral, Figs. 43 and 44. Seen from ventral, focus from medial to subdorsal

2. *The Dentes laterales* or lateral teeth (dl) show the same patterns, except that they insert more anteriorly, are shorter and also bend down earlier. So the sides of the roof are lower than the ridge of the roof.

In non-isolated basal plates these dentes laterales looked like a wall, as if they sealed the sides of the roof with the pars alaris (Riedl, 1971). This does not seem to be quite so. The isolated organ indicates that the sides are true teeth. Yet they are definitely different from the others, at least in the genus *Gnathostomula*. Not only do they bend earlier and are they much closer to the plane of the pars alaris, they also seem to be in a slightly more distant position from the rest of the teeth. And finally the "terminal tooth" seemingly can be a group of "terminal teeth" on each side, maybe even arranged above each other, forming —if not a wall—then a prop support to the margin of the roof itself.

3. *The Basis denticis* (bd), the base where the teeth of the pars centralis insert together, forms a very typical pattern in the whole family. It always is a double arch where the insertions of the dens medialis and the dentes laterales together form the three end points The rest of the smaller teeth insert on both sides of the medial

Figs. 45–49. *Gnathostomula brunidens*, basal plate. The specimen is rolled from a ventral view (Fig. 45) to a ventro-frontal view (Fig. 46), frontal (Fig. 47), and dorso-frontal (Fig. 48) to dorsal (Fig. 49) views

sagittal line along an arc whose concave side points caudally and slightly towards the lateral (Figs. 45, 50, 60, 65).

The whole dentation of the pars centralis forms a peculiar roof structure. The height of the roof is about 1 μm in *Semaeognathia* and 1.5–2 μm in species of *Gnathostomula*. The angle which is formed by the two sides of the roof is 140° in *Semaeognathia* (Fig. 67) and 100–120° in *Gnathostomula* (Figs. 47, 52, 63). The smaller height and the wider angle in *Semaeognathia* have to be considered the more conservative characters and the ancestors of the family most probably had a simple tight row of teeth all pointing frontodorsally, without forming a roof. The roof with a median ridge is an invention by this family only.

b) Pars alaris

All basal plates of the investigated specimens share in four features of the pars alaris: a pair of frontal wings, a pair of lateral ones, an

unpaired plane caudomedially, a stronger transverse axis and a flat dentation along the medial margin of the frontal wings, or serrulae (s) to be discussed in the next chapter.

The wing-shaped parts together form the five-segment pattern which is very common in gnathostomulids. Formerly, or in more conservative families, it was a much more regular and equal five-partition. This is greatly distorted, but the principle is recognizable.

The texture of the pars alaris seems midway between the lamellae and suspensorium of the jaws which were previously described. The unpaired caudal part is more lamella-like, but the paired parts are coarser in texture.

1. The Tectum caudalis (tc), or unpaired caudal part, is a very thin posterior extension of cuticularization from the broad transverse back of the basal plate. In appearance it has much in common with the tectum lateralis of the jaw, and it might also be a surface cuticularization of the epithelium of the mouth cavity; in this case the ventrocaudal portion underneath the jaws themselves.

In *Semaeognathia* it is crescent-shaped (Figs. 65, 70) with the convex side pointing caudally. This convex caudal margin can be considered a conservative character within the Gnathostomulidae since this is typical for the unpaired median part of all the lower families of the Scleroperalia, but it changes completely in the genus *Gnathostomula*. Seen from frontal and dorsofrontal (Figs. 67, 68) it also shows a distinct bend: the convex side towards the dorsal. We still know little about this dimension in more primitive basal plates in scleroperalians, yet a convex dorsal side seems to be the more likely also. Finally there is a third most obvious conservative character; its extension into the mediosagittal plane is relatively large. Taking the distance from the point where the sagittal plane joins the anterior margin of the dorsum alae to the point where it crosses the caudal margin of the tectum (2.5 μm; see Fig. 65), as 100% the distance from the caudalmost point of the basis denticis to the margin of the tectum (1.8 μm, same fig.) is correspondingly 70%.

In *Gnathostomula microstyla* the tectum caudalis is found to be a straight transverse band (Fig. 60, 64), and both of its margins are almost linear. In a frontal and frontodorsal view (Figs. 62, 63) the dorsal side is concave, spread like a strongly stretched hammock between the laterocaudal ends of the dorsum alae. The length index is about 44% (1.5 to 3.4 μm; Fig. 60). All these features are, as will be shown, intermediate between *Semaeognathia* and the two more derived species of *Gnathostomula*.

In *Gnathostomula brunidens* and *G. jenneri* the tectum is again crescent-shaped, but this time the convex side points frontally (Figs. 45, 46, 49, 54). Seen from frontal and dorsofrontal (Figs. 47, 51, 52), the dorsal
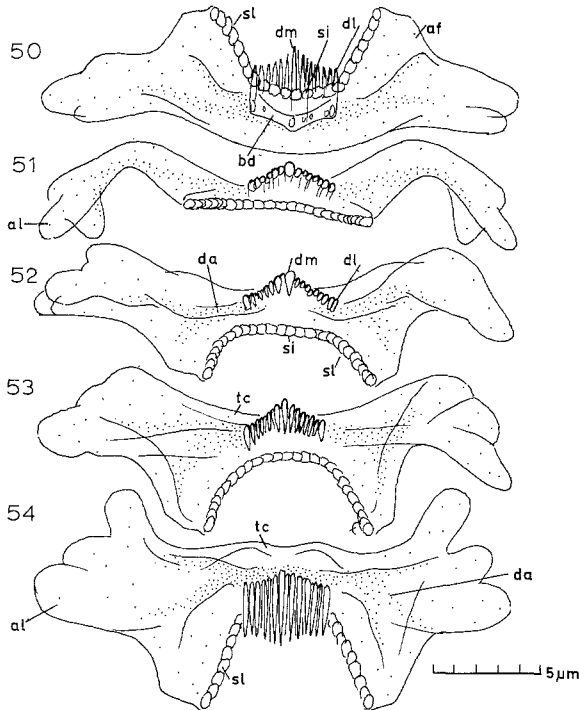
Figs. 50–54. *Gnathostomula jenneri*, basal plate. The specimen is rolled from a ventral and slightly frontal view (Fig. 50), to frontal (Fig. 51), dorso-frontal (Fig. 52), and frontodorsal (Fig. 53), to dorsal (Fig. 54) views

concavity appears so severe that the tectum almost disappears behind the dorsum alae. Also the index has the extreme values of 33–36% (4.2 to 1.5 and 3 to 2 μm; Figs. 45, 50). In addition the caudal margin of the tectum is slightly rolled upward, which is not the case in *G. brunidens* and *Semaeognathia*.

