THE GNATHOSOMA OF HERMANNIA CONVEXA (C. L. KOCH) (ACARIDA: ORIBATINA) AND COMPARATIVE REMARKS ON ITS MORPHOLOGY IN OTHER MITES

by

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With 12 text-figures

In most groups of mites the gnathosoma is rather easy to study as a whole because it can be completely separated from the idiosoma without much difficulty. In Oribatid mites, however, the membrane attaching the chelicerae to infracapitulum and rostrophragma is very thin; separation of the gnathosoma consequently results in tearing the membrane, either between chelicerae and infracapitulum, or between chelicerae and rostrophragma. In both cases the original position of the chelicerae and their exact relation to camerostome and remaining part of gnathosoma, is difficult to reconstruct. As a result of this, only parts of the Oribatid gnathosoma have been described in literature. An extensive study of the infracapitulum (especially of its ventral surface) was published by Grandjean (1957b). Its dorsal surface was studied separately by the same author (Grandjean, 1957a). Many data are also known on the chelicerae. Until recently, however, no serious, modern attempts had been made to study the Oribatid gnathosoma in its entirety.

In view of a comparative morphology of the acarid mouthparts, a better understanding of the condition in Oribatid mites was, however, indispensable. For this reason a species had to be chosen in which especially the cheliceral frame could be studied in its original position. Consequently the species should be large (in order to enable sectioning and dissection), and the prodorsum should not be too dark (in order to enable a study of the membrane by transparency). The species should moreover be present in sufficient numbers. Among the material in our collection, one species especially appeared to fulfil these requirements, viz., *Hermannia convexa* (C. L. Koch). This large size mite (length about 1.5 mm) had been collected by me in great numbers at the type-locality (Schwaighauser Forst, N. of Regensburg, Bavaria, Germany). Numerous recently moulted adults, of which the colour was still relatively clear, appeared to be present. The genus *Hermannia* has, moreover, the advantage of being not too primitive and not too highly specialized, representing a condition easily comparable with that in other Oribatid mites.

The Oribatid gnathosoma appears to have close relations to adjacent parts of the idiosomatic exoskeleton, especially to rostrum, camerostome, and podocephalic canal (cf. fig. 1). A study of the gnathosoma should consequently include descriptions of these parts. This thwarts the investigation considerably, as especially the podocephalic canal is difficult to study. It starts on the cotyloid wall of acetabulum I, hidden by acetabular tectum and trochanter I. The canal runs in the direction of the gnathosoma and is indeed distinctly present in the laterodorsal part of the infracapitulum. The connection between proximal and distal part of the canal was up to now, however, unknown.

It stands to reason that repeated investigations are needed to arrive at a complete reconstruction of the Oribatid gnathosoma. Recommencing over and over again is a time-devouring procedure, for which patience and skill are indispensable. Special care should be taken not to warm the specimens too much and too rapidly, in order not to destroy the cheliceral frame. Diluted lactic acid (two parts of lactic acid and one part of distilled water) is to be preferred. Materials in lactic acid as well as in alcohol must be used for the preparation of sections. Trochanter I should be removed with a small needle from the inside outwards. When a complete reconstruction is at last attained, the definitive figures should be prepared after new material.

In this way, I have indeed succeeded in building up a three-dimensional image of the mouthparts in question. The present paper contains the main results of the investigation. It is composed in the following way. After a description of gnathosoma and adjacent parts, a number of other characters which appeared to be of interest are mentioned. These are followed by some remarks of general importance, a glossary, and an alphabetic list of abbreviations. Figured structures are orientated according to the directions recently drawn up by me in a description of a Gamasine mite (Van der Hammen, 1964: 38).

DESCRIPTION OF GNATHOSOMA AND SOME ADJACENT PARTS

Topography. — A general survey of the region described here is given in fig. 1, in which the gnathosoma is represented in a natural position, partly hidden by the camerostome. The rostrophragma (to which the cheliceral frame is attached) is visible by transparency. Because the specimen is viewed slightly from below, the podocephalic canal can also be seen; it is partly inside acetabulum I, and its further course can be followed by transparency through the prodorsum. The description of these complicated structures is, for the sake of clearness, subdivided here into the following sections:

rostrum, camerostome, cheliceral frame, chelicerae, internal and external parts of the gnathosoma, infracapitulum, podocephalic canal, spatial relations.

Rostrum. — The cheliceral frame is dorsally attached to a structure named "cloison rostrale" by Grandjean (1934: 355); this term is translated

Fig. 1. *Hermannia convexa* (C. L. Koch); lateral (oblique) view of anterior part of prosoma (chelicerae, greater part of palp, and legs removed; the figure has been prepared after a specimen of which the left part of the body was separated by a longitudinal section); × 295.

here by rostrophragma. Rostral tectum (cf. Grandjean, 1934: 355; 1952: 33; 1958: 430, fig. 2) is replaced here by rostrum; it is not considered here a tectum. It consists of the anterior part of the prodorsum, of the rostrophragma and of the cavity between them. This cavity probably contains elements of precheliceral origin.

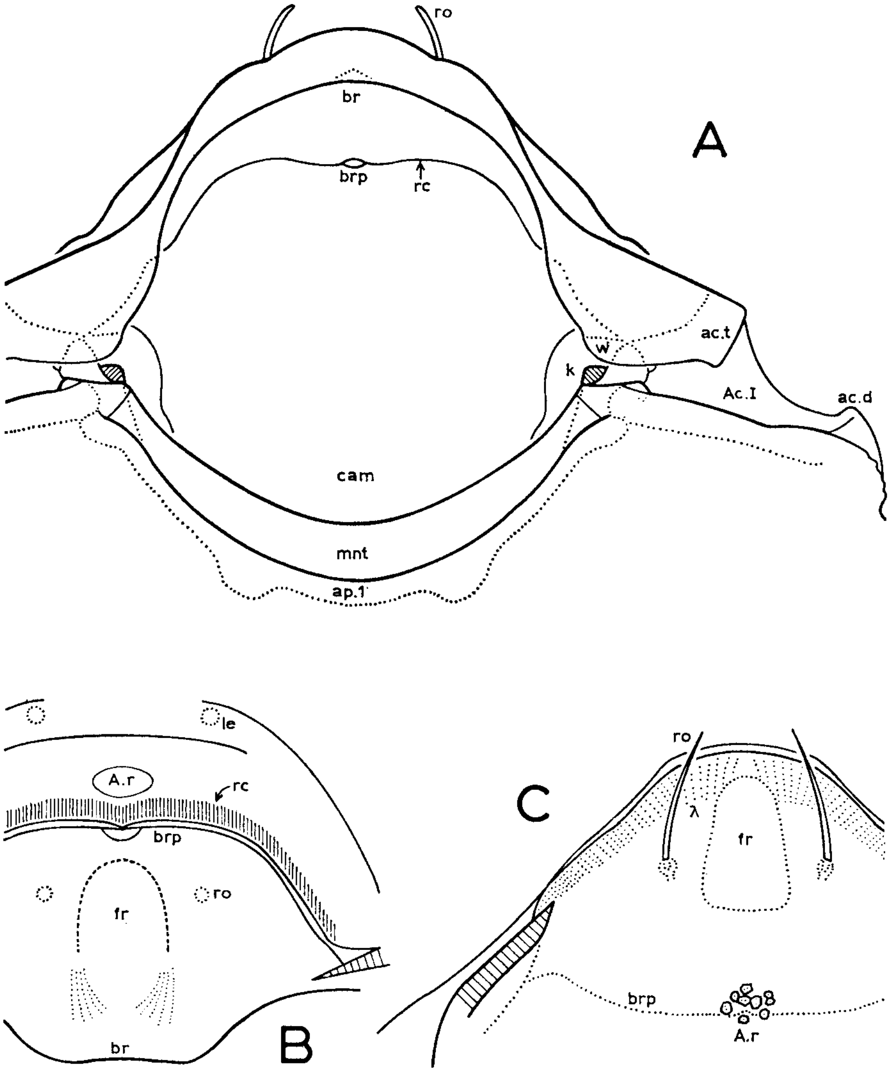

Fig. 2. *Hermannia convexa* (C. L. Koch); A, ventral view of camerostome; B, rostral part of camerostome (inner side), viewed from behind; C, dorsal view of a nearly horizontally orientated and slightly flattened rostrum; A-C, X 235.

In fig. 2C the rostrum is represented in dorsal view (slightly flattened). It has a marginal limb, of which the inner border is indicated by λ. The rostrum presents a dorsal fenestrate area (*fr*) in the shape of a distinctly vaulted clear spot. It is not impossible that, under this clear spot, nervous centres of precheliceral (rostral) origin will be discovered, homologous with the centres that innervate the naso of some primitive Oribatid mites and Endeostigmata. Posteriorly of the fenestrate area, a very small, median, rostral "porose area" is distinctly visible (fig. 2B, C: *A.r*). Because the greater part of the prodorsum represents already a porose area consisting of small pores, the rostral area with distinctly larger pores is possibly composed of sacculi. The structure is not studied here in detail. The posterior border of the rostrophragma (fig. 2C: *brp*) is visible by transparency. Because it is important to know the exact extension of the rostrophragma, its posterior border (to which the cheliceral frame is attached) is also represented in two other orientations in fig. 2A, B; in both figures the room between prodorsum and rostrophragma is indicated as rostral cavity (*rc*). Fig. 2A represents a ventral view of the camerostome; in fig. 2B the rostrum is separated and orientated in posterior view. Fig. 2A-C illustrate that the rostrophragma is a thin lamella (it is chitinous) that starts from the inner border of the rostral limb (λ) and extends in posterior direction (cf. also fig. 1, 12: *rp*). It runs nearly parallel to the prodorsum, at a small distance only. Laterally it is attached close to the lateral border of the rostrum.

Camerostome. — The camerostome is best visible in ventral view, after separation of the gnathosoma. It is represented in this orientation in fig. 2A. It contains the rostrophragma. Its anterior and lateral borders are the borders of rostrum and prodorsum. Its posterior border consists of the mentotectum (*mnt*) which protects the posterior border of the infracapitulum. Posterolaterally, a condyle for the articulation of the gnathosoma is present; the gnathosoma turns on a transverse axis passing through these condyles.

Cheliceral frame. — Grandjean (1936a: 416; 1957b: 239) subdivided the gnathosoma into two parts, of which the first was named by him "cadre mandibulaire"; Grandjean (1957b) defined it as the epimere of the cheliceral segment. Some years ago (Van der Hammen, 1961: 176) I introduced "cheliceral frame" as English translation of the term. The cheliceral frame in Oribatid mites and even in all Acarids has never been studied in its full extension. As mentioned in the introduction, it is very difficult to observe in the first mentioned group. It is represented in fig. 3 and 4 for the first time in full detail. I abandon here its definition as epimere, which in my opinion is only partly correct. Cheliceral frame is defined here as the membrane that constitutes the body wall in the region between rostrophragma and infracapitulum (line of attachment: *at*), and to which the chelicerae are movably attached by means of the cheliceral sheaths

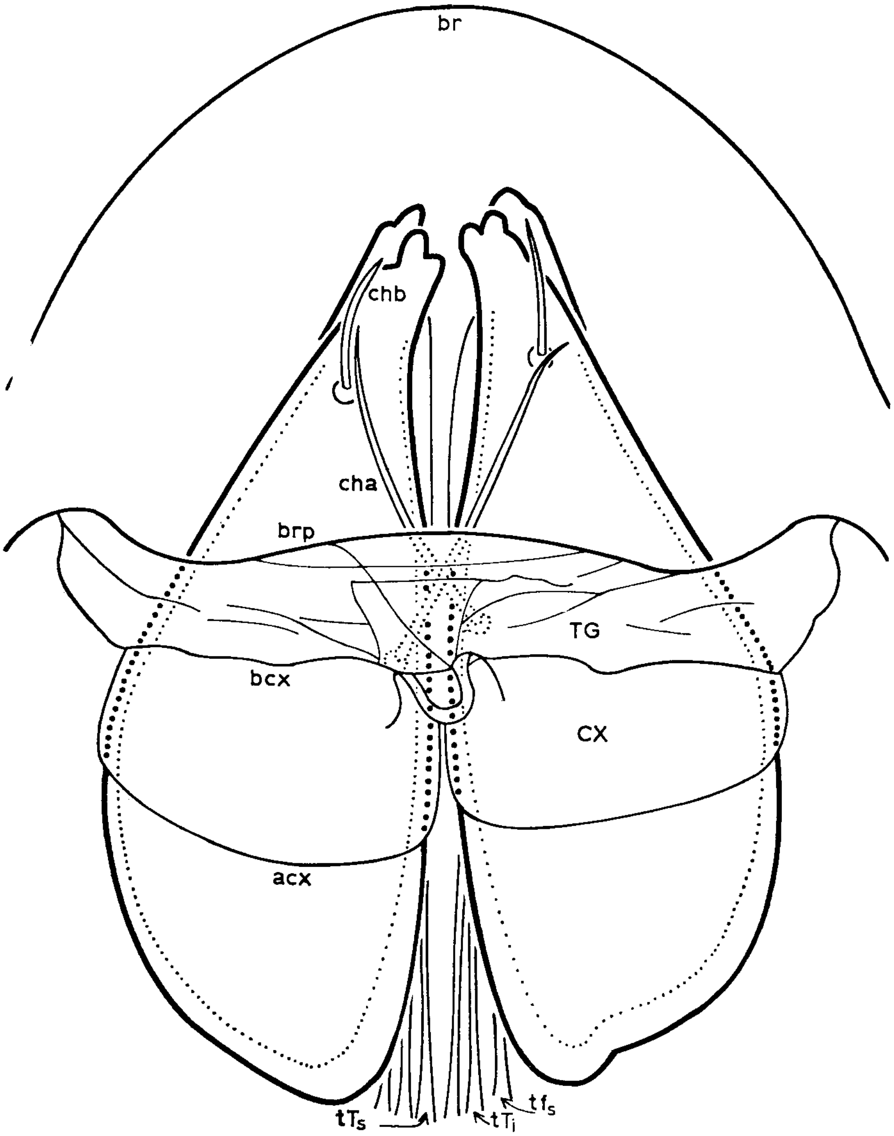

Fig. 3. *Hermannia convexa* (C. L. Koch); dorsal view of gnathosoma (observed through prodorsum) with completely retracted chelicerae (although the outline of the rostrum and the posterior border of the rostrophragma are drawn, the gnathosoma is supposed to be uncovered); × 490.

(it would also be possible to include the sheaths in the definition of the frame).

