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On the internal organization of smaridid mites (Acari, Erythraeoidea), and on the role of organismal properties for determining the course of evolutionary change

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Abstract: In the present paper the structure of the gnathosoma and of the male and female genital systems of smaridid mites is investigated. The glands of gnathosoma and prosoma are described, and the muscles which enable the wide longitudinal movability of gnathosoma and styliform chelicerae, are analysed. The role of the internalisation of the dorsal surface of the infracapitulum for guiding the chelicerae and protecting the salivary secretion pathway is discussed. The female genital system is described mainly in regard to the distal accessory organs. The genital papillae are transformed to receptacula semines, in which sperm cells become capacitated. Lipid producing glands obviously serve to protect the internal milieu against external effects. The structure of the male genital system is reconstructed. A focus is laid on the ejaculatory complex, which shows a complex pattern of accessory organs, sclerites and muscles. Finally, I discuss, which adaptive transformations have probably led to the smaridid organization and which organismal properties, e.g. developmental preconditions, constraints and key innovations, may have determined the course of evolutionary change. The evolution of the strongly derived gnathosoma is used as a particular example.

Introduction

Mites of the family Smarididae are characterised by a rather complex organization which is similar to that of the Erythraeidae (WITTE 1975a, 1975b, 1978). Compared to other groups of the Parasitengonae, e.g. Hydrachnidia (SCHMIDT 1936; MITCHELL 1962a) and Trombidioidea (BROWN 1952; MITCHELL 1962b; MOSS 1962; ROBAUX 1974; WITTE 1995), particularly the gnathosoma of the deutonymph and the adult is strongly transformed, being provided with widely protractable styliform chelicerae and having the dorsal surface of the infracapitulum transformed into an internal canal. The gnathosoma of the smaridid larva, on the contrary, maintains a rather underived organization (GRANDJEAN 1947; SOUTHCOTT 1961). This radical ontogenetic transformation of the gnathosomal organization occurs inside the calyptostasic protonymph. The male and female genital systems, which are composed of several organs, cuticular structures and muscles, have also obtained a quite complex organization.

In the present paper I will investigate the structural organization of the above-mentioned organ systems of smaridid mites using primarily *Fessonia callitricha* as an example. For some comparisons I have also investigated *Hirstiosoma* sp.

In the discussion I will deal with the mechanisms within the Parasitengonae which have probably determined the course of evolutionary transformation that has finally led to the strongly derived organization of the Smarididae. These mechanisms, on the one hand, are adaptations that have advanced the course of evolutionary change. On the other hand, however, organismal properties have probably enabled, controlled and determined to a considerable degree the sequence and the specifity of evolutionary transformations. This role of organismal properties for canalising a pathway of evolutionary change has been discussed by, e.g. RIEDL (1975); GOULD & LEWONTIN (1979); ROTH & WAKE (1985); STEARNS (1992) and WITTE & DÖRING (in press). Particular organismal properties which in the evolution of the parasitengone mites have probably enabled or delimited the pathway of evolutionary change are, e.g. developmental preconditions, constraints (which delimit the potential for evolutionary change) and structural novelties (which may enable or predispose particular subsequent transformation steps).

The phylogenetic lineage of the Parasitengonae, which finally led to the Smarididae, seems a suitable example for discussion of the interplay between selection-mediated adaptation and organismal properties that have determined the course of evolution. The reason is twofold.

On the one hand, considerable structural and functional adaptations and developmental transformations took place in this lineage. However, on the other hand, the Smarididae have maintained fairly stable original structural patterns of the organ systems in the course of evolution (WITTE 1995; WITTE & OLOMSKI in press).

Material and methods

Two species of Smarididae were investigated, which were found under stones in a vineyard in southern France (Banyuls-sur-Mer, Pyrénés-Orientales).

Fessonia callitricha (GRANDJEAN 1947), (= syn. *Oecosmaris callitricha* GRANDJEAN).

Hirstiosoma sp. The genus was determined according to SOUTHCOTT (1946, 1961).

Hirstiosoma sp. is probably identical with "*Smaris*, espèce de Collioure" described by GRANDJEAN (1947). GRANDJEAN had collected this species in the same geographical region as I did. In an addendum of his paper, GRANDJEAN followed the revisions of the Smarididae by WOMERSLEY & SOUTHCOTT (1941) and SOUTHCOTT (1946) and synonymized "his" genus *Smaris* with *Hirstiosoma* WOMERSLEY 1934.

Histology: The animals were fixed either in Bouin's fixative or formaldehyde-calcium (4%), dehydrated via an alcoholic series and embedded either via three butanol-rinses into paraffin or via Cellosolve into ester wax. Cross, sagittal and frontal sections were cut with a microtome (Jung 1140) and stained with Azan, Mayer's hemalum-chromotrop 2R or paraldehyde-fuchsin (PAF-Halmi) according to ROMEIS (1968).

Histochemical tests were carried out by means of Alcian blue for acid mucopolysaccharides (PEARSE 1968), paraldehyde-fuchsin (PAF-Halmi) for sulphated mucosubstances, etc. (PEARSE 1968), PAS-reaction according to McManus for polysaccharides, etc. (ROMEIS 1968). Tests for lipids were carried out with frozen-sections, which were stained with Sudan Black B (CAIN 1950).

