# THE MORPHOLOGY OF GLYPTHOLASPIS CONFUSA (FOÀ, 1900) (ACARIDA, GAMASINA) 

by

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Morphology has developed rather differently in each of the large groups of mites. Our knowledge on the subject is nowadays at unequal levels, so that terminology, method, and way of interpretation are difficult to compare. This has resulted at present in a more or less unsurveyable condition of acarology as a whole.
It is evident that a comparative acarid morphology is only possible when representatives of each group are studied, described, and figured according to the same method. In order to build up a survey of the mites based on these principles, I recently started a study of the Anactinotrichida according to methods used in oribatology. In 196i I published an extensive description of a species of Holothyrus, with notes on characters generally neglected in this group. Although a small note on ticks appeared afterwards (Van der Hammen, 1964), a continuation of my study in this suborder is postponed till after the study of parasitic Gamasina.
The present paper is the first of a series of studies in Gamasine morphology. I have chosen a large free-living species as starting point, because in large mites sectioning in general, and especially the study of the gnathosoma is considerably facilitated; in free-living mites evolution is, moreover, not influenced by parasitism.
On my request Dr. G. W. Krantz (Oregon State University, Corvallis, Oregon. U.S.A.) kindly sent me identified material of Glyptholaspis confusa (Foà), a large Macrochelid mite excellently suited for my purpose. I wish to express here my thanks to Dr. Krantz for his highly valued contribution.
The study resulted in a number of unexpected discoveries. One of the most interesting of these is the observation of the latero-coxal setae $e$ and $e I$, hitherto unknown in Anactinotrichid mites. Much attention is paid to the gnathosoma; the position of many parts, of which the connection was unknown, is definitely determined in the course of the present investigation. The interpretation is rather different from the ideas generally accepted in Anactinotrichid morphology. No less than eight large figures appeared to be necessary to represent the complete topography of the gnathosoma.

A series of numbered remarks is added after the description; these explain techniques and morphological views applied in the course of the present study. An alphabetic explanatory list of the terms which are introduced here in Gamasine morphology is given at the end of the paper; a list of abbreviations facilitates especially the use of the figures. Description, remarks, and definitions together must be regarded as an attempt to renew Anactinotrichid morphology on a comparable base.

Glyptholaspis confusa (Foà, 1900)
Locality. - Corvallis, Oregon, U.S.A., September 25, 1963, in horse manure; leg. Dr. G. W. Krantz.

Material. - 67 females and 4 males; only the females are described here.
Description. - The following description is principally a supplementary one. Characters which have been described in full detail by other authors (such as the sculpture of the shields) are not especially emphasized. I refer to the description published by Evans \& Browning (1956: 36) sub Macrocheles plumiventris (only the description of the female relates to the present species), and especially to the paper by Filipponi \& Pegazzano (1960: 154). Special attention is paid by me to those characters which until now generally have been neglected.

Measurements. - According to my material the length of the female idiosoma is $\mathrm{I} . \mathrm{I} 75-\mathrm{I} .485 \mathrm{~mm}$, the breadth $0.740-\mathrm{r} .050 \mathrm{~mm}$. Detailed data are published by Filipponi \& Pegazzono (1960: 159); the material of these authors shows, however, less variety than my specimens.

Habitus and colour. - The species is a large Gamasine mite. The greatest width of the idiosoma is in the posterior part, at about $2 / 3$ of its total length. The dorsal shield is entire. The large shields of the idiosoma have a conspicuous reticulate sculpture. The colour of the sclerotized parts is brown; the soft skin is whitish. The greater part of the setae are more less clavate.
The legs are relatively long. Leg I and II are directed to the front, leg III laterally, and leg IV posteriorly. Leg IV is the longest. Leg I, inserted in the soft skin, is more slender than the other legs; it bears no ambulacrum.

Cerotegument. -- When studied in a dry condition, on a carbon block, the cerotegument appears to be granular and whitish. It occurs in irregular masses. Concentrations are found on the cheliceral tectum, the ventral surface, and between the coxae. Much less, if anything, is found on the dorsal shield and on the legs.

Cuticle. - The idiosoma of the adult female presents the following scle-
rotized shields (cf. fig. $\mathrm{I}, 2,3 \mathrm{~A}$ ) : dorsal, sternal, metasternals, genital, paragenitals (the so-called accessory sclerites), ventri-anal, peritrematals (distally fused with the dorsal shield), holopodals (a fusion of exo- and endopodal shields), and metapodals. In lateral view (fig. 3A) two other small shields


Fig. I. Glyptholaspis confusa (Foà), dorsal view of female; $\times 90$.


Fig. 2. Glyptholaspis confusa (Foà), ventral view of female; $\times 90$.
are visible: posteriorly of the peritrematal shields, and posteriorly of the metapodal shield. As noted in remark 5 , the borders of some of the large shields are covered by soft, wrinkled epiostracum. Several of the smaller shields are completely covered by this soft skin; they are named here covered shields. The two pairs of laterals, the metasternals, and the metapodals are covered shields.

The sculpture of the shields is described and figured (especially by photographs) by various authors, e.g. by Filipponi \& Pegazzano (1960). Details of the sculpture of the dorsal shield are represented here in fig. 4A, D. The reticulations and the smaller elements of the sculpture are positive, i.e. the mesh-work and the granules are extending.

In fig. 4 C I have represented a transverse section through a part of the dorsal shield. The figure shows that the shield continues laterally under a wrinkled epiostracum. It appears that the uncovered sclerotized part consists of two layers; the upper layer does not continue into the covered part.

Pores and lyrifissures. - The cuticle of idiosoma and appendages presents a rather great number of pores and fissures. Typical lyrifissures are present on the appendages, e.g. as part of basitarsal and basifemoral ring; they are dealt with below, in the descriptions of chelicera, palp, and legs. A section through a basitarsal ring, showing three lyrifissures and a pore is given in fig. 4 B in order to facilitate a comparison.

The dorsal shield shows an anterior fissure near seta $d_{2}$ (fig. 4 E ). A section through this region (fig. 4 F ) reveals that the fissure probably is a lyrifissure. The sternal shield presents two pairs of real lyrifissures. The dorsal shield, and the lateral and ventral parts of the idiosoma further show a rather great number of pores. Transverse sections through two pores of the idiosoma are represented in fig. $4 \mathrm{G}, \mathrm{H}$. They have a remarkable structure. A tube runs from the epiostracum (often from a small depression in the surface) through the upper layer of the ectostracum, and debouches into a more or less bell-shaped court, a space in the lower layer of the ectostracum. For this reason the pores are named here court-pores.

Hirschmann (1960: 14) distinguishes "Areaporen" and "Anareaporen"; "Areaporen" are subdivided into "Spaltporen" and "Ovalporen". He supposes that "Spaltporen" originate from "Ovalporen". His description of the various pores is not very clear, especially because the types are not explained by figures. He creates the impression that the court of a pore is the superficial part of it. "Spaltporen" are lyrifissures; "Ovalporen" the court-pores represented here in fig. 4G, H; "Anareaporen" are apparently pores without a distinctly widened court. I distinguish lyrifissures (i) and court-pores ( $p$ ); in doubtful or transitional cases the terms fissure and pore are appropriate.

In comparing various groups of Gamasine mites it appears that courtpores can take the place of lyrifissures, or that a fissure is not always a typical lyrifissure. It appears logical to conclude that court-pores originate from lyrifissures (and not lyrifissures from court-pores as Hirschmann supposes) because the presence of lyrifissures is a general character of all groups
of Arachnida. It is interesting to remember that lyrisfissures in mites (and also in other groups of Arachnida) originally have a metameric arrangement.

Idiosoma. - The idiosoma is rather high and oval in outline; the greatest width is near coxa IV. It is represented in various aspects in fig. $1,2,3$. The dorsal shield occupies the greater part of the dorsal surface. In dorsal


Fig. 3. Glyptholaspis confusa (Foà), female; A, lateral view (anterior part with gnathosoma and leg I omitted; legs II-IV removed) ; B-D, posterior part of right peritrematal plate; $B$, viewed from below; $C$, viewed from inside; $D$, lateral view; $\mathrm{A}, \times 90 ; \mathrm{B}-\mathrm{D}, \times 295$.
view the peritrematal shield appears to extend distinctly near the stigma. In lateral and ventral view it appears that important lateral, postero-ventral and posterior regions are not sclerotized. A part of the idiosoma, in front of the dorsal shield, is also not sclerotized. The coxa of leg I is inserted in the soft skin of this area, outside the holopodal shield.

Dorsal shield. - There are 28 pairs and I (according to literature sometimes 2) unpaired setae on the dorsal shield: they are indicated here as $d_{1-8}+d_{\mathrm{x}}, m_{1-4,}, l_{1-6}$, and $m g_{1-10}$ (cf. remark 6). The dorsal shield presents one pair of lyrifissures ( $i_{1}$ ) and 21 pairs of court-pores ( $p_{1-21}$ ). Lyrifissure $i_{1}$ is situated laterally of $d_{2}$. The disposition of setae and pores is represented in fig. I .

The setae belong to three types: they are (i) simple, pointed and smooth, (2) simple, pointed, and slightly pilose, and (3) plumose. The exact shape of the plumose setae is represented in fig. 4 A . Setae $m_{3}, d_{6}, d_{\mathrm{x}}$, and $d_{8}$ are simple; $m_{4}$ and $d_{7}$ slightly pilose; and the remaining setae of the dorsal shield plumose. The position of the dorsal setae can best be studied in lateral view (fig. 3A).
The external lateral border of the dorsal shield is serrate. Under the wrinkled epiostracum the shield has an internal continuation which can be seen in lateral view as a brown border (cf. fig. 3 A ). A transverse section of the dorsal shield is represented in fig. 4 C . The sculpture of the shield is reticulate crenulate; granulations are present inside the mesh-work (fig. $4 \mathrm{~A}, \mathrm{D})$.

Ventral surface (fig. 2). - The ventral shields are partly grown together. Exo- and endopodal shields are fused to a holopodal shield. The holopodal shield is partly fused with the sternal shield, viz., in front of acetabulum II $(x)$ and in front of acetabulum III $(y)$. There is a pair of paragenital shields (generally named accessory sclerites).