2. *The Dorsum alae* (da) in Gnathostomulidae is a transverse double "y"-shaped prop support which appears as a ledge-like thickening on the dorsal side of the pars alaris. In its center, where the two "y"s from both sides meet, it supports the basis denticis and the two "v"-shaped branches divide the ala frontalis from the ala lateralis and this latter from the tectum caudalis.

This is at least the case in *Semaeognathia* and *Gnathostomula microstyla* (Figs. 60, 64, 65, 70). These patterns largely correspond to the four ledge principle dividing the five fields of the pars alaris of more conservative genera, such as *Nanognathia* and *Gnathostomaria*, and it provides additional support for the hypothesized five-partite pars alaris

principle suggested by Sterrer (1971) not only for the Gnathostomulidae but for the Gnathostomulida. The step made by Gnathostomulidae can be described as an increasing longitudinal shortening and transverse stretching of the tectum caudalis and consequently the change from a double "v" to a double "y" form of dorsum alae.

Yet this transformation seems to be the effect of an ulterior cause; and the cause may have to do with a movement of paired parts, the alae (a), towards the lateral and frontal. This must have to do with a movement of the muscles which insert on the ala lateralis and ala frontalis from probably a laterocaudal to laterofrontal position in Gnathostomulidae. So a certain change in the functions of the basal plate in this derived family seems to be the cause itself.

In *Semaeognathia* and *G. microstyla* the position of the dorsum alae is still mainly between the five fields. In *G. brunidens* and *G. jenneri* this division is obscured by thickening the middle parts of the alae themselves.

3. The Ala lateralis (al), the side wing in Gnathostomulidae, pretty much retains its lateral position—which corresponds to the main transverse axis of the basal plate—in all the species investigated. Yet two trends are observed.

First the alae laterales keep growing in an absolute scale from *Semaeognathia* to *G. microstyla* to the jenneri group with *G. jenneri* and *G. brunidens*. The maximum breadth grows from 1.8 to 2.7 to 5 and 6 μm (compare Figs. 65, 60, 49, 54); the length (from the dens lateralis to the lateral tip of the ala lateralis) from 5 to 7 to 9 and 10 μm. The thickness grows from 0.6 to 0.8 to 1 μm (compare fig. 67, 62, 51). In a relative scale, taking for example the maximum breadth of the ala lateralis in % of the maximum frontocaudal length of the basal plate, the amount grows from 25% to 35% to 65 and 67%.

Secondly, in the same sequence, this wing drastically changes its outline. In *Semaeognathia* it is a trapezoid with the smaller breadth lateral; in *G. microstyla* it is almost a rectangle and in *G. jenneri* it is a trapezoid with the smaller side medial. Finally in the *jenneri*-group, particularly in *G. jenneri* the lateral margin divides into two and three portions (Figs. 51, 54). These are most definitely steps in progressive differentiation. Less clear is the meaning of the more or less pronounced "w"-shape which these wings take on when seen from the frontal view. It is most pronounced in *G. jenneri* (Fig. 51), less so in *Semaeognathia* and *G. brunidens* (Figs. 67, 47) and the least in *G. microstyla* (Fig. 62).

4. The Ala fronatalis (af), or frontal wing of the Gnathostomulidae, very probably correspond to the lateralmost pair of fields of the general organization in gnathostomulid's basal plates. Their position as represented in the family, however, is unique. The genera *Nanognathia, Gnathosto-*
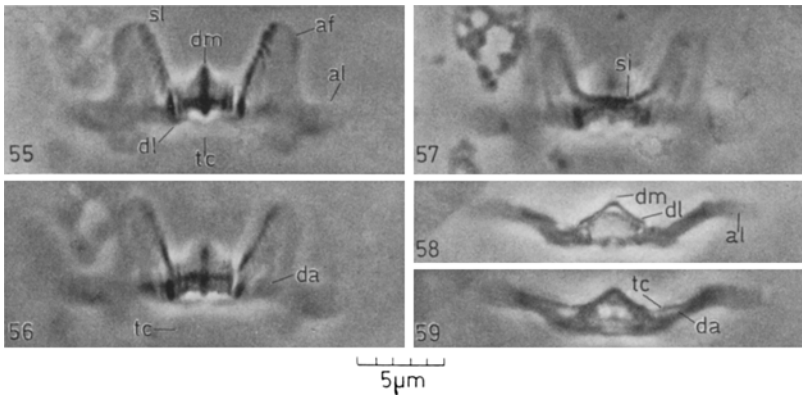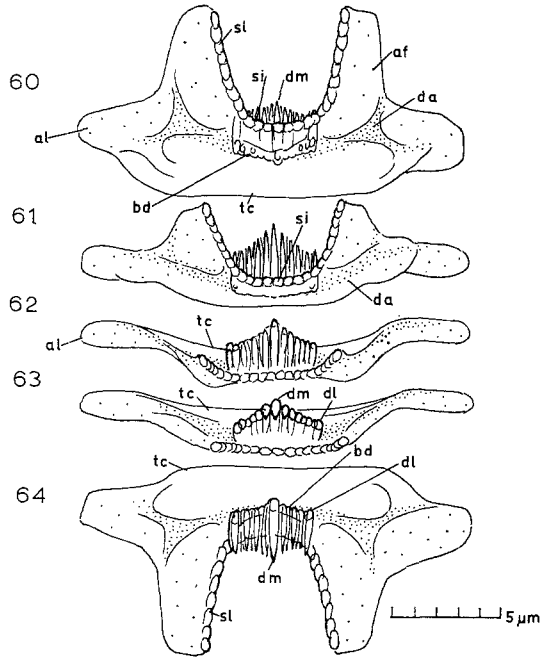
Figs. 55–59. *Gnathostomula microstyla*, basal plate. Figs. 55–57. Seen from dorsal, focus changing from dorsal to medial to ventral. Figs. 58 and 59. Seen from frontal, focus changed from frontal to caudal

maria and *Labidognathia* tend also, and assumably independently, to achieve an anterior positioning of the alae frontales in respect to the pars centralis, yet to a much smaller extent. Not more than 25% of the total sagittal length of the ala frontalis exceeds the mediofrontal margin of the basal plate, while in Gnathostomulidae it is always more than 75%.