Results

Gnathosoma

The gnathosoma of the Smarididae undergoes rigid changes in the course of ontogeny (GRANDJEAN 1947). These changes are similar to those in the Erythraeidae (GRANDJEAN 1956; 1959; WITTE 1978). In the larva, the dorsal surface of the infracapitulum forms an open groove in which lie relatively short and wide chelicerae (SOUTHCOTT 1946; GRANDJEAN 1947). In the deutonymph and the adult, on the contrary, the dorsal surface of the infracapitulum is transformed into an internal canal, in which run greatly elongated and widely protractable styliform chelicerae (Fig. 1-3).

Chelicerae

The larva of smaridid mites is still provided with chelicerae composed of a cheliceral shaft and a sickle-shaped claw (GRANDJEAN 1947; SOUTHCOTT 1946, 1961). According to GRANDJEAN (1947), the chelicerae articulate with the tip of the sigmoid pieces. This type of chelicerae can be moved only a limited distance longitudinally. The protraction is accomplished by means of a forward rotation of the sigmoid pieces, induced by contraction of the "sig-

moid muscle", the cheliceral protractor 1, as MITCHELL (1962b) and WITTE (1995) have described in the Trombidioidea (compare Fig. 12).

The styliform chelicerae of deutonymphal and adult Smarididae (Ch, Fig. 1-3) correspond to the cheliceral shafts of the larva and they are homologous with the cheliceral shafts of the mobile instars of other Parasitengonae, e.g. Hydrachnidia and Trombidioidea (MITCHELL 1962a, 1962b). The movable cheliceral digit is lost in deutonymphal and adult Smarididae. However, a movable digit is still present in adult Calyptostomatoidea, which also have styliform chelicerae (VISTORIN-THEIS 1976, 1977).

The anterior of the chelicerae runs through an internal canal of the infracapitum, the cervical canal (compare below). Longitudinal movements of each chelicerae are rigidly guided within this canal. The chelicerae are considerably elongated posteriorly into the idiosoma, and the protractor muscles of the chelicerae, which insert at the posterior tip of the chelicerae, have become correlatedly elongated (Fig. 3). Thus, they may effect wide protraction movements of the chelicerae.

The longitudinal motility of the chelicerae is fostered by the greatly elongated cheliceral sheath, which extends from the posterior part of the chelicera to the arcal sclerite. The original articulation of the chelicerae with the sigmoid pieces is abandoned, and the larval sigmoid pieces are transformed in deutonymph and adult to parts of the tracheal trunks.

With their anterior parts the chelicerae form an intercheliceral canal (ic.C, Fig. 2a). Salivary secretions are pressed into the prey and liquid food is ingested through this canal. Vertical displacement of the chelicerae is prevented by longitudinal dovetailing midway along the chelicerae (Fig. 2c).

Infracapitulum

Dorsal region: The dorsal region of the larval infracapitulum, the cervix, is transformed in the deutonymph and the adult into an internal cervical canal (Fig. 2). The development of the cervical canal takes place by fusion of the lateral keels of the infracapitulum above the chelicerae during the calyptostatic periods, as WITTE (1978) has shown for erythraeids. No cuticular membrane is left in the region of fusion, although this is still the case in the erythraeid genera *Erythraeus*, *Leptus* and *Balaustium* (WITTE 1978).

Below the chelicerae in *Hirstiosoma* the cervical canal is provided with a longitudinal salivary groove similar to that in the Erythraeidae.

In *Fessonia*, on the contrary, the same region is provided with some longitudinal folds (SaG, Fig. 1, 2c), which probably allow widening of the cervical canal when salivary secretions are transported along it.

On both sides of the salivary groove, or longitudinal folds, respectively, the cervical canal is strengthened by the cervical sclerites (CvS, Fig. 2b-c). In *Hirstiosoma*, these sclerites accompany the salivary groove along its whole length until they fuse posteriorly with the capitular sclerite. In *Fessonia*, however, they are restricted to the anterior part of the cervical canal. In the region of the pedipalps their posterior portion fuses with the anterior end of the transversal phragma (TvP, Fig. 2c). This extends in the Smarididae as a pair of sclerotised folds from the lateral wall of the infracapitulum medially. Here, the phragma fuses in *Fessonia* with the soft cuticle of the cervical canal, whereas in *Hirstiosoma* it fuses with the cervical sclerites.

The most posterior part of the cervical canal is strengthened ventrally by the capitular sclerite (CaS, Fig. 1, 2d). This sclerite continues into the arcal sclerite, which runs in a bow upward and then anteriorly (AS, Fig. 1-3). The tracheal trunks run on both sides of the arcal sclerite. In this region, they develop as longitudinal infoldings of the cuticle (Tr, Fig. 1-3). Anteriorly the tracheal trunks continue into the peritremes (Pt, Fig. 1, 2). These run dorsally on the infracapitulum and are connected by a longitudinally striated soft cuticle. A peritremal shield is lacking. A short ramus branches off and turns dorsally from the proximal portion of the tracheal trunks. Contrary to the Erythraeidae (WITTE 1978), the tracheal trunks of Smarididae lack a proximal air-chamber.