The cheliceral frame consists of three regions which are contiguous: dorsal, sternal, and ventral. The sternal region is very narrow; together with the cheliceral sheaths (which represent the coxal regions) and with the relatively small ventral part, it constitutes the cheliceral epimeric region. The dorsal part is named here tegulum; it is not regarded here as part of the cheliceral epimere, but as part of the wall of the head in front of it.

The cheliceral frame of *Hermannia convexa* is represented in fig. 3 and 4 in dorsal, lateral, and frontal view. The figures have been prepared after a specimen with completely retracted chelicerae; only in this position tegulum and cheliceral sheaths can be conclusively studied by transparency. Although the prodorsum was present, the figures are reproduced as if the gnathosoma was uncovered.

In retracted position the tegulum (fig. 3, 4: *TG*) is recognizable as an unpaired membrane, attached at the posterior border (*brp*) of the rostrophragma; this unpaired condition can be verified by studying the transverse folds of the membrane. The lateral fold, drawn in fig. 3, does not represent a lateral border; because the cheliceral frame completely separates the body cavity from the exterior, it extends everywhere from rostrophragma to infracapitulum.

The bases of the cheliceral sheaths (fig. 3, 4: *bcx*) are attached to the cheliceral frame. They represent the coxal regions of the cheliceral segment (fig. 3, 4: *CX*). The distal part of the sheaths is attached to the chelicerae; the line of attachment is indicated as *acx* (a further description of the attachment is given in the section on the chelicerae). As mentioned above, the "sternal" part between the chelicerae is very narrow (cf. fig. 3). In the dorsal median part, the transition from tegulum to sheaths is distinctly reinforced.

This reinforcement is certainly connected with the reversibility of the sheaths. The chelicerae are represented in fig. 3 and 4 in retracted position. When they are protracted, the sheaths turn "inside out". The protracted condition should be considered the original position of a coxal region; the possibility of retraction is certainly a secondarily acquired character.

Chelicerae. — Grandjean (1948: 314) recognized three cheliceral segments in Oribatid mites, viz., trochanter, principal segment, and apotele. The trochanter, which still has a proximal position in some primitive Oribatid mites, has developed a ventral, for the greater part paraxial position in the remaining Oribatids. The principal segment must be considered a fusion of femur, genu,

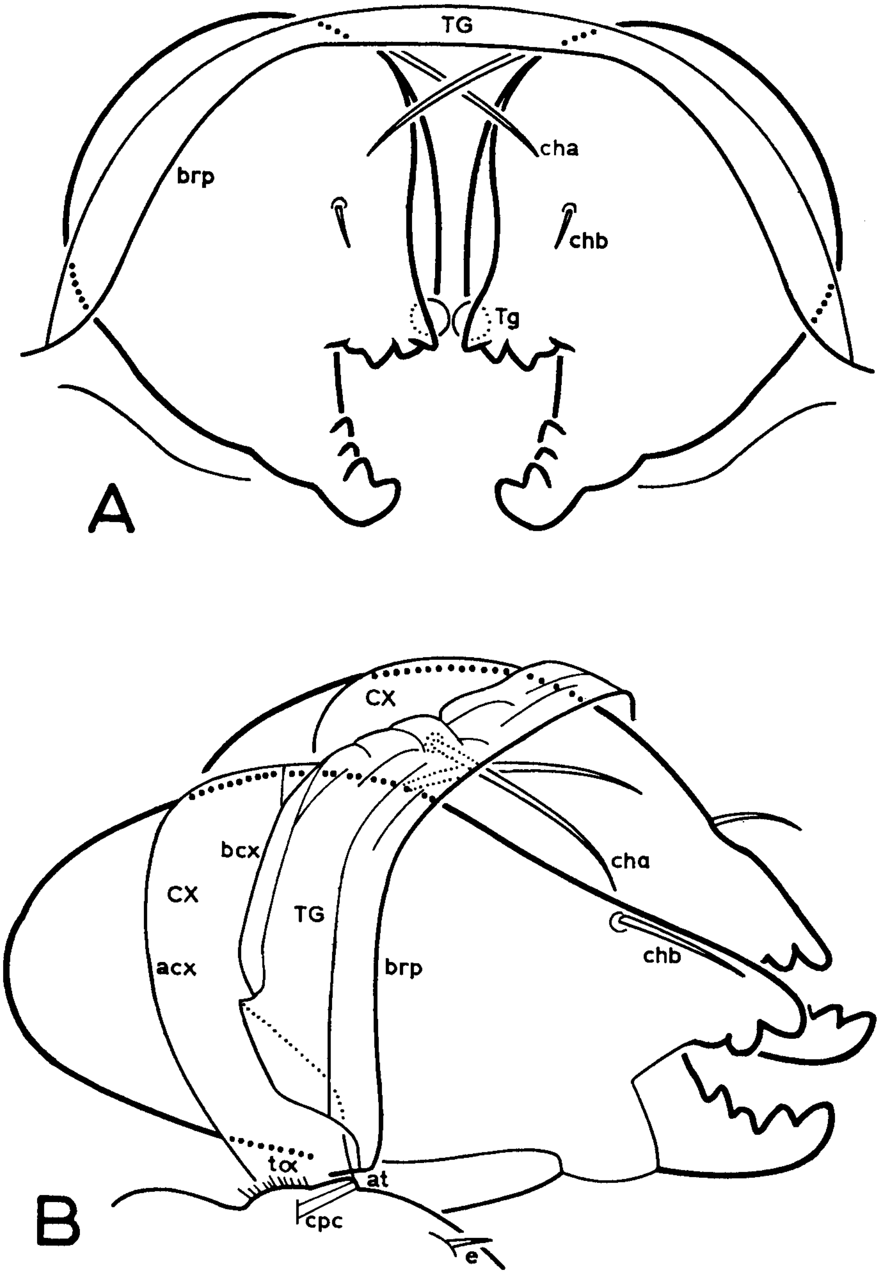

Fig. 4. *Hermannia convexa* (C. L. Koch); A, frontal view of chelicerae and cheliceral frame; B, lateral (oblique) view of chelicerae, cheliceral frame, and part of infracapitulum (although the posterior border of the rostrophragma is drawn, the gnathosoma is supposed to be uncovered); A, B, × 490.

tibia, and tarsus. These views are accepted here; they appear to be confirmed by a study of the tendons, as will be demonstrated below.

The chelicera of *Hermannia convexa* is represented in fig. 5 and 6. The apotele or movable bit is slightly longer than the fixed bit; it turns on a transverse axis passing through the condyles *k* and *k'*. The principal segment has the usual setae *cha* and *chb*; there is no lyrifissure. The trochanter is reduced to a thin paralateroventral chitinous plate with indistinct borders.

The cheliceral sheath is attached according to the line *acx*; part of the principal segment consequently is internal. The external part has a granulate structure which is nearly completely absent on the internal part (some granules are found internally, close to *acx*).

The paraxial surface of the chelicera (fig. 6A) presents a number of

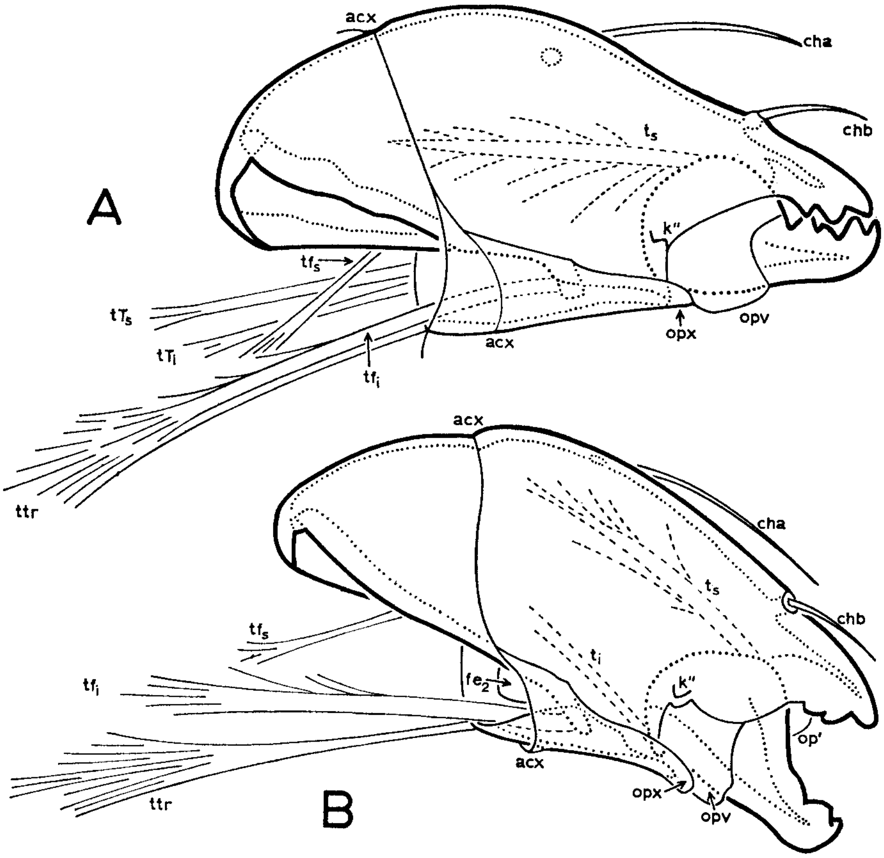

Fig. 5. *Hermannia convexa* (C. L. Koch); A, lateral (antiaxial) face of right chelicera; B, idem, but oblique view of a chelicera of which the coxal part is nearly completely removed; A, B, × 370.

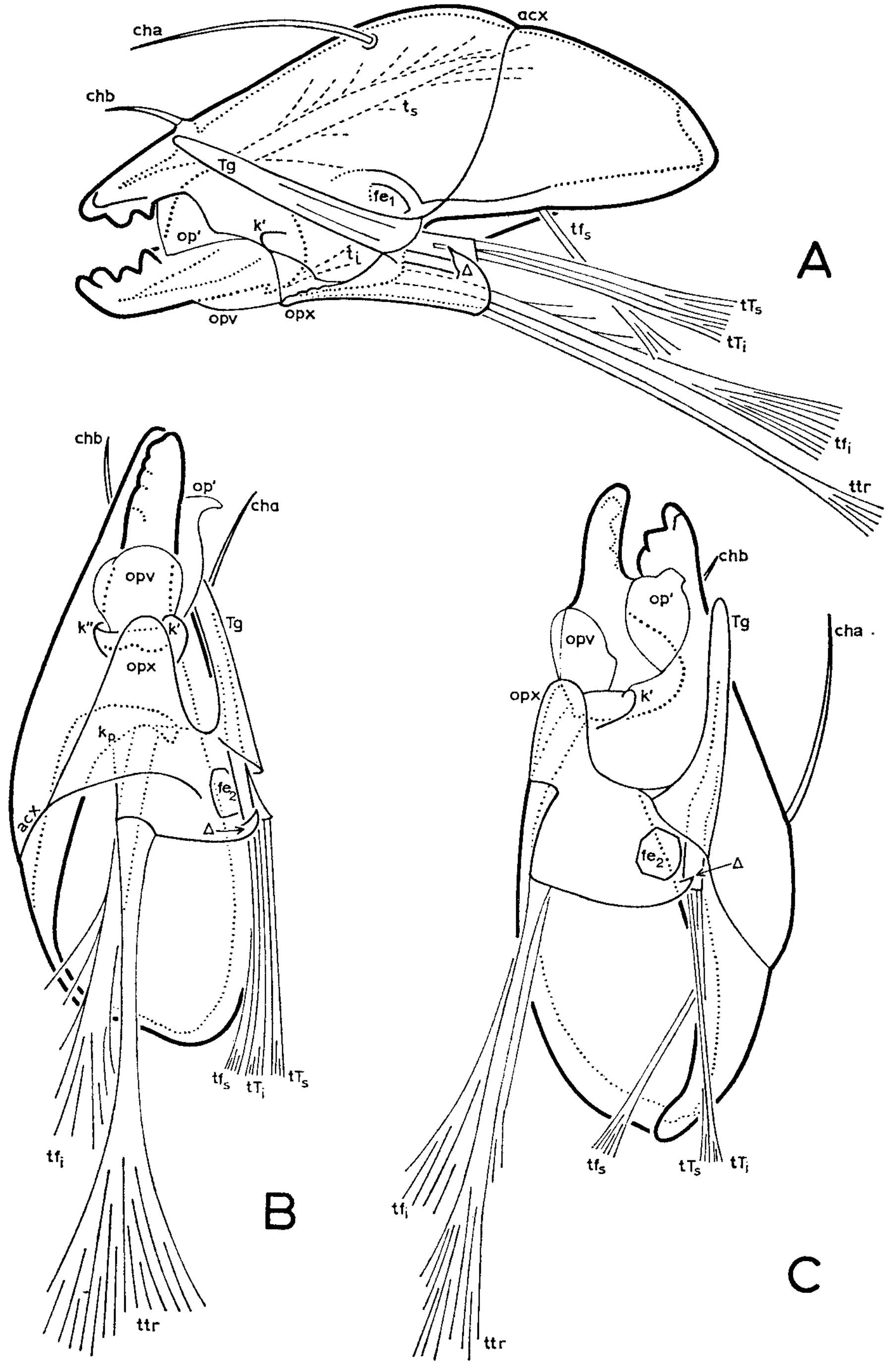

Fig. 6. *Hermannia convexa* (C. L. Koch), right chelicerae; A, lateral (paraxial) face; B, antilateroventral face (sheath partly removed); C, paralateroventral face (sheath removed); A-C, × 370.

interesting characters. Trägårdh's organ (*Tg*) is present in its usual shape and position. Its epiostracum (or complete cuticle) appears to be a continuation of the cheliceral sheath. It has an internal sclerite which articulates with a tooth (fig. 6A-C: Δ) of the trochanter; this tooth is difficult to observe, and should be studied in various orientations. The sclerite has two tendons attached to its base (tT_s and tT_i); consequently, the organ will probably be movable. The principal segment presents a paraxial fenestrate area (fe_1) dorsally of the base of Trägårdh's organ. Another fenestrate area (fe_2) is present in the paraxial region of the trochanter, ventrally of the base of Trägårdh's organ.

