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NOTES ON THE MORPHOLOGY OF *ALYCUS* *ROSEUS* C. L. KOCH

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With 7 text-figures

Recently, in my second study on Opilioacarida (Van der Hammen, 1968b), I noted that it would be interesting to make a morphological comparison between *Opilioacarus* (as primitive representative of the Anactinotrichida) on the one hand, and one of the primitive Actinotrichida on the other. It appeared that a species of *Alycus*, viz., *A. roseus* C. L. Koch (1841), was excellently suited for this purpose. Because an extensive description of *Opilioacarus texanus* (Chamberlain & Mulaik) was already published by me (Van der Hammen, 1966), it sufficed to prepare a study of the *Alycus* species according to the same principles of observing, describing and drawing.

Because the opisthosoma of *Alycus roseus* presents a distinct segmentation, and consists of the highest number of segments known from the super-order, a detailed description, moreover, appeared to be of considerable interest for a further study of soma terminology and segmentation in Actinotrichida. Both reasons have given rise to the preparation of the present paper.

The generic name *Alycus* C. L. Koch (1841:19; 1842:38) has been placed by Grandjean (1936:398), Oudemans (1937:866), and Willmann (in: Sig Thor & Willmann, 1941:133) in the synonymy of *Pachygnathus* Dugès (1834:37). This synonymy, however, is not very convincing. Dugès (1834:37, pl. 8 fig. 52) described and figured the type-species, *Pachygnathus villosus* Dugès, as presenting curved setae. This condition is not known from species now classified with the genus. Moreover, Dugès figured the idiosoma of the species as presenting a pronounced lateral constriction; this character is not present in *A. roseus*.

A redescription of *Pachygnathus villosus* after topotypic material is badly needed. However, the type-locality is not known, although it is supposed to be near Montpellier (France). Dugès collected the species in rather great numbers in autumn, under humid stones. Investigations in that season in the environs of Montpellier will possibly result in a solution.

Grandjean (1939:3) supposed that the type-species of *Pachygnathus* could be identical with *P. ornithorhynchus* Grandjean (1937b:202, fig. 8). That species, however, has no curved setae, and is rather pale in colour.

The identity of the genus *Alycus*, on the contrary, is completely certain. C. L. Koch's description and figure are distinct, whilst Willmann (in: Sig Thor & Willmann, 1941:135) records the results of a study of topotypic specimens of the type-species. Although the name *Pachygnathus* has been in current use since 1936, I have preferred here a name of which the identity is certain; a further study of the old genus *Pachygnathus*, moreover, would certainly have resulted in a subdivision and a subsequent reintroduction of the name *Alycus*.

Our knowledge on the morphology of the genus is based on the *Pachygnathus* studies by Grandjean (1936, 1937, 1937a, 1937b, 1937c), and on his detailed studies of the Endeostigmata (Grandjean, 1939, 1942, 1943). In the present paper, this knowledge is further extended, whilst new interpretations are added. A number of conclusions, of interest for comparative acarid morphology, are arranged in a series of general remarks which follow the description. It appeared too early to prepare a glossary of morphological terms; some new terms, however, are defined in a short list at the end of this paper.

***Alycus roseus* C. L. Koch, 1841**

Materials and identity. - The present description is based on a sample of some 25 specimens collected on September 9, 1965, in a garden at Arnhem (The Netherlands), in litter of a solitary yew-tree (*Taxus baccata* L.). These specimens were sent to me for identification by Mr. J. H. de Gunst (ITBON, Arnhem). The material is identical with topotypic specimens of *Pachygnathus dugesi* Grandjean (1937), originating from Mongaillard, Coulounieix (Dordogne), France (collected in litter under a spruce-fir in a park); these were kindly put at my disposal by Prof. Grandjean. According to Willmann (in: Sig Thor & Willmann, 1941:135), "cotypes" of *Pachygnathus dugesi* appeared to be identical with topotypic material of *Alycus roseus* C. L. Koch from Regensburg. The specific name *dugesi* consequently is a synonym of *roseus*. Grandjean, after having already supposed this synonymy (1939:3), later on (1942:89) definitely adopted it. Slight

differences between various populations of the species are dealt with below (cf. remark 1).

As mentioned above, the type of the genus *Pachygnathus* (*P. villosus* Dugès) is not identical with *A. roseus* as was erroneously supposed by Oudemans (1937:869) and Willmann (in: Sig Thor & Willmann 1941:135); it is considered here of uncertain identity. For this reason, the species described here is classified with the genus *Alycus*.

Measurements. — The length of the specimen represented in figs. 1-3 of the present paper is 0.535 mm (measured from the naso up to the posterior border), the breadth is 0.320; the ratio length: breadth is 1.67.

According to Grandjean (1937:56) the length varies from 0.430-0.560 mm, the ratio length: breadth from 1.65-2. In some of our specimens the "shoulders" are more distinctly developed. In some females the opisthosoma becomes strikingly plicate, which condition thwarts a description. The specimens described here are females which probably had recently moulted, and in which eggs had not yet developed. In this condition they are best suited for a detailed description.

Colour. — The colour is caused by the light brown colour of the cuticle and the violet (slightly reddish) colour of the pigment grains in the hypodermis. Together they cause the slightly pinkish colour of a specimen observed in reflected light. In alcohol (under a dissecting microscope) and in a slide (under a high power microscope), especially the violet colour is visible. The narrow intersegmental areas and the muscle attachments lack pigment grains; this is especially visible in alcohol under a dissecting microscope. In this way, segmentation is easily discernable. A detailed description of the colour of the prodorsum is given by Grandjean (1937:56-58, fig. 1A).

Tegument. — Although a thin layer of cerotegument is probably present, it is difficult to observe because observations on a carbon block are thwarted by folding of the cuticle of the drying specimens. The greater part of the cuticle is not sclerotized; its ornamentation consists of a great many, more or less parallel, winding ridges. The crests of the ridges each bear a row of pointed granules.

The prodorsum presents a central sclerite (cf. fig. 1), bearing the two pairs of bothridial setae and the interbothridials. Anteriorly the sclerite has a narrow median prolongation which continues on the naso. The genital covers and the coxal regions of the legs are also sclerotized (fig. 2); the

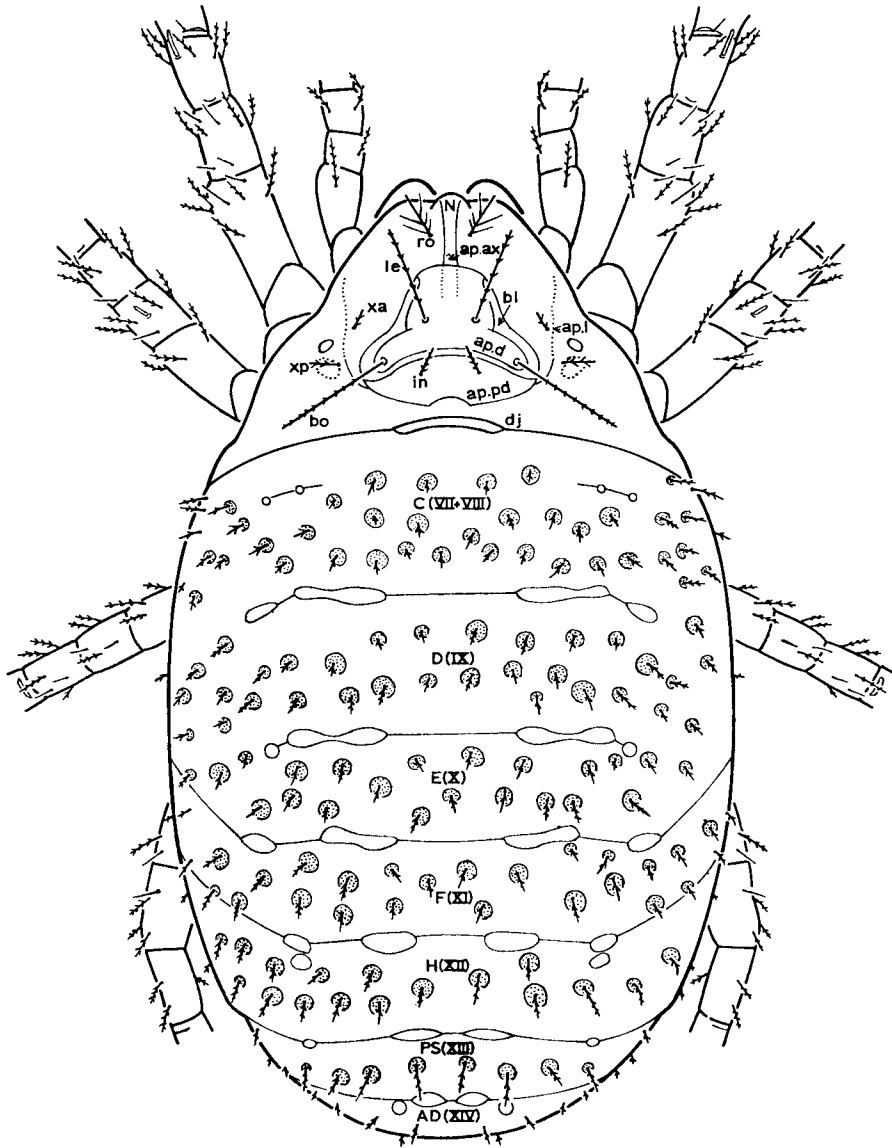


Fig. 1. *Alycus roseus* C. L. Koch, dorsal view of female; $\times 235$.

same applies to the chelicerae, the free segments of palps and legs, and parts of the infracapitulum. Small microsclerites are present at the bases of setae not inserted on larger sclerites, especially in the dorsal region of the opisthosoma (fig. 4F); these microsclerites often constitute the walls of small, funnel-shaped deepenings, at the bottom of which the setae are inserted. The surface of all sclerites (including the microsclerites) is more or less granulate; the "granules", however, have the shape of small ridges, for which reason they were named costules by Grandjean (1936:400). In the case of the larger sclerites, these costules are arranged in winding rows. In lateral view, the costules appear more or less as small cones. The borders of the large sclerites are not always distinct; transitions occur between the soft skin and the sclerotized parts.

