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Observations on the morphology of some eupodoid and endeostigmatic gnathosomata (Actinotrichida, Actinedida, Eupodoidea and Endeostigmata)

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Abstract. The paper presents a new description of the gnathosoma, especially the subcapitulum (= infracapitulum) and hypostome of some eupodoid and endeostigmatic mites. As a result of these observations a new interpretation of the subcapitulum and hypostome is offered. The subcapitulum is formed by partly fused aspidosoma limbs such as lateral lips+rutella type, hypostome type and the labrum, not by enlarged pedipalp coxae and their endites. The subcapitulum contains only preoral cavity, not the pharynx which lies in aspidosoma (idiosoma). The unpaired hypostome delimiting the subcapitulum from below continues anteriorly into free labium. It is most probably remnant of the primary limbs positioned behind the basal parts of the lateral lips+rutella, and is homologous with anactinotrichid tritosternum. The basal parts of the chelicerae and pedipalps (coxal regions) arise from aspidosoma and have no evident morphological connection with the subcapitulum. The chelicerae and pedipalps have rather functional contact with subcapitulum in order to simplify food reception.

Key words: Eupodoidea, Endeostigmata, morphology, subcapitulum, lateral lips+rutella, labrum, hypostome.

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I. INTRODUCTION

The structure of the gnathosoma of various groups of mites has been described in detail, among others, by BEKLEMISHEV (1957), GRANDJEAN (1936, 1938, 1939, 1957, 1957a), LANGE (1962), KRANTZ (1978), HAMMEN (1968, 1970, 1970a, 1980, 1989), THERON (1979), LINDQUIST (1984), WOOLLEY (1988), EVANS (1992), MORITZ (1993). In these cited above general studies there are many sources of papers presenting gnathosoma descriptions characteristic for particular groups of the Acari (e.g. PARAN 1982; ANDRE and REMACLE 1984), because so far there is no single generally acceptable terminology describing this (EVANS 1992). However, the characteristic feature of their interpretations is a conviction that a subcapitulum (=infracapitulum, EVANS 1992) contains a mouth opening and a pharynx. The same interpretation has been presented in works dealing with Eupodoidea (ZACHARDA 1980; Baker 1990; NUZZACI & DE LILLO 1991; DI PALMA 1995). The hypostome by ZACHARDA in his work on Rhagidiidae (1980) is equal with the definition of the subcapitulum.The detailed and complicated description of the gnathosoma and the infracapitulum given by HAMMEN (1968, 1980) is practically focussed on Oribatida. According to the aforementioned authors the gnathosoma is built partly of cheliceral and pedipalpal segments bearing appendages. A labrum is considered to be a precheliceral element, whereas the subcapitulum is formed by enlarged coxae of the pedipalps and their endites. WOOLLEY (1988) and MORITZ (1993) suggest that the gnathosoma is a tagma. In the present paper the author refers about a morphological study of the gnathosoma, particularly the subcapitulum, of some representatives of the Eupodoidea and the Endeostigmata with the purpose to compare the mouthparts with the previous descriptions verifying the morphological interpretation of the various parts.

Current knowledge. The most widespread knowledge on the structure of the gnathosoma, and thus of the subcapitulum, is based on GRANDJEAN'S and HAMMEN'S observations and on those presented lately by EVANS (1992) in his book as well. The compilation of a general description of the gnathosoma is presented below as well as a brief view on the structure of the aspidosoma.

The gnathosoma (=capitulum) is built of a cheliceral frame (cadre mandibulaire) and the subcapitulum (infracapitulum). It is separated from idiosoma by circumcapitular furrow and usually movably articulated to it. In some mites the gnathosoma is inserted in the prosomal cavity named the camerostome or gnathopodal cavity which contains also coxae of legs I. The cheliceral frame is considered to be segment I or its epimeron bearing the first pair of appendages, that is the chelicerae. This segment is very reduced. The dorsal part of tegument between the naso (the most frontal part of aspidosoma or idiosoma) and the cheliceral basis is referred to as tegulum, whereas the ventral part is reduced and conterminous with the dorsal part of the subcapitulum. The subcapitulum (cone buccal; hypognathum) forms the inferior part of the gnathosoma. It is a part of the pedipalpal segment or its epimeron, that is the second segment bearing the second pair of appendages – the pedipalps. The subcapitulum is formed by enlarged pedipalp coxae and their endites, and contains lips and mouth opening. Internal surfaces of the subcapitulum surround the pharynx. Free subcapitular parts, such as malapophyses (or malae), labrum and very rarely labium, delimit the pre-oral cavity leading into the mouth opening and their internal surfaces are the continuation of those of the pharynx. In some Anactinotrichida this part of the subcapitulum is defined as hypostome and the mode of formation of the pre-oral subcapitular region has not been elucidated yet. The mouth opening is triangular if three lips and three oral commissures occur or rarely quadrangular with four lips and four oral commissures. The upper lip is named labrum, the under lip is termed labium and two lateral, symmetrical lobes are known as lateral lips. Sites of the fusion of the lips are referred to as commissural lines. The most often is the situation when there are two dorsal commissures and one ventral, very rarely there are two ventral commissures. The labrum is considered to be the element of precheliceral origin, similarly as the mouth opening. It divides horizontally the pre-oral chamber (or cavity) into two spaces: dorsal and ventral, so that they create two channels. The ventral one leads into the pharynx, while the dorsal gathers secretions from subcapitular glands, e.g. the saliva. The dorsal basal part of the subcapitulum (posterior to the labrum base) named the cervix or cheliceral plate connects mesial walls of the pedipalp coxae. It is provided axially with convex part named the capitular saddle. Two cheliceral grooves (fossae mandibulaire) placed laterally to it contain cheliceral shafts. The cervix laterally to the labrum extends anteriorly into the paired malapophyses (or malae). Their dorsal parts are separated antiaxially from the ventral by large lateral ridges carrying pedipalpal coxae. Malapophyses are considered to be pedipalp endites. Their latero-ventral surfaces are named the genae and may be separated from the mentum by labiogenal articulation (restricted to Oribatida). The paraxial walls of malapophyses exceed into lateral lips. Anteriorly, the genae pass into lateral lips as well. Malapophyses are sometimes provided with structures termed the rutella (some Actinotrichida) or corniculi (Anactinotrichida). The labium is the continuation of the mentum and in some mites it is connected by lateral lips along the inferior commissural lines. In many Arachnida it is considered to be a sternit of the pedipalpal segment while in Anactinotrichida it is not present at all. The ventral part of the subcapitulum is constituted of the mentum (hysterostome). It is the unpaired element positioned posteriorly to the mouth opening and considered to be the epimeron of the second segment. The subcapitular gutter (median taenidium, subcapitular groove, deutosternal groove), restricted to Anactinotrichida, corresponds to the mentum, whereas paired genae represent surfaces situated laterally to it. The subcapitular gutter is recognized also as deutosternum and protosternum. The latter is incorporated in the anactinotrichid hypostome. The tritosternum, or the sternapophysis, is engaged along with the subcapitular gutter during the food reception (WERNZ and KRANTZ, 1976). The tritosternal laciniae are placed in being provided with transverse teeth of the deutosternal groove and cooperate with it making food reception possible. The tritosternum, paired in Opilioacarida and Holothyrida and single in other Anactinotrichida, is referred to as protuberances of the sternit of the legs I segment or as endites of leg coxae I.