The following tendons are present, beside tT_s and tT_i. The apotele has the usual two tendons t_s and t_i. Two tendons are attached to the principal segment (tf_s and tf_i); they are considered tendons of the femur, just as in the case of *Opilioacarus* (cf. Van der Hammen, 1966: 32, fig. 13A, B). It appeared impossible to establish with certainty whether k_p (at the paraxial border of femur and trochanter) represents a condyle for the articulation of the principal segment. One long tendon is attached to the trochanter (*ttr*). The action of the tendons (individually as well as in cooperation) is difficult to reconstruct. I return to this question in the section on spatial relations. The indications of the tendons are the same as those recently introduced by me (Van der Hammen, 1966) in the case of the appendages of *Opilioacarus*; they are partly different from those introduced by Grandjean (1948: 314-316, fig. 2); his t_s, t_i, $t\pi$, tv_s, tv_i correspond respectively with my t_s, t_i, tf_s, tf_i, *ttr*.

The ventral as well as the paraxial surfaces of the chelicerae present membraneous swellings which are difficult to study. They are apparently continuations of arthrodial membranes. During our annual conference in Geneva in 1966, Grandjean suggested the term oncophysis (ογκος = swelling) as collective noun for these structures. There are at least three oncophysis (cf. fig. 5, 6), which are named here: coxal oncophysis of the chelicera (*opx*), ventral oncophysis of the principal cheliceral segment (*opv*), and paraxial oncophysis of the principal cheliceral segment (*op'*); these terms can be shortened to coxal, ventral, and paraxial oncophysis. Grandjean (1959: 360) introduced the name "bouffissure paraxiale" in the case of *op'*, and "intumescence ventrale" in the case of *opv*. The exact shape of the three oncophysis is represented in fig. 5 and 6. It is not impossible that Trägårdh's organ is an oncophysis in which an internal sclerite has developed; its epiostracum (or complete cuticle) is also a continuation of an arthrodial membrane (of the cheliceral sheath). I return to the question of its homology and to other important problems concerning *Tg* in remark 3.

Internal and external parts of the gnathosoma. — As mentioned above, the cheliceral frame constitutes the body wall in part of the gnathosomatic region. Consequently, it separates internal and external parts, body cavity and the outside. Because dissection of the gnathosoma results in destruction of the cheliceral frame, the exact border between internal and external parts appears as a rule not to have been recognized. For this reason the course of this border is summarized and repeated once more in the present section. Starting with the base of the rostral limb (λ), the wall is constituted by rostrophragma and cheliceral frame (cf. fig. 12). The internal part of the chelicerae is bordered by the line *acx* (cf. fig. 5); the body cavity continues into cheliceral sheaths and chelicerae, and these certainly are protracted by hydrostatic pressure. The cheliceral frame is attached to the infracapitulum according to the line *at*, at the posterior border of the podocephalic canal. This canal consequently is external. As mentioned below, the internal part of the chitinous infracapitulum consists of the capitular apodeme. The body

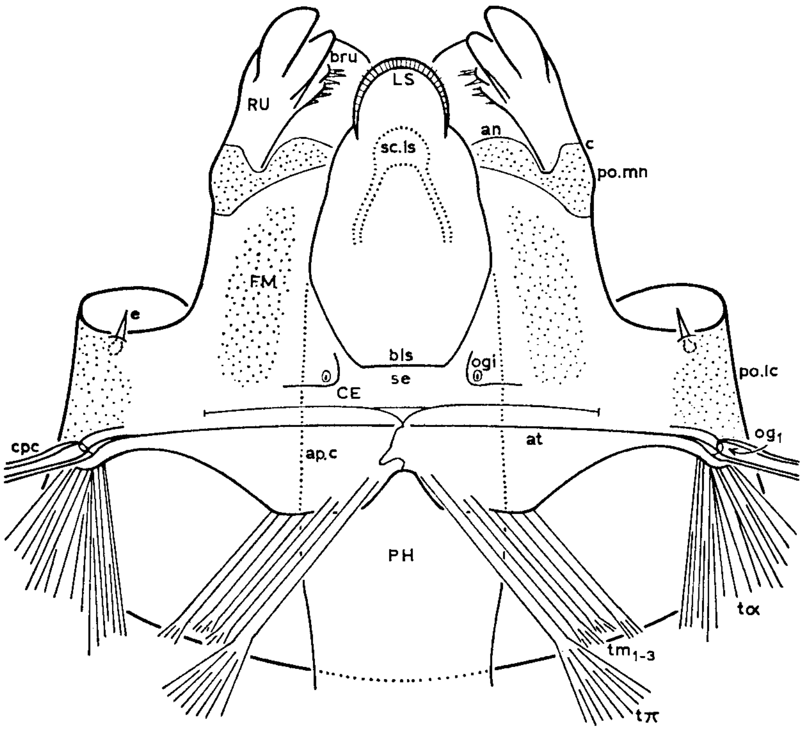

Fig. 7. *Hermannia convexa* (C. L. Koch); dorsal view of infracapitulum (chelicerae removed); × 370.

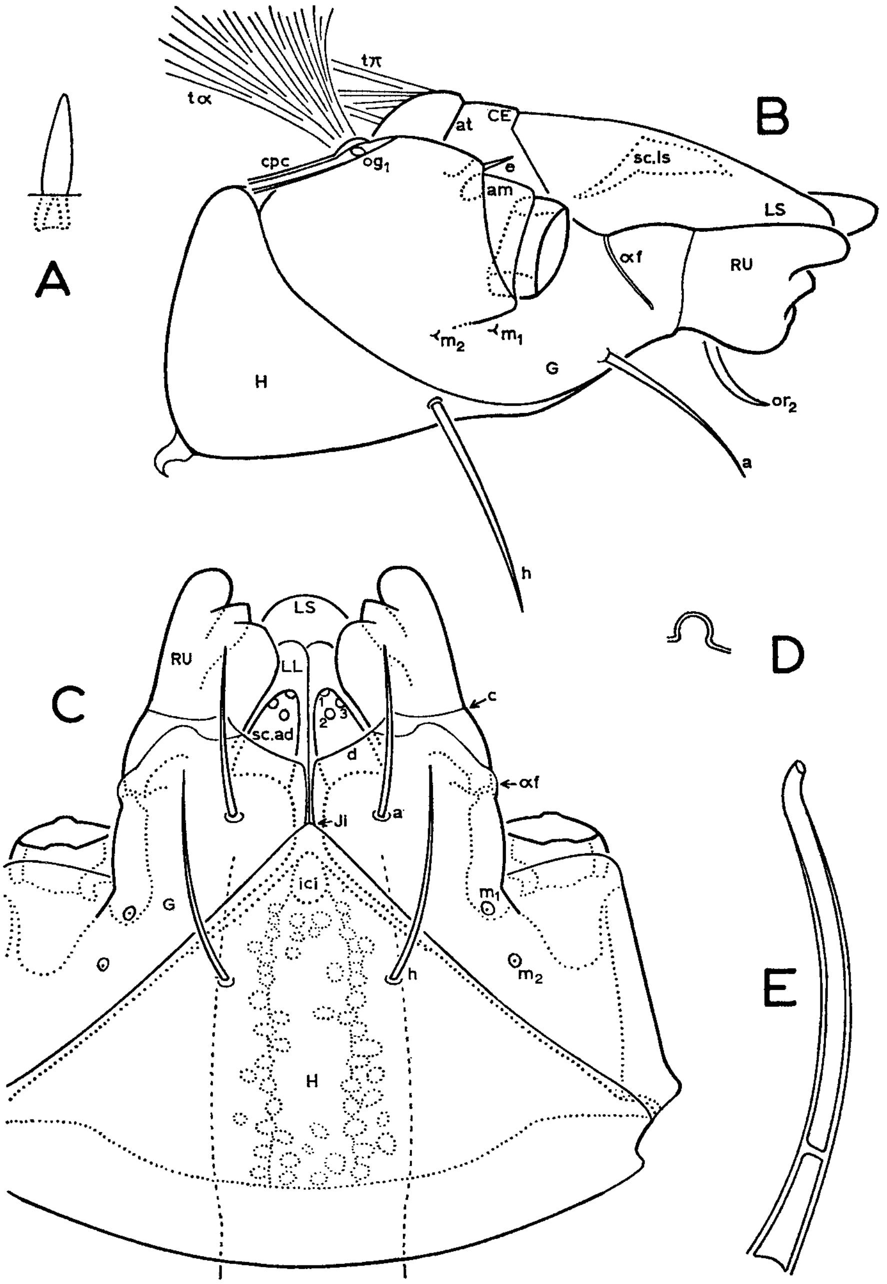

Fig. 8. *Hermannia convexa* (C. L. Koch); A, laterocoxal seta (*e*) of palp; B, lateral view of infracapitulum; C, ventral view of infracapitulum; D, transverse section of podocephalic canal in the region of acetabulum I; E, duct (*dg*1) of anterior podocephalic gland; A, D, × 1315; B, C, E, × 370.

cavity continues of course into the infracapitulum. Between infracapitulum and coxisternal region of the podosoma, the body wall consists of an arthrodial membrane, protected by the mentotectum.

Infracapitulum. — The infracapitulum is represented in fig. 7-10. Its main parts are mentum, genae, and cervix. According to Grandjean's 1957b classification, it is stenarthric; the labiogenal articulation is present, and is directed obliquely backward to a point removed from the base of the palp. In ventral view (fig. 8), the mentum is approximately triangular; in posterior view (fig. 9B), its surface appears to be strongly curved (convex). The mentum bears the usual pair of setae *h*; numerous round spots, close to the median part, represent insertions of pharyngeal muscles.

The paired region between mentum, lateral lips, and cervix represents the genae. These have a dorsal and a ventral surface. Because a section through the pair of genae is V-shaped, the dorsal surface is paraxial, the ventral surface antiaxial. The ventral genal surface bears one pair of anterior infracapitular setae (*a*), and two pairs of medians (m_1, m_2); m_1 and m_2 are reduced to very small, thin setae, although the places of insertion are distinct. The surface of the rutella is a continuation of the surface of the genae. The border between the two (collum) is distinguishable because the surface of the genae is for the greater part porous. The border can also be discovered in polarized light. A manubrial zone, belonging to the gena, is present at the base of the rutella; it is bordered by the collum (fig. 7, 8C, 9A: *c*) and by an antiaxial fissure (fig. 8A, C, 9A: *αf*); dorsally it is easily recognizable because of its being a porose area.

The rutellum belongs to the ordinary atelebasic type: it is large, but the base does not extend to the infrabuccal fissure. Dorsally, it presents the usual brush (fig. 7, 9A: ***bru***).

The lateral lips present the usual adoral sclerite which articulates with the gena. This articulation was named postadoral by Grandjean (1957b: 257). The surface of the sclerite is above the surface of the gena. This is illustrated in fig. 9A, representing an infracapitulum in dorsal view, from which one lateral lip is removed. The area of articulation is bordered by *d* (the anterior border of the gena) and *b.sc* (the base of the adoral sclerite). In anterior view (fig. 10A), the lateral lips are oval in outline; a section near the base (fig. 10B) demonstrates that the lips are less high at that level, and that the sclerite *sc.ad* is ventral and antiaxial. The usual three adoral setae are present; or_1 and or_3 are bifurcate, or_2 is not ramified.

The cervix is short and broad. Posteriorly it is bordered by the line *at*, from which the capitular apodeme is starting. Anteriorly it is partly bordered by the base of the labrum (fig. 7, 7A: *bls*). Cervix and genae pass into each other, and the transitional part is steeply sloping. Posterolaterally of the

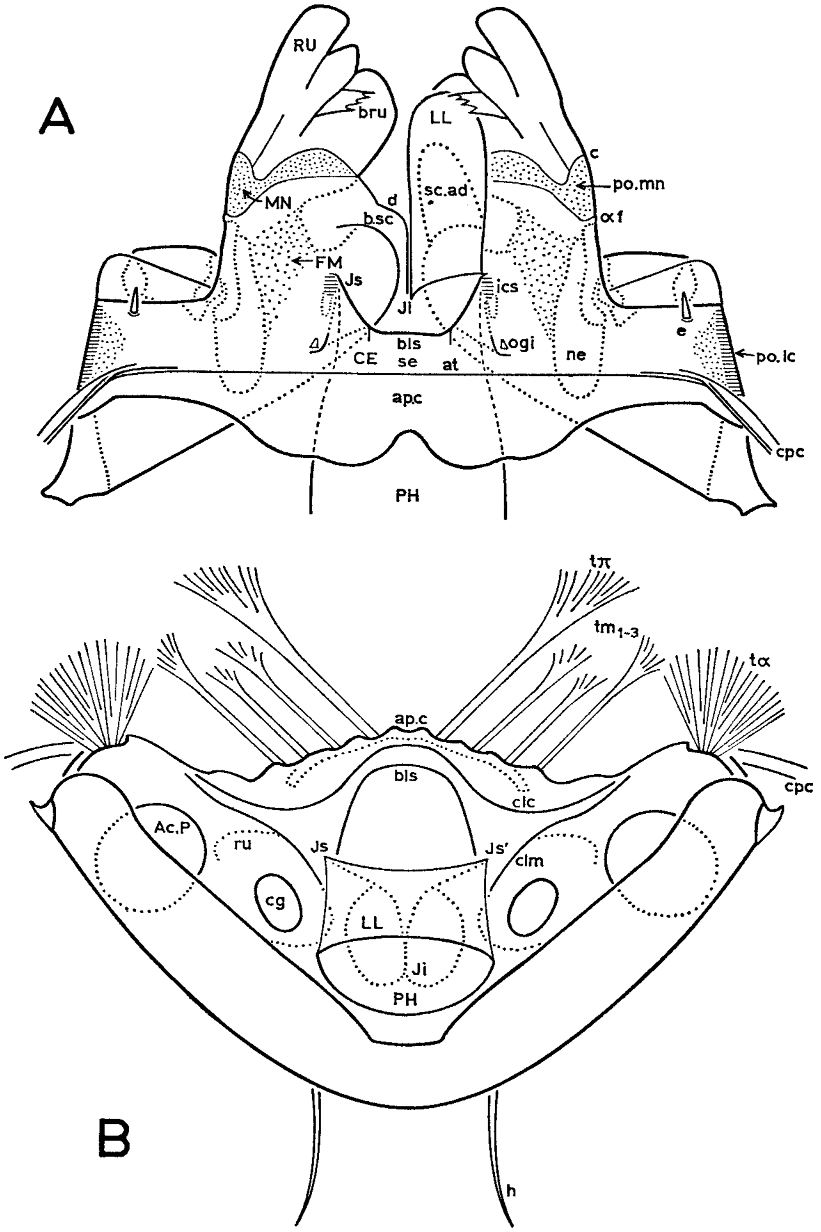

Fig. 9. *Hermannia convexa* (C. L. Koch); A, dorsal view of infracapitulum (chelicerae, labrum, and left lateral lip removed; mentum omitted; the soft parts of the right lateral lip are slightly schematized); B, infracapitulum viewed from behind; A, B, × 370.

labral base (i.e. of the capitular saddle: *se*) the pair of foramina is found and their orifice of the infracapitular glands. Part of the posterior border of the cervix is taken by the podocephalic canal which will be discussed below; its posterior border coincides with the line of attachment of the cheliceral frame. The podocephalic canal is distinct only in the lateral part of the infracapitulum; its course soon becomes obscured.