The remaining shields of the ventral surface are not fused, viz., the metasternals, genital, metapodals, and ventri-anal.
The sternal shield has two pairs of lyrifissures ( $i s_{1}, i s_{2}$ ), and three pairs of setae $\left(s_{1-3}\right)$. The metasternal shield is covered by a wrinkled epiostracum; it has one pore ( $p s_{1}$ ) and one seta ( $m s_{1}$ ). The genital shield has one pair of setae ( $g_{1}$ ). The metapodal shield is covered by weak epiostracum; it presents one seta ( $m p_{1}$ ).
The ventri-anal shield presents four pairs of setae and one impaired; three pairs are regarded here as ventrals ( $\nu_{1-3}$ ), the remaining as adanals


Fig. 4. Glyptholaspis confusa (Foà), female; A, lateral part of dorsal shield; B, transverse section through basitarsal ring of left leg III, showing three lyrifissures and a pore; C , transverse section through dorsal shield, showing the lateral continuation of the shield; $D$, central part of dorsal shield; $E$, lyrifissure $i_{1}$ and place of insertion of seta $d_{2}$ of the dorsal shield; F , transverse section through region of fig. E ; G , transverse section through dorsal shield, just beside one of the large central pores; H , sagittal section through a posterior pore $\left(p_{19}\right)$ of the dorsal shield; $\mathrm{A}, \mathrm{D}, \times 370$; $\mathrm{B}, \mathrm{C}, \mathrm{E}-\mathrm{H}, \times 710$.
$\left(a d_{1}, a d_{\mathrm{x}}\right)$. There is one pair of pores $\left(p v_{1}\right)$ on the ventri-anal shield, near the posterior border.
The anal orifice is situated on an extending part of the ventri-anal shield (cf. fig. 3A). The punctate parts of the shield (on the declivity behind the anal orifice, and at the posterior border of the shield) are probably caused by cerotegument (possibly together with a porosity of the cuticle).

The soft skin between legs I bears the so-called tritosternum; it is bifurcate and pilose. It is evident that this structure is no sternum at all, because a sternum is a distinct plate (a real sternal plate belonging to segment III is present in the Spinturnicidae). In Opilioacarida the "tritosternum" is a paired structure ; in Gamasina it is usually still forked. It must be regarded as originating from a pair of lobes or excrescences. For this reason I reject the name tritosternum and introduce here the term furca, referring to its bifurcate shape or origin.

Lateral aspect. - In lateral view (fig. 3A) the peritrematal shield, some small lateral shields, the holopodal shield, and the larger part of the soft skin can be studied.
The peritrematal shield is fused in its anterior part with the dorsal shield. It contains the peritreme, four pores, and the stigma. The peritreme (fig. 3 D ) is an open groove (not a tube as is still suggested in literature, e.g. by Hughes, 1959: 193, 195). Grandjean (1944) arranges the peritreme under his taenidia. In the diagnoses of the Macrochelidae the peritreme is characterized as "looped posteriorly and joining the stigma posteriorly". In fact the peritreme ends at the posterior border of the stigma; at this point a slit in the bottom of the groove (which had not been noticed until now) debouches into the stigma. Because the bottom of the peritreme as well as the entrance of the stigma are both punctate, the impression is created that the peritreme is looping.
The peritrematal shield is distinctly extending laterally at the place of the stigma. As mentioned above there are four pores $\left(p p_{1-4}\right)$. Pore $p p_{3}$ has a relatively very large court with irregular outline; $p p_{2}$ is at the border of the peritreme; $p p_{4}$ has a narrow canal. Pores $p p_{2}$ and $p p_{3}$ are represented in various positions in fig. 3B-D. When the peritrematal shield is separated from the idiosoma, the tracheal trunk can easily be studied; it subdivides into four branches, the posterior of which immediately afterwards subdivides again into two branches. The surface of the tracheal trunk and the bases of the primary subdivisions are brown and punctate (fig. $3 \mathrm{~B}, \mathrm{C}$ ).
As mentioned above, exo- and endopodal shields are fused to a holopodal shield. This can easily be observed after separation of the legs. In fig. 3A all coxae have been removed.

Posteriorly of the peritrematal shield a small covered lateral shield with one court-pore is found. Posteriorly of the holopodal shield two other small, covered lateral shields are found; one of these presents a relatively large court-pore.
The soft tegument, especially visible in lateral aspect, bears many setae, mostly more or less plumose or pilose. There are two orifices ( $g l_{1}, g l_{2}$ ) laterally of the ventri-anal shield; they probably represent orifices of glands.

Gnathosoma (fig. 5-12). - The gnathosoma of Glyptholaspis confusa is tube-shaped; a transverse section is nearly circular. In order to understand the complicated structure it is necessary to study the gnathosoma in dorsal, ventral, and lateral view, as well as anteriorly and posteriorly. After these observations it will be necessary to remove several parts in order to study details. Finally transverse as well as longitudinal sections must be included in the investigation.
A dorsal view of the gnathosoma (fig. 5) presents the following characters. The cheliceral tectum (TE), which is usually characterized as "tripartite" or "trifid", has an irregularly dentate anterior border which, in the median part, is more or less asymmetrically produced into a tripartite extension, of which the central part is bifurcate at the end. A ligament is attached to one of the terminal branches. Very small hairs can be observed in the anterior median part. Under the surface, a more or less striate structure can be observed. The cheliceral tectum covers the chelicerae ( CH ) when these are retracted.

At the lateral border of the infracapitulum, near the place of attachment of the cheliceral tectum, and not far from the acetabulum of the palp, a remarkable seta is present. It is whitish and pointed, with a broadened base. There can be no doubt that this is the latero-coxal seta (e), until now only known from Actinotrichida.

At various levels under the tectum and the chelicerae a number of structures can be observed which have received a confusing terminology. In the anterior part the corniculi ( CO ) (sometimes named external malae) are long and conspicuous. Between the corniculi a long, tapering labrum ( $L S$ ) is easily visible (this structure is often named epipharynx). At a lower level, partly under the labrum, a pair of pilose processes can be seen; these are named here laciniae ( $L C$ ) (in literature they are also indicated as "internal malae", "hypopharyngeal" or "hypostomal processes", etc.). Laterally of the corniculi two pairs of structures are visible that in literature are cited as "salivary styli" and "duplicationes stylorum". A thorough investigation reveals that the "salivary styli" are the free parts of efferent ducts of glands which


Fig. 5. Glyptholaspis confusa (Foà), female; dorsal view of gnathosoma; $\times 440$.
are situated in the idiosoma. The free parts of these chitinous ducts are enveloped in an epiostracal layer. Because the name "stylus" is not very appropriate, and the characterization as "salivary" uncertain, I prefer to rename the structure; I introduce here the term siphunculus (SI). According to Vitzthum (1940) the "duplicationes stylorum" are the result of a basal bifurcation of the "salivary styli". In fact they can be characterized as protective dents that arise just above and slightly laterally of the base of the siphunculi, apparently from the epiostracum. Because of their position, I introduce here the name patrocinium $(P A)$ for these structures.

At the same level as the patrocinia, but medially of these, a pair of flaps beset with hairs is partly visible. Apparently these are the structures named paralabra interna by Vitzthum (1940), paralabra externa by Hughes (1949), and hypopharyngeal styli by Gorirossi (1955). I introduce here the name labellum ( $L A$ ), which is more appropriate as will appear from the study of sections. Anteriorly of the labellum a thin pointed structure appears from below; it is named here fimbrilla (FI); I do not know if this is the structure named hypopharyngeal process by Gorirossi \& Wharton (1953). The exact topography of all these structures will become gradually clear from a study of the various aspects of the gnathosoma.

A ventral view of the gnathosoma (fig. 6) presents the following characters. The infracapitulum belongs to the anarthry type. Mentum ( $H$ ) (also named basis capituli or gnathosomal base) and genae ( $G$ ) (in literature generally recorded as hypostome or rostrum) do not present a labio-genal articulation, so that they are not separated. The usual four pairs of ventral infracapitular setae are present. It appears that these setae have exactly the same disposition as in Oribatid mites, for which reason the same notation is applied here: $h, m_{1}, m_{2}$, and $a$. These setae are named respectively: capitular seta (c.s.), external and internal posterior rostrals (ext. p.r., int. p.r.), and rostral seta (r.) by Evans (1957), and $C_{4}, C_{3}, C_{2}$, and $C_{1}$ by Hirschmann (1959).

The median part of the infracapitulum presents a rather large subcapitular groove (named protosternum + deutosternum by Gorirossi \& Wharton, 1953, capitular groove by Evans, 1957, and "Hypostom" by Hirschmann, 1959). The subcapitular groove extends from just behind the infracapitular setae $h$ to the anterior border of the genae. In literature the groove is regarded as a less sclerotized part separating the enlarged coxae of the palps. I do not accept this speculation which lacks every solid base; I might point to the fact that the groove in Holothyrus is only faintly developed. The subcapitular groove is in fact a highly specialized structure which certainly has some relation to the structure here named furca (in literature mentioned as


Fig. 6. Glyptholaspis confusa (Foà), female; ventral view of gnathosoma; $\times 440$.
tritosternum). The lack of a specialized groove in Holothyrus (the groove is present, but especially indistinct in the posterior part) is certainly connected with the lack of a furca (tritosternum). The subcapitular groove in Glyptholaspis presents 6 transverse ridges (one of these running obliquely) beset with small teeth, and a pair of smaller curved ridges between setae $a$.
The anterior part of the subcapitular groove presents a longitudinal suture which runs anteriorly to the point where the laciniae come together. By the fusion of the ventral parts of the lateral lips this point has moved relatively far to the front; for this reason it is indicated here as the anterior ventral commissure of the mouth ( $J i_{2}$ ). Although the groove and the genae are not at the same level, the structure of the mouth excludes a mobility of the ventral part.
Anteriorly the bottom of the subcapitular groove passes into a pair of long pilose processes which are generally curved downwards in the anterior part. These structures are named here laciniae (Vitzthum: laciniae; Evans: internal malae; Gorirossi: ? hypopharyngeal or hypostomal processes). Between and in front of the laciniae the labrum is easily visible.

The corniculi (specialized setae) are inserted on the genae. Their position is nearly terminal; they are long and pointed, and directed to the front. The genae present no alveolus corresponding with the root of the corniculi. It is, however, probable that these are capable of slight movements.

In ventral view the siphunculi are conspicuous. The chitinous efferent ducts ( $d g$ ) can easily be traced inside and posteriorly of the infracapitulum. The posterior part of each duct is a spiral tube; in fig. 6 it is represented at one side (folded back for the sake of room). The tips of the fimbrillae extend laterally of the corniculi. The latero-coxal seta $e$ is also conspicuous in ventral view.

In lateral view (fig. 7) the position of the chelicerae under the cheliceral tectum is easily visible. The figure moreover clearly shows the coxal region of the palp with the palpal socket and the latero-coxal seta $e$. It appears that the corniculi have a dorsal-terminal position. Siphunculus, labrum, labellum, fimbrilla, and lacinia (bent downwards in the distal part) are also partly represented in fig. 7 .

In an open slide the gnathosoma can also be studied anteriorly and posteriorly, provided that the distance between coverslip and bottom of the cavity slide is sufficiently large. In fig. 8 the gnathosoma is viewed from in front. It now appears that one of the terminal lobes of the cheliceral tectum is attached by means of a solid, asymmetrical ligament (li) to a ridge ( $d r$ ) of the dorsal surface of the infracapitulum. When the cheliceral tectum is removed, a part of the ligament is left; it is not impossible that this has been

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Fig. 8. Glyptholaspis confusa (Foà), female; gnathosoma, frontal view; $\times 440$.
regarded as a labrum by several authors. Fig. 8 clearly shows all parts surrounding the mouth. The labrum has a broad base and a narrow tip. It is flanked by the pilose labelli. The fimbrillae are visible in front of the labelli. The position of patrocinium and siphunculus laterally of the labelli is clear.