As mentioned above, the hypodermis contains a great many pigment grains; this is considered by me a primitive character (generally only present in faintly sclerotized cuticles).

Subdivision of the body. — Although the gnathosoma is movably attached to the idiosoma, the former is still distinctly the normal prolongation of the latter: chelicerae and palps have the ordinary arachnid position (cf. fig. 3). This clearly demonstrates once more that the infracapitulum (the mentum) is the coxisternal region of the palp.

The idiosoma is subdivided into stethosoma and opisthosoma. Dorsally this subdivision is represented by the disjugal furrow, laterally and ventrally the subdivision passes posteriorly of leg IV. In Acarida, gnathosoma and stethosoma together constitute the prosoma of other Arachnidea (cf. Van der Hammen, 1968a).

Prodorsum. — There are six pairs of prodorsal setae (figs. 1, 3): rostral (*ro*), anterior bothridial (= lamellar *le*), interbothridial (= interlamellar *in*), posterior bothridial (= sensillus *bo*), anterior exobothridial (*xa*), and posterior exobothridial (*xp*). Consequently, there are two pairs of bothridial setae, viz., *le* and *bo*; their bothridia are simple, but relatively deep (fig. 4B). Rostral, interbothridial, and anterior and posterior exobothridial setae are strikingly spinous; the two pairs of bothridials are long and ciliated.

Anteriorly, the prodorsum presents a distinct frontal protuberance, the naso, which is directed downwards, between the chelicerae (fig. 5 A-C). This naso (*N*) has a circular base; its shape is more or less conical. Its dorsal surface is granulate ("costulate"), its ventral surface is smooth (fig. 5B); there is no inferior eye. A rostral tectum is not present.

There are one pair of true eyes and one pair of vestigials (fig. 4C). The

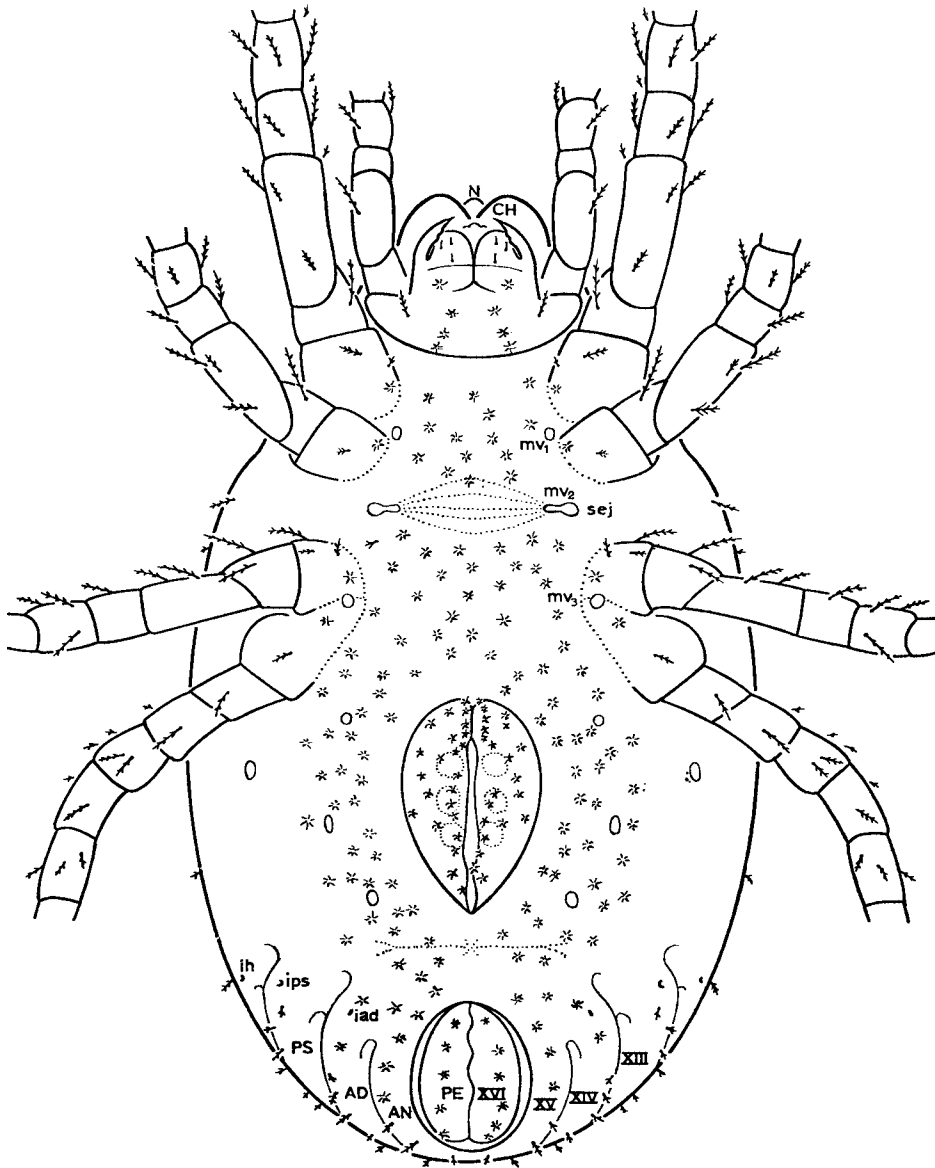


Fig. 2. *Alycus roseus* C. L. Koch, ventral view of female; $\times 235$.

vestigial eye is situated posteriorly of, but close to the anterior eye; the two still form a distinct group. The vestigial eye, recognizable as a light spot, lacks a lens; its surface is granulate; its outline is still distinctly circular.

The prodorsum presents a central sclerite (figs. 1, 4B) which bears the anterior and posterior bothridials, and the interbothridials. The central sclerite anteriorly continues on the dorsal surface of the naso. The rostral setae are inserted at the border of this anterior continuation. The prodorsum presents five internal, chitinous ridges which serve as muscle attachments: axial, dorsal, posterodorsal, and a pair of laterals; externally, they correspond with light bands without pigment grains. The axial "apodeme" (*ap.ax*) anteriorly continues into the naso, posteriorly under the central prodorsal sclerite. The dorsal "apodeme" (*ap.d*) is situated posteriorly of the posterior bothridia, the posterodorsal (*ap. pd*) posteriorly of the interbothridial setae. The lateral "apodeme" (*ap.l*) extends from the fusion of posterodorsal and dorsal apodeme up to the anterior lateral part of the prodorsum. A pair of colourless bands (*bl*) laterally border the central prodorsal sclerite; they do not correspond with an internal "apodeme". After the example of other Arachnidea (Palpigradida, Schizomida), but with modified terminology, the prodorsum could be regarded as consisting of pro-, meso-, and metastethidium (cf. remark 5), separated by dorsal and posterodorsal "apodemes".

Dorsal aspect of opisthosoma, and anal region. — Prosoma and opisthosoma are dorsally separated by the disjugal furrow (figs. 1, 3), at the internal side of which muscles are inserted. The opisthosoma strongly differs from the prosoma because of its neotrichy.

At first sight, the opisthosoma of *Alycus roseus* seems to be composed of nine segments: *C*, *D*, *E*, *F*, *H*, *PS*, *AD*, *AN*, and *PE*; these segments are separated by colourless bands which internally correspond with inter-segmental muscle attachments (fig. 4G). "Segment" *C*, however, appears to be composed of two segments: muscle attachments are present in the anterior part, laterally of the anterior central row of setae (figs. 1, 3). This condition reminds of the Opilioacarida in which group the anterior dorsal opisthosomatic division is also composed of two segments. "Segment" *C*, consequently, is composed of segments VII (generally reduced in Arachnidea) and VIII. The peranal segment is segment XVI. This number can be a base for the study of segmentation in other Actinotrichida (cf. remark 7).