The dorsal surface of the infracapitulum presents three porose areas, viz., manubrial (fig. 7: *po.mn*), laterocoxal (*po.lc*), and the porose area of the cheliceral groove (*FM*). The last-mentioned groove is a depression in which the chelicerae can move.

The laterocoxal seta (fig. 7, 8A, B, 9A, 10: *e*) has a dorsal position. It is represented separately in fig. 8A.

The capitular apodeme is notched in the median part. It is an internal lamella to which a number of tendons are attached, viz., a large antiaxial one (fig. 7-10: *tα*), three small medians (tm_{1-3}), and a paraxial (*tπ*).

The mouth is triangular (cf. fig. 9); the commissures are *Js*, *Js'*, and *Ji*. The commissural indurations are represented in fig. 9A (the two superior indurations *ics*) and 8C (the unpaired inferior induration *ici*). The pharynx soon develops, however, an oval or a crescent-shaped section.

The labrum (*LS*) is relatively large. Its base can best be studied after a separation of the upper lip itself. This base (fig. 9A: *bls*) is situated in the plane of declivity of the cervix: its dorsal border is situated posteriorly of the dorsal commissures (*Js*, *Js'*). These dorsal commissures are at the border of cervix and genae. The labrum is, in its terminal part, beset with very small teeth. It has an internal sclerite (*sc.ls*) from which a pair of tendons (fig. 12: *tls*) are starting in posterior direction. The sclerite has two posterior branches that probably articulate with the dorsal commissures. The upper lip is moved by action of the tendons, and articulates on an axis passing through the commissures.

When the infracapitulum is studied in posterior view, its internal cavities and its various external contour lines can be studied. In fig. 9B, *clc* is the dorsal contour line at the level of the cervix, *clm* that at the level of the manubrium. It is evident that the transition from cervix to genae is steeply sloping. The cavity between cervix and mentum is connected with the labrum, of which the trapezoid base is represented in fig. 9B (*bls*). The central cavity continues into the genae as genal cavity (fig. 9B: *cg*); it is also connected with the acetabulum of the palp. The genal cavity is, moreover, connected with the central cavity of the rutellum; a section at the base of the rutellum is represented in fig. 10B.

Podocephalic canal. — As mentioned above, the podocephalic canal runs from acetabulum I in the direction of the gnathosoma. Its continuation is visible by transparency through the prodorsum. The canal can further be observed in the laterodorsal part of the infracapitulum (after separation of the gnathosoma from the camerostome), and as a rule an arthrodial membrane with part of the canal remains attached to its lateral border. Consequently, it has an acetabular, a prodorsal, an arthrodial, and a capitular part. The full course of the podocephalic canal (including the connection between

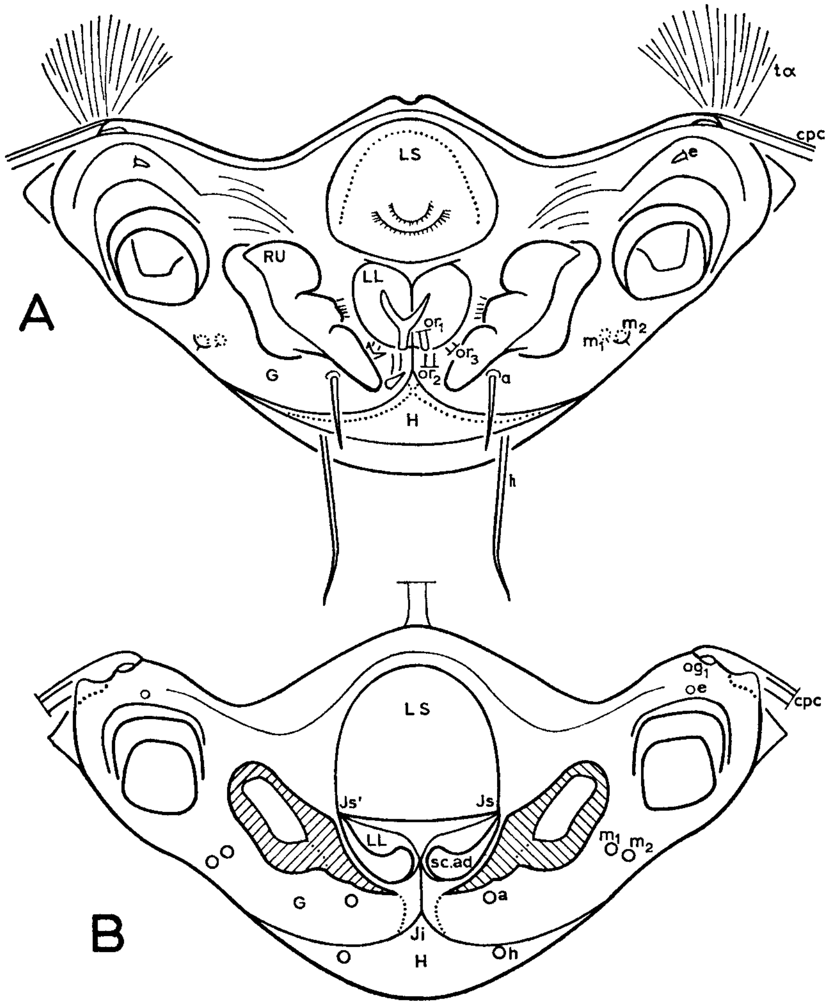

Fig. 10. *Hermannia convexa* (C. L. Koch); A, frontal view of infracapitulum; B, idem, but greater part of labrum, lateral lips, and rutella cut off; A, B, × 370.

the above-mentioned parts), and the glands debouching into it, will be described here for the first time in detail.

The course of the podocephalic canal inside acetabulum I is represented in fig. 1. Its posterior extremity *p* is just under the acetabular tooth *ac.d.* Its course from *q* to *r* can be observed when the acetabulum is studied slightly from below. A small orifice og_2 is present in the anterior half of the acetabular part. A transverse section of the canal (it is open!) is represented in fig. 8D. At *r* the canal disappears under the capitular angle *w*, and takes course to *s* and *t*, following the inner border of the angle; this course can be observed, although with some difficulty, by transparency. At *t* the podocephalic canal reaches the anterior border of its prodorsal part. From here to the infracapitulum, it is incorporated in an arthrodial membrane. This is easy to understand: the gnathosoma is movable, and the canal consequently must be adapted to following the movements.

When a gnathosoma is removed from the camerostome, part of the podocephalic canal, and of the arthrodial membrane remain attached to the infracapitulum. A small strip of the cheliceral frame remains attached to the

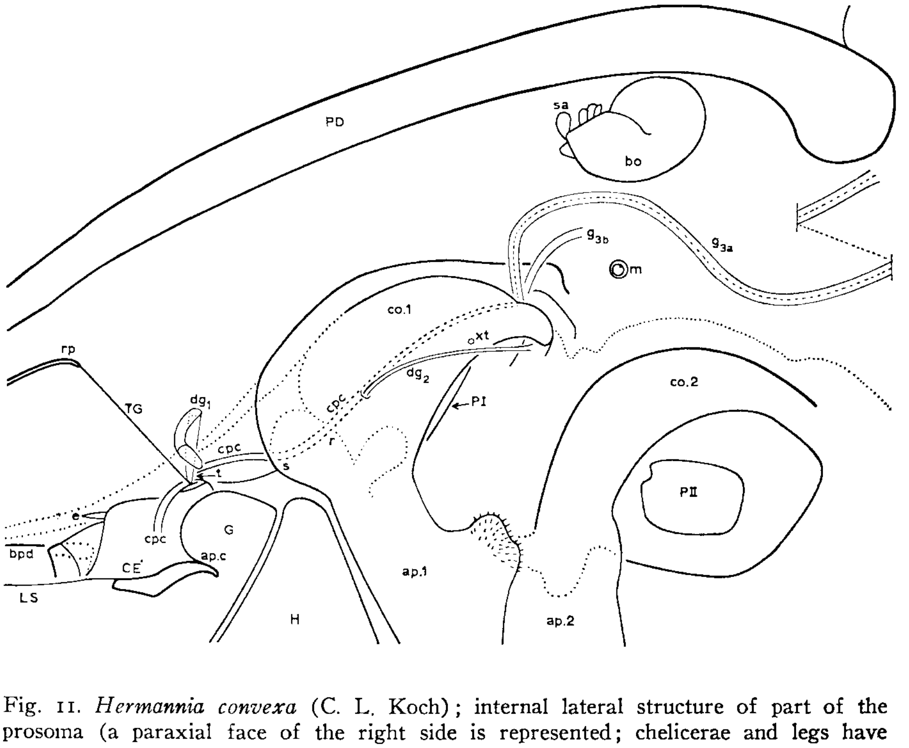

Fig. 11. *Hermannia convexa* (C. L. Koch); internal lateral structure of part of the prosoma (a paraxial face of the right side is represented; chelicerae and legs have been removed); × 295.

line *at*; it partly represents the posterior border of the canal. A small orifice og_1 in the cheliceral frame is present at a small distance from the lateral border of the infracapitulum. As a rule a long, chitinous, colourless tube remains attached to og_1, either at one side or at both. This tube is represented separately in fig. 8E; it has a transverse ridge in the posterior part, and it is much broader proximally than near its orifice og_1. The tube should be studied in various orientations; from fig. 11 it appears that it is indeed hollow.

The course of the canal in the dorsal region of the infracapitulum can be followed for a short distance only; it soon becomes indistinct when it approaches the cheliceral groove. Possibly its secretion afterwards follows the groove, just as will be the fact with the secretion of the infracapitular gland (cf. fig. 7).

Three glands debouch into the podocephalic canal; they are named here podocephalic glands. Possibly, the glands are coxal glands. The glands or their ducts can be observed when a lateral part of the prosoma is separated by a sagittal section, and studied at the paraxial side. An ideal section is represented in fig. 11; the cotyloid wall (*co.1*) of acetabulum I is visible, as well as its connection with apodeme 1 (*ap.1*). The acetabular part of the podocephalic canal can be observed by transparency. A tubiform gland with two branches (g_{3a}, g_{3b}) debouches into the posterior part of the canal, at its posterior extremity. In order to study this gland, special care should be taken not to warm the preparation too much, because the gland is destroyed by heat. The gland has a narrow central lumen. One branch (g_{3a}) is long and extends beyond the posterior border of the prodorsum into the opisthosoma. The other branch (g_{3b}) is shorter and more difficult to study.

In the anterior part of the cotyloid wall, a very narrow, chitinous duct (dg_2) debouches. Its orifice (og_2) is visible at the external side. The duct slightly widens at its base, where the gland has been destroyed by the action of lactic acid.

The prodorsal part of the canal (from *s* to *t*) is also represented in fig. 11. The duct dg_1, debouching into the infracapitular part, is represented in its original position; the figure demonstrates that its orifice is in the cheliceral frame just above the canal. The canal is everywhere external; all the glands and the ducts are internal.

It is not evident in what direction the secretion of the ducts will move. There are two outlets, a posterior and an anterior. The orifice of g_3 is close to the posterior end, og_1 close to the anterior; og_2 is about halfway. Capillary attraction will play an important role. Part of the secretion of the tubular gland will possibly arrive in the neighbourhood of acetabulum I, that of the anterior gland by way of the cheliceral groove near the mouth. It will be important to investigate the histology of the glands.

It is evident that the presence of a podocephalic canal remains one of the most mysterious characters of the Actinotrichida. A conclusive explanation of its functioning, and of that of taenidia in general, has not yet been found.

Spatial relations. — A distinct idea of the spatial relations of part of the structures mentioned above, is obtained by the study of a longitudinal (exactly median) section of a gnathosoma in its original position in the camerostome. This is a difficult task, which is unavoidably attended with numerous failures. The best way is to section complete alcohol specimens with a very sharp razor blade. The sections should pass just between the chelicerae in order to disturb the cheliceral frame as little as possible. The halves should afterwards not be touched at the plane of section. An ideal section, i.e. one which leaves a complete half undestroyed, should pass exactly beside, but parallel to the median plane. After sectioning, the halves should be warmed gently in diluted lactic acid. Before studying the material in a cavity slide, the legs should be removed. Some ten specimens had to be sectioned before arriving at the one represented in fig. 12. Most of the rejected sections can, however, be used for a repeated study of details.

In fig. 12, a gnathosoma is represented in which the chelicerae are in retracted position. Consequently, the sheaths are inverted: the surface figured is the internal one, whilst originally air was present under the surface, from *bcx* to *acx*.

A comparative study of many specimens demonstrates that the position of the cheliceral tendons, as represented in fig. 12, is indeed the natural one. It is rather difficult to reconstruct the mechanism that moves the chelicerae. All of the cheliceral tendons serve to retract (invaginate) the chelicerae; tf_s probably readjusts the chelicerae to a position parallel to the plane of the cervix; tf_i and *ttr* are certainly retractors. Retracted chelicerae extend posteriorly far beyond the capitular apodeme.

When a gnathosoma comes into operation, the infracapitulum is lowered, and consequently leaves the camerostome, whilst the protracted chelicerae at the same time turn over, and follow the course of the cheliceral groove. Because protraction is combined with turning over, the dorsal surface of the cheliceral sheaths is probably longer than the ventral. Judging from the sections, the tegulum can also be protracted, and its dorsal surface then becomes ventral; in this position it is easily comparable with the cheliceral tectum (or its base) in various other groups of mites.