Fig. 9B represents a posterior view of the gnathosoma; it shows the cheliceral sheaths, three posterior bars, the left efferent duct entering a vault, and the pharynx.

For a clear understanding of the exact position of several structures it is


Fig. 9. Glyptholaspis confusa (Foà), gnathosoma of female; A, anterior part, obliquely from above (cheliceral tectum removed) ; B, posterior view (chelicerae protruded so that only the cheliceral sheaths are visible) ; C, lateral view of anterior part (chelicerae removed, part of palpal trochanter cut off) ; A-C, $\times 440$.
necessary to gradually dissect the gnathosoma. In fig. 9C the greater part of the palp is removed; it shows the connection of cheliceral tectum and dorsal infracapitular ridge by a ligament.
After removal of cheliceral tectum and chelicerae, several other details become visible. Fig. 9A shows that labellum and patrocinium have a basal connection, and that the siphunculus passes under the patrocinium.

Fig. in B represents a dorsal view of the posterior part of the infracapitulum. It shows the dorsal shelf which I recently named cervix (Van der Hammen, 1961). A median dorsal ridge (separating two grooves in which the chelicerae can move) is also easily visible. The cervix does not reach as far behind as the base of the gnathosomal tube, but posteriorly it continues into three bars which are distinctly extending. The median bar is a prolongation of the dorsal ridge. The lateral bars support the chelicerae when these are retracted. The bars represent the capitular apodeme ( $a p . c$ ).

I prefer to use the name cervix for the dorsal part of the infracapitulum; it indicates that it is opposite to the mentum. Cervix and mentum are two faces of the infracapitulum which represents segment II. The name subcheliceral shelf could erroneously create the impression that this part belongs to the cheliceral frame, i.e. to segment I.

Further details of the gnathosoma must be learned from sections. In fig. Io a number of transverse sections are represented. It appears that the labrum is situated in a gutter ( $L G$ ) (fig. roB) and that the walls of the gutter are partly beset with teeth (fig. 10A). The labelli are a dorsal continuation of the inner lateral walls of the gutter; they are overhanging in the anterior part. The laciniae are a continuation of the ventral wall of the gutter.

A section in front of the mouth (fig. IoD) shows that the pharynx is heart-shaped. It is contained in a chamber which I name the pharyngeal chamber $(P C)$. Laterally of the pharyngeal chamber, the infracapitulum presents at each side a coxal vault ( $C V$ ). It now appears that the siphunculus enters the coxal vault dorso-medially, close to the lateral wall of the pharyngeal chamber.

The dorsal wall of the pharynx continues as the ventral wall of the labrum or upper lip. The lateral walls of the pharynx continue as the lateral lips which are very complicated in Gamasine mites, and consist of several parts. Latero-ventrally, the lateral pharyngeal walls pass into the walls of the gutter (fig. IoC). As mentioned above, the dorsal part of the gutter passes into the labelli; these are posteriorly connected with the cervix. Gutter as well as labelli must be regarded as parts of the lateral lips. The gutter has received a confusing terminology; it is named hypopharynx (although it is situated in front of the pharynx) and paralabrum internum. I introduce here the


Fig. וo. Glyptholaspis confusa (Foà), female; transverse sections through gnathosoma; A, corniculi and lacinae cut off, labrum and chelicerae removed; B, section in front of infracapitular setae $a$; C, section in front of the mouth, viewed in distal direction (labrum and chelicerae removed); D , section in front of the mouth; viewed in proximal direction (chelicerae and cheliceral tectum removed); A-D, $\times 440$.


Fig. II. Glyptholaspis confusa (Foà), female; A, longitudinal section through anterior part of gnathosoma (labrum removed), showing labial gutter; $B$, dorsal view of posterior part of gnathosoma (cheliceral tectum removed); A, B, $\times 440$.
name labial gutter, which name clearly indicates it as part of the lateral lips.
The anterior part, cut off by a transverse section in front of the mouth, is represented in fig. IoC, where it is viewed from behind. The posterior part of the labial gutter is visible here, as well as its dorsal continuation into the basal smooth part of the labellum. The figure also shows its connection with the patrocinium and the epiostracal envelope of the siphunculus.

A definitive solution of the remaining problems must be achieved by means of a study of longitudinal sections. Fig. 12 represents a section that passes exactly through the plane of symmetry; the pharynx $(P H)$ is slightly moved in order to show the underlying structure. The figure shows the gnathosoma as a tube subdivided by the cervix into a cheliceral vault and an infracapitular vault. The infracapitular vault consists of a lateral coxal vault (in fig. 12 the chitinous efferent duct leaves the posterior outlet of the vault) and a central pharyngeal chamber. Posteriorly the gnathosomal tube is not subdivided; its wall has the shape of a ring that is a continuation of cheliceral tectum and ventral and lateral walls of the infracapitulum. I regard the ring as a posterior extension of the sclerotized walls of the gnathosoma, which protects its base, and consequently must be considered a capitular retrotectum. The capitular retrotectum certainly represents a secondary acquisition; it is not present in the case of Holothyrus.

Fig. 12 further shows the central ridge of the cervix, the anterior ligament, and the posterior bars. The most interesting detail is the anterior continuation of the pharynx. The dorsal wall of the pharynx passes into the ventral wall of the labrum. Ventrally and laterally of the labrum, the left half of the labial gutter is visible. It presents three rows of teeth. It appears that the anterior part of the labial gutter is grown together with the genae (as is usual with lateral lips); the ventral part extends anteriorly as the laciniae.

The commissures of the mouth are also indicated on fig. I2. One of the dorsal commissures ( $J s$ ) is behind the base of the labrum. It is difficult to determine the exact position of the unpaired ventral commissure ( $J i$ ). I have indicated a point ventrally of $J s$ as $J i$; it is the real corner of the mouth. The point where the labial gutter is grown together with the bottom of the subcapitular groove is indicated als $J_{1}$. The point where the gutter ventrally subdivides into the laciniae is indicated as $J i_{2}$.

In fig. irA a longitudinal section is represented from which the labrum is removed. From this section it is at last clear that the fimbrilla is the anterior dorsal process of the labial gutter. Fimbrillae as well as laciniae must also be regarded as parts of the lateral lips.

These details complete the description of the extremely complicated gna-
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thosoma. The exact position of all structures is clarified, and fig. 5-12 together represent a complete topography.

Chelicera. - The chelicerae are 3 -segmented. The homology of the segments is uncertain, except for the terminal one which represents the apotele. The dimensions of the basal segment can be derived from fig. 12. Fig. 13 represents the distal part of the right chelicera. The movable bit (or movable finger) is the apotele, the fixed bit (or fixed finger) is the terminal part of segment 2.

The various faces of a chelicera are easily recognizable. The antiaxial face (fig. I3A) presents a lateral lyrifissure $i \alpha$, a dorsal seta $d$, the small orifice of a gland ( $g c$ ) at the base of the fixed bit, and a specialized seta generally indicated as pilus dentilis; the last-mentioned term is too long, for which reason I introduce here the name cheliseta (cs). The antiaxial ventral seta $v^{\prime \prime}$ is the smaller one of the pair of plumose brush-like setae.

The paraxial face (fig. $13 B$ ) presents a dorsal lyrifissure id on the fixed bit. A part of seta $d$ is visible in this orientation; ventral seta $v^{\prime}$ is the larger one of the two brushes.

A dorsal view (fig. 13C) distinctly shows the dorsal seta $d$ and lyrifissure id. The pair of brushes is best visible in ventral view (fig. I3D, E). In dorsal as well as in ventral view, the ridges on the teeth are clearly visible by transparency.

The apotele of the chelicerae is movable by means of three muscles: a rather large median one $\left(t_{1}\right)$ attached to a dorsal condyle; a median one with ventral attachment $\left(t_{2}\right)$ and a lateral paraxial muscle $\left(t_{3}\right)$ attached to a lateral chitinous bar.

Palp. - The palp consists of six segments. The proximal segments are partly represented in fig. 5-7, the distal segments in fig. 14. Tarsus and tibia together have the shape of one segment. The apotele (fig. 14A, C) has a three-pronged seta with a paraxial ventral position. Genu and tibia present a rather large dorsal lyrifissure at the posterior border (fig. I4C). Tibia and tarsus have a large number of setae.

The tarsus presents a dorsal group of three hollow setae, and a more or less terminal group of five; these probably represent eupathidia (cf. fig. r4A-C: $\zeta$ ). The large antiaxial hollow seta $\omega$ probably represents a solenidion (fig. $\mathrm{I} 4 \mathrm{~B}, \mathrm{C}$ ). According to a preliminary observation the formula of the palp (from trochanter to apotele) is about $2-5-6-\mathrm{I} 3-\mathrm{I} 5-\mathrm{I}$.

Legs. - Leg I is inserted in the soft skin; legs II-IV are inserted in acetabula of the holopodal plate. Leg I, which lacks the apotele, and presents


Fig. 13. Glyptholaspis confusa (Foà), distal part of right chelicera of female; A, lateral (antiaxial) face; B, lateral (paraxial) face; C, dorsal face; D, ventral face; E , ventral setae $v^{\prime}$ and $v^{\prime \prime} ; \mathrm{A}-\mathrm{D}, \times 370 ; \mathrm{E}, \times 710$.


Fig. 14. Glyptholaspis confusa (Foà), right palp of female; A, lateral (paraxial) face of femur (distal part), genu, tibia, tarsus, and apotele; B, lateral (antiaxial) face of genu (distal part), tibia, and tarsus; $C$, dorsal face of genu, tibia, tarsus, and apotele; A-C, $\times 440$.
numerous hollow setae at the tip, certainly has no walking, but a sensory function. Leg II-IV present pretarsus and apotele.

Legs I and II are directed forward, leg IV posteriorly; these legs consequently present an antiaxial and a paraxial surface. Leg III is directed more or less laterally, and consequently presents an anterior and a posterior surface. Arranged according to length (without pretarsus and apotele) the sequence of the legs is: IV, I, II, III. In comparison with II-IV, leg I is slender with rather differently shaped segments.

The formulae of the legs (apotele included) are the following (sensory setae also counted): I: ( $2+\mathrm{I}-5-\mathrm{I} 3-\mathrm{II}-12-\mathrm{I} 8+\infty-\mathrm{o}$ ) ; II: (2-5-II-II-ro-18-2); III: (2-5-6-7-7-18-2); IV: (1-5-6-6-7-18-2).

Leg I is represented in fig. 15 . Coxa I has two ordinary setae with a more or less ventral position ( $l v^{\prime \prime}$ and $v^{\prime \prime}$ ), of which $v^{\prime \prime}$ is long and pointed, and $l v^{\prime \prime}$ rather blunt. At the paraxial surface, near the anterior border, a specialized seta is present, which is rather small, whitish, and pointed, and shows exactly the same shape as the latero-coxal seta or spine at the base of the palp. There can be no doubt that this represents the latero-coxal seta of leg I, eI, until now unknown from the Anactinotrichida; this seta is represented in fig. ${ }_{5} \mathrm{G}$. A remarkable "sacculus" (sa) debouches at the anterior ventral border of coxa I (fig. ${ }_{5} \mathrm{~A}, \mathrm{G}$ ); its function is unknown.