Latero-coxal region: In the Smarididae, the infracapitular region behind of the pedipalps, the latero-coxal region, is posteriorly elongated rod-like (Lcx, Fig. 1, 3). SOUTHCOTT (1961) has called these elongations "cornua".

Pharynx and buccal cavity: In *Fessonia* the pharynx is elongate (Ph, Fig. 1-3). It is provided with alternating flexor and dilator muscles. In *Hirstiosoma*, on the contrary, the pharynx is short and is provided only with dilator muscles. The anterior opening of the pharynx is overlapped by the labrum (La, Fig. 1-3).

The cervical canal continues into the buccal cavity (b.c., Fig. 1, 2), anterior to the pharynx opening and the labrum. The buccal-cavity is formed by the lateral lips, which are fused in the ventral and the postero-dorsal region of the cavity.

Glands of gnathosoma and prosoma

The glands of the gnathosoma and the prosoma apparently have three main functions: (1) production of salivary secretions, (2) protection of the internal milieu, (3) osmoregulation

Podocephalic glands and infracapitular gland: In the Parasitengonae and other Prostigmata the podocephalic gland system is usually composed of four pairs of podocephalic glands, which open into internal podocephalic ducts (ALBERTI 1973; ALBERTI & STORCH 1974; WITTE 1978, 1995). Three pairs of these glands are acinous salivary glands, whereas the most posteriorly located glands are tubular coxal glands (4th podocephalic gland). These have an osmoregulatory function (ALBERTI & STORCH 1977; OLOMSKI, 1995). There is, moreover, a pair of acinous infracapitular glands, of which the ducts in most groups open directly onto the cervix or into the cervical canal, respectively. In larval Trombiculidae SHATROV (1982) described the same number of acionous and tubular glands.

In the Smarididae this gland system has changed in the following respects:

1. The ducts of the podocephalic and the infracapitular glands are considerably elongated (pG 1 and 2, iG, Fig. 1). Obviously, the evolution of this feature took place correlated with the evolution of a wide longitudinal motility of the gnathosoma.

2. The 3rd podocephalic glands are reduced in *Fessonia* as well as in *Hirstiosoma*. This conclusion about the reduction of just this one pair of glands is based on a comparison with the Erythraeidae. In *Erythraeus* the 3rd podocephalic glands show large vacuoles containing a few small secretion granula that stain with Anilin-blue (WITTE 1978). A gland producing such a secretion is lacking in the Smarididae. The first and the second podocephalic glands, however, produce secretion droplets which stain with Orange G in the Smarididae as well as in *Erythraeus*.

3. In *Fessonia* the ducts of the infracapitular glands open into the distal podocephalic duct. In *Hirstiosoma*, however, they still open directly into the cervical canal.

Buccal glands: A pair of buccal glands is located on both sides of the buccal cavity and at the most anterior part of the cervical canal (BG, Fig. 2). The buccal glands lack a lumen in the Smarididae. The gland cells release an oily secretion immediately into the buccal cavity and into the anterior portion of the cervical canal. In deutonymphs and adults, the secretion probably seals the mouth opening and, moreover, the axial pathway of salivary secretions within

the intercheliceral canal into the prey and the pathway of liquid food via the same canal from the prey into the pharynx.

Labial glands: Labial glands are lacking at least in adult smaridids. These lipid-producing glands are located in the anterior part of the lateral lips in some erythraeids (WITTE 1978).

Intercheliceral gland: A small tubular intercheliceral gland (= tracheal gland) occurs in adult *Hirstiosoma*. It opens between the tracheal trunks into the posterior part of the cervical canal. This gland is lacking in adult *Fessonia*. However, GRANDJEAN (1947) has described it in the larva of this species (glande intermandibulaire), in which it is still quite large.

The different sizes of this gland in the larva and the postlarval mobile instars correspond with its probable function, as I have described in the Erythraeidae (WITTE 1978). In the larva, the lipidaceous secretion seals the space between both chelicerae, whereas the space between chelicerae and cervix is mainly sealed by secretions of the buccal glands. In this way the pathway of salivary secretions along the cervix seems protected against desiccation. In deutonymphs and adults, however, the pathway of salivary secretions is protected mainly by structural internalisation (compare above).

Pharyngeal glands: A pair of pharyngeal glands opens into the pharynx (PG, d.PG, Fig. 1, 2). The function of these glands is unknown.

Aspidosomal glands: A pair of aspidosomal glands is located below the prodorsal shield close to the crista metopica (asp.G, Fig. 1). These glands belong to the type of subcuticular glands, which are quite common in the Erythraeoidea (WITTE 1978). They release a secretion into the narrow space between cuticle and epidermis.

Muscles of gnathosoma

The muscles of the smaridid gnathosoma may be homologised quite well with those of the Erythraeidae (WITTE 1978). Most of the muscles are also found in Calyptostomatoidea (WITTE 1995), Trombidioidea (MITCHELL 1962b; SHATROV 1981; WITTE 1995) and Hydrachnidia (MITCHELL 1962a). In order to assume a common terminology in dealing with these muscles, I will use in this paper the terms which MITCHELL (1962a, 1962b) has introduced for Hydrachnidia and Trombiculidae.