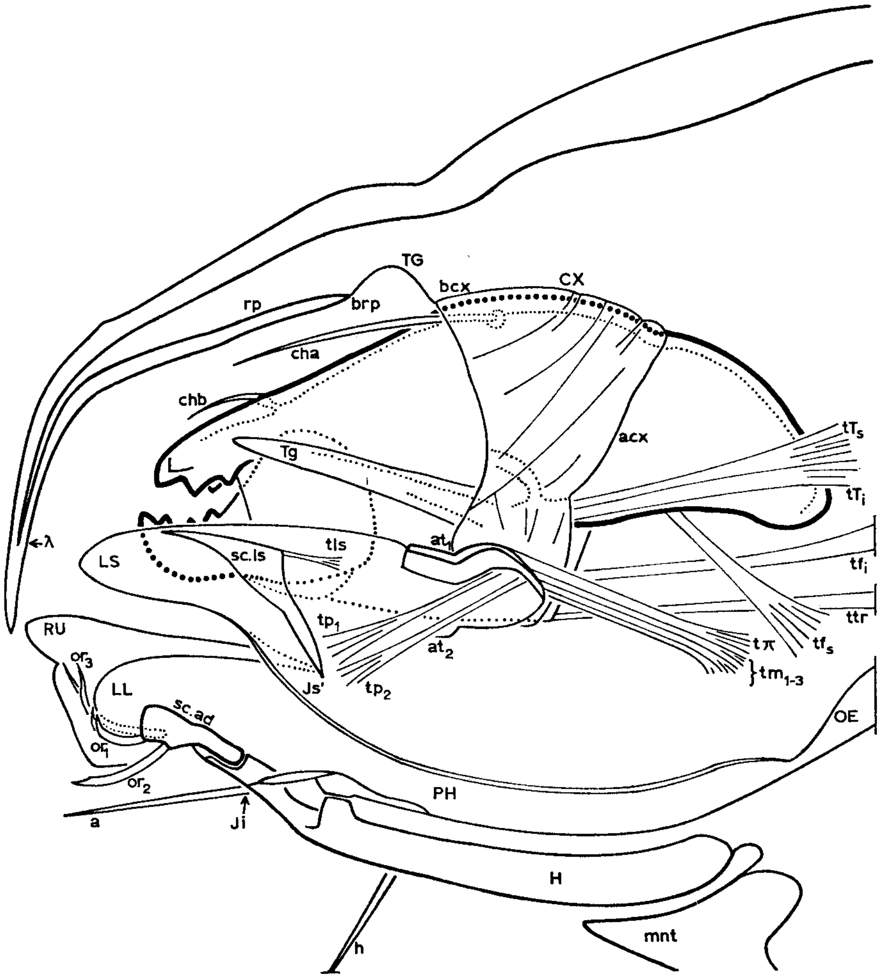

Fig. 12. *Hermannia convexa* (C. L. Koch); longitudinal (median) section of gnathosoma in camerostome (chelicerae nearly completely retracted); × 370.

Fig. 12 demonstrates also the position of the lips with regard to each other and to the pharynx; it demonstrates at the same time the commissures and articulations. The pharynx is recognizable by its well-developed wall; posteriorly it passes into the oesophagus. Tendons attached at the ventral wall of the cervix run in anteroventral direction; their muscles can be attached to the dorsal pharyngeal wall, or to the lateral lips.

The tendons attached to the capitular apodeme retract the infracapitulum as a whole; on that occasion it turns on an axis passing through the condyles of the camerostome.

STRAY OBSERVATIONS ON *HERMANNIA CONVEXA* (C. L. KOCH)

Occurrence. — *Hermannia convexa* has been collected by me in great numbers at Koch's type-locality, the Schwaighauser Forst, N. of Regensburg (Bavaria, Germany). It was found in various samples, taken in different parts of the forest. Apparently, it has a localized occurrence, because according to my data it is absent from other localities in the surroundings of Regensburg; it appeared to be also absent from the remaining of Koch's type-localities in the Oberpfalz (Wernberg, Pleystein, Neumarkt).

The Schwaighauser Forst is an extensive forest of spruce-firs, in places mixed with some deciduous trees (especially beeches); it has an undergrowth of e.g. *Vaccinium*. Samples of litter and moss collected here, appeared to contain a great variety of species, often in considerable numbers of specimens. *Hermannia convexa* is one of the common species of the forest.

There are only a few records of the species in literature, which confirms its localized occurrence. Its area of distribution in Europe is apparently restricted to the central part.

Prodorsum. — There are two relatively large fenestrate areas (clear spots) between the bothridia; they extend from bothridia to interlamellar setae, and anteriorly up to halfway the lamellar setae. They are situated in front of the racemiform spots, two masses of pigment grains near the posterior border of the prosoma, not far from the centre of the body cavity. It is as yet difficult to connect these two structures; it is a relatively long way from the fenestrate areas to the pigment spots, and the light should enter obliquely (from in front and from laterally) in order to reach the spots. The shape of the pigment spots is rather irregular; in reality they are no spots but three-dimensional masses. They are rather firmly attached, because warming in lactic acid, and sectioning do not change their position, even when the greater part of the internal structures have become transparent. I recall that the racemiform organ was already known from the genus *Hermannia*; it was recorded for *Hermannia reticulata* Thorell by Grandjean (1965: 105).

A number of sacculi are attached to the bothridium (fig. 1, 11: *sa*). These are respiratory organs (cf. Grandjean, 1967a: 249-252). They start from the bottom of the bothridium and run in anterior and dorsal direction. They can best be observed when a bothridium is studied separately from the inside. In this orientation it appears that a large porose area occupies the paraxial surface; a tendon is attached to the ventral paraxial part of the bothridium.

Notogaster. — As mentioned already by Sellnick (1923), some species of the genus *Hermannia* present a small, central notogastral porose area. It is situated about halfway between the setae of row *e* and row *f*. It resembles the central prodorsal porose area. Probably it is also no true porose area, but an area of sacculi. I have paid no special attention to it. It should be subject of further investigations.

Ventral region of opisthosoma. — There are two anal setae, nine or ten genitals, and two or three aggenitals. There is a strongly developed preanal organ with two large tendons, and a small postanal organ, apparently with one tendon; these serve as locking pieces of the anal orifice.

Ventral region of the podosoma. — The formula of the epimeres is 3-1-6 (7)-7. Consequently there is a distinctly developed neotrichy of epimeres 3 and 4.

Lateral region of podosoma. — The laterocoxal seta *el* is apparently not present in *Hermannia*, unless it should be incorporated in the acetabular tectum which has an extraordinary development in the genus. No trace of the seta could be discovered with the aid of polarized light. According to Grandjean (1962: 403), *el* is frequently lacking in Nothroidea.

Palp. — The tarsus of the palp has nine setae; *acm*, (*ul*), and *sul* are eupathids. The solenidion ω is inserted close to the base of the segment, proximally of *cm*.

Ovoviviparity. — A number of females in our collection contained eggs, prelarvae, and larvae; consequently, *Hermannia convexa* is ovoviviparous. According to Grandjean, who had a look at the material in 1966, the prelarva belongs to the Nothroid type. One female studied by me was captured at the moment of depositing a larva. This larva was still partly in the ovipositor, and was apparently fixed in this position. Its dorsal and ventral surfaces were orientated parallel to the lateral borders of the adult; in this way it is evidently adapted to the proportions of the genital orifice. The anterior part of the body, in front of leg III, was still in the ovipositor. After separation of the larva, it appeared that part of the dorsal surface was still covered by "membranes", certainly representing egg-shell and prelarval skin. Although the action of lactic acid may have contributed to the liberation of the larva, it appears evident that the larva indeed hatches at the moment of being deposited.

Although I have made no special study of the literature on the subject, it appears that ovoviviparity (in literature recorded as viviparity) is restricted to a few groups. It is recorded for *Trimalaconothrus* and *Trhypochthoniellus*, and according to unpublished observations by Grandjean, it also occurs in *Hygroribates marinus* (Banks) and *Hermannia reticulata* Thorell. Ovoviviparity is apparently more often found in species with an aquatic way of life; its occurrence in *Hermannia* proves, however, that this is no general rule. Further investigations on this subject, and a survey of the published data will be very interesting.

REMARKS

REMARK 1. THE SEGMENTATION OF THE GNATHOSOMA AND OF THE ANTERIOR PROSOMATIC REGION IN GENERAL

In order to understand the segmentation of the anterior prosomatic region, a morphological synthesis should be outlined, reconstructed from anatomical, embryological, and histological data. Because these are up to now nearly completely wanting in the case of mites, the problem should be approximated by comparing the main data known from other groups of Arachnida. These have been summarized by Vandel (1949), Millot (1949), and Dawydoff (1949), and a very important addition, based on the study of the nervous system of Araneida, was published by Legendre (1958). The following is for the greater part based on the results of the last-mentioned author.

Apart from the acron (its ganglion is still recognizable as the central body; the rostral gland also originates from the acron), the following precheliceral segments can be distinguished in spiders: one or more metameres to which the eyes belong; a preantennular metamere (with cerebroid ganglion and fugacious appendages of the vesiculae laterales); and the segment of the tritocephalon (with rostral ganglion, and labrum). The last-mentioned segment is followed by the segments of chelicerae and palp, between which a fugacious segment probably has been present.

According to Legendre (1958), Arachnida are characterized by the absence of deutocerebron and segment of antennae 2; the last-mentioned character is also met with in Insects. Other characters exhibited by the development of the nervous system have some analogy with the Myriapods. As to Crustacea, these are the Arthropods presenting the least affinity with Arachnida.

In view of the uncertain number of precheliceral segments, arachnologists as a rule indicate the cheliceral segment as segment I. The comparative arachnid morphology is based on this numbering. Giving the number I to the precheliceral segments together (as has recently been done by Evans, Sheals & Macfarlane, 1961: 37) is confusing. These authors (1961: 37) have moreover homologized the prosomatic and cephalothoracic appendages in Arthropods in a way that does not take into account the data mentioned above.

In view of a correct interpretation of the gnathosoma, it is of considerable interest to know which parts of gnathosoma and prodorsum are of precheliceral origin. Judging from the facts mentioned above, at least the labrum is of rostral origin. An important part of the precheliceral segments is, however, present in the prodorsum, e.g. naso, eyes (if present), various parts of the central nervous system, etc.

It is to be expected that further studies on the internal anatomy of the prosoma, especially of Opilioacarida on the one hand and Endeostigmata on the other, will be important contributions to our concept of the precheliceral region.

Up to now I have considered the complete infracapitulum to be part of the segment of the palp, not taking into account its complicated organogeny. From the above it will be evident that at least the labrum and its base should be excluded from this definition.

It is also evident that the gnathosoma cannot be defined as a fusion of precheliceral, cheliceral, and palpal segments, the tergites of which constitute the gnathosomal roof, as has erroneously been done by Hughes (1959: 135). The gnathosoma should be defined as parts of precheliceral, cheliceral, and palpal segments having fused, the remaining parts of these segments being incorporated in the prodorsum.

REMARK 2. OBSERVATIONS ON THE SOMA-TERMINOLOGY

The term gnathosoma is conceived here in its practical sense (cf. Grandjean 1937b: 377): it is the anterior mobile part of the body separated off by the circumcapitular furrow. The presence of a separate gnathosoma is a special character of mites.

On three occasions I have briefly mentioned the soma-terminology. The first time (1961: 176), I pointed to the incompleteness of this terminology; in that case the term prodorsum would, however, have been appropriate. The second time (1963: 445) I gave a short history of the soma-terminology, and demonstrated, on theoretical grounds, that the body of mites is primarily composed of prosoma and opisthosoma. This opinion was confirmed by me (Van der Hammen, 1966: 51) in a study of *Opilioacarus*.

The term prosoma was introduced by Lankester (1881) in a comparative study of Xiphosura and Scorpionida. In the greater part of this paper he used the term cephalothorax, but at the end, in his final remarks, he introduced a subdivision of the body into prosoma, mesosoma, and metasoma. These names have been repeated by him in later papers, e.g. Lankester (1882, 1882a), and Lankester, Benham & Beck (1885); the last-mentioned paper was cited by Oudemans (1911) as the first introduction of the term prosoma.

Börner (1904) introduced the term opisthosoma, and Reuter (1909) the terms gnathosoma, proterosoma, and hysterosoma. Finally, Oudemans (1911) tried to complete the soma-terminology, and after correspondence with Reuter he introduced the terms idiosoma, propodosoma, metapodosoma, and podosoma; according to him the last-mentioned three terms had been created by Reuter in correspondence; their first introduction should consequently be cited as Reuter in Oudemans (1911).

According to my present opinion, the terms prosoma and opisthosoma have a theoretical base; they are now also applied to other groups of Arachnida. Gnathosoma, idiosoma, and podosoma have a practical value in descriptions. The terms proterosoma, hysterosoma, propodosoma, and metapodosoma are, in my opinion, misleading because they are founded on a confusion of sejugal and disjugal furrow; their use should be dissuaded.

REMARK 3. TRÄGÅRDH'S ORGAN AND THE ONCOPHYSIS OF THE CHELICERAE

The name Trägårdh's organ was introduced by Grandjean (1936: 38, 47, 64, 92, 102) without, however, mentioning that it concerned a new term. It was described by him already two years earlier (Grandjean, 1934a: 245) without naming it, and on that occasion he referred to its discovery by Trägårdh (1910). The organ has afterwards been mentioned on several occasions by Grandjean, and a comparative study of it was published by him in 1959. In the last-mentioned paper he demonstrated that it is known from higher Oribatid mites and Nothroidea (with few exceptions), but that it is not known with certainty from the remaining primitive Oribatid mites.

In the present paper I have demonstrated that the epiostracum (or cuticle) of Trägårdh's organ is a continuation of the cheliceral sheath. It takes, moreover, the place of a laterocoxal seta in species with free coxae. Consequently, it could hypothetically be derived from an oncophysis or from a laterocoxal seta; the first hypothesis appears to be the most plausible one. Both hypothesis explain why Trägårdh's organ has not yet been found in most primitive Oribatid mites. Its base should be looked for at the line of attachment of the cheliceral sheath to the chelicera. This line has a proximal position in these mites, and Trägårdh's organ, consequently, would have a position slightly different from that in higher Oribatid mites.

As mentioned above, three other oncophysis are distinguished here in Oribatid mites: coxal (*opx*), ventral (*opv*), and paraxial oncophysis (*op'*). The question arises now whether these are also found in other groups of mites. An oncophysis in Prostigmata has indeed been described in the case of *Smaris* and *Balaustium* by Grandjean (1947: 20, fig. 3H, J; 1957: 145); this probably concerns the paraxial oncophysis *op'*. The arthrodial membrane and its terminal flap, described by me in *Opilioacarus texanus* (Chamberlin & Mulaik) (cf. Van der Hammen, 1966: 33, fig. 13A-C, E) relates to the ventral oncophysis *opv*. The brush-like "setae" *v'* and *v''*, described by me in the case of *Glyptholaspis confusa* (Foà) (Gamasina), are also parts of a ventral oncophysis. Probably, the presence of oncophysis is a general character of the Acarid chelicera; their function is as yet, however, unknown.