The subcapitulum is separated internally from the cheliceral frame by the capitular apodeme, while from the sternal region of the segment III by the subcapitular apodeme. Both are considered to be an ancestral character. On individual faces of the subcapitulum are inserted setae of different number, morphology and function.

The aspidosoma is considered to be a part of the body, not the tagma. It is built of parts of the precheliceral, cheliceral and pedipalpal segments. It is separated from the podosoma by the abjugal furrow and dorsally from opisthosoma by disjugal or “das” furrow. The prodorsum with the frontally inserted naso is its dorsal part. The naso is treated as the precheliceral element. The formation mode of the gnathosoma during embryonic growth is not clear as yet but seems very complicated. The role of the pedipalpal and cheliceral sternites in subcapitulum formation in the process of gnathosomatization is unknown. They are probably reduced or completely obliterated.

II. MATERIAL AND METHODS

The representative description of the gnathosoma, mainly the subcapitulum, is based on drawings of specimens of the following species (together approximately 50 specimens): *Cocceupodes* THOR, 1934 (= *Cocceupodes* „L” in JESIONOWSKA, 1991, = *C. filiformis* in JESIONOWSKA, 1992) and *Eupodes voxencollinus* sensu STRANDTMANN and PRASSE, 1977 from the Eupodidae, and *Protopenthalodes coniunctus* JESIONOWSKA, 1989 from the Penthalodidae, with *Alycus ornithorhynchus* GRANDJEAN, 1937 and *Orthacarus tremli* ZACHVATKIN, 1949 belonging to Endeostigmata as a comparision. In the case of *A. ornithorhynchus* and *O. tremli* I chose respectively the larval and nymphal instars because a separateness of the subcapitulum and the coxal regions of the pedipalps is the most visible.

General statements concerning the morphology of the gnathosoma in this paper are the results of studies of the superfamily Eupodoidea, particularly Eupodidae (JESIONOWSKA, 1992) and numerous representatives of genera from the group Endeostigmata (e.g. *Alicorhagia* BERLESE, 1910, *Alycus* KOCH, 1842, *Orthacarus* ZACHVATKIN, 1949, *Terpnacarus* GRANDJEAN, 1939). The observations concern not only mature individuals but larval and nymphal instars as well, in which the separate character of particular elements of the gnathosoma, especially the subcapitulum, is more visible.

The material examined also includes 19 species from the family Eupodidae representing the following genera: *Benoinyssus* FAIN, 1958, *Caleupodes* BAKER, 1987, *Claveupodes* STRANDTMANN & PRASSE, 1977, *Hawaiieupodes* STRANDTMANN & GOFF, 1978, *Linopodes* KOCH, 1836, *Protereunetes* sensu STRANDTMANN, 1967. Observations of the larval gnathosoma in *Penthaleus* KOCH, 1835 and *Penthalodes* MURRAY, 1877 are also included. The material (with exception of *Benoinyssus* and *Hawaiieupodes*) was collected in Poland and is deposited in the author’s collection. All illustrations are original and were made using a compound microscope equipped with a phase-contrast optical system and an immersion objective.