In Table 1 the various muscles of the gnathosoma are characterised in regard to insertion and origin. Moreover, the terms which I have used to denominate the muscles of Erythraeidae are named (WITTE 1978).

designation of muscle	origin	insertion	designation in Erythraeidae (WITTE 1978)
protractor capituli 1 (protr. cap. 1)	anterior tip of crista metopica	posterior tip of latero-coxal region	dorsal protractor of gnathosoma
protractor capituli 2 (protr. cap. 2)	posterior margin of coxa I	posterior tip of latero-coxal region	ventral protractor of gnathosoma
retractor capituli 1 (retr. cap. 1)	posterior tip of crista metopica	posterior tip of latero-coxal region	dorsal retractor of gnathosoma
retractor capituli 2 (retr. cap. 2)	crista metopica, region of posterior sensory field	posterior portion of peritreme	retractor of trachea
retractor capituli 3, ventral ramus (retr. cap. 3, v.)	posterior margin of coxa I	postero-ventral margin of infracpitulum	ventral retractor of gnathosoma, anterior ramus
retractor capituli 3, dorsal ramus (retr. cap. 3, d.)	posterior margin of coxa I	transversal phragma of infracapitulum	ventral retractor of gnathosoma, posterior ramus
protractor chelicerae 1 (protr. chel. 1)	arcal sclerite and distal portion of tracheal trunk	posterior tip of chelicera	medial protractor of chelicera
protractor chelicerae 2 (protr. chel. 2)	transversal phragma of infra-capitulum	posterior tip of chelicera	lateral protractor of chelicera

retractor chelicerae (retr. chel. 1)	crista metopica, region of posterior sensory field	last third of chelicera, dorsal surface	posterior retractor of chelicera
retractor chelicerae 2 (retr. chel. 2)	crista metopica, posterior portion	posterior tip of chelicera	anterior retractor of chelicera
retractor chelicerae 3 (retr. chel. 3)	arcal sclerite	mid-portion of chelicera, internal surface	internal retractor of chelicera
retractor of labrum	cervical sclerite	posterior tip of labral sclerite	labral muscle
dilator of pharynx	dorso-lateral cuticle of infracapitulum and transversal phragma	concave dorsal surface of pharynx	levator of pharynx
flexor of pharynx	dorso-lateral horns of pharynx		constrictor of pharynx
levator palpi	lateral wall of latero-coxal region	postero-dorsal margin of trochanter	
depressor palpi	ventral wall of infracapitulum	ventral margin of trochanter	
abductor palpi	cuticle of latero-coxal region behind articulation-condyle of palp-acetabulum	ventro-lateral margin of trochanter	

Tab. 1: Muscles of gnathosoma of *Fessonia callitricha*.

The muscle system of deutonymphal and adult Smarididae is characterised by some properties, which evolution obviously correlated with the evolution of styliform chelicerae and with a wide longitudinal mobility of the gnathosoma (Fig. 3). This becomes obvious from a comparison with a probably rather underived parasitengone muscle system, as it is found, e.g. in the Trombidioidea (MITCHELL 1962b; WITTE 1995).

The indirect mode of cheliceral protraction by means of cheliceral protractor 1, the "sigmoid muscle" is changed to direct protraction. Additionally, there evolved a second cheliceral protractor (protr.chel.2, Fig. 3) which is longer then the original one. When the chelicerae pierce the cuticle of a prey, both protractors will act together. The subsequent protraction of the chelicerae deep into the prey, however, is carried out only by the longer protractor 2. In addition, the cheliceral retractors demonstrate a considerably different length in the Smarididae (retr.chel.1-3, Fig. 3). This enables the chelicerae to retract even if the gnathosoma is retracted completely into the idiosoma (Fig. 3). A wide protraction of the gnathosoma is enabled by two pairs of greatly elongated protractor muscles. The retractor muscles of the gnathosoma have also developed rather different lengths. A complete retraction of the gnathosoma appears to be enabled only by action of capitulum retractor 2 (Fig. 3).

It should be noted that the two rami of capitulum retractor 3 are attached to the posterior margin of coxa 1, but do not originate on the endosternite as they do in most Erythraeidae and in Calyptostomidae (WITTE 1995). There exists, moreover, a labrum-retractor (retr.labr., Fig. 3) and three extrinsic palpal muscles (Table 1, not figured).

Female genital system

The main functions of the female genital organs are: (1) formation of eggs, (2) capacitation and storage of transferred sperm cells, (3) protection of the internal milieu in the distal region of the genital tract against environmental inflicts.

Ovary and paired oviducts

The ovary of *Fessonia* and *Hirstiosoma* is horseshoe-shaped (Ov, Fig. 4). Both arms are directed posteriorly and continue into the paired oviducts (pO, Fig. 4). These turn anteriorly, run along both sides of the distal genital tract, turn again in a loop posteriorly and enter from the anterior side the distal unpaired part of the genital tract.