The opisthosoma presents a distinct neotrichy, especially developed in the anterior segments. All dorsal setae are inserted on microsclerites (fig. 4F). The setae are distinctly spinous. "Segment" *C* (= VII + VIII) presents

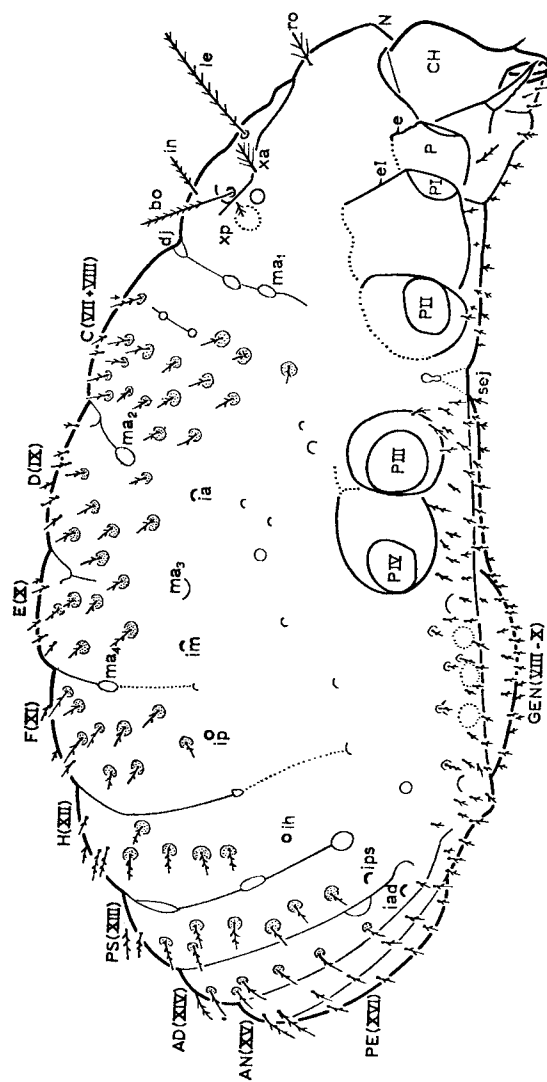


Fig. 3. *Alycus roseus* C. L. Koch, lateral view of female; $\times 235$.

some three rows of setae, segments *D-H* (IX-XII) some two rows; *PS-PE* (XIII-XVI) present only one row. The paraproctal lips (segment *PE*) each bear 4-6 often asymmetrically arranged setae.

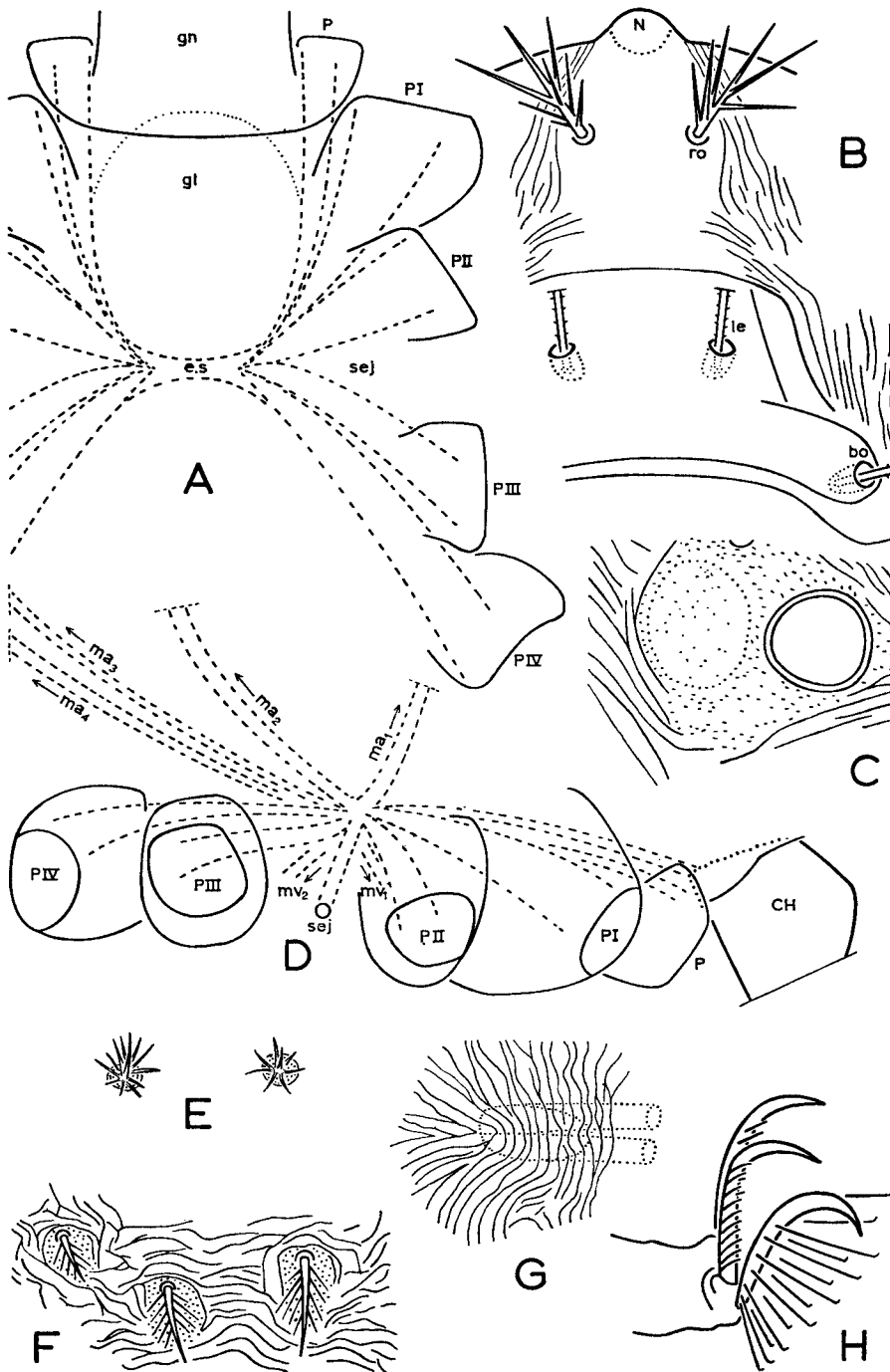
There are six pairs of lyrifissures which have the shape of cupules: *ia*, *im*, *ip*, *ih*, *ips*, *iad*; there is no anal lyrifissure *ian*. Consequently the two posterior segments (*AN*, *PE*) and apparently the two anterior (*C*) lack lyrifissures. This means that the lyrifissures *ia*, *im*, and *ip* belong to the segments *D*, *E*, and *F* respectively. This is a discovery of fundamental importance to the comparative morphology of all Actinotrichida (cf. remark 8).

The shape of the opisthosoma is slightly variable. In the specimen figured here, it is nearly parallel-sided; the shoulders, however, can be slightly more pronounced. Although the peranal segment is the posterior one, its position is ventral; this means that the posterior part of the opisthosoma is curved downwards.

Genital region. — Just as in other Endeostigmata, the progenital lips (genital covers) (figs. 2, 3) are rather large; they are separated by a distinct interval from the anal orifice. The lips are sclerotized. There is a great number of (pro)genital setae; these are generally asymmetrically arranged. In the figured specimen the number is 21-23; according to Grandjean (1937:60) it varies from 18-24. Just as in other Actinotrichida, the longitudinal orifice between the progenital lips gives entry into the progenital chamber (in order to avoid confusion, progenital is introduced here instead of pregenital; in arachnology pregenital refers to the pregenital segment, i.e. segment VII, in front of the genital segment). The progenital chamber (fig. 7A) contains three pairs of genital papillae (*Pg*₁₋₃). Between the anterior pair of papillae, the true genital orifice (*og*) of the female is visible; it is triangular. One pair of eugenital setae (Ψ_1) is present near the posterior border of the orifice. In Arachnidea the genital orifice is in segment VIII. Consequently, the anterior genital papilla belongs to the VIIIth segment, the median and posterior papilla to the IXth and Xth respectively. The longitudinal opening between the progenital lips is named here secondary genital orifice.

This interpretation of the genital region is very important for a clear apprehension of the opisthosomatic structure. A progenital chamber extending over three segments is apparently a unique character of the Actinotrichida (cf. remark 9).

Ventral and adgenital region. — This area is characterized by a strongly developed neotrichy (fig. 2). A number of important muscle attachments is present in the adgenital region.



Coxisternal region. — This region is also neotrichous (fig. 2). There is a large sejugal interval. It appears that an endosternite is present in this region (fig. 4A, D). This endosternite has the shape of a narrow, transverse band, connected with muscles from chelicerae, palps, and all legs. Ventrally, the endosternite is connected with the pair of muscle attachments in the sejugal interval (mv_2), and with the muscle attachments between legs I and II (mv_1), and legs III and IV (mv_3) (fig. 2). Dorsally, the endosternite is connected with the muscle attachments in the disjugal fold (fig. 3: ma_1), between segments *C* and *D* (ma_2), *D* and *E* (ma_3), and *E* and *F* (ma_4). This correlation of the sejugal interval with an endosternite is very interesting; in Opilioacarida (where no sejugal interval is present) an endosternite appeared to be present between legs III and IV (cf. Van der Hammen, 1966: fig. 5A); however, this must be subject of further investigations (cf. remark 10).