There is a definite sequence of shapes of the alae frontales in Gnathostomulidae. Yet the decision about the progression is less easy. If, however, the interpretation of the direction in the other trends found in jaws and basal plates of the family was correct, support is gained for interpreting the ala frontalis trend in the same direction: namely from *Semaeognathia* to *Gnathostomula microstyla* to the "jenneri-group" of the latter genus.

In this sense the ala frontalis becomes more compact and relatively smaller. The length/breadth index decreases from 2 to 1.6 to about 1 and 0.8. The relative size, e.g. the length of the ala frontalis in percent of the span of the whole basal plate, also reduces from *Semaeognathia*'s 35% to 28% in *G. microstyla* and to 23 and 19% in *G. jenneri* and *G. brunidens* respectively (compare Figs. 65, 60, 50, 45).

Semaeognathia however shows features in the ala frontalis which are very different from all the species of *Gnathostomula*. The median margins of the alae frontales remain separate in their caudal portion (Figs. 65, 66, 68). They swing caudo-laterally in this area and end at the ventral side of the pars alaris. This is a most fundamental difference from the genus *Gnathostomula* (Figs. 45, 50, 60) where the

Figs. 60–64. *Gnathostomula microstyla*, basal plate. The specimen is rolled from a ventral view (Fig. 60), to ventro-frontal (Fig. 61), frontal (Fig. 62), and frontal with slight tilt dorsally (Fig. 63), to dorsal (Fig. 64) views

two median margins fuse fully to form an unbroken arc underneath the roof of the pars centralis and ventrofrontal to the basis denticis.

Finally the ala frontalis is also more separate from the ala frontalis in *Semaeognathia*. It sits somewhat underneath the ala lateralis (Fig. 67) and doesn't fuse laterally either with this wing, as is the case in *Gnathostomula* species (Figs. 47, 51, 63). As a consequence the caudolateral margin of the ala frontalis can only be seen, in *Semaeognathia*, underneath the frontomedial part of the ala lateralis (Figs. 65, 66, 68, 70).

With regard to the phylogeny of these features, one may be a conservative, the other a specialized character. The lack of fusion of the medial margins seems to show a conservative situation, because these margins were always separate in more primitive families. The partial separation and overlapping of the two wings is a speciality of the genus *Semaeognathia*.

c) Serrula

The medial margin of the alae frontales of all known species of the family Gnathostomulidae shows a unique feature which is still not found

in one of the other families. This is a cover by scale-like plates about 0.5 μm in diameter, which optically resemble teeth in their texture. Like these they also seem to be a surface product of the mouth epithelium and extend uncovered into the mouth cavity. But unlike the rest of the dentation in the family these structures are more flat and their distal ends remain close to the surface on which they insert.

This forms a serrated margin which shall be called the serrula (s) in the family under investigation. These scales or flat teeth form a striated pattern, being longer than broad, and placed in an oblique position pointing anteriorly. The more anterior scale also may overlap its posterior neighbor, but this is rather an assumption and beyond the reach of light microscopy.

1. The Serrula lateralis (sl) is of different lengths. In *Semaeognathia* it borders 3/4 of the medial margin of the ala frontalis. The anteriormost part of the medial margin is free, but also the caudomedial part of the margin is unprotected (Fig. 70). In *Gnathostomula microstyla* and *G. jenneri*, the serrula lateralis covers the entire length of the margin (Figs. 64, 54).

In *G. brunidens*, however, the tip of the ala frontalis is not quite reached by the serrula (Figs. 45, 49), but it can't be decided whether these are primary or secondary conditions. This is particularly so because the tip of the alae frontales in *Gnathostomula* species gains a shoulder-like broadening, not existing in *Semaeognathia*, which by itself could, as a later adaptation, extend the former end-point of the serrula lateralis.

Seven to ten scale-like teeth generally seem to cover the margin of the ala frontalis. However strong irregularity is observable, not only from specimen to specimen in a species, but even between the right and the left sides of the same organ.

2. The Serrula infundibula (si) is a unique feature, so far only observed within the genus *Gnathostomula*. As outlined above the caudal ends of the median margin of the alae frontales fuse only in *Gnathostomula*, forming a transverse crest underneath the roof of the pars centralis—a structure one could call an infundibulum. This infundibulum seems also covered with a serrula, the serrula infundibula (Figs. 45, 50, 60), having about 5 to 10 scale-like teeth, as many as light microscopy can show. In *Semaeognathia* this infundibulum does not exist and also no trace of a serrula infundibula is found.

This lack of an infundibulum as well as of a serrula infundibula is one of the major differences of the cuticularized parts in the two genera of the family Gnathostomulidae.

At this point the question becomes of interest whether the lack or the presence of the infundibulum-serrula infundibula character is the more conservative status. Two approaches seem initially feasible.
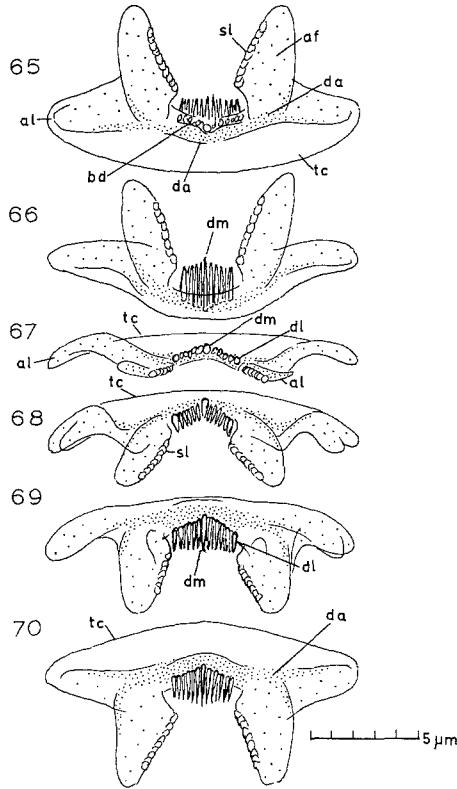
Figs. 65–70. *Semaeognathia sterreri*, basal plate. The specimen is rolled from a ventral view (Fig. 65), to fronto-ventral (Fig. 66), frontal (Fig. 67), dorso-frontal (Fig. 68), and fronto-dorsal (Fig. 69), to dorsal (Fig. 70) views

The dentation of the anterior margin of the basal plate in the more conservative families of the gnathostomulids is, if developed at all, much less pronounced. The teeth are smaller, less distinct or less tightly arranged and the area of dentation is more vaguely limited but covers a wider portion of the basal plate's anterior margin. The genera *Pterognathia*, *Labidognathia* or *Gnathostomaria* represent such types. And in addition all lower genera of gnathostomulids, even if they don't have any teeth at all, or if the dentation is too small to be seen by the light microscope, show, in their basal plates, most of the differentiation on a wide portion of this anterior margin. So most of this margin may be the logical place for further development of dentation.