The oocytes already migrate into peripheral pouches of the ovary at the beginning of their growing phase (e.p., Fig. 4, 5). The pouches are formed from the basement membrane of the ovary epithelium and are ensheathed by some muscle fibres. Egg cells in the pouches undergo phases of previtellogenesis and vitellogenesis. Cells remain in the lumen of the ovary, which obviously function as nurse cells (n.c., Fig. 4, 5). Nutritive cords can be recognised running between nurse cells and egg cells at the beginning of vitellogenesis. The nurse cells and their nuclei are already considerably enlarged at this time. It remains unresolved whether later in the course of egg-development, the nurse cells become multinucleated, as it is the case in erythraeids (WITTE 1975b), since vitellogenesis had just begun in the specimens which I have investigated. Extra-ovarian nutritive cells (fat-body), as they are found in several groups of Prostigmata (HENKING 1882; SCHMIDT 1936; ALBERTI 1974), are lacking in all Erythraeoidea.

Distal female genital organs

The distal portion of the female genital tract has an ectodermal origin. It is provided with a cuticular intima. The unpaired oviduct, the vagina and some accessory organs belong to this part of the genital tract in both species investigated. Accessory organs are the dorsal accessory gland, the lipid gland of the vagina, two pairs of genital papillae, which are transformed to receptacula seminis and the distal gland accessory. A pair of progenital pouches is found only in *Fessonia* (WITTE 1995).

Unpaired oviduct: The unpaired oviduct of the Prostigmata is also termed uterus (VITZTHUM 1943; MATHUR & LEROUX 1970) or oviduct II (ALBERTI 1974; ALBERTI & CROOKER 1985). In Smarididae, like in Erythraeidae (WITTE 1975b), it is provided with a cuticular intima. In *Fessonia*, the cuticular intimata in the distal part of the unpaired oviduct is provided anteriorly with numerous spines, and posteriorly with cuticular hairs (uO, Fig. 4). The epithelium of the unpaired oviduct is constituted by relatively squamous cells, and it forms several longitudinal folds.

The unpaired oviduct is provided with a wide layer of circular muscles and some longitudinal muscles (Fig. 4, 5a).

Dorsal accessory gland: The dorsal accessory gland opens into the posterior region of the unpaired oviduct (dG, Fig. 4, 5b). In *Fessonia* it forms a wide alveole within which the glandular cells are quite large. The cytoplasma is basophilic. The secretion is obviously a protein with a mucopolysaccharide component. It stains with Anilin-blue and with paraldehyde-fuchsin.

In *Hirstiosoma* the lumen of the gland contains only few acidophilic secretion-droplets.

Vagina: In *Fessonia* and *Hirstiosoma* the vagina (V, Fig. 4, 5) is provided with cuticular strengthenings that are located dorso-medially in the anterior and the posterior roof of the vagina and anteriorly to the entry of the unpaired oviduct (cu.S., Fig. 4). In *Fessonia*, moreover, a pair of cuticular strengthenings is located between the vaginal lipid gland and the genital acetabulae (Fig. 4). This strengthening is lacking in *Hirstiosoma*. The intima of the vagina is arranged in some folds distally to the genital papillae. The epithelium forms the glandular epithelium of the distal accessory gland in this region. Finally, proximally to the progenital lips, the vagina shows a pair of deep invaginations, the progenital pouches (Fig. 4, 5).

Vaginal lipid gland: In *Fessonia* as well as in *Hirstiosoma* the vaginal lipid gland consists of an anterior and a posterior lobe (lG, Fig. 4,5). Both lobes together nearly surround the proximal part of the vagina. The cuticular intima is widely separated from the epithelium, so that there is a wide lumen filled with secretions. The apex of the glandular cells is filled with several vacuoles, and the secretion in the lumen of the gland contains lipids (Sudanblack B-staining) as well as proteins.

The secretion probably contributes to the protection of the internal milieu of the genital tract from external affects and it might seal and protect eggs, as is the case in erythraeids (WITTE 1978).

Genital papillae and receptacula seminis: In *Fessonia* and *Hirstiosoma* two pairs of genital papillae are located distally to the lobes of the lipid gland (g.p., Fig. 4, 5a). Each organ is surrounded by a cuticular margin.

The function of these organs apparently differs from their function in other Actinotrichida, in which they probably are involved in uptake of water or ions (ALBERTI 1977, 1979; ALBERTI & LÖWENFELD 1990). In *Fessonia* the anterior part of the anterior papillae as well as the posterior part of the posterior papillae form deep pouches. These pouches serve as receptacula seminis R.s., Fig. 4, 5b, 6). The sperm cells, which probably have been taken up with a spermatophore, are arranged close to each other in one layer on the surface of the receptaculum cells (Sp, Fig. 6b).

In *Hirstiosoma* the genital papillae lack pouches. However, even in this species, sperm cells are arranged closely to each other on the surface of the papillae (Sp, Fig. 6c). Sperm cells are to be found only rarely outside the cuticular frame of the genital papillae. EM-pictures from *Hirstiosoma* show that the cell apices of the genital papillae are provided with numerous cisternes

and infoldings of the cell membrane. The sperm cells become capacitated upon contact with the surface of the genital papillae (Fig. 7a, b). In the figures presented here, the peripheral cisternes of the sperm cells, which characterize the non-capacitated sperm cells in the testes (Fig. 7c) are already reduced. The sperm cells have developed numerous microfilaments in the region of contact to the receptaculum cells. In the anterior part of the sperm cells several mitochondria and small vesicles are located.