Lateral region of podosoma. — The pleural regions are glabrous. The coxal regions of the legs are distinctly differentiated. The coxal region of leg I has a small supracoxal seta eI (fig. 7C), similar to the supracoxal seta e of the palp; the coxal region of leg II has no supracoxal seta. The podoccephalic canal is present as a superficial taenidium.

Gnathosoma. — The general position of the gnathosoma is represented in figs. 2, 3; it is terminal and slightly inclined. There is no rostral tectum and no camerostome. Chelicerae and palps have the same position as in other groups of Arachnidea; the presence of an infracapitulum, however, remains an important difference in comparison with the general Arachnid condition. The gnathosoma, moreover, can easily be separated as a whole: the chelicerae remain attached to the infracapitulum.

Alycus roseus clearly demonstrates the primitive condition of the tegulum: it is still nothing but part of the front wall of the body (cf. fig. 5A-C: TG). Apart from the simple tegulum, the cheliceral frame consists of a rather large interspace between the chelicerae, and of the attachment of the chelicerae to the infracapitulum. The three parts of the cheliceral frame together constitute the complete front wall (cf. Van der Hammen, 1968: 7-9). There is a

Fig. 4. *Alycus roseus* C. L. Koch, female; A, ventral view of endosternite; B, dorsal view of median part of prodorsum; C, lateral view of lateral eyes; D, lateral view of endosternite; E, ventral view of two sternal setae of the segment of leg II; F, dorsal view of three dorsal setae of segment *F* (= XI); G, dorsal view of right dorsal muscle attachment between segments *D* (= IX) and *E* (= X); H lateral (paraxial) view of the claws of left leg II; A, $\times 370$; B, $\times 690$; C, $\times 1315$; D, $\times 370$; E, F, G, $\times 690$; H, $\times 1315$.

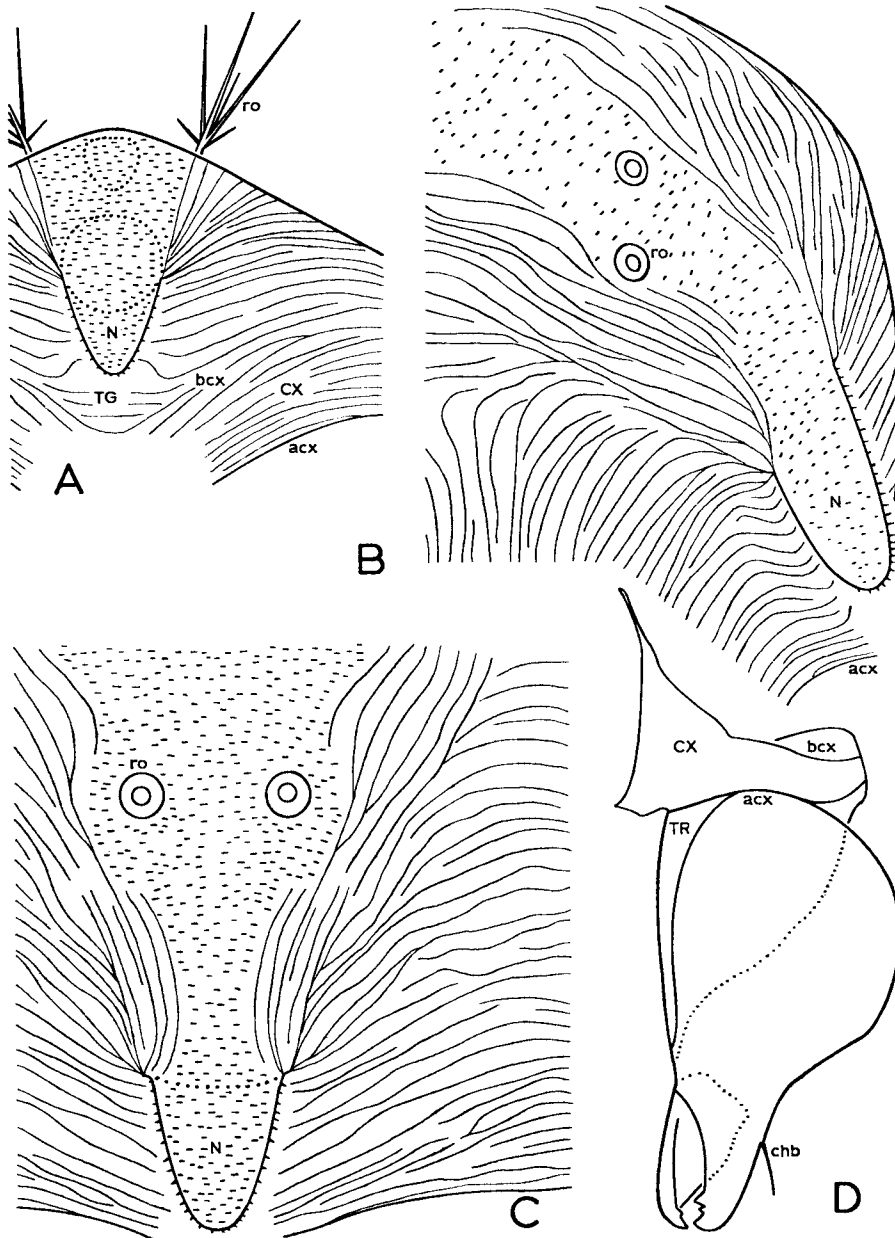


Fig. 5. *Alycus roseus* C. L. Koch, female; A-C, naso and adjoining parts of prosoma; A, ventral view; B, lateral view; C, frontal view; D, lateral (antiaxial) view of right chelicera with coxal region; A-C, $\times 1315$; D, $\times 710$.

distinct coxal region of the chelicera, which is attached to the tegulum according to a line *bcr* (fig. 5A-D). The gnathosoma as a whole is represented in lateral view in fig. 6A; in this figure the chelicera is slightly raised in order to show the labrum. The primitive condition of the cheliceral frame is here at once evident.

The infracapitulum is anarthric: there is no labiogenal articulation; mentum and genae are consequently not separated. In contradistinction to the last-mentioned parts, the lateral lips are not sclerotized. There is a distinct difference of level between the base of the lateral lips and the anterior border of the genae.

There are three pairs of simple, strongly curved adoral setae. The rutellum belongs to the narrow, primitive type. Its shape is represented in lateral and ventral view in fig. 6A, B respectively. In the Dutch specimens it ends in a single point; it has some three rounded ventral teeth. Apart from the lateral lips, there are a three-lobed labrum, and a small, rounded, unpaired underlip. Consequently, the mouth has four commissures (fig. 6B: *Js, Js', Ji, Ji'*). There are a variable number of infracapitular setae: one pair of anteriors (*a*), one to three pairs of medians (*m₁₋₃*), and one pair of hysterosomatics (*h*); they are as a rule asymmetrically arranged. The pharynx has a dorsal sclerite (fig. 6B: *sc.ph*) which is anteriorly pointed; the terminal, pointed part extends into the labrum as labral sclerite (*sc. ls*).

Chelicera. — The chelicera (figs. 5D, 6A) has only one seta (*chb*) with an anterior, dorsal position; a comparison with other species of the genus demonstrates that the posterior seta (*cha*) has disappeared. The trochanter is small and oblique; its position is especially ventral and paraxial.

The coxal regions of the chelicerae serve as sheaths: they can be invaginated and evaginated. They are attached at the base of the chelicerae (fig. 5D: *acr*). The fixed jaw of the chelicerae has three teeth (including a large one), the movable jaw two.

Palp. — A left palp in lateral (antiaxial) view was described and figured in detail by Grandjean (1937: 58, fig. 1B). The formula of the palp is 0-2-1-3-14; the tarsus bears one small solenidion ω .