Trochanter I has no dorsal setae, two laterals ( $l^{\prime}, l^{\prime \prime}$ ), two latero-ventrals ( $l v^{\prime}, l v^{\prime \prime}$ ), and one ventral ( $v^{\prime \prime}$ ); they are rather short, except $v^{\prime \prime}$ which is long and pointed as the corresponding seta of the coxa. The antiaxial surface presents a very small latero-dorsal "pore" of uncertain homology.

The basifemoral ring is complete (fig. $15 \mathrm{~A}, \mathrm{D}-\mathrm{F}$ ). It presents two lyrifissures, both at the antiaxial surface: one dorsal (ifd) and one lateral (if"); ifd is probably composed of three lyrifissures as is shown in fig. ${ }_{5} \mathrm{D}, \mathrm{E}$. The "basifemur" bears no setae; the distal part presents i3 setae, some of which are relatively large and pilose, others are small, pointed, and smooth. I have made no attempt to establish whether any of the dorsal setae is really $d$; the number of verticils is apparently three. The setae of the femur have received no notation.

The in setae of the genu are mostly strong and pilose. The same applies to the 12 setae of the tibia; here some ventral setae are long and pointed.

Tarsus I (fig. ${ }_{55} \mathrm{C}$ ) has no basitarsal ring; at the place of the ring, a ventral lyrifissure (itav) is present. It is the only lyrifissure of the segment. Pretarsus and apotele are lacking, but tarsus I presents at the tip a field of numerous hollow sensory setae. The tip is not sclerotized. The hollow setae remind of eupathidia except a small hollow paraxial seta (not figured), inserted between the "eupathidia"; this seta is shorter and less pointed, and


Fig. I5. Glyptholaspis confusa (Foà), leg I of female; A-C, lateral (antiaxial) face; A, coxa, trochanter, and femur; B, genu and tibia; C, tarsus; D-F, basifemoral ring; D, obliquely from above, showing composed lyrifissure ifd; E, lateral (antiaxial) face, showing lyrifissures ifd and if"; F, lateral (paraxial) face; G, ventral view of distal part of coxa and proximal part of trochanter, showing coxal "sacculus" and latero-coxal seta eI; A-C, $\times 245 ; \mathrm{D}-\mathrm{G}, \times 470$.


Fig. 16. Glyptholaspis confusa (Foà), leg II of female; A-C, lateral (antiaxial) face; A , femur and genu; B, tibia; C, tarsus and apotele; D, dorsal face of part of tarsus; E, lateral (paraxial) face of basitarsal ring; A-E, $\times 245$.
possibly represents a solenidion. Tarsus I is composed of at least four verticils. Two anterior dorsal groups of three setae ( $l d^{\prime \prime}, d, l d^{\prime}$ ) probably also represent eupathidia. The setae of the tarsus are relatively long and pointed.

Leg II is represented in fig. i6. Coxa II has two plumose latero-ventral setae; the formula of the segment is ( $\mathrm{I}-\mathrm{O}-\mathrm{I}$ ) (cf. remark 9).

Trochanter II has no dorsal seta, four plumose laterals ( $l d^{\prime}, l v^{\prime} l d^{\prime \prime}, l v^{\prime \prime}$ ) and one simple ventral that probably is an antiaxial one $\left(v^{\prime \prime}\right)$; the formula of the segment consequently is ( $2-\mathrm{O}-3$ ).

The basifemoral ring is incomplete; it is interrupted in the ventral antiaxial part. There is an isolated antiaxial lyrifissure ( $i f^{\prime \prime}$ ), and a dorsal paraxial one ( $i f^{\prime}$ ) that forms part of the ring.
Femur II is apparently composed of three verticils. There are two probably dorsal setae, the dorsal seta of the proximal (basifemoral) verticil being lost. The paraxial setae are more or less simple, the dorsals small and only slightly pilose, the antiaxials more or less plumose. The formula of the segment consequently is (3-2-6).
Genu II is composed of three verticils. It is impossible to conclude whether the three plumose setae with a dorsal position are really $d$. Apart from these three setae, genu II bears two paraxial laterals, four antiaxial laterals, and two ventrals.

Tibia II is composed of two verticils. There are two possibly dorsal plumose setae. The paraxial setae are more or less simple, the antiaxials more or less plumose.

The basitarsal ring has small interruptions in the antiaxial and paraxial parts. The false articulation has three lyrifissures: an antiaxial (ita"), a ventral (itav), and a dorsal paraxial (ita'). Proximally of the antiaxial interruption of the ring is a pore. The tarsus further shows a dorsal lyrifissure (itad), about halfway the segment. A very small antiaxial fissure at the base of the tarsus possibly represents the proximal lyrifissure itap ${ }^{\prime \prime}$.
Pretarsus and apotele resemble those of leg III. They are dealt with below.
Leg III is represented in fig. I7; pretarsus and apotele III moreover in fig. 19.

Coxa III has two plumose ventral setae. Trochanter III has five setae.
The basifemoral ring is complete; there are two lyrifissures ( $i f^{\prime \prime}$ and $i f^{\prime}$ ). Femur III is apparently composed of three verticils. There are two possibly dorsal setae. The basifemoral verticil is reduced to $v^{\prime}$. The formula of the segment probably is (2-2-2); $l^{\prime \prime}$ and $l d^{\prime \prime}$ have a remarkable shape (fig. 17A).
Genu III is composed of two verticils, together consisting of seven plumose setae. Tibia III bears also seven more or less plumose setae, probably belonging to two verticils.


Fig. 17. Glyptholaspis confusa (Foà), female; lateral (posterior) face of leg III; A, femur; B, genu and tibia; C, tarsus and apotele; A-C, $\times 245$.

Tarsus III has 18 setae. It nearly exactly corresponds with tarsus II; it has lyrifissures and a pore at corresponding places. A section through the basitarsal ring is represented in fig. $3^{3} \mathrm{~B}$; this figure clearly demonstrates that the tarsal wall is thickened internally as well as externally at the places where the ring is interrupted.
Pretarsus and apotele III are represented in fig. 19 in various projections. The pretarsus has a pair of lateral internal chitinous pieces, and a central pair of tendons. The pulvillus is apparently a continuation of the epiostracum of the pretarsus; it is more or less lobate. There are two claws that have a lateral position. Posteriorly and slightly dorsally of the claws there is a pair of "laterodistal pretarsal elements" (Krantz, 1962). They have a dentate distal border; when observed obliquely (fig. ${ }_{17} \mathrm{C}$ ) the surface appears to be beset with a few dents. There is also a pair of anterior "elements", apparently not observed till now; these have the shape of a simple seta. Both structures have no appropriate name, for which reason


Fig. 18. Glyptholaspis confusa (Foà), female; lateral (paraxial) face of leg IV; A, femur ; B, genu; C, tibia; D, part of tarsus; E, part of pretarsus and apotele (oblique view) ; A-E, $\times 245$.

I introduce here the terms anterior and posterior paradactyli (apd, ppd).
The greater part of leg IV is represented in fig. 18. Coxa IV (cf. fig. 2) has one plumose ventral seta. Trochanter IV has five plumose setae.

The basifemoral ring has a ventral paraxial interruption; there are a paraxial lyrifissure ( $i f^{\prime \prime}$ ), and a dorsal antiaxial ( $i f^{\prime}$ ) which is not composed. The paraxial surface of the basifemur presents a pore. There are no basifemoral setae. I have indicated the femoral setae as $d, l d_{1}{ }^{\prime \prime}, l d^{\prime \prime}{ }_{2}, l^{\prime}, l v^{\prime \prime}, l v^{\prime}$; I am not certain about the notation $d$. The femoral setae are more or less


Fig. 19. Glyptholaspis confusa (Foà), female, pretarsus and apotele of right leg III; A, dorsal view; $B$, ventral view; $C$, viewed from in front; $D$, lateral (posterior) face; A-D, $\times 490$.
plumose, with the exception of $l v^{\prime \prime}$ which has a remarkable conical shape.
Genu IV is probably composed of two verticils; it presents six plumose setae. Tibia IV bears seven plumose setae, originally probably belonging to two verticils.
Tarsus IV is similar to tarsus II and III, except for its being more elongate. Pretarsus and apotele are represented in oblique view in fig. 18E; an anterior setiform, and a posterior dentate paradactylus are visible in this orientation.

## REMARKS

## REMARK I. TECHNIQUES

The techniques applied in the course of the present study are nearly unknown in Gamasine morphology. They have been introduced by Grandjean and are now used by several investigators working on actinotrichid morphology. Because the methods permit of observations that are much more detailed, a summary is given here in the interest of workers in other groups of mites.

I might remark that an acarological laboratory should be equipped with three different types of microscopes: one microscope for sorting, preparation of slides, and dissection; a second for observation on a carbon block; and a third for observation by transmitted light.

## A. Observation on a carbon block.

This method, described by Grandjean (1949), is particularly well adapted for the study of general habitus, colour, sculpture, and cerotegument. It should be the beginning of every investigation, because it shows the mites nearly in natural condition, legs and setae not moved through the influence of a coverslip.

The disposition required for this observation is represented in fig. 20; the method is as follows.

With a pipette a block of porous carbon $(B)$ is moistened with 75 per cent alcohol. It is placed on the stage of a binocular dissecting microscope, and part of the surface is kept moist with alcohol siphoned through a capillary tube $(S)$ from a small reservoir $(R)$ on the block. A small region near the opening of the tube is saturated with liquid, so that the surface is very black. The specimen $(A)$ is placed in the alcohol running out of the siphon; for observation it is slightly moved so that it does not touch the moist spot, but still stays in an atmosphere nearly saturated with vapour. In this position it does not desiccate, and as soon as the alcohol covering its surface is evaporated, the conditions for observation are favorable. The specimen can easily be orientated in the position required. As soon as there appears to be some risk for desiccation, the mite is returned to the moist spot and the investigation recommences.

The specimen should be strongly illuminated by a large source of light. For that purpose a loo-watt bulb of milk glass $(E)$ is mounted in such a way that it can be placed close to the carbon block; the light should be screened at the upper side in order not to trouble the eye. The illumination of the specimen can be improved by a system of lenses ( $L$ ), provided that


Fig. 20. Schematic representation of the observation of a specimen on a carbon block.
the rays still enter from different directions. Various condensers can be used; in the case of a condenser of a microscope, the front lens should be removed. In order to absorb the heat and to prevent desiccation, a cell (C) containing water is placed between bulb and microscope. I remark that lowvoltage equipment, suggested in this connection by Evans, Sheals \& Macfarlane (1961), must be dissuaded because it does not satisfy the condition of diffuse light.

The present method allows the use of magnifications ranging to $100 \times$. B. Observation by transmitted light.