III. RESULTS

Representatives of the Eupodoidea. The subcapitulum is conical, muscled and ornamented on almost all the external surface. The ornamentation is characteristic for particular genera and it looks differently according to where it occurs on the subcapitulum. The subcapitulum (Figs 1-3) is composed of the following partly fused elements: the paired lateral lips (LL), the upper lip or labrum (LB), and the hypostome (H) which tapers to the small under lip or labium (LI). The lateral lips, labrum and hypostome originate at the level of the basal parts of the chelicerae and pedipalps. The lateral lips are fused with the labrum along 3/4 of their length (stitches of fusion are well visible, st, Figs 1,2). The dorsoparaxial surfaces of the lateral lips are smooth (non-ornamented) and connected by hyaline cuticle, of probably membraneous character. This cuticle seems to cover the labrum along the length of its fusion with the lateral lips (see in *Penthaleus* and *Penthalodes*). The free, antiaxial distal parts of the lateral lips are folded, smooth and there is 1 or 2 pairs of weakly visible, nude adoral setae on them. The paraxial free surfaces of the lateral lips are strongly sclerotized similar to the ventral surface of the distal part of the labrum. Free parts of the lateral lips are longer on the ventral side than on the dorsal one. There is a pair of „n” setae on the ventral face of the lateral lips and a pair of „m” setae situated antiaxially, on the sides of the bases of the lateral lips. The „m” setae are usually slender and shorter than the „n” setae. The pair of „n” setae are inserted at the level of the labium base (e.g. *Penthaleus*), or close to it (approx. 1/3 of the length of the lateral lips free part; e.g. *Cocceupodes*, Fig. 1), or distinctly before its apex (e.g. *Eupodes voxencollinus*). Lateral antiaxial faces of the lateral lips are divided by longitudinal linear ornament into dorsal and ventral parts (lo; Figs 2, 3). The bases of dorsal parts of the lateral lips partly fuse with the coxal regions of the pedipalps (cxp, Fig. 3). The labium (LI) is small, subtriangular and distinctly shorter than the lateral lips free parts and the labrum. The labium tops the hypostome (Figs 1, 3) which is spreading between internal sclerotized lines (sc, lying just under the tegument) directed obliquely from the labium to the base of the subcapitulum. The hypostome (H) composes only a subtriangular ventral surface of the

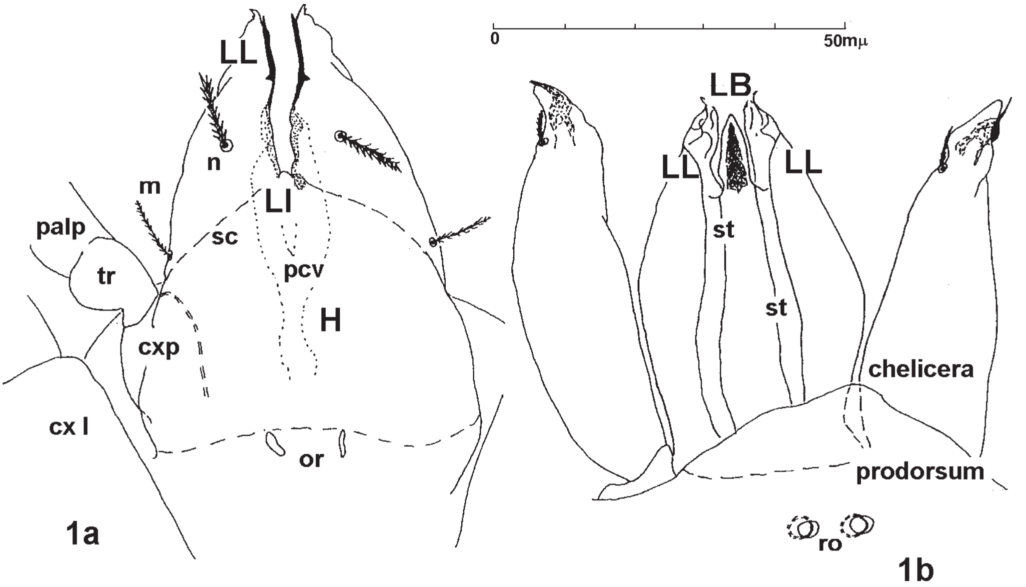

Fig. 1. *Cocceupodes* sp. (= *Cocceupodes „L”* in JESIONOWSKA, 1991), female. Subcapitulum: a-ventral aspect (labrum removed), b-dorsal aspect. Abbreviations: **cx I**, coxal region of leg I; **cxp**, coxal region of pedipalp; **tr**, pedipalp trochanter; **H**, hypostome; **LB**, labrum; **LI**, labium; **LL**, lateral lip; **n**, **m**, setae; **or**, orifices; **pcv**, preoral cavity; **ro**, bothridia of rostral setae; **sc**, internal sclerotized lines; **st**, stitches of junctions of the lateral lips with labrum.

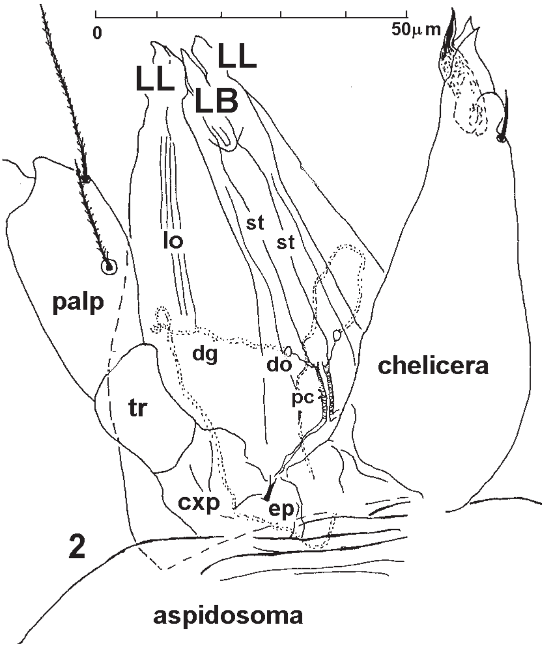

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Fig. 2. *Eupodes voxencollinus* (sensu STRANDTMANN and PRASSE, 1977), male. Gnathosoma. Subcapitulum – dorsolateral aspect. Abbreviations: **cxp**, coxal region of pedipalp; **dg**, duct; **do**, orifices of ducts; **ep**, supracoxal seta of pedipalp; **LB**, labrum; **LL**, lateral lip; **lo**, linear ornamentation divides lateral lip; **pc**, outlet of podocephalic canal; **st**, stitches of junctions of the lateral lips with labrum; **tr**, trochanter of pedipalp.