Legs. — Parts of the legs are represented in figs. 1 and 2; leg I is represented in detail in fig. 7B, D, E, part of leg IV in fig. 7F, the ambulacrum of leg II in fig. 4H. Legs I-III consist of six primary segments: trochanter, femur, genu, tibia, tarsus, and apotele. Leg IV presents seven segments: there are two femora. The articulation between the two femora (cf. fig. 7F) is a monovalent, primary one (cf. Van der Hammen, 1966: 54-57). Consequently, the proximal segment is not trochanter 2 (an articu-

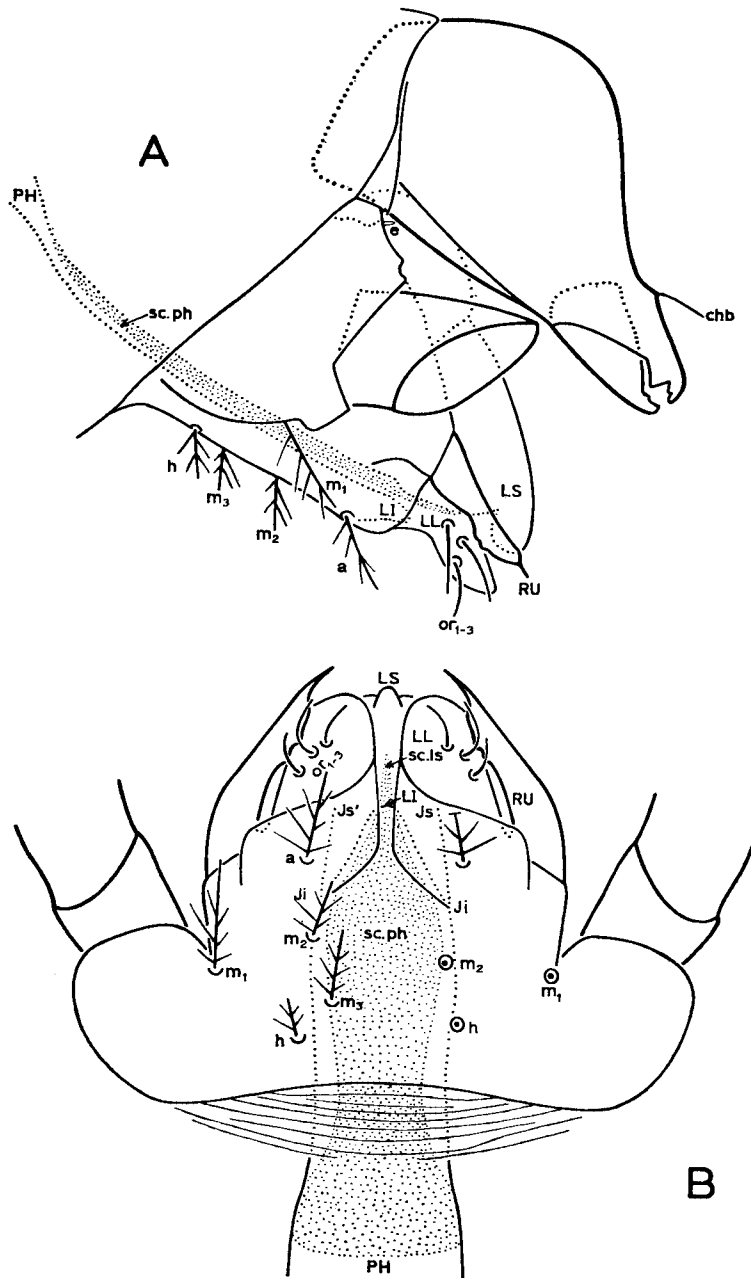


Fig. 6. *Alycus roseus* C. L. Koch, gnathosoma of female; A, lateral view (chelicera slightly raised); B, ventral view; A-B, $\times 710$.

lation trochanter 2/femur is bivalent) and no basifemur (an articulation basifemur/telofemur is a secondary one). For this reason I introduce here the names femur 1 and femur 2 for the two femora of Actinotrichida, and the notation *tfe* for the tendon of femur 2. This further perfection of the terminology of the leg segments augments its value for comparative morphology.

The formulae of the legs are the following (the formula of leg IV has seven numbers instead of six, because of the presence of two femora): I (1-6-5-6-42-3); II (1-5-4-5-29-3); III (2-3-3-4-25-3); IV (1-3-3-4-5-23-3). The formulae of the solenidions are the following (the formulae have four numbers because solenidions occur also on some femora): I (2-4-1-2); II (0-2-2-1); III (0-2-2-0); IV (1-1-0-0). The number of solenidions on femur IV relates to femur 2. The presence of solenidions on some femora distinctly distinguishes the species from the Oribatida.

In fig. 7E, F, I have reserved the notation *d* for the unpaired dorsal seta; the paired dorsals have received the notations *ld'* and *ld''*. The setae of tarsus I (fig. 7B, D, E) are arranged in rows, viz., a pair of laterodorsal rows: (*p*), (*it*), (*tc*), (*ft*), (*ld*₁), (*ld*₂), *ld*₃'; a pair of laterals: (*a*), (*pl*), (*l*₁), (*l*₂), (*l*₃); a pair of lateroventrals: (*lv*₁), (*lv*₂), (*lv*₃), (*lv*₄); a pair of ventrals: (*u*), (*pv*), (*v*₁), (*v*₂), (*v*₃); and an unpaired medioventral: *s*.

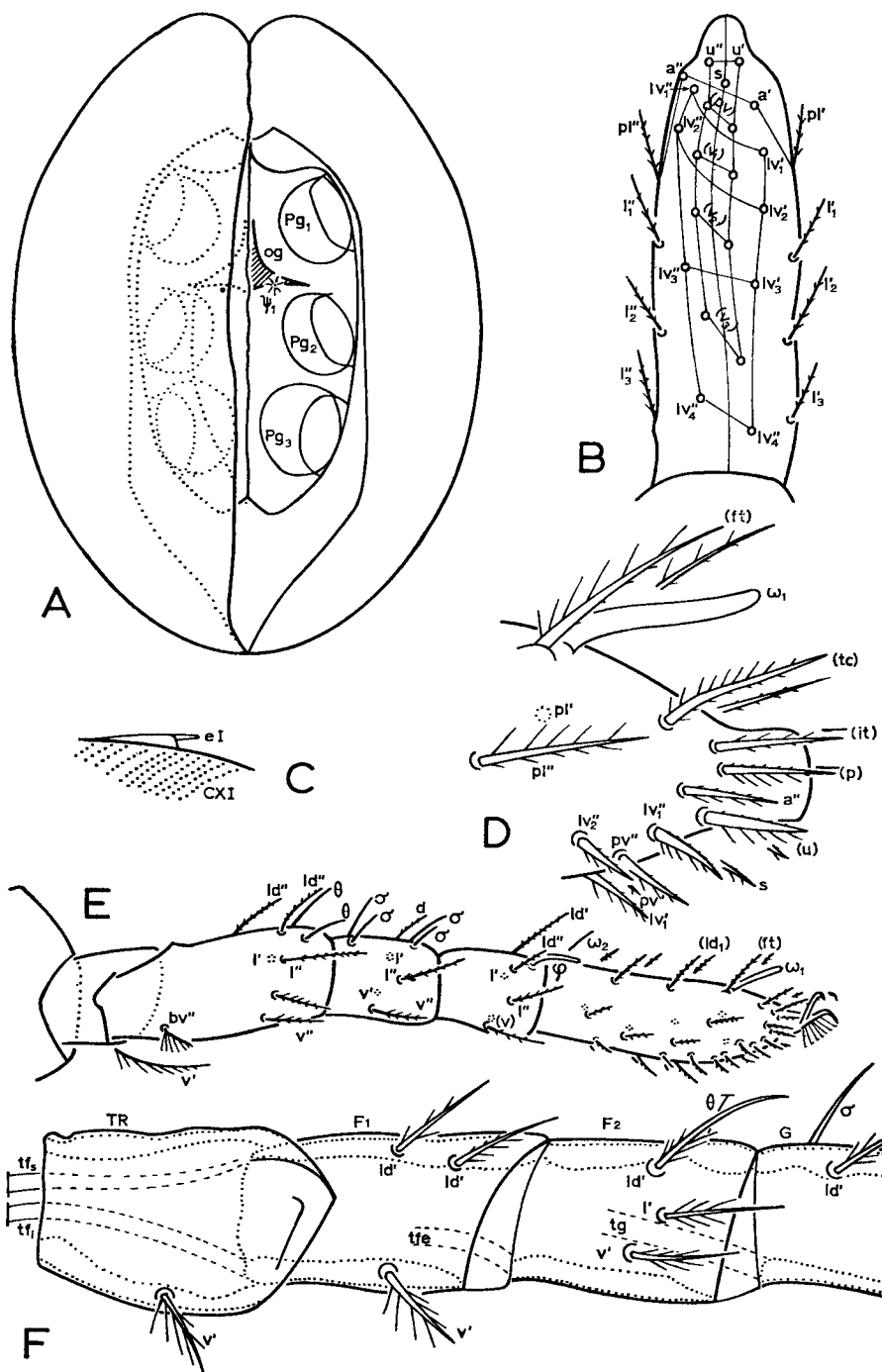
In the Dutch specimens, femur 1 IV has three setae; Grandjean (1937:61) mentions two setae for the specimens from Mongaillard near Coulounieix (Dordogne, France).

The apotele has three claws which bear hairs (fig. 4H). When observed under favourable conditions, the hairs of the median claw appear to be suddenly bent in the terminal part, in this way resembling the tenent hairs of some Tetranychidae; they are probably tenent hairs indeed. The possession of claws of this type is also a character that profoundly separates *Alycus roseus* from the Oribatida.