The present method is based on the use of open preparations; the best medium is diluted lactic acid (two parts of lactic acid, and one part of distilled water). The material for study should be warmed (e.g. in a cavity slide) in the same lactic acid that is later on used as medium. This can take place on a warming plate; even boiling for a very short time can be necessary. Specimens or parts of specimens cieared in this way are studied in cavity
slides, a range of slides being required in order to suit mites of different measurements.
A cavity slide of suitable depth is chosen according to the size of the specimen. A rectangular coverslip is placed on one half of the cavity, and a small quantity of lactic acid (just sufficient to fill the space between slide and coverslip by capillarity) is introduced at a place $t$ (cf. fig. 2IA).


Fig. 21. Schematic representation of the manipulation of a specimen in a cavity slide (after Grandjean, 1949) ; A, slide and coverslip; B, cavity and specimen in position; C, transverse section through cavity, coverslip, and specimen.

The empty slide is placed on the stage of a binocular dissecting microscope in transmitted light. The specimen is introduced at a place $m$ where the cavity has the largest depth, then pushed parallel to the border of the coverslip till it touches the two surfaces of the closed cavity at a place $a$. At this place it is easy to bring the specimen in the position required. Manipulations with a fine needle, or slight movements of the coverslip (e.g. with the left forefinger at a place $d$ ) are sufficient. A vertical section $c c^{\prime}$ (fig. 2rB) at the level of the specimen results in fig. 2 IC .
The specimen is now ready for observation under a high power microscope. The use of a phase contrast microscope for all observations should be dissuaded. The study of mites in transmitted light requires specially adapted techniques. A microscope should be used with apochromatic objectives and compensating eyepieces; the stage of the microscope should be revolving. In order to obtain satisfying results with the study in polarized light, the analyzer should be inside the body tube. The illumination described below should have its maximum of intensity in cases where polarizers are added; in polarized light it may also be necessary to change to the monocular tube, otherwise only used for drawing.
The illumination of the microscope is of considerable importance. For the observation of mites it should be as heterogeneous as possible. This is achieved by the following method (cf. Grandjean, 1949).

A microscope lamp, from which condenser and diaphragm are removed, is mounted on a stand and placed at a distance of about 60 cm from the microscope; the distance must be larger in the case of high magnifications, smaller when these are low. A 6 -volt flat filament bulb is used as source of light; a variable supply of current is introduced by a rheostat transformer. The light should be as feeble as possible, but dark-coloured mites and the investigation in polarized light require a higher intensity.
The diaphragm of the microscope must be completely open; by means of the plane mirror an image ( $I M$ ) of the source of light is formed through condenser and microscope. The image should always be small in comparison with the field. Conditions of illumination can be changed by lowering (or more rarely raising) the condenser; this results in a slightly larger but less brilliant image $I M^{\prime}$.
For observation or drawing the image $I M^{\prime}$ is moved in the dark field by means of the mirror, in such a way illuminating successively all parts of the object. In the case of observations only, the same result is obtained by moving the slide by means of the mechanical stage. As a rule the detail studied is in the centre of the image $I M^{\prime}$; certain characters are, however, better visible when they are illuminated obliquely.

## C. Preparation of sections.

In the course of the present investigation a number of specimens have been dissected in order to study further details. Small needles are used for dissecting; sectioning is carried out by hand under a binocular microscope, only with the help of a razor blade. After some experience, objects cleared in lactic acid can easily be cut in this way.

For a morphological study, this method must be preferred over the use of a microtome, at least as a starting point. Sectioning with a razor blade results in pieces that still distinctly show course, connection, and mutual relation of the parts; it must be strongly recommended for further acarological investigations.

The sections can be studied in various orientations in cavity slides. Results of this method are represented in fig. $4 \mathrm{~B}, \mathrm{C}, \mathrm{F}-\mathrm{H}$, ro, irA, 12.

REMARK 2. DIRECTIONS FOR THE ORIENTATION OF FIGURED STRUCTURES
With the exception of oribatologists, acarologists have no common usage as to the orientation of figured mites. Each author has his own way of representing animals and structures, or even no special way at all. In one paper homologous structures (represented with the aim of enabling com-
parisons) are often figured in different positions, in this way thwarting a comparative study. Among ig figures of Macrochelid chelicerae published by Evans \& Browning (1956) (without explanation about their position), 4 represent right antiaxial faces, 7 right paraxials, 5 left antiaxials, and 3 left paraxials. Of 47 figures of Macrochelid chelicerae published by Evans \& Hyatt ( 1963 ), 12 represent right antiaxial faces, 4 right paraxials, 20 left antiaxials, and II are of uncertain position because the figures are too in complete. Since the various faces of the chelicerae are distinctly different from each other, it is evident that in this way a comparative investigation is not tacilitated. Similar lists as for the chelicerae could be made for legs, mouth parts, and lateral faces of the idiosoma.
It is evident that figures should be prepared by all authors in such a way that comparisons can easily be made. For this reason I have introduced in the present paper (with some alterations) the way of drawing used in papers on Oribatid mites. The following directions are of general interest.

Figures of dorsal and ventral faces of the idiosoma or of the complete mite have raised no differences; they are nearly always orientated vertically on the page (cf. fig. $\mathrm{I}, 2$ ). The usage of combining dorsal and ventral faces as halfs of one figure, separated by a median line, must be dissuaded. This type of figures prevents the reader to form a distinct notion of the median part which is of essential importance. I do not know if this way of drawing is found in papers on Gamasine mites; it is not probable since several unpaired structures are found here.

Figures of lateral faces of the idiosoma should be orientated in such a way that the anterior part is at the right, the posterior part at the left (cf. fig. 3A).
The same principles should be applied to the gnathosoma (cf. fig. 5-7, etc.). Special attention must be paid to the appendages, since these present anterior and posterior, antiaxial and paraxial faces. It is preferable to draw the right chelicera, in which case the antiaxial face is orientated from left to right, the paraxial from right to left ; dorsal and ventral faces can be orientated vertically (cf. fig. 13). The same should be applied to the palp (cf. fig. 14) ; if one face only is represented in the case of the palp, it is preferable to figure the paraxial one (cf. fig. 14A), because the apotele is invisible in antiaxial view. The legs pose further problems. In Oribatid mites it is usual to represent the antiaxial face of the legs (if only one face is figured) because these surfaces have as a rule preserved more setae. In order to have all legs orientated from left to right, legs I and II are figured in this group from the right side, legs III and IV from the left. In the case of Glyptholaspis I have figured all legs from the right side (cf. fig. 15-19); lyrifissures
and false articulations are distinct examples of the law of parallel homology (cf. Grandjean, 1939). If only one face of each leg is represented, it is preferable to figure the posterior one which in legs I and II is the antiaxial surface, in leg IV the paraxial (leg III has no distinct antiaxial and paraxial faces since it is orientated laterally). Anterior faces of the legs are consequently orientated from right to left (cf. fig. $15 \mathrm{~F}, \mathrm{I} 6 \mathrm{E}$ ), dorsal and ventral faces vertically (cf. fig. ${ }^{5} \mathrm{G}, 16 \mathrm{D}, 19 \mathrm{~A}, \mathrm{~B}$ ).
When the above-mentioned directions are generally adopted, different papers and even different descriptions in one paper will be much easier to compare; it will, moreover, at once be distinct which face was figured in a paper consulted.

## REMARK 3. SCIENTIFIC APPROACH TO TERMINOLOGY

Progress of science is a process that is closely connected with a continuous revaluation of terms and concepts, and a rejection or correction of outworn opinions. This requires of course a certain adaptibility of the investigator. It results, however, in a clear and logical terminology. The oribatologist, who is used to the renovations in Oribatid morphological terminology, is rather surprised when he finds that nearly nothing of this has entered into the morphology of other groups of mites. Revision of terminology is one of the first things that has to be done in Anactinotrichida.
The aim of a morphological study must be the understanding of a structure. When appears that structures have been misinterpreted by previous authors, and consequently received erroneous or misleading names, it will be necessary to create a new terminology. This can easily be done in the present case, since very few names appear to be generally accepted, especially in the case of the gnathosoma.

In 1961, in a study on Holothyrus, I published already some critical notes on the terminology of the Gamasine gnathosoma, and introduced a number of new terms. In the present paper this renovation is continued.

## REMARK 4. THE TERMINOLOGY OF THE TEGUMENT

There appears to be some confusion in the terminology of the various layers of the tegument. This is for instance evident from the book by Evans, Sheals \& Macfarlane ( 1961 ); on p. 5 these authors characterize the epiostracum as "non-chitinous", but on the same page they deal with "epiostracal chitin". Apparently there is no uniformity in the use of these terms.

I have followed Grandjean's 1951 terminology, distinguishing cerotegument, epiostracum, ectostracum, and hypodermis. The cerotegument (also
named tectostracum) is the superficial layer which develops by exsudation; in Gamasine mites it often has a cement-like appearance. The epiostracum is a thin, elastic, colourless layer which covers the ectostracum. The ectostracum is a thick layer which becomes coloured by sclerotization; in sclerotized parts two ectostracal layers can often be distinguished. Epiostracum and ectostracum together form the cuticle. The hypodermis is the layer which consist of living cells.

REMARK 5. THE DELIMITATION OF THE SCLEROTIZED SHIELDS OF THE IDIOSOMA AND THE CONDITION OF THE EPIOSTRACUM

After heating with lactic acid, the various shields can easily be separated from the remaining idiosoma. When the dorsal shield is separated in this way, it appears that the dentate margin, generally regarded as its border, is not the real outer border. The shield continues under a wrinkled surface which is apparently the epiostracum; in a cleared specimen this part has indeed the same brown colour as the remaining part of the shield. A section reveals that the sclerotized shield s.str. consists of two layers, whilst the marginal part apparently consists only of the sclerotized lower layer, covered by a thin, weak epiostracum.

It appears that several shields, or borders of shields of the lateral and ventral surfaces show the same condition (e.g. metasternal and metapodal shields, the borders of peritrematal, genital, and holopodal shields), which explains the difficulty in tracing the real delimitation at the ventral surface.
It will be interesting to study the condition of the epiostracum of the various shields in different genera. Until now no attention has apparently been paid to this character.

REMARK 6. The chaEtotaxy of the idiosoma
Fissures and pores of the dorsal shield appear to have a more or less metameric arrangement. If they originate from lyrifissures (as was supposed above), their position originally corresponded with the borders of the segments. When transverse rows of pores are connected by lines, we state indeed that they separate transverse rows of setae. A comparative study of pores and setae would probably result in a better system of notation of the setae of the Gamasine idiosoma. I might remark that the secondary increase of the number of pores by plethotaxy (cf. Grandjean, 1943) is here not taken into consideration.

It is evident that a comparative study of the chaetotaxy of the idiosoma should include the lateral regions, as a rule omitted up to now. Possible metameric arrangements are best visible when mites are studied in lateral view
(cf. fig. 3 A ). The anal segment must be regarded as the posterior segment of the idiosoma.

In the present paper I have followed the current artificial system for the setae of the dorsal shield, distinguishing dorsal $(d)$, median ( $m$ ), lateral ( $l$ ), and marginal ( $m g$ ) series. Most authors use capitals for these setae, but I have adapted the system to the usage of oribatologists, indicating setae with small letters, and reserving capitals for segments, organs, etc.