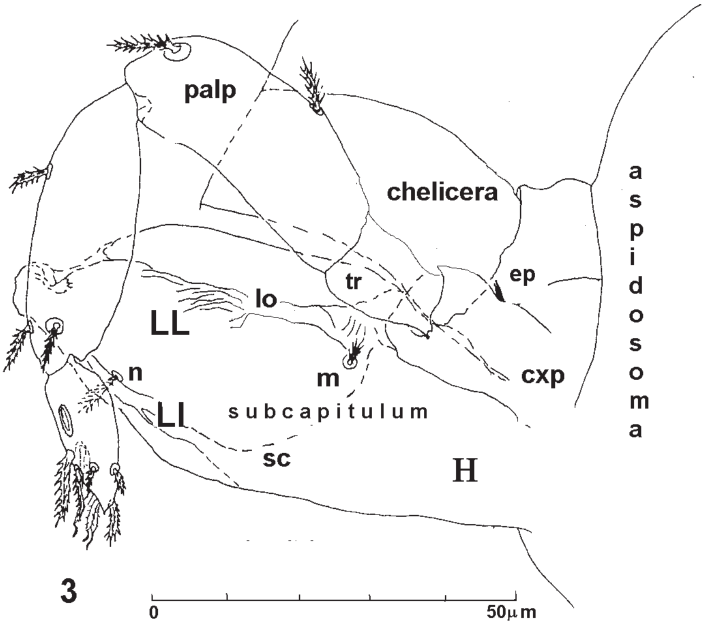

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Fig. 3. *Protopenthalodes coniunctus* JESIONOWSKA, 1989, female. Gnathosoma: lateral aspect. Abbreviations: **cxp**, coxal region of pedipalp; **ep**, supracoxal seta of pedipalp; **H**, hypostome; **LI**, labium; **LL**, lateral lip; **lo**, linear ornamentation divides lateral lip; **m**, **n**, setae; **sc**, internal sclerotized lines; **tr**, trochanter of pedipalp.

subcapitulum (Fig. 1). The lateral lips do not constitute a part of the hypostome. A proper mouth opening is situated inside, at the base of the subcapitulum. The subcapitulum contains on its length only a preoral cavity (pcv, Fig. 1a) and its sclerotized walls and muscles probably act as (or form) a „sucking pump" (cf DI PALMA 1995, Fig. 16). In the genus *Cocceupodes*, there is a pair of orifices at the base of the hypostome, whose role is not known (or, Fig. 1). In *Eupodes voxencollinus* there is a pair of the orifices on the dorsal part of the subcapitulum (do, Fig. 2) which issue from thin ducts (dg) leading towards the interior of the subcapitulum. These ducts are winding and reach into the idiosoma. Probably, these represent the ducts of subcapitular glands (Hammen 1980). The podocephalic canals (pc, Fig. 2) have their outlets posterior to those orifices (do, Fig. 2). The pedipalps arise from anterolateral walls of the aspidosoma. They are situated laterally and dorsally to the subcapitulum in such a way that the coxal regions of the pedipalps (cxp) are partly fused with the dorsolateral part of the subcapitulum base (Fig. 3). The coxal regions of the pedipalps are not visible from beneath. There is a supracoxal seta (ep) on the dorsal side of the coxal regions of the pedipalps. Chelicerae (independent, according to EVANS, 1992 three-segmented) arise from the anterior wall of the aspidosoma and they lie close to one another, clearly over the base of the subcapitulum, between and slightly dorsally to the pedipalpal bases (the coxal regions). The length of the chelicerae is almost the same as the length of the subcapitulum. Number of the subcapitular setae is the same in all instars.

Representatives of the Endeostigmata (Figs 4, 5). The subcapitulum, similar to that of the Eupodoidea, is composed of the following partly fused elements: the paired lateral lips with rutella (LL, ru), the upper lip or labrum (LB) and the hypostome (H) which tapers to the under lip or labium (LI). The lateral lips, hypostome and labrum originate at the level of the basal parts of the pedipalps. In the larva of *Alycus ornithorhynchus* (Fig. 4) the lateral lips are cylindrical and distinctly separated from the coxal regions of the pedipalps (cxp). An ornamentation diminishes on distal parts of the lateral lips where a pair of adoral setae (ad) and antiaxially short papillate process (pap, Fig. 4a) are inserted. There are protuberances (pru) terminated with rutella (ru) on the dorsal side of the lateral lips. The length of the rutellum is almost the same as the unornamented distal part of the lateral lip. The hypostome (H) is on the ventral side of the subcapitulum. It is composed of a basal part fused with the bases of the lateral lips and of the free labium. The labium is partly overlapped by paraxial surfaces of the lateral lips in larva while in the adult it is covered completely. The labium is short, almost 1/3 of the ventral free lateral lips length. The lateral lips are fused with the labrum dorsally along almost 2/3 of their length. Free parts of the lateral lips are longer on the ventral than on the dorsal face. The proximal part of the labrum is convex and steep, then it transforms into a freely projecting, three-lobed distal part (Fig. 4b). The ventral surface of the labrum is equipped with a sclerite whose base attaches to an ovate strongly sclerotized rim (P) lying inside the subcapitulum at the level of the bases of the pedipalpal coxal regions (Figs 4b, 5b). A general structure of the subcapitulum of the tritonymph of *Orthacarus tremli*, shown in Fig. 5, is similar. Its differences, among others, relate to the characteristics for succeeding juvenile instars of elongation of the basal part of the subcapitulum, of augmented number of setae, and of changes in shape of rutella as well as to the ornamentation. The position of the chelicerae and pedipalps in relation to the subcapitulum of these taxa are similar to that of the Eupodoidea.