But, and the alternative is now defined more precisely, in the case of the genus *Gnathostomula* does the dentation of the pars centralis or

that of the serrula infundibula represent the primary pattern? Here
we found two rows above each other.

Version I: The primary dentation has gradually spread over to the
total margin. In *Gnathostomula* it is represented by the serrulae laterales
and infundibula. The infundibulum is the primary frontal margin of the
organ and the dentation of the pars centralis is a secondary differentiation.
Gnathostomula would represent the more conservative and *Semaeognathia*
the more derived condition.

Version II: The primary dentation becomes gradually centralized to
form the one of the pars centralis and is in *Gnathostomula* represented
by the roof-forming group only. The dentation of the serrulae is
secondary and the infundibulum group is the newest addition. *Semaeo-
gnathia* would consequently represent a more conservative and
Gnathostomula the more derived stage.

The second version seems to be far more likely for the following
reasons. First: As soon as the differentiation of teeth occurs, at least
in Bursovaginoidea, a tendency for centralization is found at the same
time. Isolated basal plates of *Labidognathia longicollis* confirm this
increase of differentiation towards the sagittal plane. Second: Most of
the margin of the ala frontalis may not reach the mouth cavity in more
conservative species but may be covered by the suspending tissues.
Serrulae may be developed only if the margin reaches the epithelium
surface and this seems to happen first laterally and later caudally.
Third: No reason is seen for substituting the serrula infundibula with the
teeth of the pars centralis in *Semaeognathia*, and not in *Gnathostomula*;
but good reasons can be seen for completing and fusing the serrula
itself. Fourth: *Semaeognathia* has, in the majority of the characters,
proved to be the more conservative of the two genera of Gnathosto-
mulidae; this must also influence the interpretation.

The serrulae of the Gnathostomulidae seem to be an additional and
secondary differentiation, even though the scales of the serrulae themsel-
ves may show a primitive tooth structure, as for instance the primary
teeth of the basal plate of conservative Scleroperalia.

D. Discussion

This last chapter shall serve to correlate the different trends and
principles observed and to use this more generalized information to
discuss overall relationships. So we will not follow single structural
units but combine them in the different levels of the hierarchic patterns
of similarities, from the general to the specific.

In order to facilitate the use of an overview of the systematic
grouping of Gnathostomulida as initially put forth in several papers by

R. Riedl and by W. Sterrer and recently summarized (Sterrer, 1971), we list the groups described and defined today:

Order	Suborder	Family	Genus	Author
Filospermoidea {		Haplognathiidae	*Haplognathia*	Sterrer
		Pterognathiidae	*Pterognathia*	Sterrer
Bursovaginoidea {	Scleroperalia {	Agnathiellidae	*Agnathiella*	Sterrer
		Mesognathariidae {	*Mesognatharia*	Sterrer
			Labidognathia	Riedl
		Gnathostomariidae	*Gnathostomaria*	Ax
		Onychognathiidae {	*Onychognathia*	Riedl
			Nanognathia	Sterrer
		Gnathostomulidae {	*Semaeognathia*	Riedl
			Gnathostomula	Ax
	Conophoralia {	Austrognathiidae {	*Austrognathia*	Sterrer
			Austrognatharia	Sterrer

The species of the family Gnathostomulidae described today (see also Riedl, 1970, 1971) are the following:

Semaeognathia sterreri	Riedl	*Gnathostomula maldivarum*	Gerlach
Gnathostomula arabica	Riedl	*Gnathostomula mediocristata*	Riedl
Gnathostomula armata	Riedl	*Gnathostomula mediterranea*	Sterrer
Gnathostomula axi	Kirsteuer	*Gnathostomula microstyla*	Riedl
Gnathostomula brunidens	Riedl	*Gnathostomula murmanica*	Mamkaev
Gnathostomula jenneri	Riedl	*Gnathostomula nigrostoma*	Riedl
Gnathostomula karlingi	Riedl	*Gnathostomula paradoxa*	Ax
		Gnathostomula peregrina	Kirsteuer

I. Gnathostomulida and Scleroperalia

The trends of the "outer framework" which allows discussion of the position of the family Gnathostomulidae within the higher categories, can be sorted into three levels. These are the phenomena which are typical for the the phylum (or class) Gnathostomulida, for the order Bursovaginoidea, and the suborder Scleroperalia (compare for terminology Sterrer, 1971). Although the trends within phylum and suborder can be discussed together conveniently, the order contains different problems. This has to do with the relationship of the suborders, particularly of the families Gnathostomulidae and Austrognathiidae and will be discussed in the next chapter.

1. The Five-Alae System of the basal plate, since it is also found in Gnathostomulidae, endorses the applicability of this principle (Sterrer,
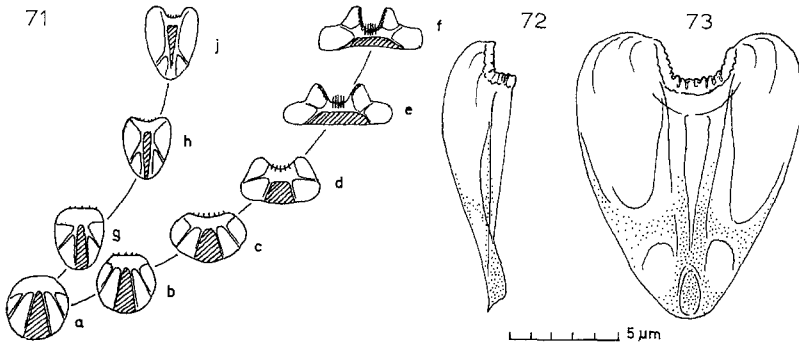
Figs. 71–73. Theory of the "five-partition" of basal plates as in two trends of Scleroperalia. Fig. 71 a–j. From conservative types (a, b) to ancestral forms of Gnathostomariida (c) and Onychognathiidae (d) to Gnathostomulidae (e) and *Gnathostomula* (f), and to hypothetical forms of Mesognathariidae (g, h) to *Lab-.idognathia* (j). Figs. 72–73. *Labidognathia longicollis*, basal plate. Fig. 72. Seen from right. Fig. 73. Seen from ventral

1971) in an even more general sense. If so, proof for the homology of the five parts is then desirable. The two paired portions may be the insertions for the suspension of the basal plate and could correspond to two pairs of muscles (as indicated by the anatomy of *Pterognathia swedmarki*: Sterrer, 1968, Figs. 86–89 rbp, dbp).