REMARKS

REMARK 1. DISTRIBUTION AND VARIABILITY OF THE SPECIES

The type-locality of the species is the forest in the neighbourhood of the Schuttfelsen, near Sinzing, SW of Regensburg, Bavaria Germany. Although the identity of the species is certain (cf. Willmann in: Sig Thor & Willmann, 1941:135), a redescription after topotypic material is still wanting; consequently, details on e.g. gnathosoma and leg chaetotaxy are not known. Differences appear to exist between various populations. The specimens described here have a rutellum with a broad base, a concave median ventral border, three rounded ventral teeth, and one terminal point. This rutellum



is intermediate between that of the specimens described as *dugesi* Grandjean (1937:56) and as *dugesi denasutus* Grandjean (1937b:199); it is apparently nearly similar to that of the specimens from the North of France mentioned by Grandjean (1937:58). As mentioned above, in the section on the legs, there is a slight difference in chaetotaxy between the Dutch specimens and those from Dordogne (France). When the specimens from The Netherlands and those from the North of France should appear to be identical with those from the type locality, they should represent the typical subspecies *Alycus roseus roseus* (C. L. Koch, 1841); in that case the specimens from Dordogne should be named *A. roseus dugesi* (Grandjean, 1937), the subspecies from Strasbourg *A. roseus denasutus* (Grandjean, 1937b).

Willmann & Sig Thor (1941:136) mention the species from Europe (France, Germany, Switzerland, The Netherlands). It was afterwards recorded from Denmark (Haarlov, 1957:25, sub *Pachygnathus villosus*). The specimens recorded as *Alycus ?roseus* from Australia by Womersley (1944: 139, fig. 3 F-I) probably represent nymphs of a different species; they are small, and the ambulacrum presents an empodium; the anterior bothridial setae are very close together, and the opisthosoma has a slight constriction.

REMARK 2. THE MORPHOLOGY OF *ALYCUS* AS CONTRIBUTION TO A MORE DISTINCT DELIMITATION OF ACTINEDIDA AND ORIBATIDA

Recently (Van der Hammen, 1968a), I drew the attention once more to the difficulty in preparing clear definitions distinguishing Actinedida (= Trombidiformes) and Oribatida. The groups are distinctly separated as to the greater part of their representatives; however, they are apparently rather closely related as far as the primitive species are concerned. In the present description of *Alycus roseus*, mention is made of a number of details that are fundamentally different from the condition in (adult) Oribatid mites. I enumerate the following typically Actinedid characters of the species, as contribution to a better understanding of the diagnostics of the two orders. (1) There is no rostral tectum; the naso extends unprotected between the chelicerae. (2) The prodorsum has two pairs of bothridial setae. (3) Although there are opisthosomatic microsclerites, a notogaster or notogastral sclerite is not present. (4) Some of the femora present solenidions. (5) The claws

Fig. 7. *Alycus roseus* C. L. Koch, female; A, ventral view of genital region (the left progenital lip is supposed to be removed); B, ventral view of right tarsus I (the ventral setae are represented by their place of insertion only); C, lateral view of laterocoxal seta *cI*; D, lateral (antiaxial) view of distal part of right tarsus I; E, lateral (antiaxial) view of right tarsus I; F, lateral (antiaxial) view of trochanter, femur 1, femur 2, and proximal part of genu of left leg IV; A, B, $\times 690$; C, D, $\times 1315$; E, $\times 370$; F, $\times 710$.

present tenent hairs; in the case of legs I-III, the median claw is replaced by an empodium in the larval stage, in the case of leg IV in the protonymphal stage (cf. Grandjean, 1937a:136, 138, fig. 4C). Some of these characters apply to all or nearly all Actinedida (1, 3), others have only a restricted validity (2, 4, 5); all of them, however, serve to distinguish the species from the Oribatida.

It may be added here that another trend demonstrated by the Endeostigmata consists in the tendency to reduce the number of nymphs from three to two (some *Alicorhagia* and *Bimichaelia* species; cf. Grandjean, 1942: 134). This trend, together with the characters mentioned above, exactly suits into the evolutionary pattern of the Actinedida.

Summarizing, we could say that primitive Actinedida and Oribatida, although externally still resembling each other in many characters, were already definitely separated by their internal disposition, by possibilities present in germ.

REMARK 3. THE PRIMITIVE CHARACTERS OF THE ACARIDA, AND THE FUNDAMENTAL DIFFERENCES BETWEEN ACTINOTRICHIDA AND ANACTINOTRICHIDA

When we compare the figures of the present paper with those prepared by me for *Opilioacarus texanus* Chamberlin & Mulaik, 1942 (cf. Van der Hammen, 1966), especially fig. 3 of both papers, we are at first sight astonished by a remarkable similarity. This similarity is not caused by the uniform style of drawing; uniformity of style, on the contrary, is favourable because it eliminates all artificial differences. The similarity of two primitive species of completely different groups, and with completely different adaptations, is apparently caused by essential and primitive acarid characters. It is interesting to summarize these characters here, and to analyse afterwards which characters, different in the two species, are essential differences between the two superorders.

As a result of the comparison (and taking into account the characters known from other primitive mites), the following list of primitive or original acarid characters can be prepared (some of these characters have persisted in most mites). (1) The body is for the greater part only faintly sclerotized in a more or less leathery way. (2) There are coloured pigment grains in the hypodermis. (3) The body consists of prosoma and opisthosoma; the prosoma in its turn of gnathosoma and stethosoma. (4) The dorsal surface of the prosoma (the prodorsum) is subdivided by one or two transverse furrows. (5) The opisthosoma presents a distinct segmentation; there are intersegmental furrows, internally corresponding with muscle attach-

ments; there are primitively no separate tergites, sternites, and pleurites. (6) The prosoma presents eyes. (7) The gnathosoma presents an anarthric infracapitulum; there are a labrum and a pair of lateral lips (a primitive, unpaired underlip is not yet known from Anactinotrichida); there are adoral setae, one of which can develop into a rutellum. (8) The chelicerae consist of three segments: trochanter, principal cheliceral segment, and apotele; the coxal region of the chelicerae is functioning as sheath. Some characters need further investigation; they are not yet included in this list; this concerns the rostral lobe, and the sternal and genital verrucae or papillae (cf. Van der Hammen, 1966: 10, 53; 1968b: 62).

A further analysis results in the following list of primitive and original, exclusively Actinotrichid characters. (1) A primitive number of sixteen segments. (2) The presence of a naso. (3) The presence of six pairs of prodorsal setae. (4) A basic number of six or seven pairs of opisthosomatic lyrifissures or cupules. (5) A genital orifice debouching into a progenital chamber which extends over three segments (VIII-X) and contains three pairs of genital papillae (the larva has a metahomologous Claparède's organ); the secondary genital orifice is longitudinal. (6) The presence of a sejugal interval, corresponding with an endosternite. (7) Three pairs of (coxal) glands, debouching into a podocephalic canal. (8) The condition of the cheliceral frame which is still nothing but the front wall of the body. (9) The presence of an unpaired underlip. (10) The presence of two femora (originally apparently in all legs). However, it will be interesting to investigate the tendons of femur I of *Sphaerolichus barbarus* Grandjean (1938: 98, fig. 20); this femur is apparently subdivided into three parts, and the telofemur is functionally a genu. (11) The presence of solenidions on femur, genu, tibia, and tarsus. (12) A characteristic basic pattern of the tarsal setae. (13) The presence on the legs of only one lyrifissure, dorsally at the base of the tarsus.

The following characters occurring in Acarida are regarded here as primitive and exclusively Anactinotrichid. (1) A number of nineteen segments. (2) The presence of a great number of opisthosomatic lyrifissures, four pairs of which have developed into tracheae. (3) A transverse genital orifice. (4) The absence of a sejugal interval. (5) The presence of sternal taenidia passing into a median subcapitular groove. (6) The presence of a pair of sternapophyses in the region of leg I. (7) Chelicerae with a dorsal and an antiaxial lyrifissure. (8) A palp with an apotele bearing claws. (9) The presence of an important number of lyrifissures on the legs, some of which are associated with secondary articulations. (10) The presence

of free coxae, two trochanteres (in the case of legs III and IV), and of secondary articulations in femora and tarsi. (11) The presence of a pretarsus with two pairs of setae.

Opilioacarus is more primitive than *Alycus* because of: the terminal position of the anus; the simple, transverse genital orifice; the presence of palpal claws; and possibly because of the greater number of segments. *Alycus*, in its turn, is more primitive because of its cheliceral frame which has still the typical Arachnid shape of front wall of the body; because of the presence of an unpaired underlip; and possibly because of the presence of a naso. A further evaluation of these characters is in the field of comparative Arachnid morphology.

REMARK 4. RESTRICTION AND COMPLETION OF THE SOMA TERMINOLOGY

Recently (Van der Hammen, 1968a), I pointed once more to the incorrectness of part of the soma terminology because of a confusion of sejugal and disjugal furrows. As a result of this, I rejected the terms proterosoma, propodosoma, metapodosoma, and hysterosoma. However, it appeared that no term existed for the prosoma without the gnathosoma, although logically both parts of the prosoma should receive names. During my investigations of the last years, I had indeed been repeatedly in need of it, for which reason I introduced the term stethosoma.

The soma terminology can now be summarized in the following table.

	gnathosoma	} prosoma
idiosoma	stethosoma	
	opisthosoma	

The term podosoma does not enter into this table because of its imprecise definition in the dorsal region. I have not rejected it because of its practical value in descriptions (as far as lateral and ventral face of the idiosoma are concerned).