IV. DISCUSSION

Several questions can be pointed out on the basis of the present morphological study. They are contained in three sections presented below.

Comparison between eupodoid and endeostigmatic gnathosomata.

The number of setae on the subcapitulum in larval and nymphal instars of Eupodoidea is the same as in adults (cf JESIONOWSKA 1996) in contrast to the examples from Endeostigmata. The coxal regions (cxp) of pedipalps in Endeostigmata are more distinctly separated from the subcapitulum than in Eupodoidea, where they are not visible on the ventral face. This can be explained by the

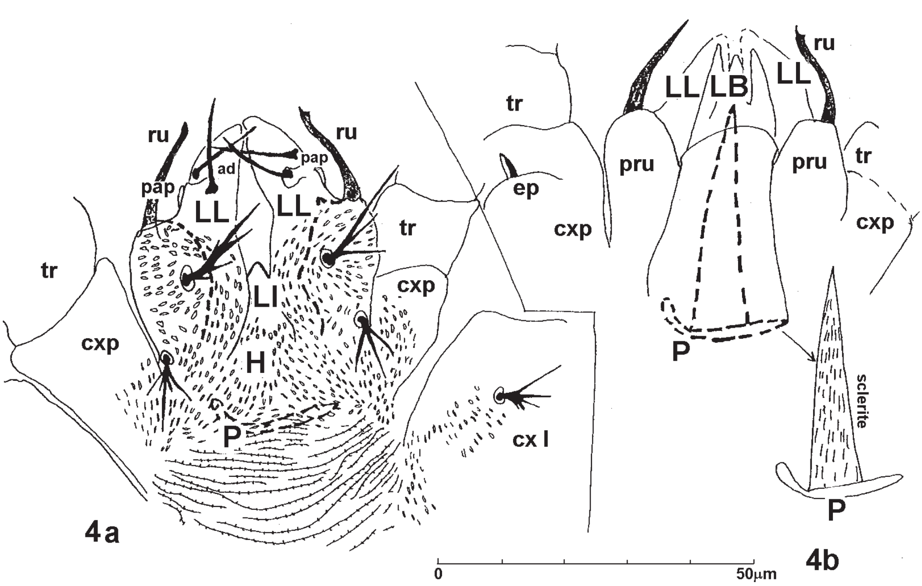

Fig. 4. *Alycus ornithorhynchus* GRANDJEAN, 1937, larva. Subcapitulum: a-ventral aspect (without labrum), b-dorsal aspect. Abbreviations: ad, adoral setae; **cx I**, coxal region of leg I; **cxp**, coxal region of pedipalp; **ep**,supracoxal seta of pedipalp; **H**, hypostome; **LB**, labrum; **LI**, labium; **LL**, lateral lip; P, sclerotized rim; **pap**, papillate process; **pru**, protuberance; **ru**, rutellum; **tr**, trochanter of pedipalp.

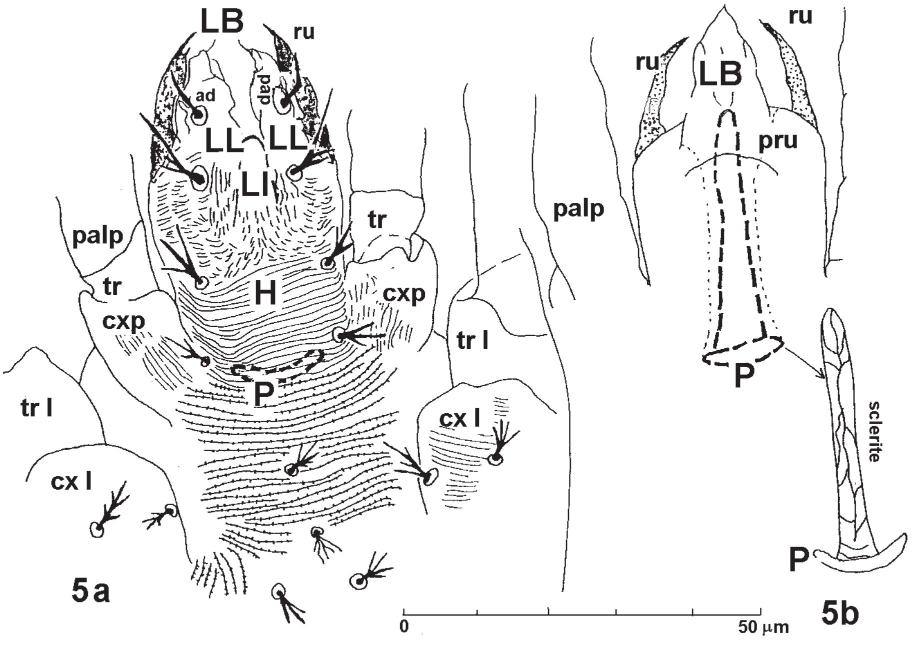

Fig. 5. *Orthacarus tremli* ZACHVATKIN, 1949, tritonymph. Subcapitulum: a-ventral aspect, b-dorsal aspect. Abbreviations: ad, adoral seta; **cx I**, coxal region of leg I; **cxp**, coxal region of pedipalp; **H** , hypostome; **LB**, labrum; **LI**, labium; **LL**, lateral lip; **P**, sclerotized rim; **pap**, papillate process; **pru**, protuberance; **ru**, rutellum; **tr**, trochanter of pedipalp; **tr I**, trochanter of leg I.