REMARK 4. THE TROCHANTER OF THE CHELICERAE

Recently (Van der Hammen, 1966: 32), I homologized the proximal segment of the chelicerae in *Opilioacarus* with a trochanter, on account of its bivalent articulation with the principal segment. Further investigations, especially a study of the tendons, will probably demonstrate that the same applies to most Anactinotrichida with a 3-segmented chelicera.

Grandjean (1948: 314) pointed to the probability of the cheliceral trochanter being present in Oribatid mites. His view is confirmed in the present paper by a study of the tendons. A trochanter is further e.g. recorded in Endeostigmata and Bdellidae (Grandjean, 1939a: 26), and *Labidostomma* (Grandjean, 1942a: 415). It is not impossible that the ephippial pillar ("pilier éphippial") of the chelicerae of *Smaris* (cf. Grandjean, 1947: 21, fig. 3H) and *Balaustium* (cf. Grandjean, 1957: 145, fig. 5B) is a remainder of this trochanter; a study of the tendons will in this case also be very important.

Although the cheliceral trochanter is not yet recorded from Acarina (Acaridei), it seems plausible to suppose that its presence in mites will prove to be a more or less general condition. The segment tends to be reduced, whilst its position at the same time tends to become paraxial.

REMARK 5. THE PODOCEPHALIC CANAL

The name podocephalic canal ("canal podocéphalique") was introduced by Grandjean (1937: 286) in a paper on *Otodectes* (Acaridei). He mentioned that, beside in Acaridei, the canal is also present in Bdellidae, and apparently constitutes a constant character of Prostigmata. Shortly afterwards (1937a: 388), he returned to the subject, and recorded anew, in detail, its occurrence in Acaridei. An extensive description of the canal in Bdellidae was published shortly afterwards (Grandjean, 1938: 7). On that occasion Grandjean mentioned that it can be external (a canal) or internal (a tube), with numerous transitions. According to him, the ducts of three glands debouch into the canal (or in the tube, when the canal has become internal). In a survey of the literature, he reported that the canal had been described by Michael and by Sig Thor (as common duct of the salivary glands) and by Oudemans (erroneously as tracheal trunk). The canal was subsequently recorded by Grandjean from the following groups: *Retetydeus* and other Prostigmata (1938a: 282, 285); Tydaeidae and probably all Actinotrichida (1938b: 379); Endeostigmata (1939a: 46); *Labidostomma* (1942: fig. 3B); *Anystis* (1943: 76); *Apostigmaeus* (1944: 109); Smarisidae (1947: 25, fig. 1A).

Extensive data on the canal in Oribatid mites are apparently scarce. Grandjean (1939: 110-117, fig. 1-3) described the glands debouching in the lateral region of the podosoma in some Oribatid mites; in this paper he pointed to a possible homology of a lateral band in *Eulohmannia* (at the border of which band two glands are debouching) with the podocephalic canal. The canal has afterwards been recorded by him from Palaeacaroidea (Grandjean, 1954: 206, 220, 236, 254, fig. 2B). The occurrence of it in the antiaxial part of the subcheliceral epimeric furrow was mentioned three years later (Grandjean, 1957b: 241); this part had been figured by him shortly before (Grandjean, 1957a: fig. 1). The course of the canal inside acetabulum I was mentioned as a casual remark in a note on laterocoxal seta *el* (Grandjean, 1962: 403). Parts of the canal have afterwards also been described by him in papers on *Collohmannia* (Grandjean, 1966: 336) and *Staurobates* (Grandjean, 1967: 702).

Although the above list is probably not complete, it appears that all descriptions of the podocephalic canal, as far as Oribatid mites are concerned, are incomplete. As a rule, only part of the canal is mentioned, and more than two glands had not been described. The discovery of three glands or ducts during the present investigation, and the description of the full course of the canal, demonstrate its mutual resemblance in the three groups of Actinotrichida. The presence of the canal is apparently an important character of the order.

REMARK 6. THE INGESTION OF SOLID FOOD

Grandjean (1957b: 273) pointed to the correlation between the presence of rutella (in Oribatid mites, Endeostigmata, and *Opilioacarus*) and the ingestion of solid food. The groups in question apparently belong to the few Arachnida presenting this way of life. The ingestion of fluid food, which occurs in most Arachnida is, however, a specialization that probably has developed from the intake of solid material. From this it would appear that mites with a rutellum are less removed from their original way of life than other Arachnida. It would at least be illogical to suppose that evolution of the ingestion in Oribatid mites, Endeostigmata, and *Opilioacarus* passed from the ingestion of solid food, by way of fluid, to solid again. Grandjean (1957b: 273) supposed that the ancestors of mites with rutella feeded in an unknown way, but different from their descendants, because instead of a rutellum they had only a seta. In my opinion, the development of rutella must have been a specialization of a primitive condition that in its main features resembled already the present way of life. The problem could be approached by studying the way of feeding, or the contents of the gut of mites with very primitive rutella (e.g. *Heterochthonius, Eniochthonius, Hypochthonius,* etc.), or of species without rutella (but with rutellar setae at homologous places), chosen from groups where rutella are usually present (*Speleorchestes, Sphaerolichus*). Grandjean (1939a: 48, 93), however, supposed on account of the structure of chelicerae and anterior legs, that *Sphaerolichus,* which has setae instead of rutella, probably sucks his prey. The controversial problem is important enough to be studied anew in detail. I suppose that rutella can be present in primitive representatives of all groups of Acarida. It would e.g. be very interesting to discover their occurrence in primitive Acarina (Acaridei).

REMARK 7. THE GNATHOSOMA OF MITES IN COMPARISON WITH THE MOUTHPARTS IN OTHER ARACHNIDA

The study of the cheliceral frame, and its interpretation as part of the body wall, have demonstrated that, in principle, the Acarid gnathosoma is typically arachnoid. The development of the tegulum into structures as the so-called cheliceral tectum in Mesostigmata, should be considered of secondary origin. On the contrary, I regard the presence of an infracapitulum, i.e. of the palpal epimeric region, as a primitive condition, no more present in other Arachnida. This primitive condition, while retaining its epimeric character, has been subject of a considerable evolution. It will be interesting to develop a comparative morphology of the Arachnid mouthparts, with the primitive condition in mites (i.e. the presence of the palpal epimere) as starting point.

As a rule, mites have been considered very specialized Arachnida, having lost most of their typically arachnoid characters. I am, on the contrary, convinced that Acarid morphology holds the key to many problems in general arachnology.

GLOSSARY

The present glossary is a survey of terms applied to the gnathosoma of

Oribatid mites. It contains all names mentioned above in connection with the mouthparts; it is supplemented with a number of terms referring to conditions not found in *Hermannia*. The list is probably not yet complete. Synonyms have, moreover, not been included; adding these to the glossary, would have required a time-devouring historical study. When explanations have been slightly modified in comparison with those previously published by me, the present ones should be regarded as the correct definitions.

ACETABULAR TECTUM. — The tectum surrounding part of the acetabulum in higher Oribatid mites; it is strongly developed anteriorly in the case of legs I and II; the reverse applies to legs III and IV. The structure of the acetabular tecta in *Hermannia* is rather exceptional; the tecta (and especially their limbs) surround the acetabula anteriorly, dorsally, and posteriorly.

ACETABULAR TOOTH. — The posterior, dentiform part of acetabular tectum I in *Hermannia*.

ACETABULUM. — A cavity in the lateral part of the podosomatic exoskeleton, into which the leg is articulated; it is filled nearly completely by the trochanter. In higher Oribatid mites it has an internal orifice and an external; the wall between the two is the cotyloid wall.

ACETABULUM I. — The acetabulum of leg I.

ADORAL SCLERITE. — The sclerite occupying part of the ventral surface of the lateral lips, and bearing (part of) the adoral setae. In the case of postadoral articulation, it is movably connected with the sclerite of the genae.

ADORAL SETAE. — The setae in front of the postadoral articulation, inserted on the lateral lips. Their number is three or two.

ANARTHRY. The condition of the ventral surface of the infracapitulum, characterized by the absence of labiogenal articulation.

ANTERIOR CHELICERAL SETA. — One of the two setae that are usually present on the dorsal surface of the chelicerae; it is indicated as *chb*.

ANTERIOR INFRACAPITULAR SETA. — The anterior seta of the gena; when postadoral and labiogenal articulation are both present, the seta *a* is inserted between them.

ANTERIOR PODOCEPHALIC GLAND. — The gland of which the duct debouches into the podocephalic canal, in the laterodorsal part of the infracapitulum.

ANTIAXIAL. — The side turned away from an axis. The term is also found in compound words as antilateral, antilateroventral, etc.

ANTIAXIAL MANUBRIAL FISSURE. — The fissure representing the antiaxial part of the manubrial articulation.

APOTELE. — The terminal segment of the appendages, originally bearing the claw(s). In the case of the chelicerae it is the movable bit. As a rule the apotele is moved by means of two tendons (t_s and t_i).

ARTHRODIAL MEMBRANE. — The soft, often retractable membrane, connecting two segments of an appendage. The membrane is usually referred to as synarthrodial; because synarthrosis is generally used for immovable articulations, the name has been changed by me into arthrodial, the meaning of which is, moreover, unmistakable.

ARTICULAR FOSSETTE. — Small groove in the laterodorsal part of the infracapitulum, posteriorly of tendon $t\alpha$, corresponding with the condyle k of the camerostome.

ARTICULATION. — The joining of two structures; it is here always applied to movable connections.

ATELEBASIC RUTELLA. — Ordinary (not specialized) rutella, which are more or less broad, but of which the bases do not reach to the infrabuccal fissure.

ATTACHMENT OF CHELICERAL SHEATH. — The distal border of the sheath; it separates an anterior external part of the chelicera from a posterior internal.

BASE OF CHELICERAL SHEATH. — The line of attachment of the cheliceral sheath to the cheliceral frame (especially to the tegulum).

BRUSH OF RUTELLUM. — The brush or comb in the dorsal (paraxial) part of the rutellum; there are one or (exceptionally) two brushes.

CAMEROSTOME. — The cavity anteriorly of the podosoma, in which the gnathosoma is lying; the latter is movable, and articulates with the podosomatic condyles k.

CAPITULAR ANGLE. — A projecting angle at the posterior lateral border of the prodorsum; it is at the same time the produced part of acetabular tectum I.

CAPITULAR APODEME. — An internal chitinous lamella, starting from the border of infracapitulum and cheliceral frame. In Nothroidea and higher Oribatid mites it is notched in the middle; in Phthiracaroidea it is, on the contrary, produced in this part. The pharyngeal cupola of *Cosmochthonius* and *Haplochthonius* is a hypertrophied capitular apodeme. In all species, tendons are starting from the posterior border of the apodeme; the number and position of these (although more or less constant in each species) is variable.

CAPITULAR EPIMERIC FURROW. — The line of attachment of the cheliceral frame to the infracapitulum; it is at the same time the bottom of the small interval between chelicerae and cervix. In many Actinotrichida, the antiaxial part of the furrow is occupied by the podocephalic canal.

CAPITULAR SADDLE. — The convex median part of the cervix.

CENTRAL CAVITY OF INFRACAPITULUM. — The space between cervix and mentum.

CERVIX. — The dorsal surface of the infracapitulum, posteriorly bordered by the capitular epimeric furrow. Anteriorly, it constitutes the base of the labrum. Near the superior commissures of the mouth, it passes into the dorsal surface of the genae.

CHELA. — The pair of pincers or jaws of the chelicerae; it is composed of the fixed and the movable bit.

CHELICERAE. — The anterior pair of appendages, transformed into feeding organs. They generally consist of three segments: trochanter, principal segment, and apotele; the principal segment is a fusion of femur, genu, tibia, and tarsus.

CHELICERAL EPIMERIC REGION. — The sternal and ventral region of the cheliceral frame, together with the cheliceral sheaths.

CHELICERAL FRAME. — The membrane that constitutes the body wall in the region between rostrophragma and infracapitulum, and to which the chelicerae are movably attached by means of the cheliceral sheaths. These sheaths can eventually be included in the definition of the frame.

CHELICERAL GROOVE. — A longitudinal depression in the dorsal surface of the infracapitulum, in which the chelicerae can move. Cheliceral grooves start at both sides of the capitular saddle (the convex median part of the cervix), and continue on both sides of the labrum.

CHELICERAL SETAE. — The setae inserted on the chelicerae. In Oribatid mites they occur only on the dorsal surface of the principal segment.

CHELICERAL SHEATH. — The membraneous coxal region of a chelicera. It is proximally attached to the cheliceral frame, distally to the chelicerae. It can be protracted (certainly by means of hydrostatic pressure) as well as retracted and invaginated (by means of the cheliceral tendons).

COLLUM. — The superficial limit of the rutellum, i.e. the border between its external layers and the cuticle of the gena.

COMMISSURAL INDURATIONS. — Chitinous thickenings, extending from the lips, along the commissural lines, to the cuticle of the infracapitulum. There are two superior commissural indurations and one inferior (it is unknown whether two inferior indurations are found in species with an unpaired underlip).

COMMISSURE OF THE MOUTH. — The external point of a commissural line where two lips meet. There are three or four commissures: two superiors (*Js*, *Js'*) and one or two inferiors (*Ji*, *Ji'*), depending on the absence or presence of an unpaired underlip.

CONDYLE. — A process forming articulation with an opposite structure.

COTYLOID WALL. —The chitinous wall between internal and external orifice of an acetabulum.

COXAL GLANDS. — Glands debouching in the coxae or coxal regions of the appendages. Part or all of the podocephalic glands are supposed to be coxal.

COXAL ONCOPHYSIS. — The membraneous swelling in the ventral region of the chelicerae, starting from the line of attachment of the cheliceral sheath.

COXAL REGION. — Lateral part (at both sides) of an epimere, surrounding the orifice of an appendage. Coxal regions take the place of free coxae in several groups of mites; the two regions are homologous (because of the occurrence of laterocoxal setae in both), but it is unknown which of the two conditions is the primitive one. In Oribatid mites coxae have certainly never been free segments. The coxal region of the cheliceral epimere consists of the two cheliceral sheaths.

COXISTERNAL REGION. — A complete epimere (consisting of a coxal and a sternal part) or the epimeres together.

CUTICLE. — The chitinous part of the tegument, consisting of epiostracum and ectostracum (sometimes an endostracum can also be distinguished).

DIARTHRY. — The condition of the ventral surface of the infracapitulum, characterized by the presence of a labiogenal articulation which extends to the base of the palp. The mentum is consequently large and not triangular; the genae ar small.