Distal accessory gland: The epithelium distal to the genital acetabulae is glandular (di.G, Fig. 4, 5). In *Fessonia*, this epithelium looks similar to that of the lipid gland. The intima is separated from the glandular cells and a lipidaceous secretion is stored in the lumen below the intima (Sudanblack B). The secretion is additionally provided with an acidophilous proteinaceous secretion component. In *Hirstiosoma* this glandular region shows only squamous cells, and there is only a narrow subcuticular space.

Progenital pouches: In *Fessonia*, proximal to the progenital lips, the vagina epithelium forms deep progenital pouches (pr.p., Fig. 4, 5a), which GRANDJEAN (1947) has termed "sacs prégénitaux".

The cuticular intima of these pouches is provided with papillae, which may hinder the collaps of the pouches. Numerous circular folds allow an enlargement of the volume of the pouches. This can be achieved by means of a dilator muscle, which inserts at the proximal end of the pouches (Mu, Fig. 5a) and originates on the coxa III.

One may hypothesise that a rapid expansion of the pouch, which probably is filled with a liquid secretion, may be important for the uptake of a spermatophore head. Thus sucking it into the vagina.

Male genital system

Only little is known about the mode of sperm transfer in the Smarididae. However, I have found spermatophores in *Hirstiosoma*. *Hirstiosoma* produces small stalked droplet spermatophores, of which the droplets are provided with a whitish sheath. In the vicinity of the spermatophores, moreover, I found several secretion threads on the ground. These are probably signalling threads. The internal structure of the spermatophores remains uninvestigated.

Spermatophores of *Fessonia* have not been detected so far. However, since in *Fessonia* as well as in *Hirstiosoma* the structure and histology of the male genital organs as well as the secretions of testes and accessory glands are very similar to those of the Erythraeidae, in particular of *Erythraeus* and *Charle-*

tonia (WITTE 1975a, 1977; WITTE & OLOMSKI in press), it seems likely that spermatophores are built in a similar way in Smarididae and Erythraeidae.

Testes and vasa deferentia

Fessonia and *Hirstiosoma* have a pair of tube-shaped testes, which are connected by a testis-bridge at their posterior part (Fig. 1, 2). Testes as well as the testis-bridge show a dorsal germinal part and a ventral glandular part.

In the reproductive period of males, non-capacitated sperm cells and spermatophore secretions are stored in a matrix secretion in the lumen of the glandular part.

The paired vasa deferentia run from the glandular part of the testes towards the ejaculatory complex (Fig. 1, 2). Before they enter the ejaculatory complex they join to a short unpaired vas deferens.

Distal male genital tract and accessory organs

The distal male genital tract is composed of three sections: an unpaired vas deferens, the ejaculatory duct and the progenital chamber (Fig. 8). These sections are provided with a cuticular intima and have an ectodermal origin. The unpaired vas deferens projects a short distance into the ejaculatory duct. It is composed of cylindrical, apparently glandular cells and is provided externally with a few circular muscles. The ejaculatory duct and progenital chamber are separated by the eugenital lips (eu.l., Fig. 8, 10). Distally the progenital chamber is delimited by progenital lips (pr.l., Fig. 8, 10).

The ejaculatory duct is provided with the following accessory glands (Fig. 8, 10):

1. Lateral accessory glands (lat.acc.gl.)
2. Posterior organa membranoidea (post.org.membr.). Of these, in *Fessonia*, the posterior portion extends into the progenital chamber.

The progenital chamber is provided with the following accessory organs:

3. Anterior organa membranoidea (ant.org.membr.)
4. Anterior accessory gland (ant.acc.gl.)
5. Two pairs of genital papillae (alv.gen.pap.), which in *Fessonia* are transformed to alveoles. Fields of cells, possessing a glandular appearance, may be found in the same region in *Hirstiosoma* (Fig. 11b).

MITCHELL (1962a) introduced the term "ejaculatory complex" for the ensemble of ejaculatory duct and progenital chamber including associated sclerites, muscles and accessory organs.

Spatial structure of ejaculatory complex: The spatial structure of the ejaculatory complex of the Smarididae is quite similar to that of some Erythraeidae, in particular *Erythraeus* (WITTE 1975) and *Charletonia* (WITTE & OLOMSKI in press). In the following discussion, I shall refer to Fig. 8 and 10, unless otherwise specified.

The ejaculatory duct is divided by a wide anterior projection (AntPrj) into a large central chamber (CentCmb) and a semi-hemispherical anterior chamber (AntCmb), which has a narrow, crescent-shaped cross-section. The unpaired vas deferens enters the ejaculatory complex in a deep invagination of the anterior projection. Immediately posterior to the anterior projection, the anterodorsal part of the central chamber forms a dome-shaped transversally extended proximal chamber (PrxCmb).

Laterally, the central chamber is delimited by lateral projections (LatPrj), which separate a pair of lateral chambers (LatCmb) from the central chamber. These lateral projections in the Erythraeoidea are homologous to the medial projections of the Hydrachnidia as described by WITTE & OLOMSKI (in press).