I have tried to trace any progress in Hirschmann's 1957 system of notation, which recently has been followed by a few authors. This system is based on two principles: the subdivision of the body into podosoma and opisthosoma, and the arrangement of setae in transverse, as well as in longitudinal and oblique rows. Both principles appear to be misleading. It is in fact impossible to trace the anterior and posterior dorsal border of the podosoma since we do not know if the tergites of the podosoma are still in existence. Recently (Van der Hammen, 1963) I pointed to the fact that the tergites of the podosoma tend to disappear in several groups of Arachnida, and probably also in Actinotrichid mites. There is further still no evidence at all that the posterior border of the podonotal, and the anterior border of the opisthonotal shields of the protonymph represent borders of tagmata. Apart from this, the anterior dorsal region of the idiosoma certainly includes the tergites of segments I and II (i.e. the segments of chelicerae and palps). For these reasons I regard Hirschmann's subdivision of the body into anterior and posterior parts as probably artificial and useless for a notation. As to the arrangement of setae in rows, it is evident that only a metameric arrangement, i.e. the arrangement in transverse rows has phylogenetic value. The metameric relations of pores and lyrifissures have not been studied by Hirschmann. I am of the opinion that these will be of much help in developing a chaetotaxy on the base of metamerism.

A few words must be added here on Hirschmann's "Gangsystematik". Hirschmann (1957) starts from the correct principle that all stases must be included in a phylogenetic study. He over-estimates, however, the value of "Gangmerkmale", i.e. characters that are constant throughout post-embryonic ontogeny. "Gangmerkmale" point to parallel phylogeny of the stases, or even to the absence of evolution. Diverging phylogenies, which are very important in acarology (I may point for instance to the origin of calyptostases and elattostases), are in this way arbitrarily neglected. "Gangsystematik" is in fact systematics not paying attention to the course of phylogeny. It is illustrative that only vol. 2 of Stammer's "Beiträge" (Stammer, i963) is based on the principles of the "Gangsystematik", whilst in vol. I (Stammer, 1957, 1959), dealing with groups in which elattostases and calyptostases are found, these views are not applied.

The "Gangsystematik" is explained in a dogmatic way by Bernhard (1963). According to him a genus should present at least one character that is constant throughout post-embryonic development. It is sufficient to apply this definition to the classification of caterpillars, pupae, and butterflies to illustrate its final impossibility.

REMARK 7. SUMMARY OF THE MORPHOLOGY AND TERMINOLOGY OF THE GAMASINE GNATHOSOMA

The Gamasine gnathosoma has the shape of a tube. It primarily consists of a cheliceral frame (segment I) and an infracapitulum (segment II). The cheliceral frame has developed a cheliceral tectum which is grown together with lateral and ventral parts of the infracapitulum, constituting the wall of the gnathosomal tube. Posteriorly, this wall has developed a secondary extension which is named here capitular retrotectum.
The tube is divided by the dorsal wall of the infracapitulum into a dorsal cheliceral vault and a ventral infracapitular vault. The infracapitular vault contains a pair of lateral coxal vaults and a median pharyngeal chamber.

The cheliceral frame consists of the cheliceral sheaths and their attachment to the infracapitulum, and of the cheliceral tectum. The frame is an epimere of which the sternal part is lost; only the coxal region is still present (cf. Grandjean, 1957, 1957a).

The infracapitulum is also an epimere. Here the coxisternal part is still present; it bears the infracapitular setae which consequently are epimeric setae; a latero-coxal seta is present in the coxal region. The epimeric character of the infracapitulum is definitely proved by the existence of a capitular apodeme at the border of segments I and II. I may remark that Gorirossi \& Wharton (1953) regard subcheliceral plate (i.e. cervix) and tentorium (apparently the connecting part between cervix and coxal region) as apodemes, but did not notice the apodematal character of the posterior bars. Gorirossi (1955) even recognizes apodemes in the wall of the pre-oral cavity. Apodemes are, however, by definition the internal extensions of the chitinous skeleton, arising from the borders of the segments.

The infracapitulum has a dorsal shelf (cervix), a lateral wall (which is the outer wall of the coxal vault), and a ventral wall (mentum). The cervix presents a dorsal ridge, separating two grooves in which the chelicerae can move; in the case of Glyptholaspis a ligament attaches the cheliceral tectum to the anterior border of the ridge. The posterior border of the cervix presents three bars which constitute the capitular apodeme. Anteriorly the cervix continues in the parts constituting the dorsal walls of the pre-oral
cavity. The lateral wall of the coxal vault presents the latero-coxal setae. The anterior part of the coxal vault constitutes the socket of the palp.

The mentum passes anteriorly into the genae which form the lateroventral walls of the pre-oral cavity. A subcapitular groove is present in the median part of mentum and genae. This groove must not be regarded as a less sclerotized part separating two coxal extensions, but as a highly specialized structure which has some relation to the furca (syn. tritosternum). It presents transverse rows of teeth, emphasizing its high degree of specialization.
The anterior part of the groove (separating the genae) is often named protosternum, the posterior part deutosternum, the furca tritosternum, because of a supposed relation to respectively segments I, II, and III. It is evident that protosternum and deutosternum, as parts of the infracapitulum, both belong to segment II. None of the three structures is a sternum.

The ventral surface of the infracapitulum bears four pairs of setae with exactly the same position as in the Actinotrichida. They must be considered homologous, for which reason the same notation is introduced here: hysterostomal ( $h$ ), median ( $m_{1}, m_{2}$ ), and anterior (a).

The mouth is situated inside the infracapitulum; it is the entrance to the pharynx. The position of the mouth is dorsally of the infracapitular groove, near the transition of mentum into genae. There are three lips; a section through the pharynx consequently is more or less triangular. The dorsal wall of the pharynx continues as the ventral wall of the labrum. The labrum is attached to the cervix. The lateral walls of the pharynx continue as the lateral lips which are extremely complicated in Gamasine mites. These lips are grown together in the ventral median part, in this way forming a labial gutter. The anterior ventral part of the labial gutter is attached to the genae, just as the lateral lips of the Actinotrichida. Anteriorly, the labial gutter passes into two pairs of processes: a ventral pair of laciniae (which are also a continuation of the bottom of the subcapitular groove) and a dorsal pair of fimbrillae. Dorsally, the walls of the labial gutter pass into the labelli, pilose flaps which are posteriorly connected with the cervix. Labelli and genae are the walls of the pre-oral cavity.

Laterally the labelli are connected with the patrocinia which have the appearance of protective dents situated dorsally of the siphunculi. These siphunculi are the terminal parts of efferent ducts of glands which are situated in the idiosoma. The ducts run through the coxal vault and leave the infracapitulum dorso-medially of the acetabulum of the palp. At this place the siphunculi arise; they consist of the continuation of the duct, enveloped
in an epiostracal layer which at the base is attached to the lateral wall of the genae.

The present description of the gnathosoma is mainly topographic. Up to now interpretations of the gnathosoma have been generally based on speculations which as a rule lacked the base of a completely understood topography. The infracapitulum is not the result of a gradual extension of coxal regions, but an epimere from the border of which starts an apodeme.

I remark that in the present paper no attention is paid to Snodgrass (1948). The study by this author (especially the acarological part of it) is entirely based on literature records. This risky process leads to the discovery of structures which are not present at all. On p. 67 Snodgrass recognizes for instance a cheliceral tectum (for which he was certainly looking) in Oribatid mites, solely by interpretation of a 1897 Berlese figure. Every serious acarologist will identify this so-called tectum at once with the prodorsum.

## remark 8. the gnathosoma of holothyrus

In the light of the present study of the gnathosoma it is necessary to make some corrections and additions to my ig6 paper on Holothyrus. I regard the gnathosoma of Holothyrus as very important because it is partly less complicated than the gnathosoma of Glyptholaspis. For the moment I prefer, however, to avoid the characterization as more primitive.

It is interesting enough to recall that the gnathosoma of Holothyrus is situated in a camerostome, protected by a rostral tectum, just as in certain Uropodini, in this way differing from the Gamasini.

One of the outstanding characters of Holothyrus is the large number of infracapitular setae (possibly neotrichy). They take the place of $m$ and $a$; apparently there is no seta $h$. A large number of infracapitular setae is also found in Opilioacarus.

In 196i I applied the term mentum to the whole ventral surface of the infracapitulum of Holothyrus. I now prefer to distinguish the genae, just as I have done in the present paper. I must correct here an error I have made in 196I: the infracapitular setae $l d m$ and the corniculi are not inserted on the cervix, but on a dorsal ridge connected with the genae. The cervix (or subcheliceral shelf) passes anteriorly into the dorsal lobes of the lateral lips; these lobes are probably homologous with the structures here named labellum. It is evident that the lateral lips of Holothyrus have dorsal and ventral lobes; in recent discussions I noticed that the thin labellum had not been recognized as a separate dorsal lobe by several acarologists who had studied the genus. It will be useful to publish figures of sections (especially longitudinal) through the gnathosoma of Holothyrus.

The large lateral ridges of Holothyrus are homologous with the coxal vault of Glyptholaspis. It is interesting to see that these lateral ridges extend to the posterior border of the infracapitulum, whilst the coxal vault of Glyptholaspis confusa is relatively shorter. This supports my conception of the basal ring of the Gamasine gnathosoma as a secondary extension, a capitular retrotectum, to which cheliceral tectum as well as infracapitulum have contributed.

## REMARK 9. THE CHAETOTAXY OF THE LEGS

Grandjean (1940) pointed to the fact that the fundamental element of a leg is a ring, originally bearing a verticil of setae. Primitively the verticil consisted of seven setae (a number also found in other groups of Arachnida), viz., one unpaired dorsal seta ( $d$ ), two pairs of laterals (here named $l d$ and $l v$ ) and one pair of ventrals (here named $v$ ).

One of the essential conditions for the application of this notation is the exact definition of the unpaired dorsal seta $d$. A comparative study is required in order to arrive at a definite solution.

It is regrettable that Evans ( 1963 ), in a study on the chaetotaxy of the legs in the free-living Gamasina, did not pay attention to the definition of the unpaired dorsal seta $d$, nor to the recognition of verticils. The setae indicated by him as dorsals (mostly paired) are in fact mostly $l d$; his ventral setae are often $l v$. Consequently his formulae

$$
\text { (antero-laterals/ } \frac{\text { dorsals }}{\text { ventrals }} / \text { postero-laterals) }
$$

have little or no comparative value. A formula giving for each segment three numbers, viz., anterior ( $\left.l d^{\prime}, l v^{\prime}, v^{\prime}\right)$ - dorsal ( $d$ ) - posterior ( $l d^{\prime \prime}, l v^{\prime \prime}, v^{\prime \prime}$ ) would be more logical.
It must be noted here that in Actinotrichid mites verticils of seven setae are only present in exceptional cases (Palaeacaroidea). I do not know whether they are found in Gamasine mites. The notation must be adapted to the degree of deficency. When only one (or one pair) of lateral setae is present, the notation $l d$ or $l v$ can be replaced by $l$, especially when the seta has a position which is exactly lateral.
The dorsal setae are apparently in regression. The few observations I have made point to the fact that there can be a reduction in size, as well as a retardation during ontogeny.