DUCT OF ANTERIOR PODOCEPHALIC GLAND. — A large duct debouching into the infracapitular part of the podocephalic canal; its orifice is in the cheliceral frame. In *Hermannia* the duct often remains attached to the infracapitulum (i.e. by means of a small part of the cheliceral frame) when the infracapitulum is separated from the idiosoma.

DUCT OF INFRACAPITULAR GLAND. — Narrow duct debouching into the dorsal region of the infracapitulum. The orifice is in the so-called foramen, a transparent part (the ectostracum is lacking) of the cervix, at both sides of the capitular saddle.

DUCT OF MEDIAN PODOCEPHALIC GLAND. — A narrow, chitinous duct, debouching into the acetabular region of the podocephalic canal.

EPIMERE. — The coxisternal region of one prosomatic segment.

EPIOSTRACUM. — The outermost layer of the chitinous cuticle. It is thin, elastic, and colourless.

EXTERNAL ACETABULAR ORIFICE. — The apparent orifice formed by the development of an acetabular tectum.

FENESTRATE AREA. — A clear spot in the surrounding, darker cuticle.

FENESTRATE AREA OF CHELICERAL TROCHANTER. — A clear spot posteroventrally of the base of Trägårdh's organ.

FENESTRATE AREA OF PRINCIPAL CHELICERAL SEGMENT. — A clear spot anterodorsally of the base of Trägårdh's organ.

FENESTRATE AREA OF ROSTRUM. — A median clear spot in the anterior part of the prodorsum, between the rostral setae.

FIXED BIT. — The immovable part of the chela.

FORAMEN. — A clear spot in the cervix, at both sides of the capitular saddle, characterized by the absence of the ectostracum; it contains the orifice of the infracapitular gland.

GENAE. — The paired region which is a continuation of mentum and cervix, and which anteriorly passes into the lateral lips. The genae present a dorsal (paraxial), and a ventral (antiaxial) surface.

GENAL CAVITY. — The central cavity inside the genae; it is a continuation of the central cavity of the infracapitulum.

GENAL SCLERITE. — The single sclerite occupying the surface of the genae.

GNATHOSOMA. — The mouthparts in mites. They constitute a part of the body, which secondarily has become mobile. The gnathosoma is separated off from the idiosoma by the circumcapitular furrow.

INFERIOR COMMISSURAL INDURATION. — The chitinous thickening of the infracapitular wall, which is in connection with the inferior commissural line.

INFERIOR COMMISSURE OF THE MOUTH. — The external point of the line where the lateral lips meet.

INFRABUCCAL FISSURE. — Fissure in the plane of symmetry, between two lateral lips. It is directly visible at the ventral surface of the infracapitulum.

INFRACAPITULAR GLAND. — The gland which is supposed to be salivary; it debouches at the dorsal surface of the infracapitulum.

INFRACAPITULAR SETAE. — The epimeric setae of the infracapitulum. They have nearly always a ventral position; a pair of latero-dorsals is only present in Opilioacarida and Holothyrina.

INFRACAPITULUM. — The ventral part of the gnathosoma bearing labrum and palp. It consists of mentum, cervix, and genae, and it contains mouth and pharynx.

INTERNAL ACETABULAR ORIFICE. — The true orifice in the podosoma, at the bottom of the acetabulum, to which the trochanter of a leg is attached.

LABIOGENAL ARTICULATION. — The articulation between mentum and genae. It starts from the inferior commissure of the mouth, and runs obliquely backwards (to the posterior border) or transversely (to the lateral border of the mentum). The labiogenal articulation is often absent; it can also be incomplete.

LABRAL SCLERITE. — The dorsal sclerite of the labrum; it presents two posterior branches which run in lateroventral direction, and probably articulate with the superior commissural indurations.

LABRAL TENDONS. — The small tendons attached to the posterior border of the labral sclerite, and by which the labrum is raised.

LABRUM. — The upper lip. It is apparently of precheliceral origin (in some Arthropods it is even paired at a certain stage of embryological development). Its ventral surface is a continuation of the dorsal wall of the pharynx. Its base is attached to the cervix.

LARGE LATERAL RIDGES. — The large ridges at the lateral border of the infracapitulum, between dorsal and ventral surface.

LATERAL LIPS. — The paired lateroventral lips which meet in the plane of symmetry, at the ventral surface of the infracapitulum. Their dorsal paraxial surface is a continuation of the ventral wall of the pharynx.

LATEROCOXAL POROSE AREA. — The porose area in the laterodorsal part of the infracapitulum, posteriorly of the laterocoxal seta.

LATEROCOXAL SETAE. — Setae of the coxal region or of the free coxae of palp, leg I, and leg II. They can be partly reduced (e.g. *eI* and *eII* in *Opilioacarus*), or multiplied (e.g. *eII* in *Anystis*).

LIPS. — Morphologically the anterior prolongations of pharynx and infracapitulum, in front of the mouth; embryologically they are of different origin. There can be three or four lips: labrum, lateral lips, and underlip (occurring only in some primitive mites).

MANUBRIAL ARTICULATION. — The articulation at the base of the manubrium, i.e. between the basal tubercle of the rutellum (or the manubrial zone) and the gena.

MANUBRIAL POROSE AREA. — The dorsal and paraxial porose area of the manubrium.

MANUBRIAL ZONE. — The manubrium in higher Oribatid mites with large rutellum. It belongs to the gena. It is situated between collum and antiaxial manubrial fissure. It is well-defined only in the antiaxial region.

MANUBRIUM. — The basic tubercle of the rutellum.

MEDIAN INFRACAPITULAR SETAE. — The setae (one or more pairs) inserted about halfway the anterior and posterior infracapitular setae, near the base of the palp. They belong to the genae.

MENTOTECTUM. — The tectum (especially in higher Oribatid mites) which protects the ventral gnatho-podosomatic articulation. It starts from epimeric furrow I, and it is part of the podosoma. It overlaps the posterior ventral border of the gnathosoma. A primitive mentotectum consists of two parts, because of an interruption in the median sternal part; at a higher developed stage the two parts have fused.

MENTUM. — The unpaired posterior region of the ventral infracapitular surface, anteriorly bordered by the labiogenal articulation (when this is present).

MOUTH. — The anterior orifice of the pharynx, inside the infracapitulum, bordered by lips. Its shape is defined by the number of commissures: when three commissures are present, the mouth is triangular; when four commissures are present (i.e. when there is an underlip), its is quadrangular.

MOUTHPARTS. — The feeding organs in general, which in mites have developed as a separate gnathosoma.

MOVABLE BIT. — The movable part of the chela. It is the apotele of the chelicera; two tendons (t_s, t_i) are attached to its base.

NASO. — The unpaired frontal protuberance of the anterior prosomatic extremity. In the rare cases where it occurs, it is often nearly entirely occupied by a depigmentated inferior eye. The naso is undoubtedly of precheliceral origin.

OESOPHAGUS. — The part of the gut between pharynx and stomach.

ONCOPHYSIS. — Membraneous swellings in the ventral and paraxial region of the chelicera, starting from, or connected with arthrodial membranes.

PALPS. — The second pair of appendages, articulating with the infracapitulum. They are part of the feeding organs.

PALPAL ACETABULUM. — The acetabulum in each of the large lateral ridges of the infracapitulum.

PANTELEBASIC RUTELLA. — Ordinary (not specialized), broad rutella, of which the bases reach at the infrabuccal fissure.

PARAXIAL. — The side turned to an axis. The term is also found in compound words as paralateral, paralateroventral, etc.

PARAXIAL MANUBRIAL FISSURE. — The fissure visible in ventral view, representing the paraxial part of the manubrial articulation.

PARAXIAL ONCOPHYSIS. — The membraneous swelling in the paraxial region of the chelicerae, which starts from the base of the fixed bit. It is connected with the arthrodial membrane of the movable bit.

PHARYNGEAL CUPOLA. — The hypertrophied capitular apodeme in some Enarthronata. It has the shape of a vault which is dorsally closed.

PHARYNX. — The anterior part of the gut, functioning as suctorial apparatus. It is provided with numerous muscles. A transverse section can be triangular, quadrangular, or hexagonal (only in Opilioacarida). In Oribatid mites this section soon becomes oval or crescent-shaped.

PODOCEPHALIC CANAL. — An open canal (a taenidium) running from the posterior part of acetabulum I to the laterodorsal region of the infracapitulum. Three glands are debouching into it.

PODOCEPHALIC GLANDS. — The glands debouching into the podocephalic canal. There are two orifices in the acetabular region, and one in the infracapitular. The podocephalic glands are possibly coxal glands.

POROSE AREA. — A limited area with distinct pores (macropores) which traverse the ectostracum.

POSTADORAL ARTICULAR DIFFERENCE OF LEVEL. — The difference in level between adoral and genal sclerite: the base of the lateral lips is above the ventral surface of the gena. It is a secondary condition; primarily the two parts are in the same plane.

POSTADORAL ARTICULATION. — The articulation between lateral lips and genae.

POSTADORAL FURROW. — The furrow separating lateral lips and genae. Originally these surfaces are in the same plane; in part of the primitive, and in all higher Oribatid mites, the furrow has, however, developed into an articular difference of level.

POSTERIOR CHELICERAL SETA. — One of the two setae that are usually present on the dorsal surface of the chelicerae; it is indicated as *cha.*

POSTERIOR INFRACAPITULAR SETA. — The hysterostomatic seta, or seta of the mentum.

POSTERIOR PODOCEPHALIC GLAND. — The tubiform gland debouching into the posterior part of the podocephalic canal. In *Hermannia* it has two branches. It is supposed to be a coxal gland.

PRIMITIVE RUTELLA. — Rutella with a narrow base, as well as a narrow median part.

PRINCIPAL CHELICERAL SEGMENT. — The largest part of the chelicerae, bearing the fixed bit. It is supposed to be a fusion of femur, genu, tibia, and tarsus.

PRODORSUM. — The dorsal part of the prosoma (without the gnathosoma). Posteriorly it is bordered by the disjugal fold.

RIB OF THE DORSAL INFRACAPITULAR WALL. — A strong internal process of the cervix, to which delator muscles of the pharynx are attached. It continues posteriorly under the capitular apodeme.

RIDGE OF COAPTATION OF THE INFRACAPITULUM WITH THE BORDER OF THE CAMEROSTOME. — The ridge which can be present in the lateral part of the infracapitulum (it continues on the genae). It is adjusted to the lateral border of the camerostome. The two coapt when the camerostome is closed by the infracapitulum.

ROSTRAL CAVITY. — The cavity between anterior part of prodorsum and rostrophragma. It is supposed to contain elements of precheliceral origin.

ROSTRAL LIMB. — The external prolongation of the rostral exoskeleton, which dorsally protects the gnathosoma. It has no internal cavity, and it has the appearance of a thin, transparent, chitinous border.

ROSTROPHRAGMA. — The chitinous lamella which starts from the base of the rostral limb, and extends to the base of the cheliceral frame.

ROSTRUM. — The anterior part of the idiosoma. It consists of the anterior part of the prodorsum, the rostrophragma, and the rostral cavity.

RUTELLAR BRUSH. — See: brush of rutellum.

RUTELLAR SETA. — The ordinary, primitive, not evolved seta, which takes the place of a rutellum. It occurs in some Endeostigmata.

RUTELLUM. — A specialized infracapitular seta, which generally has taken the shape of a thick, solid, dentate lamella. It is inserted in the anterior part of the genae, in such a way that its surface appears to be the prolongation of the surface of the gena. There are four types of rutella: primitive, ordinary atelebasic, ordinary pantelebasic, and specialized suctorial.

SACCULI. — Small invaginated parts of the ectostracum, of which the wall is partly porous. They are supposed to have a respiratory function.

SALIVARY GLAND. — A gland of which the secretion, transported to the mouth, has a digestive or auxiliary ingestive function. The infracapitular glands are supposed to be salivary. This supposition needs reinvestigation.

SECONDARY INFRACAPITULAR ARTICULATIONS. — The articulations at the base of manubrium, lateral lips, and genae, i.e. respectively manubrial, postadoral, and labiogenal articulations.

STENARTHRY. — The condition of the ventral surface of the infracapitulum, characterized by the presence of a labiogenal articulation which extends obliquely backwards to a point removed from the base of the palp. The mentum is consequently triangular; the genae are large.

SUCTORIAL GNATHOSOMA. — Gnathosoma characterized by chelicerae which are elongated (with small chela) or styliform (without chela). There is no labiogenal articulation; the rutellum belongs to the suctorial type.

SUCTORIAL RUTELLA. — Pantelebasic rutella which constitute a membraneous tube; the two rutella are not fused, and the tube consequently is no true tube.

SUPERIOR COMMISSURAL INDURATIONS. — The chitinous thickenings of the infracapitular wall, which are in connection with the superior commissural lines.

SUPERIOR COMMISSURES OF THE MOUTH. — The external parts of the two lines where labrum and lateral lips meet.

TEGULUM. — The dorsal part of the cheliceral frame; it is a membrane which extends from rostrophragma to chelicerae.

TENDON. — A cord or bundle of connective tissue between a muscle or a muscle bundle and its place of insertion. A tendon consists of material resisting lactic acid, whilst muscles are dissolved in this medium.

TRÄGÅRDH'S ORGAN. — A long protuberance of conical shape at the paraxial surface of the chelicerae. Its cuticle is a continuation of the cheliceral sheath; it is supposed here to be an oncophysis. In *Hermannia convexa* it has an internal sclerite which articulates with the trochanter; the sclerite has two basal tendons. The function of Trägårdh's organ is unknown.

TROCHANTER. — In Oribatid mites, the trochanter is the first free segment of the appendages. The trochanter of the chelicerae (in higher Oribatid mites) is generally reduced to a ventral paraxial chitinous piece.

TUBIFORM PODOCEPHALIC GLAND. — The gland debouching into the posterior part of the podocephalic canal. In *Hermannia convexa* it has two branches; one of these surpasses the posterior border of the prosoma. The tubiform podocephalic gland is supposed to be a coxal gland.

UNDERLIP. — The small unpaired lip which, in some primitive mites (some Endeostigmata and Palaeacaroidea), is intercalated ventrally between the lateral lips. This primitive character is correlated with the occurrence of a quadrangular mouth and four commissures.

VENTRAL ONCOPHYSIS. — The membraneous swelling in the ventral region of the chelicera, which is a continuation of the arthrodial membrane of the principal cheliceral segment.