The lateral accessory glands open into the proximal part of the lateral chambers. In *Fessonia*, moreover, the distal part of the lateral chambers is accompanied by the posterior organa membranoidea. Distal to the eugenital lips, the ejaculatory complex widens to the progenital chamber (PrgCmb), of which the lateral walls are strengthened by the operculum (Opc). The anterior accessory gland opens anteriorly into the progenital chamber, and two pairs of rudimentary genital "papillae" are located distally to the operculum.

Lateral accessory glands (lat.acc.gl., Fig. 8): In the Smarididae, each lateral accessory glands consists of three tubes. The intima is provided with numerous papillae. The glands produce a lipidaceous secretion (Sudanblack B-staining). Their function in erythraeids (WITTE 1975a) may indicate their function also in the Smarididae. In erythraeids the secretion serves to glue the spermatophore stalk to the ground and the head to the stalk. In *Leptus* and *Abrolophus*, moreover, the secretion provides the sheath-material for the droplet.

Organa membranoidea (ant.org.membr. and post.org.membr., Fig. 8): The anterior and the posterior organa membranoidea are glandular epithelia, which produce a lipidaceous secretion. This probably contributes to the protection of the internal milieu in the region of the ejaculatory complex.

Anterior accessory gland (ant.acc.gl., Fig. 8): This gland forms a large alveole. The cylindrical cells produce an oily secretion (Sudanblack B-staining). The secretion probably protects the internal milieu of the distal genital tract.

Genital papillae (alv.gen.pap. Fig. 8, 10): Contrary to the literature, in which the existence of genital papillae in male Erythraeoidea is denied (GRANDJEAN 1946; SOUTHCOTT 1961), two pairs of these organs exist at least in the male *Fessonia callitricha.*

As in other Parasitengonae, these are located distal to the operculum and, as in female *Fessonia* (compare above), are transformed to alveoli. However, their diameter is only about 7 µm in the male compared to about 25 µm in the female. It is remarkable that even in the male, agglomerations of a few sperm cells can be frequently found in the alveoles. This may indicate that they are even physiologically similar to the female genital papillae.

The male of *Hirstiosoma* has probably also retained genital papillae. Fields of glandular cells are located in *Hirstiosoma* in the same regions in which in *Fessonia* alveolareous genital papillae are to be found. However, unlike in other Prostigmata, these lack a cuticular margin (Fig. 11b).

Sclerite system of ejaculatory complex

In regard to the terminology of the sclerites of the ejaculatory complex I will refer mainly to FEIDER (1959), who has introduced a terminology for the Trombidioidea.

In regard to sclerites, which were not described by FEIDER, I will preferably use the terminology proposed by BARR (1972) for *Hydrachnidia.* Contrary to BARR (1972) I found that most of the sclerites of Hydrachnidia and *Trombidia* (including the Erythraeoidea) may be homologized well. WITTE & OLOMSKI (in press, Table 1) have compared the probably homologous sclerites of *Fessonia callitricha* and *Thyas barbigera.*

In *Fessonia* the ejaculatory complex is provided with the following sclerites:

Operculum (Opc, Fig. 8-10): The operculum (amphioid-sclerite, eugenital sclerite) is a clasp-shaped sclerite, which is composed of two longitudinal arms that run along the lateral wall of the progenital chamber, distal to the eugenital lips. The anterior ends of these sclerites are joined by a small zone of flexible cuticle. The longitudinal sclerites of the operculum are provided with a row of eugenital setae (in *Fessonia* 17-19 on each side). These are lacking only on the anterior portion of the operculum.

The anterior part of the operculum is provided with wing-shaped lateral arms (Fig. 9). This part of the operculum is surely homologous with the anterior arm sclerite of Hydrachnidia. The posterior ends of the operculum continue into the hypapodemes.

Anterior keel (AntKl, Fig. 8, 9): The anterior keel is located medially in the roof of the anterior part of the progenital chamber. It is formed of two parallel plates, which are dorsally fused. Anteriorly these plates become flexible and accompany the entry of the duct of the anterior accessory gland into the progenital chamber. Posteriorly the anterior keel joins the distal ends of the anteromedial sclerites.

Anteromedial sclerites (AmdScl, Fig. 8, 9): The anteromedial sclerites run side-by-side in the antero-distal wall of the anterior chamber. They are connected by a flexible cuticle. Distally, the sclerites diverge slightly.

Furca (Frc, Fig. 8, 9): Both, the central and distal portions of the furca are identical with the sclerotised posterior wall of the anterior chamber. Apically, the furca continues into a pair of sclerotised arms, and a pair of posterior rami turn in a sharp angle posteriorly from the lateral border of the mid-furca. These rami run on both sides of the anterior projection towards the proximal chamber sclerite, with which they are joined via a flexible cuticle. Ventro-distally, the posterior rami of the furca are provided with many cuticular hairs. (In the Erythraeidae these probably function in the course of spermatophore formation as a weir that allows only the stalk secretion to enter the anterior chamber.)

Proximal chamber sclerite (PrxCmbScl, Fig. 9): The wall of the proximal chamber is sclerotised and forms the proximal chamber sclerite. The sclerite extends transversally between the proximal ends of the apodemes.