Within this hypothesis the trends observed find an easy explanation. It would be sufficient to assume that these two pairs of muscles exited mainly caudally in conservative types as dilators and retractors of the mouth cavity, but later moved more laterally and even frontolaterally for better control of the basal plate. The mechanical response of the field of insertion would be (Fig. 71 a–f): 1. shortening of the longitudinal axis, 2. extension of the transverse span, 3. expansion of the unpaired part, 4. movement of the paired parts frontally into the main transverse axis, 5. transforming the frontal margin from convex to concave, 6. relative increase and dominance of the caudomedial pair—the future alae laterales—, 7. reduction of the length of the pars centralis, 8. elongation and compression of the dentation, 9. changing the caudal margin from convex to straight (even to concave in "jenneri" type of *Gnathostomula*), 10. contraction of paired laterofrontal parts,—the future alae frontales—with the mouth cavity of the serrulae laterales in Gnathostomulidae, 11. contraction of medial part, fusion of alae frontales and formation of the serrula infundibula in *Gnathostomula*.

Some of these steps are evident in Filospermoidea toward *Pterognathia*, all of them in Bursovaginoidea toward Gnathostomulidae and

Gnathostomula. But there are most definite side lines. In Filospermoidea the organ becomes shortened and increases in span without moving the paired fields frontally and without compressing the pars centralis. Conophoralia move in a special direction from near the root of the Gnathostomulidae, as will be discussed later. But here three-partite basal plates seem to exist as well, at least in Onychognathiidae and Mesognathariidae.

From the latter *Labidognathia* basal plates were isolated and compared (Figs. 72, 73). It is possible that the five-partition is still found; the principal difference seems to be a lateral reduction of the unpaired field, a movement of decreased mediocaudal fields caudally, and a strong increase of the laterofrontal fields. The medial field is even folded, keel-like, and the medial parts of the former double "∧" patterns have fused caudally to form a " ⋀ " pattern (Fig. 71g–j). But this needs proof by intermediate forms and the anatomy of the suspending tissues.
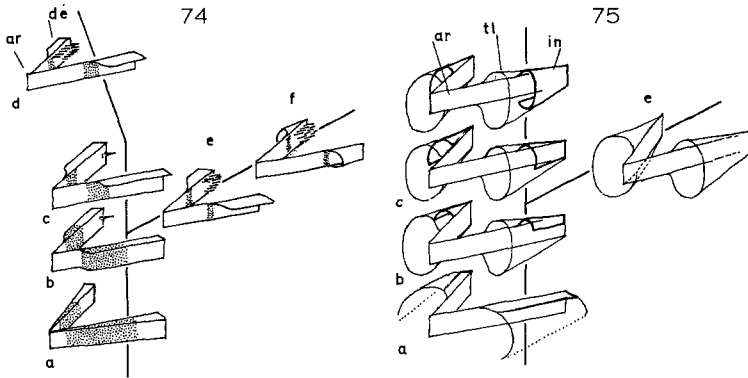
2. The Articularium-Dentarium Division of the jaws is clear in most of the genera of the Gnathostomulida. The principle involved obviously has to do with the difference in mechanical requirements, while the articularium has to permit lateral flexibility and to prevent twisting like the proximal end of forceps, the dentarium must keep more rigid against each stress.

In some Filospermoidea this is achieved by a reduction of the lateromedial diameter in the proximal portion of the jaw branches. In others a definite increase in thickness defines the boundary between the stiff and the flexible portions. In a third group the whole branch is thinned in the lateromedial direction and the stiffness of the distal portion is obtained through an "L" profile. This "L" is formed by a lateral extension of the dorsal margin and since it ends abruptly caudally, it defines the boundary of the flexible articularium very well.

However the flexible articularium and the tooth-bearing tip, the dentarium, are both very short, particularly in conservative filospermoids, and a long middle beam of rather slight flexibility connects the two (Fig. 74). Only in the most derived types of the genus *Pterognathia*, which is characterized by lamellarization, are both these portions longer (e.g. *Pterognathia sorex*, Sterrer, 1968). The middle part becomes small and less distinct, and a division into only articularium and dentarium is almost achieved.

So this specialization of the anterior and posterior parts of the handles of the forceps is correlated with general lamellarization—and functionally this is probably a necessity.

In Scleroperalia even the most conservative genera already show lamellarized jaws. Consequently the distinction between articularium and dentarium emerges much earlier, but the trend is similar. The more

Figs. 74 and 75. Theory of the jaw "lamellarization" in Gnathostomulida
Fig. 74 a–f. Division between articularium and dentarium in Gnathostomulida
(intermediate area dotted), lower filospermoids (a, b), *Haplognathia* (c), *Pterognathia*
(d), side branch towards bursovaginoids (e, f). Fig. 75 a–e. Formation of the in-
volucrum in Bursovaginoidea (tectum lateralis with thin line), lower Scleroperalia
(a, b), Onychognathiidae and Gnathostomulidae (c and following),
side branch towards Austrognathiidae (e)

the dentarium specializes, the more the boundary between dentarium
and articularium becomes distinct (compare Fig. 75).

This spezialization of the dentarium is correlated with the devel-
opment of the involucrum and connected with a concentration and
centralization of functions. The dentation, previously forming a basket
open caudally and extending further caudally on the ventral side, becomes
restricted and forms three defined arcs. The outer cuticularization becomes
differentiated into lamella externa and tectum lateralis, and the inser-
tions of the apophyses become restricted to the lamella interna and
externa.