ALPHABETIC LIST OF ABBREVIATIONS USED IN FIG. 1-12

a, anterior genal seta.
ac.d, acetabular tooth.
Ac.P, acetabulum of palp.
ac.t, acetabular tectum.
acx, attachment of cheliceral sheath.
Ac.I, acetabulum I.
Ac.II, acetabulum II.
am, arthrodial membrane.
an, anterior paraxial border of gena.
ap.c, capitular apodeme.
ap.1, apodeme 1.
ap.2, apodeme 2.
A.r, rostral porose area.
at, capitular epimeric furrow.
at_1, at_2, median, resp. lateral part of capitular epimeric furrow.
bcx, base of cheliceral sheath.
bls, base of labrum.
bo, bothridium.
bo.e, border of external acetabular orifice.
bo.i, border of internal acetabular orifice.
bpd, lateral border of prodorsum.
br, lateral border of rostrum.
brp, posterior border of rostrophragma.
bru, brush of rutellum.
b.sc, base of adoral sclerite.
c, collum of rutellum.
cam, camerostome.
CE, cervix.
cg, internal genal cavity.
cha, posterior seta of chelicerae.
chb, anterior seta of chelicerae.
clc, dorsal contour line of infracapitulum at level of cervix.
clm, dorsal contour line of infracapitulum at level of manubrium.
co.1, cotyloid wall of acetabulum I.
co.2, cotyloid wall of acetabulum II.
cpc, podocephalic canal.
CX, cheliceral sheath.

d, postadoral articular difference of level.
dg_1, duct of anterior podocephalic gland.
dg_2, duct of median podocephalic gland.
e, laterocoxal seta of palp.
ex, exobothridial seta 1).
fe_1, fenestrate area of principal cheliceral segment.
fe_2, fenestrate area of cheliceral trochanter.
FM, cheliceral groove.
fr, fenestrate area of rostrum.
G, gena.
g_{3a}, g_{3b}, branches of tubiform podocephalic gland.
h, seta of mentum.
H, mentum.
ici, inferior commissural induration.
ics, superior commissural induration.
il, interlamellar seta.
Ji, inferior commissure of mouth.
Js, *Js'*, superior commissures of mouth.
k, condyle for the articulation of the gnathosoma.
k', *k''*, condyles for the articulation of the cheliceral apotele.
k_p, supposed "condyle" for the articulation of the principal cheliceral segment.
le, lamellar seta.
LL, lateral lip.
LS, labrum.
m, lateral prodorsal mark.
m_1, m_2, median infracapitular setae.
MN, manubrium.
mnt, mentotectum.
ne, internal rib of dorsal infracapitular wall.
OE, oesophagus.
og_1, orifice of anterior podocephalic gland.
og_2, orifice of median podocephalic gland.
ogi, orifice of infracapitular gland.
op', paraxial oncophysis of principal cheliceral segment.
opv, ventral oncophysis of principal cheliceral segment.
opx, coxal oncophysis of chelicera.
or_1, or_2, or_3, adoral setae.
p, posterior extremity of podocephalic canal.
PD, prodorsum.
PH, pharynx.
po.lc, laterocoxal porose area of infracapitulum.
po.mn, porose area of manubrium.
PI, leg I.
PII, leg II.
q, posterior acetabular part of podocephalic canal.
r, anterior acetabular part of podocephalic canal.
rc, rostral cavity.
ro, rostral seta.
rp, rostrophragma.
ru, basal contour line of rutellum.
RU, rutellum.
s, transition of acetabular part of podocephalic canal into prodorsal.
sa, bothridial sacculi.
sc.ad, adoral sclerite.
sc.ls, internal sclerite of labrum.
se, capitular saddle.
sens, sensillus.
t, anterior extremity of prodorsal part of podocephalic canal.
t_i, inferior tendon of cheliceral apotele.
t_s, superior tendon of cheliceral apotele.
tf_i, inferior tendon of principal cheliceral segment.
tf_s, superior tendon of principal cheliceral segment.
Tg, Trägårdh's organ.
TG, tegulum.
tls, tendons attached to labral sclerite.
tm_{1-3}, median tendons starting from capitular apodeme.
tp_1, tp_2, tendons attached to dorsal wall of infracapitulum, and running in anteroventral direction.
tT_i, inferior tendon attached to Trägårdh's organ.
tT_s, superior tendon attached to Trägårdh's organ.
ttr, tendon of cheliceral trochanter.
tα, posterior antiaxial tendon of infracapitulum.
tπ, paraxial tendon starting from capitular apodeme.

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1) The following terms have been derived from bothridium, and are accepted by me: trichobothrium (= bothridium + bothridial seta), bothridial seta, exobothridial seta.

w, capitular angle.
xt, place of attachment of tendon on cotyloid wall I.
αf, antiaxial manubrial fissure.
Δ, articular tooth on cheliceral trochanter.
λ, base of rostral limb.
1, 2, 3, adoral setae.
1a, 1b, 1c, setae of epimere I.

SUMMARY

In the present paper a detailed description is given of the gnathosoma of *Hermannia convexa* (C. L. Koch), a large Oribatid mite. It is the first modern study dealing with a complete Oribatid gnathosoma. Special attention is paid to the way of attachment of the chelicerae, and the distinction of internal and external parts of the gnathosoma. The description comprises studies of rostrum, camerostome, cheliceral frame, chelicerae, infracapitulum, podocephalic canal, as well as of various sections. The complete course of the podocephalic canal, and the exact shape of the cheliceral frame are described here for the first time. The paper includes stray observations on occurrence, idiosomatic morphology, and ovoviviparity of the species. A number of general remarks deal with segmentation; soma-terminology; Trägårdh's organ and the oncophysis of the chelicerae; cheliceral trochanter; podocephalic canal; the ingestion of solid food; and the gnathosoma of mites in comparison with the mouthparts of other Arachnida. In a glossary, a survey is given of terms applied to the gnathosoma of Oribatid mites. Among the new terms introduced here, I point to tegulum (the dorsal part of the cheliceral frame, extending from rostrophragma to chelicerae) and oncophysis (the membraneous swellings in the ventral and paraxial region of the chelicerae); rostrophragma is introduced here as translation of the French "cloison rostrale".

REFERENCES

Börner, C., 1904. Beiträge zur Morphologie der Arthropoden I. Ein Beitrag zur Kenntnis der Pedipalpen. — Zoologica, Stuttgart **17** (5) (42): 1-174, 7 pl., 114 text-fig.

Dawydoff, C., 1949. Développement embryonnaire des Arachnides. — In: P.-P. Grassé, Traité de Zoologie **6**: 320-385, fig. 97-157.

Evans, G. O., J. G. Sheals & D. Macfarlane, 1961. The terrestrial Acari of the British Isles. An introduction to their morphology, biology and classification **1**. Introduction and biology. — London.

Grandjean, F., 1934. Observations sur les Oribates (6e série). — Bull. Mus. Nat. Hist. Nat. (2) **6**: 353-360, fig. 1-3.

——, 1934a. Oribates de l'Afrique du Nord (2me série). — Bull. Soc. Hist. Nat. Afr. Nord **25**: 235-252, fig. 1-5.

——, 1936. Les Oribates de Jean Frédéric Hermann et de son père. — Ann. Soc. Ent. France **105**: 27-110, fig. 1-14.

——, 1936a. Un acarien synthétique: Opilioacarus segmentatus With. — Bull. Soc. Hist. Nat. Afr. Nord **27**: 413-444, fig. 1-5.

——, 1937. Otodectes cynotis (Hering) et les prétendues trachées des Acaridiae. — Bull. Soc. Zool. France **62**: 280-290, fig. 1-2.

——, 1937a. Sur quelques caractères des Acaridiae libres. — Bull. Soc. Zool. France **62**: 388-398, fig. 1-3.

——, 1937b. Remarques sur la terminologie des divisions du corps chez les Acariens. — Bull. Mus. Nat. Hist. Nat. (2) **9**: 373-378.

——, 1938. Observations sur les Bdelles (Acariens). — Ann. Soc. Ent. France **107**: 1-24, fig. 1-4.

——, 1938a. Retetydeus et les stigmates mandibulaires des Acariens prostigmatiques. — Bull. Mus. Nat. Hist. Nat. (2) **10**: 279-286, fig. 1-2.

——, 1938b. Observations sur les Tydeidae (1re série). — Bull. Mus. Nat. Hist. Nat. (2) **10**: 377-384, fig. 1-2.

——, 1939. Observations sur les Oribates (11e série). — Bull. Mus. Nat. Hist. Nat. (2) **11**: 110-117, fig. 1-3.

——, 1939a. Quelques genres d'Acariens appartenant au groupe des Endeostigmata. — Ann. Sci. Nat. Zool. (11) **2**: 1-122, fig. 1-25.

——, 1942. Observations sur les Labidostommidae (2e série). — Bull. Mus. Nat. Hist. Nat. (2) **14**: 185-192, fig. 1-3.

——, 1942a. Observations sur les Labidostommidae (Acariens) (4e série). — Bull. Mus. Nat. Hist. Nat. (2) **14**: 414-418, fig. A-F.

——, 1943. Le développement postlarvaire d' "Anystis" (Acarien). — Mém. Mus. Nat. Hist. Nat. (n.s.) **18**: 33-77, fig. 1-13.

——, 1944. Observations sur les Acariens de la famille des Stigmaeidae. — Arch. Sci. Phys. Nat. (5) **26**: 104-131, fig. 1-5.

——, 1947. Étude sur les Smarisidae et quelques autres Érythroïdes (Acariens). — Arch. Zool. Exp. Gen. **85**: 1-126, fig. 1-11.

——, 1948. L'origine de la pince mandibulaire chez les Acariens actinochitineux. — Arch. Sci. Phys. Nat. Genève (5) **29**: 305-355, fig. 1-4.

——, 1952. Au sujet de l'ectosquelette du podosoma chez les Oribates supérieurs et de sa terminologie. — Bull. Soc. Zool. France **77**: 13-36, fig. 1-2.

——, 1954. Étude sur les Palaeacaroïdes (Acariens, Oribates). — Mém. Mus. Nat. Hist. Nat. (n.s.), sér. A., Zool. **7**: 179-274, fig. 1-25.

——, 1957. Les stases du développement ontogénétique chez Balaustium florale (Acarien, Erythroïde). Première partie. — Ann. Soc. Ent. France **125**: 135-152, fig. 1-5.

——, 1957a. Observations sur les Oribates (37e série). — Bull. Mus. Nat. Hist. Nat. (2) **29**: 88-95, fig. 1-2.

——, 1957b. L'infracapitulum et la manducation chez les Oribates et d'autres Acariens. — Ann. Sci. Nat., Zool. (11) **19**: 233-281, fig. 1-7.

——, 1958. Au sujet du naso et de son oeil infère chez les Oribates et les Endeostigmates (Acariens). — Bull. Mus. Nat. Hist. Nat. (2) **30**: 427-435, fig. 1-2.

——, 1959. Observations sur les Oribates (40e série). — Bull. Mus. Nat. Hist. Nat. **31**: 359-366, fig. A-C.

——, 1962. Nouvelles observations sur les Oribates (2e série). — Acarologia **4**: 396-422, fig. 1-4.

——, 1965. Nouvelles observations sur les Oribates (4e série). — Acarologia **7**: 91-112, fig. 1-2.

——, 1966. Collohmannia gigantea Selln. (Oribate). Première partie. — Acarologia **8**: 328-357, fig. 1-8.

——, 1967. Les Staurobatidae n. fam. (Oribates). — Acarologia **8**: 696-727, fig. 1-8.

——, 1967a. Nouvelles observations sur les Oribates (5e série). — Acarologia **9**: 242-272, fig. 1-4.

HAMMEN, L. VAN DER, 1961. Description of Holothyrus grandjeani nov. spec., and notes on the classification of the mites. — Nova Guinea, Zool. **9**: 173-194, fig. 1-9, pl. 6.

——, 1963. The addition of segments during the postembryonic ontogenesis of the Actinotrichida (Acarida) and its importance for the recognition of the primary subdivision of the body and the original segmentation. — Acarologia **5**: 443-454.

——, 1964. The morphology of Glyptholaspis confusa (Foà, 1900) (Acarida, Gamasina). — Zool. Verh. **71**: 1-56, fig. 1-21.

——, 1966. Studies on Opilioacarida (Arachnida). I. Description of Opilioacarus texanus (Chamberlin & Mulaik) and revised classification of the genera. — Zool. Verh. **86**: 1-80, fig. 1-21.

HUGHES, T. E., 1959. Mites, or the Acari. — London.

LANKESTER, E. Ray, 1881. Limulus an Arachnid. — Quart. Journ. Micr. Sci. (n.s.) **21**: 504-548, 609-649, fig. 1-20.

——, 1882. On the coxal glands of Scorpio hitherto undescribed and corresponding to the brick-red glands of Limulus. — Proc. Roy. Soc. London **24**: 95-101, fig. 1.

——, 1882a. Note on the differences in the position of the ganglia of the ventral nerve-cord in three species of scorpion. — Proc. Roy. Soc. London **24**: 101-104, fig. 2-4.

LANKESTER, E. RAY, W. B. S. BENHAM & E. J. BECK, 1885. On the muscular and endoskeletal systems of Limulus and Scorpio; with some notes on the anatomy and generic characters of scorpions. — Trans. Zool. Soc. London **11**: 311-384, pl. 72-83.

LEGENDRE, R., 1958. Contributions à l'étude du système nerveux des Aranéides. — Ann. Biol. **34**: 193-223, fig. 1-11.

MILLOT, J., 1949. Classe des Arachnides (Arachnida). I. Morphologie générale et anatomie interne. — In: P.-P. GRASSÉ, Traité de Zoologie **6**: 263-319, fig. 47-96.

OUDEMANS, A. C., 1911. Acarologische aantekeningen XXXVIII. — Ent. Ber. **3**: 183-191.

REUTER, E., 1909. Zur Morphologie und Ontogenie der Acariden. Mit besonderer Berücksichtigung von Pediculopsis graminum (E. Reut.). — Ann. Soc. Fenn. **36** 4: 1-288, pl. 1-6.

SELLNICK, M., 1923. Die Gattung Hermannia Nicolet. — Acari **2**.

TRÄGÅRDH, I., 1910. Acariden aus dem Sarekgebirge. — Naturwissenschaftliche Untersuchungen des Sarekgebirges in Schwedish-Lappland **4** Zool.: 375-586, fig. 1-362.

VANDEL, A., 1949. Généralités. Composition de l'embranchement. — In: P.-P. GRASSÉ, Traité de Zoologie **6**: 79-158, fig. 1-36.