REMARK IO. ADDITIONAL CHARACTERS FOR THE SEPARATION OF ACTINOTRICHIDA AND ANACTINOTRICHIDA

In 196I I published a summary of the differential characters of the three
orders of mites. A few additions and corrections must be added here with regard to Actinotrichida and Anactinotrichida. These remarks concern development, moulting, latero-coxal setae, and the subdivision of the body.
r. There appear to be primarily 4 stases of development in the Anactinotrichida: larva, protonymph, deutonymph, and adult. Prelarva and tritonymph are unknown in this group. Differences in the number of stases can be derived from this original cycle.

In the Actinotrichida there are primarily 6 stases of development: prelarva, larva, protonymph, deutonymph, tritonymph, and adult. In this group differences can be derived from the original cycle of 6 stases.
2. There appears to be an important and very interesting difference in moulting between the two groups. Moulting in the Anactinotrichida resembles moulting in many other groups of Arachnida: the legs of a stase develop inside the leg of the preceding stase.

In the Actinotrichida on the contrary, legs develop inside the idiosoma of the preceding stase, apparently as the result of a much more advanced histolysis. It is not impossible that there is some relation between this way of moulting and the tendency to develop regressive stases. I do not know whether a comparable way of moulting is also found in other groups of Arachnida. In Actinotrichida this way appears to be general. It will be important to pay more attention to this highly interesting character.
3. In 196i I mentioned the presence of specialized latero-coxal setae as a character of the Actinotrichida. It is interesting to return here to these very important structures. Latero-coxal (or supra-coxal) setae can be present in the coxal regions of palp (e), leg I (eI), and leg II (eII). In the Opilioacarida $e I$ and $e I I$ are known (Grandjean, 1936). Recently, Grandjean (I962) summarized our knowledge on the latero-coxal setae in the Actinotrichida: $e$ is probably constantly occurring in this group; $e I$ is common, but nevertheless lacks in many systematic units; $e I I$ is only known from some Prostigmata.

Up to now latero-coxal setae had never been recorded from Anactinotrichida. In the present paper the occurrence of $e$, and $e I$ in Glyptholaspis confusa is described; it is the first record for this group. It clearly demonstrates the homology of the fixed coxal region of the palp, with the free coxa of leg I. It will be worth while to study the latero-coxal setae in many more species.
4. Recently (Van der Hammen, ig63) I demonstrated that the body of the Actinotrichid mites is primarily subdivided into prosoma and opisthosoma. The (dorsal) furrow separating prosoma and opisthosoma was named disjugal (replacing the misleading term dorso-sejugal), whilst the furrow
separating coxisternal regions II and III kept its name sejugal. A sejugal furrow or interval, present in the Actinotrichida, is absent in the Anactinotrichida. A disjugal furrow has neither been described from this group. There is still no sufficient proof that podonotal and opisthonotal shield represent dorsal parts of prosoma and opisthosoma respectively. It will be necessary to study a possible post-embryonic addition of segments, just as I have done in the case of the Actinotrichida (combined with further studies on the original segmentation), in order to solve this problem (cf. Van der Hammen, 1963). Up to now it appears that the body of the Anactinotrichida shows no distinct subdivision into prosoma and opisthosoma.
alphabetic list (ARRANGED according to the first catchword) of new OR LITTLE KNOWN TERMS, HERE INTRODUCED INTO GAMASINE MORPHOLOGY, WITH DEFINITIONS AND CURRENT SYNONYMS
A training in Oribatid morphology has been the starting point of the present study. This implies not only that the techniques summarized in remarks 1 and 2 are introduced here, but also that the morphological views partly explained in remarks 3 to to have influenced the course of the investigation. This has resulted in the introduction of an important number of terms hitherto unknown in Gamasine morphology. Part of these terms have been introduced by Grandjean in Actinotrichid morphology; others have recently been created by myself; a number of terms is new. In order to facilitate the use of these terms, an alphabetic list is given here, arranged according to the first catchword, with definitions and some of the current synonyms. The author of each term is mentioned, except when the origin could not be traced with certainty. The present list is no historical study; consequently the list of synonyms is an anthology. A definition is only given if necessary; sometimes a reference to a synonym appeared to be sufficient.

Anarthry (Grandjean). - The absence of labio-genal articulation.
Anterior infracapitular setae (Grandjean). - Syn. distal setae (Gorirossi \& Wharton, 1953), rostral setae (Evans \& Browning, 1956), "Coxalhaare" $\mathrm{C}_{1}$ (Hirschmann, 1959).
Antiaxial. - Used here for the surface of an appendage not facing the idiosoma.
Apotele (Grandjean). - The terminal segment of the appendages. In the case of the legs it is reduced to a basal piece bearing the claws. In the palp it bears the "tined seta". The movable bit (or digit) is the apotele of the chelicerae.

Basifemoral ring. - The false articulation of the femur, which in Anactinotrichida passes through two lyrifissures.

Basitarsal ring. - The false articulation of the tarsus, which in Anactinotrichida passes through three lyrifissures.
Calyptostase (Grandjean). - A regressive stase which has lost its appendages or at least the use of them: it does not eat, and it cannot move by means of legs. Calyptostases are not known from Anactinotrichida.

Capirular apodeme (Grandjean). - The apodeme starting from the border between cheliceral frame and infracapitulum. It consist of large bars. The existence of the capitular apodeme is the proof of the epimeric character of the infracapitulum.
Capitular retrotectum (new). -- The posterior extension of cheliceral tectum and infracapitulum, constituting a basal ring.

Cerotegument (Grandjean). - The superficial cement- or wax-like layer of the tegument, developed by exsudation through the chitinous layers. Syn. tectostracum.

Cervix (Van der Hammen). - The dorsal wall of the infracapitulum, which anteriorly of the mouth passes into the labelli. Syn. epistome + subcheliceral plate (Gorirossi \& Wharton, 1953).
Cheliceral frame (Grandjean). - The segment of the chelicerae (segment I). The epimere is strongly reduced; it has no sternal region. The coxal region consists of the cheliceral sheaths and their attachment to segment 1I; from the line of attachment the capitular apodeme arises. The cheliceral tectum is a secondary extension of the cheliceral frame.

Cheliceral tectum (new). - Syn. tectum.
Cheliceral vault (Grandjean). - The room between cheliceral tectum and the dorsal surface of the infracapitulum.

Cheliseta (new). - The specialized seta laterally of the teeth of the fixed bit (or finger) of the chelicerae. Syn. pilus dentilis.

Commissure of tife mouth (Grandjean). - The external point of a commissural line where two lips meet. In Glyptholaspis confusa (and probably in all Gamasine mites) there are three commissures: two superior commissures ( $J s$ ) which are the meeting points of labrum and lateral lips, and one inferior ( $J i$ ) which is the meeting point of the pair of lateral lips. Because the Gamasine lateral lips are generally more or less grown together in the ventral part, I distinguish a point $J i$, ventrally of $J_{s}$ (which is the real lower corner of the mouth); a point $J i_{1}$ where the labial gutter is grown together with the bottom of the subcapitular groove (this point is homologous with $J i$ in Actinotrochida); and a point $J_{i_{2}}$ (the only external one) where the lateral lips divide into a pair of laciniae.

Court-pore (new). - Syn. pore (auct.), "Ovalpore" (Hirschmann, r960).

Covered shield (new). - A sclerotized shield covered by a weak, wrinkled epiostracum.
Coxal vault (new). - The coxal region of the palp constitutes a separate vault which posteriorly passes into the infracapitular vault; anteriorly it constitutes the palpal socket. The vault is separated by a lateral wall from the pharyngeal chamber.

Disjugal furrow (Van der Hammen).-- The (dorsal) furrow separating prosoma and opisthosoma. The existence of it in Gamasine mites is not yet proved.

Elattostase (Grandjean). - A regressive stase in which the mouth parts are considerably reduced, but in which the legs are strongly developed. Elattostases are not known from Anactinotrichida.

Eupathid (Grandjean). -- A hollow seta. It is easily recognizable in Actinotrichida because of the presence of actinopilin. In Anactinotrichida it is not recognizable with certainty, although the shape of a seta can sometimes suggest a homology.

Fimbrillae (new). - The anterior dorsal processes of the labial gutter.
Furca (new). - Syn. tritosternum.
Genae (Grandjean). - The paired ventro-lateral walls of the pre-oral cavity between mentum and the extensions of the lateral lips. The genae are separated by the anterior part of the subcapitular groove.

Holopodal shield (new). - The shield which can be regarded as a fusion of exo- and endopodal shields.
Hysterostomal setae (Grandjean). - The posterior pair of infracapitular setae. Syn. gnathosomal setae (Gorirossi \& Wharton, 1953), capitular setae (Evans \& Browning, 1956), "Coxalhaare" $\mathrm{C}_{4}$ (Hirschmann, 1959).

Infracapitular setae (Grandjean). - The setae on the ventral surface of the infracapitulum: one pair of hysterostomal ( $h$ ), one or more pairs of median (in Gamasine mites $m_{1}, m_{2}$ ), and one pair of anterior setae (a). With the exception of Opiliocarida and Holothyrina (which present a large number of infracapitular setae) these are recognizable in all groups of mites; they must be regarded as homologous. Syn. "Coxalhaare" (Hirschmann, 1959). (It is evident that the infracapitular setae are no coxal, but epimeric setae; only the specialized seta $\varepsilon$ is latero-coxal).

Infracapitular vault (new). - The room between dorsal and ventral wall of the infracapitulum. It has a central pharyngeal chamber, and a pair of lateral coxal vaults.

Infracapitulum (Grandjean). - The epimere of the palpal segment
(segment II), containing pharynx, mouth, and lips. The border of this epimere and segment I (the cheliceral frame) is still distinct because of the existence of a capitular apodeme. In Gamasine mites the infra-capitulum is fused with segment I to a gnathosomal tube. The epimeric character of the infracapitulum is proved; this is in contradistinction to the current unfounded interpretation of the Gamasine gnathosoma as mainly originating from coxal extensions.
Labeili (new). - Pilose flaps which are laterally attached to the dorsal border of the labial gutter, and posteriorly to the cervix. Syn. paralabra interna (Vitzthum, 1940), paralabra externa (Hughes, 1959), hypopharyngeal styli (Gorirossi \& Wharton, 1953).
Labial gutter (new). - The gutter-shaped part of the latero-ventral continuation of the pharynx into the pre-oral cavity. It belongs to the lateral lips. About half-way its length, the labial gutter is grown together with the bottom of the subcapitular groove. Latero-dorsally it passes into the labelli. It has a pair of anterior dorsal processes (the fimbrillae), and a pair of anterior ventrals (the laciniae). Syn. hypopharynx (Gorirossi \& Wrarton, 1953).

Labio-genal articulation (Grandjean). - The articulation which separates mentum and genae. It is absent in Gamasine mites.