Consequently the specialization in the articularium corresponds to a
restriction to the sole function of articulation. And the disappearance of
the intermediate field, or the increasing evidence of the boundary between
the articularium and dentarium has to do with a better sorting and
centralization of all the functions of these two portions.

Summarizing. Comparable trends are found in basal plates and jaws
of both orders of Gnathostomulida. But the similarity might be based
mainly on analogous processes.

The basal plate changes from a shield-like protection of the ventral
mouth cavity into a support for dentation, connected with comparable
changes in form and suspension. But the degree of differentiation in
Scleroperalia is not nearly reached in Filospermoidea.

The basic trend in jaw differentiation is lamellarization. Together
with specialization and centralization of functions it leads in a com-
parable way to the separation of articularium, dentarium, and sus-

pensorium. But Scleroperalia not only reach a much higher degree of differentiation than Filospermoidea, their most conservative genera are already more advanced than the more derived of the latter,.

A common root of the Filospermoidea and Bursovaginoidea is as clear as is the difference in their levels of organization.

II. Bursovaginoidea

The next pertinent problem centers around the levels of organization in the two suborders of bursovaginoids: Scleroperalia versus Conophoralia. The latter quite obviously originates from the former, but at a farily high level of organization.

1. The Formation of the Involucrum is a special feature of the highest families of the Bursovaginoidea: particularly Gnathostomulidae and Austrognathiidae. But these two families had to be placed in two different suborders.

This process of forming a pair of hollow cones must be seen in connection with the articularium-dentarium differentiation, in connection with the centralization of the dentation, and with the specialization of the suspensorium.

Though a lateral extension of the dorsal margin of the articularium-dentarium lamella is common in Gnathostomulida, the restriction of this feature (Fig. 75) to the dentarium is found only in the most derived families, and its bending towards the ventral is restricted to the highest Scleroperalia. One also can assume a very thin cuticularization of the entire dorsal and lateral surfaces of the jaw system as a general feature in Gnathostomulida, or at least in Bursovaginoidea. But though this tectum lateralis may escape observation in many cases, it is observed in many others. The lamella externa seems to be a thickening of the distal part of the tectum lateralis. So the matrix for its formation was prefabricated, however only its limitation and its boundary became distinct, which must be due to special mechanical reasons.

In Labidognathiidae and Onychognathiidae several experiments seem to be carried out to strengthen the tectum very close to the arcus of the dentarium. This includes also the strengthening of dorsolateral strips of the tectum, as in *Labidognathia* and others, presumably to serve as insertion for the muscle system.

In Gnathostomulidae the dentarium has, by means of three archs of comparable length, become a well-limited area; in addition the insertion of the apophysis is close to the former's caudal end. So the field which has to resist pull and push without becoming distorted is well-limited also. It seems logical to strengthen the former tectum lateralis to this precise limit—defined as the apertura caudalis. In addition the division of the insertion of the apophysis in two fibulae,

of which one, the fibula lateralis, is connected with the lamella externa, must contribute to the necessity for maintaining the strength of the involucrum.

In Austrognathiidae the development of the involucrum must have also started from the tectum. The difference, however, is that there seems to be no defined limitation between a strong lamella externa and a thin tectum lateralis. This is probably in connection with a difference in the insertion of the muscles. But this needs further proof.

In summarizing one can assume the potential of surface cuticularization for Gnathostomulida jaws in general. All jaws of Bursovaginoidea show some lamellarization of the tectum lateralis. Some of the lower Scleroperalia show regional strengthening of the tectum, but only in Gnathostomulidae does the thickened anterior part of the tectum reach lateroventrally down and fuse with the apophysis to form a closed involucrum. In Conophoralia (Austrognathiidae) a similar effect is achieved by strengthening a wide portion of the tectum. The root of this development seems to be close to the one of the Gnathostomulidae and functionally it is an involucrum: a long involucrum when compared with the short one of the former family.

2. A Process of Stretching the basal plate into a transverse position was found for both orders. In the bursovaginoids the most derived families in this respect are again Gnathostomulidae and Austrognathiidae. Common to both families is the transverse stretching of the dorsum alae, the caudal reduction of the tectum, the centralization of the dentation, and presumably a reduction of the ala frontalis and an enlargement of the ala lateralis in the more derived genera (*Gnathostomula, Austrognathia,* and *Austrognatharia*).

The remarkable difference, however, between this "winged" basal plates (as Sterrer, 1971, correctly describes it), can easily be seen by the final position of the dentation. In Gnathostomulidae the teeth bend forward and extend the frontal margin of the dorsum alae. In Austrognathiidae they stand upright or bend caudally. Furthermore the basis denticis in the first group is in an anterior, and in the second a posterior position.

This is related to the position of the central part of the dorsum alae itself. In Gnathostomulidae it is fairly frontal, since a tectum caudalis is, though reduced, always represented, but an infundibulum by fusion of the alae frontales is, if represented, small and covered by the dentation. In Austrognathiidae, however, the tectum caudalis may be different, and in addition a fairly broad band of the pars alaris is found frontal to the dorsum alae.

Since the trend to fuse the alae frontales is observed in Gnathostomulidae, this mediofrontal part in Austrognathiidae might very well

represent the homologous part. But this trend would have started much earlier in the latter group, or the more conservative Austrognathiidae would still be unknown to us. Yet, a common principle for the winged basal plates is very likely and so is the common derivation of the two families. The consequence is to derive the suborder Conophoralia from a fairly highly developed part of the main branch of the Scleroperalia: as for instance the mammals are derived from reptiles, or amphibians from fishes.

3. The situation is similar with regard to *the cauda system*. This system seems to substitute for the more conservative principle of extending the symphysis laterally, as with Filospermoidea and primitive Scleroperalia. However the cauda system is already found in Onychognathiidae, preceding Gnathostomulidae.

It is likely that the knowledge of the finer organization of the cauda in onychognathians and austrognathians will also clarify the position of the latter's origin. The diversity found in Gnathostomulidae speaks for it. But isolated jaws in both of these bordering families have not yet been investigated.

So a fairly recent derivation of the suborder Conophoralia from the Scleroperalia is supported by all the additional information collected here. The root seems to originate between the Onychognathiidae and the Gnathostomulidae.

III. Gnathostomulidae

Strong endorsement for the gnathostomulid system as we see it today is also found in the diversity patterns within the family Gnathostomulidae. As one expects from a system representing degrees of natural relationship, defined trends must be found at all systematic levels and they must link up with each other in a logical way. Within the family level three systems are of particular interest.