fact that Endeostigmata have a better developed pedipalpal segment of the aspidosoma. The hypostome as an individual element contributing to the subcapitulum is more clearly isolated in Endeostigmata than in Eupodoidea, although its part fused with the lateral lips is bigger in Eupodoidea. I suppose that the place of oblique sclerotized lines (sc, Figs 1, 3) in Eupodoidea can be treated as an equivalent of the regions on the labium overlapped by the paraxial surfaces of the lateral lips in Endeostigmata. The distal non-ornamented parts of the lateral lips in relation to the length of the subcapitulum are relatively shorter in Eupodoidea than in Endeostigmata. The Eupodoidea have no separate, discrete rutella. The dorsal part of the lateral lips of Eupodoidea, separated from the ventral one by antiaxial ornamentation lines (lo, Figs 2, 3) is probably homologous with the dorsal protuberances (pru, Figs 4b, 5b) terminating with rutella (ru, Figs 4, 5) in Endeostigmata. The proximal part of the labrum in Endeostigmata is convex and sloping, shorter than the distal part or equal. This is different from Eupodoidea, where it is flat and longer than the distal part. The proximal convex part of the labrum may be homologous with the transparent surface covering the labrum in Eupodoidea. In these two groups the labium is distinctly shorter than the free, ventral parts of the lateral lips and the labrum is fused with the lateral lips almost along its total length. The free parts of the lateral lips are longer on the ventral than on the dorsal face in both groups. The coxal regions of eupodoid and endeostigmatic pedipalps bear dorsally the supracoxal seta (ep). The positions of the basal parts of the chelicerae and of the pedipalps in relation to the subcapitulum are also similar. The characteristic sclerite leading all along the ventral part of the labrum in Endeostigmata (Figs 4b, 5b) may be comparable with the similar one observed in larvae of *Brevipalpia* ZACHARDA, 1980 (Rhagidiidae). The above observations on the structure of the eupodoid and endeostigmatic gnathosomata, especially the subcapitulum, form the basis for a new interpretation of the acarine gnathosoma.

Comment on the current knowledge with presentation of new proposition.