REMARK 5. THE SUBDIVISION OF THE PRODORSUM

As mentioned above, the prodorsum of *Alycus roseus* presents in its posterior part two transverse, colourless bands corresponding with internal apodemes: the dorsal and the posterodorsal. The transverse bands subdivide the prodorsum into three parts: a large anterior, a small median, and a small posterior. In the case of *Opilioacarus* (cf. Van der Hammen, 1966: 10, fig. 1), the prodorsum is subdivided by one furrow into two parts.

When we compare these subdivisions with those of other Arachnidea with divided prodorsum (Palpigradida, Schizomida, Solpugida), we state that the conditions are certainly primitive and homologous. However, because the prodorsum of *Alycus* and *Opilioacarus* is only partly or faintly sclerotized, the terms pro-, meso-, and metapeltidium, or pro- and postpeltidium are not applicable. For this reason the terms pro-, meso-, and metastethidium are introduced here for the three prodorsal subdivisions of *Alycus*, the terms pro- and poststethidium for the two of *Opilioacarus*.

REMARK 6. THE PRODORSAL SETAE OF THE ACTINOTRICHIDA

The prodorsal setae of Oribatida and those of primitive Actinedida (= Trombidiformes) are without doubt homologous. The primitive number is six pairs: rostrals, anterior bothridials (= lamellars), interbothridials (= interlamellars), posterior bothridials (= sensilli), anterior exobothridials, and posterior exobothridials. In Oribatid mites, this primitive number is generally still present, with the exception of one of the pairs of exobothridial setae which is lacking in the higher developed species. (However, both exobothridial setae and the sensillus can also be lacking). In higher Actinedida, and Acaridida, the number is generally smaller, and homologization seems difficult. The regression of setae, however, is passing according to laws. Two of these laws concern the regression of the posterior bothridials. Besides, there will be a certain priority among the setae; the rostrals e.g. are probably never lacking (they are probably present in nearly all Arachnidea). Establishing homologies will be very interesting. For this reason, it will be important to make comparative investigations of the prodorsal setae in other groups of Actinedida, and in Acaridida.

REMARK 7. THE POSTLARVAL ADDITION OF PARAPROCTAL SEGMENTS AND THE TOTAL NUMBER OF SEGMENTS IN VARIOUS ACTINOTRICHIDA

In the present paper we have established the primitive number of segments in Actinotrichida. The paraproctal segments have received the numbers XIII (*PS*), XIV (*AD*), XV (*AN*), and XVI (*PE*). Each of these segments has a fixed base level: larval (*PS*), protonymphal (*AD*), deutonymphal (*AN*), and tritonymphal (*PE*). From this it follows that we can establish the total number of segments in studying the postlarval addition of segments. When there is no postlarval addition (many higher Actinedida), the total number is 13. When the protonymph only adds a segment (Caeculidae, Anystidae, Bdellidae ad part., *Torpacarus* (Lohmanniidae)), the total number is 14. When proto- and deutonymph both add a segment,

the total number is 15 (the greater part of the Oribatida). A total number of 16 segments is apparently found only in some primitive Oribatida and Endeostigmata.

According to Knülle (1959:369), the postlarval addition of segments in Acaridida is essentially different. The larval paraproctal segment should be *F*, the protonymph should add *H* and *PS*, whilst *AD* should be added by the adult. This remarkable development emphasizes the gap between Acaridida on the one hand, and Oribatida and Actinedida (Tarsonemida not included) on the other; a further study of it will be very important.

REMARK 8. THE ATTRIBUTION OF THE OPISTHOSOMATIC LYRIFISSURES AND CUPULES TO THE CORRESPONDING SEGMENTS

The opisthosomatic lyrifissures or cupules constitute a pair of longitudinal rows; they are distinctly segmentally arranged. Up till now, only the posteriors have been attributed to definite segments, viz., *ih*, *ips*, *iad*, and *ian* (to *H*, *PS*, *AD*, and *AN* respectively). The present study demonstrates that *im* distinctly belongs to *E*, *ip* to *F*. The cupule *ia* is situated at the border of *C* and *D*. It is logical to suppose that originally all opisthosomatic segments had lyrifissures or cupules, and that in the course of evolution they disappeared in the anterior and posterior parts. The peranal segment has indeed no lyrifissure, whilst *ian* is often absent. The hypothesis seems plausible that the lyrifissures of *C* have also disappeared, and that consequently *ia* belongs to *D*. This hypothesis is adopted in the present paper.

REMARK 9. THE TERMINOLOGY OF THE GENITAL REGION IN THE ACTINOTRICHIDA

The longitudinal orifice between the progenital lips (or genital lips or genital covers) is a secondary orifice that gives entry into a progenital chamber (progenital is preferred here over pregenital, because the latter term refers in Arachnology to segment VII). This progenital chamber contains primitively three pairs of genital papillae, which number, however, can be reduced or multiplied. The chamber extends over three segments, viz., the nos. VIII-X, each pair of papillae (when three pairs are present) corresponding with one segment. The progenital chamber presents also the true (or primary) genital (or eugenital) orifice situated at the level of the anterior pair of papillae, i.e. in segment VIII. In Actinotrichida the orifice is apparently always triangular. Close to the orifice, the eugenital setae are present. In the female the orifice and its surrounding region can secondarily develop into an ovipositor which preserves its ternary character.

The above-mentioned structure of the genital region is generally neglected;

the present interpretation should be the base for further investigations into its comparative morphology in various groups of Actinotrichida.

REMARK 10. THE CORRELATION OF THE SEJUGAL INTERVAL WITH AN ENDOSTERNITE

Up till now the meaning of the sejugal interval (although it constitutes a general character of the Actinotrichida) had not been discovered. In the present paper it is apparently for the first time correlated with an endosternite. In Arachnidea endosternites have various shapes. In *Opilioacarus texanus* Chamberlain & Mulaik (cf. Van der Hammen, 1966: fig. 5A), an endosternite is apparently present between legs III and IV; it is not impossible that more than one endosternite is present in that species. The condition in Actinotrichida is apparently unique: an internal, transverse band in the sejugal region, dorsally and ventrally attached to various parts of the idiosoma, and on which muscles from all appendages are inserted. It will be very interesting to investigate its presence in other groups of Actinotrichida, and to make further studies of the possible presence of endosternites in Anactinotrichida; in the last-mentioned group they will probably be differently shaped, and they will certainly have a different position.

REMARK 11. THE TERMINOLOGY OF THE TWO FEMORA IN PRIMITIVE ACTINOTRICHIDA

In my first study on Opilioacarida (Van der Hammen, 1966:54-57), I further developed the terminology of the leg segments in paying special attention to the way of articulation. A distinction was made between primary and secondary articulations, the latter being characterized by the absence of tendons. In the case of the primary articulations, much value was attached to the presence of one or two tendons. The prefixes *basi* and *telo* were reserved for secondary articulations. The two trochanteres of leg III and IV of Opilioacarida, consequently, were named trochanter 1 and trochanter 2 (instead of *basi-* and *telotrochanter*).

The principles of this terminology are now also applied to the femora of *Alycus*. In the present species, leg IV presents two femora; the articulation between the two segments is primary and monovalent. This means that, according to my terminology, they cannot be named *basi-* and *telofemur*; this means also that the distal segment is no trochanter 2. For this reason femur 1 and femur 2 are introduced here as new terms replacing the previous names of *basi-* and *telofemur*. The last-mentioned two names remain of course appropriate in the case of the two secondary divisions of the femur in Anactinotrichida.

LIST OF NEW TERMS

FEMUR 1. — The proximal femur in Actinotrichida (when two femora are present). It is a primary segment; its articulation with the trochanter is bivalent, that with femur 2 monovalent.

FEMUR 2. — The distal femur in Actinotrichida (when two femora are present). It is a primary segment; its articulation with femur 1 and with the genu is monovalent.

MESOSTETHIDIUM. — The median part of the prodorsum when this is subdivided by two transverse furrows.

METASTETHIDIUM. — The posterior part of the prodorsum when this is subdivided by two transverse furrows.

POSTSTETHIDIUM. — The posterior part of the prodorsum when this is subdivided by one transverse furrow.

PRIMARY GENITAL ORIFICE. — The triangular opening inside the progenital chamber, which represents the true genital (eugenital) orifice.

PROGENITAL CHAMBER. — The room between primary and secondary genital orifice. It contains the genital papillae.

PROGENITAL LIPS. — The lips at both sides of the secondary genital orifice.

PROSTETHIDIUM. — The anterior part of the prodorsum when this is subdivided by one or two transverse furrows.

SECONDARY GENITAL ORIFICE. — The opening between the progenital lips (in Actinotrichida it is usually longitudinal), which gives entry into the progenital chamber.

STETHOSOMA. — The prosoma without the gnathosoma.