1. *The Infundibulum Formation* in all *Gnathostomula* species and its absence in *Semaeognathia* is, as seen, one of the most striking differences between the two genera. It also fits very well with the trend which changes the position, and probably the function, of the alae frontales in higher Scleroperalia.

Yet there is still the question of how the Austrognathiidae have to be interpreted in this respect. This was discussed above. The frontal lamella of austrognathians could very well correspond to the alae frontales of Gnathostomulidae. If so, a general trend would incorporate both of the most derived families of the Bursovaginoidea. But since one genus of these two families does not show an infundibulum—this is *Semaeognathia*—one would expect that the Austrognathiidae would have found an independent way of accomplishing the same goal of fusing the frontal wings.

The serrula formation could provide the necessary proof. If it remains a unique feature in Gnathostomulidae and does not appear in Austrognathiidae, the former hypothesis would gain in likelihood. If all austrognathians were to have serrulae, the conservative position of *Semaeognathia* within the Gnathostomulidae could be weakened in this interesting point.

2. *The "Fibularization"* of the apophysis system might be another feature of high specialization of Gnathostomulidae. Though fibulae can in general only be seen in isolated jaws and the families more closely related to Gnathostomulidae, such as Onychognathiidae and Austrognathiidae, have not been investigated in this respect, one can assume that there will be remarkable differences.

The fibulae mediales and laterales could be expected in other apophyses, but the fibula radialis is a most peculiar structure, which, as described above, must be involved in strengthening the thin hollow cone of the involucrum during longitudinal stress. This point may merit some elaboration.

Due to its position in the conservative *Semaeognathia* and in the more conservative species of *Gnathostomula*, namely in *G. microstyla*, the fibula radialis seems to have originated together with the rest of the apophysis system in a most ventral position within the cone. Probably it emerged together with the formation of the fenestra ventralis, to provide the strength which would otherwise have been lost by allowing only a window built. Later however, by a dorsal migration of its medial insertion, it became one of the six edges in the formation of an almost equilateral three-sided pyramid, one of the strongest spatial structures known.

The three edges leading to the tip of the pyramid (Fig. 76) are the arcus dorsalis, the arcus ventralis, and the fibula lateralis together with the ventral margin of the lamella externa. The three edges of the base of the pyramid (corresponding to the apertura caudalis) vary due to the position of the fibula radialis. The more conservative condition would be fibula radialis versus lamella interna versus lamella externa. The more advanced situation would fully release the lamella externa from taking tension: fibula radialis versus lamella interna versus the caudal frame of the fenestra ventralis.

3. *Twist of the Fibula radialis.* As already mentioned, the insertion of this fibula changes while the others generally stay the same. It is primarily the medial insertion (Fig. 77) which moves dorsally, from near the caudal end of the arcus ventralis to the arcus dorsalis; from *Semaeognathia* and *G. microstyla* to *G. brunidens* repectively. In its dorsoventral position, as it might be recalled, the fibula seems to be replaced by a ligament; see *G. brunidens* and *G. jenneri*. The following functional consequences can now be summarized.
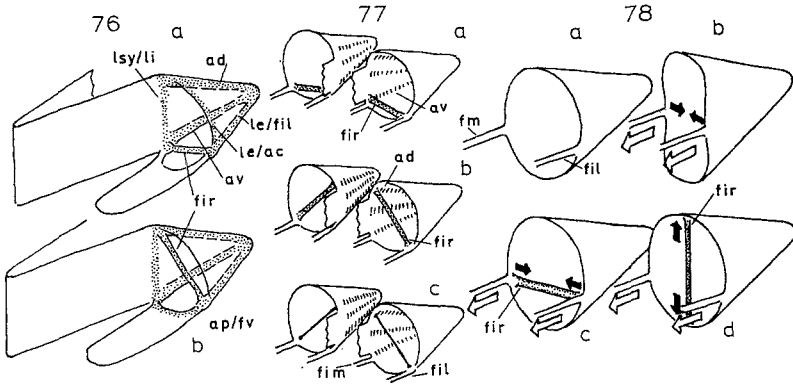
Figs. 76–78. Theory of "fibularization" in Gnathostomulidae. Fig. 76a and b. The six props (dotted) of the involucrum, conservative type (a), the derived type (b), note substitution of le/ac by fir and of fir by ap/fv. Fig. 77a–c. Position of fibula radialis, *Semaeognathia* and *G. microstyla* (a), *G. brunidens* (b), *G. jenneri* (c). Fig. 78a–d. Tensions within the involucrum, muscle tension in theoretical case without fibula radialis (a to b), pressure tension in conservative construction (c), pulling tension in derived types (d)

The involucrum forms a hollow and thin-walled cone (Fig. 78). Muscle tension from caudolateral is applied against its caudal margin by means of the apophysis and in both a medial and lateral position (fibulae lateralis et medialis). Against this tension the tip of this cone is kept in position by the articularium-lamella interna axis. Under such conditions the relatively flexible walls of the cone would bend inwards. To prevent this bending, which may affect the tissues in the cone, support has to be provided. The most logical position is a prop extending from the insertion of the fibula medialis to the insertion of the fibula lateralis. This is evidenced in *Semaeognathia* and *G. microstyla*.

The same function is retained if the prop rotates 90° about the longitudinal axis of the cone. The only difference is that pulling tension replaces the previous pressure tension. But a solid connection fills both functions. This seems to be the case in *G. brunidens*.

However, as soon as the function of withstanding pressure-tension is changed to that of withstanding pulling-tension, a prop can be replaced by a sinew, much as the wooden spoke of a cart can be replaced by the wire spoke in a bicycle. This seems to be represented by *G. jenneri*.

4. *The Cauda Specialization.* The principle difference in the cauda between the genera *Semaeognathia* and *Gnathostomula* is found in the dorsoventral length of the symphysis where it originates.