The purpose of this paper is to propose a new interpretation of the structure of the gnathosoma, particularly the subcapitulum. This means that the sense of general terminology existing hitherto for the elements building the subcapitulum is completely modified. According to my interpretation the subcapitulum is a separate structure created by fused limbs of the lateral lips+rutella type (or analogically of the lateral lips+corniculi type for Anactinotrichida; treated as a notional unit), hypostome type and the labrum. The entire structure surrounds only the pre-oral cavity, not the pharynx. Such an opinion results from observations on the morphology of the aspidosoma, which is treated by me as the tagma, and not as a part of the body. It is formed by the reduced (vestigial) segments: first and second sensory segment, lateral lips+rutella type segment, and cheliceral and pedipalpal ones (JESIONOWSKA 1991, 1992). The last three (not two) segments bear appendages. Thus, the cheliceral frame, bilding entirely the frontal wall of the aspidosoma (or idiosoma; dorsal part termed tegulum), contains the area between the naso and the dorsal part of the subcapitulum, that is it constitutes the frontal part of the cheliceral segment. The subcapitulum situated under the chelicerae is formed by the labrum and fused limbs which I call the lateral lips+rutella and hypostome. Their bases situated at the level of the basal parts of the chelicerae and pedipalps one are fused to each other as well as with the labrum basis and the hypostome that continues anteriorly into free labium. Thus the subcapitulum is not built of enlarged pedipalp coxae either their endites. That is why the terms such as lateral lips+rutella, labrum, hypostome and labium obtain a new meaning in this work. The proximal part of the labrum is combined of the basal parts of the lateral lips+rutella while its unfused distal part lies between free portions of the subcapitulum. The proximal part may be covered by hyaline cuticle of probably membranous character, which is spread between the paraxial walls of the lateral lips+rutella (e.g. *Penthalodes*). The dorsal part of the subcapitulum posterior to the free labrum base, i.e. the part of the labrum connected with lateral lips+rutella, is termed by other authors the cervix or subcheliceral plate, that is the element joined the paraxial walls of the enlarged pedipalp coxae. But this part of membranous character may correspond to the capitular saddle. On the dorsal part of the subcapitulum in the Eupodidae there are paired outlets of the subcapitular glands and podocephalic canals. Laterally to the fused part of the labrum (cervix) there are paired cheliceral grooves, in which cheliceral shafts are located. It seems probable that they press on the "membrane" causing discharge of secretions of the subcapitular glands, e.g. saliva. The excretion flows then to the preoral chamber which is divided horizontally by free part of labrum into dorsal and ventral space (cf ANDRE & REMACLE 1984). This room, termed the pre-oral cavity, in my interpretation is only a prolongation of the preoral chamber contained as, a whole in the subcapitulum, not of the pharynx. Most probably the free part of the labrum, depending on its position, controls the food reception in such a way that if it is lowered (moved down) then the fluids (e.g. saliva) flow on the prey but if it is upraised then the melted tissues are pulled into the preoral cavity (or to the pharynx according to the existing interpretation). In order that this activity might be efficient the subcapitulum had to be formed by the fusion of limbs with the labrum and development of the sucking pump by means of muscles (cf. pharyngeal pump, NUZZACI & DE LILLO 1991). In my opinion, the mouth opening located according to other authors at the level of the free basal subcapitular parts, is only the orifice leading into the pre-oral cavity which is enclosed in the fused part of the subcapitulum, and the real mouth opening is placed internally at the subcapitulum base. At this level in the Endeostigmata is situated a characteristic strongly sclerotized rim, the role of which is unknown. The real mouth opening passes into the pharynx located entirely in the idiosoma, not in the subcapitulum. This channel is surrounded with central nervous system which is found only in the anterior part of the prosoma (or idiosoma), not in the gnathosoma (EVANS 1992). Thus, I propose to recognize that part of the alimentary canal, or at least its portion called the oesophagus as the real pharynx. Consequently, I am of the opinion that the aspidosoma is just the tagma, not the gnathosoma. Ventrally, the pre-oral chamber is limited by the hypostome which continues anteriorly in free underlip or the labium. It is referred to as the mentum, however, I do not treat it as the sternit or epimer of the pedipalpal segment but as a remnant of primary limbs. It is positioned anteriorly to the mouth opening, not posteriorly to it. In the Endeostigmata the base of the hypostome, continuing anteriorly into free conspicuous labium, is fused with the ventral, paraxial parts of the lateral lips+rutella. In the Eupodoidea the labium is much smaller and the hypostomal part connected with lateral lips is distinctly larger and separated internally from lateral lips by sclerites "sc". Most likely they are homologous with the oribatid labiogenal articulation. The ventral part of the subcapitulum anteriorly to the mentum is termed the genae, whereas the dorsolateral parts as malapophyses passing frontally into paraxial lateral lips. In my interpretation these sections are only the adequate surfaces of the whole lateral lips+rutella considered as limbs and not as the endites of the palpcoxae. In both groups (Endeostigmata and Eupodoidea), characteristically, the dorsal, free parts of lateral lips+rutella are shorter than the ventral ones. This feature also evolved most likely as a result of adaptation to the way of food reception, namely to food sucking. This would speak for the conception of the limbous formation of the subcapitulum. This also means that the shape of the oral orifice, in the sense of existing interpretation, is neither triangular nor quadrangular. In my opinion, the commissural lines and oral commissures showing the shape of the orifice (pre-oral orifice not oral) are only sutures (or sites) along which the particular parts of the subcapitulum such as the paired lateral lips+rutella, single labrum and hypostome with labium are fused. The hypostome is treated by me as a remnant of the limbs which were inserted behind the lateral lips+ rutella. I consider it to be homologous with the tritosternum of Anactinotrichida that have no labium. Hence the area of the anactinotrichid subcapitular groove is the site of fusion of the limbs of lateral lips+corniculi type (or malae+corniculi) but not the mentum or protosternum and deutosternum. By means of the tritosternum cooperating with this part of the subcapitulum the efficient food reception is possible (WERNZ & KRANTZ 1976). In my interpretation it seems that the actinotrichid hypostome performs similar function in primitive representatives. The tritosternum (dual in Opilioacarida and Holothyrida, single in other Anactionotrichida) is most probably a relict of ancient limbs (remnant limbs), not the endites of leg coxae I or the process of the sternum of segment III. Its position, namely its basis arising from a separate tegument (EVANS 1992) posterior to the lateral lips+rutella bases (similar to the hypostome) and not from the leg coxae I or sternite III, suggests the "limbous" character of this part of the gnathosoma as well. I think that the pedipalpal coxae do not form the basal part of the subcapitulum but rather arise from the anterolateral walls of the aspidosoma, being only partly fused with the subcapitulum. Similarly, the chelicerae originate from the anterodorsal part, and the subcapitulum from the anteroventral one of the aspidosoma wall. Thus, the morphological connection of the pedipalpal coxae with the subcapitular base are rather inconsiderable. Consequently, in both instances the gnathosoma is not accomodated in any supporting cavity.

The structure and function of the subcapitulum evolutionally resulted from the way of the food reception. This means that formation of anterior part of the preoral cavity by free subcapitular parts is connected with sinking them into the body of prey to taste and distinguish its kind and then to release digestive fluids. The role of the fused part of the subcapitulum is to enable the melted tissues to be sucked into the posterior preoral cavity in order to direct them further to the alimentary canal, this way making the food swallowing possible. Therefore, the fusion of some elements and the arrangement of muscles of the subcapitulum as the sucking pump was necessary (cf pharyngeal pump in NUZZACI & DE LILLO 1991). This also caused that this type of food reception became effective and allowed to preserve characteristic for Arachnida morphology of the prosoma in correlation with their specific way of living. The role of the labrum and most probably the chelicerae is the cooperation in directing the fluids and melted tissues flow; for example, if free labral part is down then saliva rises to the prey, and if it is up then the liquid food enters the preoral chamber. While the shafts of the chelicerae press the cheliceral grooves and possibly the "membrane" covering the fused labral part, thereby they regulate discharge of fluids from the subcapitular glands. Further investigations are needed to explain all morphological and functional obscurities and to propose new nomenclature for particular parts of the subcapitulum as well.