ALPHABETIC LIST OF ABBREVIATIONS USED IN FIGS. 1-7

<i>a</i> , anterior infracapitular seta.	<i>CX</i> , cheliceral sheath (coxal region of chelicera).
<i>a'</i> , <i>a''</i> , antelateral setae of tarsus.	<i>CXI</i> , coxal region of leg I.
<i>acx</i> , attachment of cheliceral sheath to chelicera.	<i>d</i> , unpaired dorsal seta of legs.
<i>AD</i> , adanal segment (segment XIV).	<i>D</i> , segment IX.
<i>AN</i> , anal segment (segment XV).	<i>dj</i> , disjugal furrow.
<i>ap.ax</i> , axial "apodeme" of prodorsum.	<i>E</i> , segment X.
<i>ap.d</i> , dorsal "apodeme" of prodorsum.	<i>e.s.</i> , endosternite.
<i>ap.l</i> , lateral apodeme of prodorsum.	<i>e, eI</i> , laterocoxal setae of palp, resp. leg I.
<i>ap.pd</i> , posterodorsal apodeme of prodorsum.	<i>F</i> , segment XI.
<i>bcs</i> , base of cheliceral sheath.	<i>(ft)</i> , fastigial setae of tarsus.
<i>bl</i> , colourless lateral prodorsal band.	<i>F1</i> , femur 1.
<i>bo</i> , bothridial seta (= sensillus).	<i>F2</i> , femur 2.
<i>bv''</i> , basiventral seta of femur.	<i>G</i> , genu.
<i>C</i> , anterior opisthosomatic division, consisting of segments VII and VIII.	<i>gl</i> , gland.
<i>CH</i> , chelicera.	<i>gn</i> , gnathosoma.
<i>chb</i> , (anterior) seta of chelicera.	<i>h</i> , posterior infracapitular seta.
	<i>H</i> , segment XII.

- ia*, cupule (lyrifissure) of segment D (IX).
iad, cupule (lyrifissure) of segment AD (XIV).
ih, cupule (lyrifissure) of segment H (XII).
im, cupule (lyrifissure) of segment E (X).
in, interbothridial (= interlamellar) seta.
ip, cupule (lyrifissure) of segment F (XI).
ips, cupule (lyrifissure) of segment PS (XIII).
(it), iter setae of tarsus.
Ji, *Ji'*, inferior commissures of mouth.
Js, *Js'*, superior commissures of mouth.
l', *l''*, *l'_{1-3}*, *l''_{1-3}*, lateral setae of legs.
ld', *ld''*, (*ld*), laterodorsal setae of legs.
le, anterior bothridial (= lamellar) seta.
LI, underlip.
LL, lateral lip.
LS, labrum.
lv'_{1-4}, *lv''_{1-4}*, lateroventral setae of tarsus.
m_{1-3}, median infracapitular setae.
ma_{1-4}, dorsal attachments of muscles of endosternite.
mv_{1-3}, ventral attachments of muscles of endosternite.
N, naso.
og, primary genital orifice.
or_{1-3}, adoral setae.
(p), proral setae of tarsus.
P, palp.
PE, peranal segment (segment XVI).
Pg_{1-3}, genital papillae.
PH, pharynx.
pl', *pl''*, primilateral setae of tarsus.
PS, pseudanal segment (segment XIII).
(pv), primiventral setae of tarsus.
PI-IV, legs I-IV.
ro, rostral seta.
RU, rutellum.
s, subunguinal seta of tarsus.
sc.ls, labral sclerite.
sc.ph, dorsal pharyngeal sclerite.
scj, sejugal interval.
(tc), tectal setae of tarsus.
tf_i, inferior tendon of femur or femur 1.
tf_s, superior tendon of femur or femur 1.
tfe, tendon of femur 2.
tg, tendon of genu.
TG, tegulum.
TR, trochanter.
(u), *u'*, *u''*, unguinal setae of tarsus.
v', *v''*, (*v_{1-3}*), etc., ventral setae of legs.
xa, anterior exobothridial seta.
xp, posterior exobothridial seta.
θ, solenidion of femur.
σ, solenidion of genu.
φ, solenidion of tibia.
ψ_1, eugenital seta.
ω, solenidion of tarsus.
 VII-XVI, opisthosomatic segments.
', right (in the case of symmetrical pairs).
', *''*, anterior and posterior (in the case of setae of the appendages).
(), a pair (of setae).

SUMMARY

In the present paper a detailed description is given of *Alycus roseus* C. L. Koch (= *Pachygnathus dugesi* Grandjean); the species is a representative of the Endeostigmata, a primitive group of Actinedida (= Trombidiformes). The description is prepared in order to enable a comparison between primitive representatives of Actino- and Anactinotrichida; it is at the same time a fundamental study of segmentation and soma terminology in the first-mentioned superorder. Special attention is paid also to the homology of the prodorsal setae, to the genital region, and to the sejugal interval (which is correlated here with an endosternite). A number of new terms is introduced, viz., stethosoma for the prosoma without the gnathosoma; pro-, meso-, and metastethidium for the three subdivisions of the prodorsum; primary and secondary genital orifice and progenital chamber (instead of pregenital); and femur 1 and 2 for the two Actinotrichid femora.

REFERENCES

- DUGÈS, A., 1834. Recherches sur l'ordre des Acariens. Troisième mémoire. — Ann. Sci. Nat. (2), 2, Zool.: 18-63 (sep. 1-46), pls. 7-8.

- GRANDJEAN, F., 1936. Le genre *Pachygnathus* Dugès (*Alycus* Koch) (Acariens). 1re partie. — Bull. Mus. Nat. Hist. Nat. (2), 8: 398-405.
- , 1937. Le genre *Pachygnathus* Dugès (*Alycus* Koch) (Acariens). (Deuxième partie). — Bull. Mus. Nat. Hist. Nat. (2), 9: 56-61, figs. 1-3.
- , 1937a. Le genre *Pachygnathus* Dugès (*Alycus* Koch) (Acariens). (Troisième partie). — Bull. Mus. Nat. Hist. Nat. (2), 9: 134-138, figs. 4-5.
- , 1937b. Le genre *Pachygnathus* Dugès (*Alycus* Koch) (Acariens). (Quatrième partie). — Bull. Mus. Nat. Hist. Nat. (2), 9: 199-205, figs. 6-8.
- , 1937c. Le genre *Pachygnathus* Dugès (*Alycus* Koch) (Acariens). Cinquième et dernière partie. — Bull. Mus. Nat. Hist. Nat. (2), 9: 262-269: fig. 9.
- , 1939. Quelques genres d'Acariens appartenant au groupe des Endeostigmata. — Ann. Sci. Nat., Zool. (11), 2: 1-122, figs. 1-25.
- , 1942. Quelques genres d'Acariens appartenant au groupe des Endeostigmata (2e série.) Première partie. — Ann. Sci. Nat., Zool. (11), 4: 1-135.
- , 1943. Quelques genres d'Acariens appartenant au groupe des Endeostigmata (2e série.) Deuxième partie. — Ann. Sci. Nat., Zool. (11), 5: 1-59 (sep. 137-195), figs. 1-18.
- HAARLØV, N., 1957. Microarthropods from Danish soils. Systematics. — Spol. Zool. Mus. Haun., 17: 1-60, figs. 1-21.
- HAMMEN, L. VAN DER, 1966. Studies on Opilioacarida (Arachnida) I. Description of *Opilioacarus texanus* (Chamberlin & Mulaik) and revised classification of the genera. — Zool. Verh., 86: 1-80, figs. 1-21.
- , 1968. The gnathosoma of *Hermannia convexa* (C. L. Koch) (Acarida: Oribatina) and comparative remarks on its morphology in other mites. — Zool. Verh., 93: 1-45, figs. 1-12.
- , 1968a. Introduction générale à la classification, la terminologie morphologique, l'ontogenèse et l'évolution des Acariens. — Acarologia, 10: 401-412.
- , 1968b. Studies on Opilioacarida (Arachnida) II. Redescription of *Paracarus hexophthalmus* (Redikorzev). — Zool. Meded., 43: 57-76, figs. 1-4.
- KNÜLLE, W., 1959. Morphologische und entwicklungsgeschichtliche Untersuchungen zum phylogenetischen System der Acari: Acariformes Zachv. II. Acaridae: Acaridae. Grundlagen der Getreidemilben-Systematik. — Mitt. Zool. Mus. Berlin, 55: 347-417, figs. 1-47.
- KOCH, C. L., 1841. Deutschlands Crustaceen, Myriapoden und Arachniden, 37. — Regensburg, 1841: 1-24.
- , 1842. Uebersicht des Arachnidensystems, 3. — Nürnberg, 1842: 1-131, pls. 1-13.
- OUDEMANS, A. C., 1937. Kritisch historisch overzicht der acarologie. Derde gedeelte. 1805-1850. Band C. — Leiden, 1937: xxiv, 799-1348, figs. 350-579.
- THOR, SIG & C. WILLMANN, 1941. Acarina. Eupodidae, Penthalodidae, Penthaleidae, Rhagidiidae, Pachygnathidae, Cunaxidae. — Das Tierreich, 71a: i-xxviii, 1-186, figs. 1-252.
- WOMERSLEY, H., 1944. Australian Acarina, families Alycidae and Nanorchestidae. — Trans. Roy. Soc. S. Austr., 68: 133-143, figs. 1-5.