In *Semaeognathia* the symphysis was described as short, while all the investigated species of *Gnathostomula* show a fairly broad symphysis.
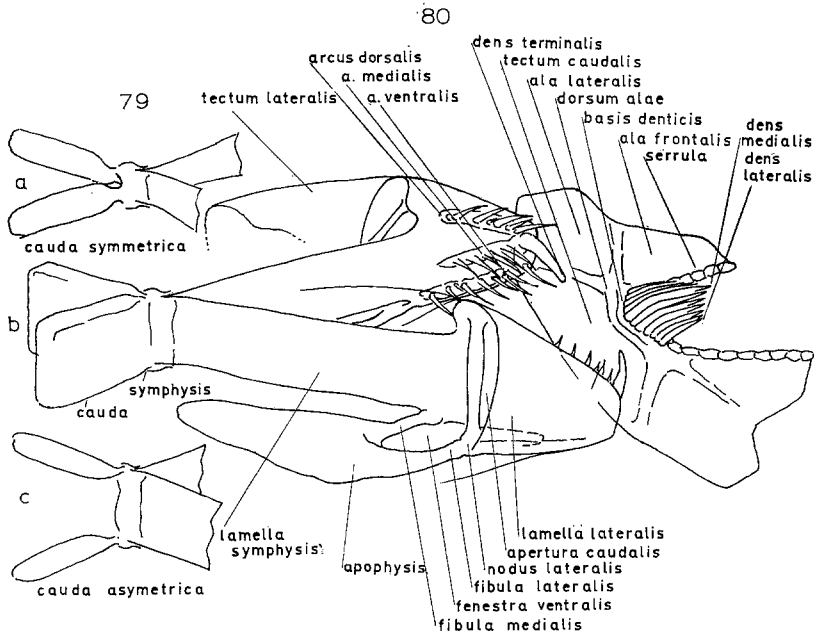
Figs. 79 and 80. General organization within Gnathostomulidae. Fig. 79 a–c. Types of cauda: *Semaeognathia* (a), *G. microstyla* (b), *G. brunidens* and *G. jenneri* (c). Fig. 80. Jaws and basal plate of *Gnathostomula*, in natural position, seen from right and somewhat from caudo-dorsal

Neither of these opposite characters can be recognized as the more conservative status with any certainty. On the contrary, a medium breadth might represent the more primitive patterns; and both of these fairly highly derived genera could follow different trends in this respect.

The consequence of this seemingly small difference, however, is that, in contrast to the narrow field where the cuticularized caudae can originate in *Semaeognathia* (Fig. 79), a wider potential variety is possible in *Gnathostomula*.

In the more conservative *G. microstyla* the cuticularized caudae were found as high as the symphysis. This is a striking difference, yet both caudae systems are still symmetrical.

However in *G. brunidens* and *G. jenneri* the cuticularized caudae are slender again with a small field of origin. One originates at the dorsal, the other at the ventral end of the symphysis. Since, in addition, it is very likely that these two caudae are homologous to those of *G. microstyla* and *Semaeognathia,* one must be the left and the other the right one. And if this is so, the pattern of a "cauda symmetrica" has changed into a "cauda asymmetrica".

More material is required to define whether the dorsal portion—the cauda dorsalis—represents the cauda dexter and the cauda ventralis the cauda sinister or the other way around. And this is even more so in order to decide whether all derived species of the genus *Gnathostomula* are following one trend, say the "cauda dorsalis sinister" direction, or whether two opposite trends are realized. Under these circumstances a functional understaining of the structures within the cauda system would be even more desirable.

IV. Gnathostomula

The degrees of relationship among the 14 species of the genus *Gnathostomula* described today have been investigated recently (Riedl, 1971). Based mainly on patterns of bursa, bursa cycles, and penis apparatus, four groups of species were defined: I *jenneri* type, II *paradoxa* type, III *mediterranea* type, and IV the *microstyla* type.

It is of interest to see that these subdivisions are fully endorsed by the additional characters found in isolated jaws and basal plates.

1. The Cauda Typology. In the *jenneri* type the "cauda dorsoventralis" i.e. the "cauda asymmetrica" has been found to be represented not only in *G. jenneri* but also in *G. brunidens*. Indications are given that *G. nigro-stoma* also shows this cauda type.

In the *paradoxa* type no isolated jaws were investigated, but a "lateral tube cauda" is clearly reconstructible in *G. armata* and pro-bably also in *G. mediocristata* and in *G. paradoxa*. In the latter species the cauda is not documented in line drawings, but the two circles, though not specified, as in the center of the section of fig. 20 of AX (1956), are probably meant to represent these special caudae. Due to size and position they seem to correspond with cross-sections through the cuticularized tube-shaped caudae.

The *mediterranea*-type also seems to have this "lateral tube caudae". So it is clearly derived from *G. arabica* and *G. karlingi*, but it is not yet investigated in *G. axi* and *G. mediterrenea* which belong to the same type because of characters in the genital system (full literature in Riedl, 1971, and in Sterrer, 1971).

With *G. microstyla*, which forms the fourth type by itself, yet another cauda type is represented. The two caudae, as described above, could be labelled "lateral cushion caudae", being symmetrical but having a high area of origin along the symphysis.

2. Fibula radialis Typology. The fibulae are, as said, only visible in isolated jaws, which are investigated only in species belonging to two of the types mentioned here. But again the "vertical fibula radialis" is similarly represented in type I, i.e. in *G. jenneri* and in *G. brunidens*, while in type IV—*G. microstyla*—a "horizontal fibula radialis" was found.

List of Abbreviations

a	alae	fv	fenestra ventralis
ac	apertura caudalis	fvc	fenestra ventrocaudalis
acl	´apertura caudolateralis	fvf	fenestra ventrofrontalis
acm	apertura caudomedialis	i	incisura
ad	arcus dorsalis	id	incisura dorsalis
af	ala frontalis	in	involucrum
al	ala lateralis	iv	incisura ventralis
am	arcus medialis	n	nodi
ap	apophysis	nl	nodus lateralis
ar	articularium	nm	nodus medialis
av	arcus ventralis	l	lamellae
bd	basis denticis	li	lamella interna
c	cauda	le	lamella externa
ad	cauda dorsalis	lsy	lamella symphysis
cv	cauda ventralis	pa	pars alaris
(d)	(dexter)	pc	pars centralis
da	dorsum alae	s	serrula
de	dentarium	(s)	(sinister)
dl	dens lateralis	si	serrula infundibula
dm	dens medialis	sl	serrula lateralis
dt	dens terminalis	su	suspensorium
fi	fibulae	sy	symphysis
fim	fibula medialis	tc	tectum caudalis
fil	fibula lateralis	tl	tectum lateralis
fir	fibula radialis		

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