V. GENERAL CONSIDERATIONS

It seems that the role of the pedipalpal coxae and their endites in forming the acarine subcapitulum or their mouthparts as in other Chelicerata is overestimated. In my opinion the terms used for spider descriptions, like the pedipalpal coxae and their endites (=apophyses) forming the preoral cavity, and the labium described as a sternite of the pedipalpal segment (EVANS 1992) all require a new interpretation. I suppose that the so-called well developed spider endites of the pedipalpal coxae (=maxillae, cylindrical, oriented forward; cf EVANS 1992, Fig. 5.1.A) correspond to the acarine lateral lips+rutella (or lateral lips+ corniculi – these terms reflect notional units), and the labium to the hypostome in my meaning. Another example is the Palpigradi, in which the pedipalps are not involved in food ingestion (SAVORY 1977; EVANS 1992), the pedipalpal coxae have no endites similar to those in the Scorpiones (SAVORY 1977; WEYGOLDT & PAULUS 1979), and a separate prominence (rostrum) is adapted (specialized) for food reception (BEKLEMISZEV 1957; HAMMEN 1969; SAVORY 1977; WEYGOLDT & PAULUS 1979). Probably this prominence, similar to a rostrum of the Solifugae, is homologous with the acarine subcapitulum. In the Solifugae the rostrum situated underneath the chelicerae is formed by the labrum, lateral lips and labium whose basal parts are fused together, and yet the pedipalpal coxae do not create a preoral cavity (MORITZ 1993). Is the rostrum of the Solifugae and Palpigradi which contains a preoral cavity (MORITZ 1993), like the acarine subcapitulum? Also, some facts support the opinion that the lateral lips+rutella (or lateral lips+corniculi) should be considered to be the limbs, not the endites: (1) in Eupodoidea and Endeostigmata the coxal regions of the pedipalps and locomotory legs are weakly sclerotized and their free parts are very short; at the same time sternal part of the podosoma is developed; (2) the strongly sclerotized coxae of the locomotory legs in many Parasitiformes do not form endites, and diameter of the coxae of legs I, although they are elongated, are distinctly smaller than others; 3) fusion of the leg coxae I with prosomal cavity and formation of so-called gnathopodal cavity, not endites in some Parasitiformes. These show that a tendency towards creation of endites in mites is unlikely. Additionally, many observations reported by EVANS (1992) and BEKLEMISHEV (1957) point out the frequent phenomenon of fusion of the chelicerae (e.g. Raphignathoidea, Tetranychoidea) or basal articles of the chelicerae and pedipalps (e.g. Cheyletidae). These confirm a conception that the subcapitulum can be formed without a necessity of development of extra elements as endites or of coxal enlargement. Endites are useful in water environments for creatures having a ventral food gutter to gain food particles. Many Arachnida (Parasitiformes, Thelyphonida, Amblypygi, Araneae, Schizomida, Palpigradi) do not have endites on leg coxae but have an expansive sternal shield; if „endites" exist, they are only on the pedipalpal coxae. The question is open if there are really endites among Acari?

The processes marked with asterisks in Aeschlimann and Hess' paper (1984, Fig. 7), and named as coxal lobes of the pedipalps, are noteworthy. I suppose that these are the buds of the lateral lips+rutella (treated as a notional unit), because it seems unlikely that only the coxal lobes of the pedipalps would appear individually during embryonic development nor would those of the chelicerae and locomotory legs appear as well. The buds (metameres) denoted with asterisks and metameres of the pedipalps lie posteriorly to the stomodeum and growing later during embryonic development, similar to the chelicerae, they migrate forward and locate laterally to the stomodeum (Aeschlimann & Hess 1984) and probably form the subcapitulum finally. Thus, I prefer a „non-coxal" and „non-endital" conception of the subcapitulum structure. The most primitive situation of the mouth opening is on the ventral side of the „prosoma" (e.g. Merostomata) and its caudal displacement bordered by the anterior leg coxae (Weygoldt & Paulus 1979). Therefore, formation of a separate rostrum with a terminal position of the „mouth opening", as for instance in Acari or Palpigradi, seems to be created by the fused limbs of aspidosoma with the labrum.

VI. CONCLUSION

Observations on the morphological structure of some endeostigmatic and eupodoid gna thosomata lead to the conclusion that the subcapitulum is constituted by aspidosoma limbs (lateral lips+rutella and hypostome) fused with the labrum. According to this interpretation the subcapitulum does not contain neither the mouth opening nor the pharynx. It contains only the preoral cavity. The real mouth orifice is located inside at the base of the subcapitulum and the pharynx lies in the idiosoma. The aspidosoma is segmented tagma and the chelicerae and pedipalps are its appendages, similar to these ones forming the subcapitulum. That is why the cheliceral and pedipalpal segments do not build the gnathosoma but they are parts of the aspidosoma. In author's opinion the term "hypostome" relating to the unpaired, separate element tapered to the labium forms only the ventral side of the subcapitulum. Therefore, the hypostome encloses the preoral cavity from underneath. Most probably it is homologous with the part called "tritosternum" in Anactinotrichida which have no labium. Some terms describing the subcapitulum are the same but used herein in a new sense, because as yet there is no satisfactory agreed system describing gnathosoma. In author's opinion the chelicerae and the pedipalps arise from aspidosoma and have no evident morphological connection with the subcapitulum, this means that it is formed neither by enlarged pedipalp coxae nor their endites. The coxal regions of the pedipalps instead fix (stabilize) the base of the subcapitulum dorsolaterally, while the hypostome (probably fused limbs; cf dual tritosternum in Opilioacarida) reinforces the lateral lips underneath. A partial fusion of the subcapitulum structural elements improves the efficiency of that structure, that is swallowing of food as well as the cooperation between the chelicerae and pedipalps. The authors's interpretation excludes existence of endites of the pedipalp coxae and their participation in the subcapitulum formation. More detailed study will be continued, including TEM investigation.

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