Laciniae. - The anterior ventral processes of the labial gutter, and at the same time the anterior paired continuation of the bottom of the subcapitular groove. The laciniae are part of the lateral lips. Syn. internal malae (Evans, 1957), hypopharyngeal processes (Gorirossi \& Wharton, 1953).

Lateral lips (Grandjean). - The continuation of the lateral walls of the pharynx into and in front of the pre-oral cavity. These lips are highly developed in Gamasine mites, and consist of labial gutter, labelli, fimbrillae, and laciniae.
Latero-coxal setae (Grandjean). - The specialized spiniform setae of the coxal region of the palp (e) and of the free coxae or the coxal regions of the legs (eI, eII; the setae are not known from legs III and IV). In Glyptholaspis confusa $e$ and $e I$ are present, eII is absent (eII is not known from Gamasine mites).

Lyrifissure. - Syn. lyriform pore (Evans, 1957), lyriform fissure (Van der Hammen, 196r; Evans, 1963), "Spaltpore" (Hirschmann, 1960).

Median infracapitular setae (Grandjean). - Syn. medial + lateral setae (Gorirossi \& Wharton, 1953), internal + external posterior rostrals (Evans \& Browning, 1956), "Coxalhaare" $\mathrm{C}_{3}, \mathrm{C}_{2}$ (Hirschmann, 1959).

Mentum (Grandjean). - The posterior part of the ventral surface of the
infracapituium, which anteriorly passes into the paired genae. The mentum is also indicated as hysterostome ( $H$ ).

Neotrichy (Grandjean). - The presence of additional setae, new in phylogenetic sense.

Paradactyli (new). - The epiostracal extensions latero-dorsally of the claws of the legs. In Glyptholaspis confusa there are anterior and posterior paradactyli. Syn. laterodistal pretarsal elements (Krantz, 1962).

Paragenital shields (new). - The lateral sclerites bordering in the Macrochelidae at both sides the genital shield. Syn. accessory sclerites.

Paraxial. -- Used, in dealing with appendages, for the surface alongside te idiosoma.

Patrocinium (new). - A "protective" dent, arising from the epiostracum enveloping the base of the siphunculus. Syn. duplicationis stylorum (Vitzthum, 1940).
Puaryngeal chamber (new). - The central part of the infracapitulum, separated by lateral walls from the coxal vaults. Posteriorly, the chamber passes into the infracapitular vault. The mouth is situated in the anterior entrance of the chamber.

Plethotaxy (Grandjean). - The secondary increase in number of a certain organ, corresponding with an apparently disorderly insertion. The homology of each organ individually is obscured, and a notation is finally impossible.

Sejugal furrow. - The furrow separating the coxisternal regions of legs I and II from those of legs III and IV. The furrow is not present in Anactinotrichida.

Siphunculus (new). - Syn. salivary stylus.
Solenidion (Grandjean). - A hollow sensory seta, without basal bulb. It is easily recognizable in Actinotrichida by the absence of actinopilin. In Anactinotrichida it is not recognizable with certainty, although the shape can sometimes suggest a homology.

Stase (Grandjean). - The interval between two moults, as well as the animal itself during this period. There are four stases in Gamasine mites: larva, protonymph, deutonymph, and adult. The term stase must be preferred over stage. Stage has various meanings: two stases can be present in one immobile stage; one stase can consist of a mobile and an immobile stage.

Subcapitular groove (new). - The longitudinal groove in the sternal part of the infracapitulum, running from about the hysterostomal setae ( $h$ ) to the laciniae. The groove passes the mentum, and separates the genae. Syn. protosternum + deutosternum (Gorirossi \& Wharton, 1953), capitular groove (Evans \& Browning, 1956), "Hypostom" (Hirschmann, 1959).

Taenidium (Grandjean). - Collective noun for long, narrow grooves at the surface of the body, which are in relation with stigmata, glands, or the mouth. The peritreme is a taenidium.
Verticil (Grandjean). - A whorl of setae on palp and legs. The primitive number of setae composing the verticil appears to be seven (one dorsal, a pair of latero-dorsals, a pair of latero-ventrals, and a pair of ventrals).

## ALPHABETIC LIST OF ABBREVIATIONS USED IN FIG. I-I9

$a$, anterior infracapitular seta
$a d_{1}, a d_{x}$, adanal setae.
ap.c, capitular apodeme.
apd, anterior paradactylus.
$C H$, chelicera.
$C O$, corniculus.
$c s$, cheliseta.
$C V$, coxal vauit.
$d$, dorsal seta of the appendages (incl. chelicerae).
$d g$, efferent duct of gland.
$d r$, dorsal ridge of the cervix.
$d_{1-8}, d_{x}$, setae of the dorsal series of the dorsal shield.
$e$, latero-coxal seta of the palp.
$e I$, latero-coxal seta of leg J.
FI, fimbrilla.
$G$, gena.
$g c$, orifice of a gland in the fixed bit of the chelicerae.
$g l_{1-2}$, orifices of glands, laterally of the ventri-anal shield.
$g_{1}$, seta of genital shield.
$h$, hysterostomal or posterior infracapitular seta.
$H$, mentum.
id, dorsal lyrifissure of the chelicera.
$i f^{\prime}, i f^{\prime \prime}$, lateral (anterior, resp. posterior) lyrifissures of the femur.
$i f d$, dorsal lyrifissure of the femur.
$i s_{1-2}$, lyrifissures of sternal shield.
ita', ita", lateral (anterior, resp. posterior) lyrifissures of the tarsus.
itad, dorsal lyrifissure of the tarsus.
itap ${ }^{\prime \prime}$, supposed proximal lyrifissure of the tarsus.
itav, ventral lyrifissure of the tarsus.
$i \alpha$, antiaxial lyrifissure of the chelicera.
$i_{1}$, lyrifissure of dorsal shield.
$J i, J i_{1}, J i_{2}$, ventral commissure of the mouth.
$J_{s}$, dorsal commissure of the mouth.
$l^{\prime}, l^{\prime \prime}$, lateral setae of the appendages.
I.A, labellum.
$L C$, lacinia.
$l d^{\prime}, l d^{\prime \prime}$, latero-dorsal setae of the appendages.
$l i$, ligament attaching the cheliceral tectum to the dorsal ridge of the cervix.
$L G$, labial gutter.
$L S$, labrum.
$l v^{\prime}, l v^{\prime \prime}$, latero-ventral setae of the appendages.
$l_{1-6}$, setae of the lateral series of the dorsal shield.
$m g_{1-10}$, setae of the marginal series of the dorsal shield.
$m s_{1}$, seta of metasternal shield.
$m p_{1}$, seta of metapodal shield.
$m_{1-2}$, median infracapitular setae.
$m_{1-4}$, setae of the median series of the dorsal shield.
$P A$, patrocinium.
$P C$, pharyngeal chamber.
Pry, pharynx.
ppd, posterior paradactylus.
$p p_{1-4}$, pores of the peritrematal shield.
$p s_{1}$, pore of metasternal shield.
$p v_{1}$, pore of ventrianal shield.
$p_{1-21}$ pores of the dorsal shield.
sa, "sacculus" of coxa I.
$S I$, siphunculus.
$s_{1-3}$, sternal setae.
$T E$, cheliceral tectum.
$t_{1-3}$, muscles (tendons) of the chelicera.
$v^{\prime}, v^{\prime \prime}$, ventral setae of the appendages (incl. chelicerae).
$v_{1-3}$, ventral setae of the ventrianal shield.
$x$, fusion of sternal and holopodal shield in front of acetabulum II.
$y$, fusion of sternal and holopodal shield in front of acetabulum III.
$\zeta$, hollow seta resembling a eupathid.
$\omega$, hollow seta resembling a solenidion.

## SUMMARY

In the present paper a detailed description is given of a large Macrochelid mite. It is an example of a morphological study of the Gamasina according to methods and views hitherto especially employed in Oribatid morphology.

The application of these methods resulted in the observation of several unknown or insufficiently studied structures. The following list is a concise summary of the main results.
I. Four layers of the tegument are distinguished: cerotegument, epiostracum, ectostracum, and hypodermis. The so-called "pores" are distinguished here into court-pores and lyrifissures. It is demonstrated that borders of sclerotized shields of the idiosoma, or even complete shields can be covered by weak, wrinkled epiostracum.
2. The peritreme, which is an open groove and no tube, is not looping; a split in the bottom debouches into the stigma. The peritrematal plate presents several court-pores.
3. The gnathosoma is regarded as consisting of a cheliceral frame and an infracapitulum. The epimeric character of both parts is especially emphasized; this view is proved by the existence of a capitular apodeme, starting from the border of the two epimeres. The infracapitular setae are consequently epimeric, and no coxal setae. A latero-coxal seta $e$, hitherto unknown in Camasina, appears to be present in the coxal region of the palp.

The basal ring of the gnathosoma is considered here a secondary extension: a capitular retrotectum. The cheliceral tectum is attached by means of a ligament to the anterior border of the median dorsal ridge of the infracapitulum.

The infracapitular setae appear to be homologous with those in Actinotrichid mites. Consequently, they are named here hysterostomal ( $h$ ), median ( $m_{1}, m_{2}$ ), and anterior (a). The ventral surface of the infracapitulum is regarded as consisting of mentum and genae; the dorsal surface is named cervix.

The cervix subdivides the gnathosomal tube into a cheliceral vault and an infracapitular vault. The infracapitular vault contains a median pharyngeal chamber, and a pair of lateral coxal vaults.

A pair of efferent ducts of glands run from the idiosoma through the coxal vaults to the siphunculi (syn. salivary styli). It appears that the so-called "duplicationes stylorum" are thin "protective" dents, arising near the base of the siphunculi; they are named here patrocinia.

The pre-oral continuations of the pharyngeal walls are named here lips. The dorsal continuation is the labrum or upper lip; the latero-ventral continuations are named lateral lips. The lateral lips are very complicated in Gamasine mites. The ventral part is fused to a labial gutter (syn. hypopharynx) which in the anterior part is grown together with the genae. The labial gutter has a pair of anterior dorsal processes (the fimbrillae), and a pair of anterior ventrals (the laciniae). The laciniae are at the same time a prolongation of the bottom of the subcapitular groove. Dorsally, the walls of the labial gutter pass into the labelli, pilose flaps, also attached to genae and cervix. Labelli and genae are the walls of the pre-oral cavity.

The name tritosternum, indicating a structure which is no sternum at all, is abandoned here and replaced by furca.
4. Chelicera and palp are figured in various projections. The face; are distinctly different. Authors should mention the orientation, especially in the case of the chelicera.
5. The value of the determination of verticils and a possible dorsal seta $d$ for a comparative study of leg chaetoxaxy is especially emphasized. A specialized laterocoxal seta el appears to be present on the coxa of leg $I$; it is the first record of this seta for this group of mites. Special attention is paid to lyrifissures, false articulations, and ambulacra.
6. Methods and techniques applied in the course of the present study are summarized, and some morphological views are explained.
7. A list of terms introduced in Gamasine morphology is added at the end of the paper, accompanied by definitions and, if nevessary, by an anthology of synonyms.

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