Apodemes (Apd, Fig. 8-10): The apodemes are a pair of elongated sclerites which strengthen the lateral wall of the lateral projections. Antero-dorsally, they reach the proximal chamber sclerite, and their posterior margin is joined with the posterior margin of the hypapodemes. Distally the apodemes are provided with two setae.

Hypapodemes (HypApd, Fig. 9): The hypapodemes are a rigid pair of sclerites located in the postero-lateral wall of the lateral chambers. Distally, the hypapodemes continue into the posterior ends of the operculum and join with the apodemes with their dorsal tip and lateral margin.

Distal sclerites (DisSc, Fig. 9, 10): Proximal to the eugenital lips, the distal sclerites run longitudinally in the wall of the ejaculatory complex. Each scle-

rite forms a phragma, which is posteriorly fused with the hypapodeme. Anteriorly, the sclerite ends near the anterior keel and the antero-medial sclerite.

Dorsal cuticular strengthening of central chamber (cu.S, Fig. 10): This flexible strengthening runs dorso-medially in the central chamber. It is probably homologous to the "Prägesklerit" of the erythraeid mite *Abrolophus* (WITTE 1975a).

Posterior keel (PosKl, Fig. 8, 9): In Smarididae, as in Erythraeidae, the posterior keel is a clasp-shaped sclerite. It is located medially in the posterior wall of the ejaculatory complex, forming the border between the central chamber and progenital chamber.

The sclerite can probably be homologised with the posterior keel of the Hydrachnidia (BARR 1972) because the same muscles (M3 and M5) insert at it in Smarididae and Hydrachnidia (WITTE & OLOMSKI in press).

Mediale sclerite of lateral projections (MdScl, Fig. 10): This sclerite runs in the medial wall of the proximal region of the lateral projections.

Muscles of ejaculatory complex

The muscles of the ejaculatory complex of *Fessonia* are characterised in Table 2 in regard to their insertion and origin and in regard to their possible function. The muscles are mainly shown in Fig. 8 and 9. This is the first time that these muscles have been described in the Erythraeoidea.

In order to produce a common terminology for the muscles of all Parasitengonae, I will use the same indices for the intrinsic muscles which BARR (1972) used for the Hydrachnidia. In regard to the extrinsic muscles, I will use – so far as possible – the terminology which MITCHELL (1957) introduced for *Thyas barbigera*. (For *Blankaartia*, however, MITCHELL (1962b) used some of these terms for other muscles!)

The intrinsic muscles of Erythraeoidea are named M1-M13.

The muscle-groups 1-5 described by BARR (1972) for Hydrachnidia are probably homologous to the muscles M1 - M5 of *Fessonia*. Moreover, a homolog to M7 and maybe to M8 of *Fessonia* exist in the water mite *Thyas barbigera* (as well as in *Piersigia intermedia* and *Hydrovolzia placophora*) (WITTE & OLOMSKI, in press).

The muscle-group 6, by BARR described, is an extrinsic muscle, which is named here in accordance with MITCHELL (1957) ventral muscle 7 (Ventr. 7). The other extrinsic muscles of Smarididae are named here Gen 1, Gen 2 and Gen 4-6.

Gen 1 and Gen 2 of Smarididae correspond with muscles of *Thyas* (MITCHELL 1957). Gen 3 of *Thyas* has no homolog in the Erythraeoidea. The terms Gen 4 and Gen 5 were introduced for extrinsic muscles by WITTE & OLOMSKI (in press). These muscles were not described by MITCHELL (1957) for *Thyas*, and they are not homologous to the intrinsic muscles Gen 4 and Gen 5 of *Blankaartia* (MITCHELL 1962b). Gen 6 of the Smarididae, however, seems to be homologous to Gen 6 of *Blankaartia* (MITCHELL 1962b).

Function of the male genital system

Since spermatophores of Smarididae are so far only known from *Hirstiosoma*, and since these have not been investigated histologically, I will deal only briefly with the probable function of the male genital organs. It is likely, however, that at least the basic functions of the smaridid genital organs are similar to those of the Erythraeidae, since in both families the structure of the genital system and the secretions of testes and accessory glands correspond greatly (compare for erythraeids WITTE 1975a; WITTE & OLOMSKI in press).

In view of this situation, it may be assumed that the following main steps of spermatophore formation are common to both families. However, I will stress that these functions have been investigated experimentally only for the Erythraeidae (WITTE 1975a).

Non-capacitated sperm cells and droplets of proteinaceous spermatophore secretions are released into the lumen of the glandular part of the testes. There they are stored within a matrix fluid. Prior to spermatophore formation, the formation of relative large uniform complexes of stalk-secretion, sheath-secretion and sperm takes place in the paired vasa deferentia. This aggregation of secretion-complexes is caused by resorption of the matrix fluid in the vasa deferentia.

The final separation of stalk-secretion, sperm and sheath secretion takes place in the ejaculatory complex.

The stalk secretions are released via the anterior chamber. The anterior chamber is probably widened by actions of muscles M7 and M8 in order to take up the stalk secretion. Thereafter, the stalk secretion is pressed by muscle M4 out of the distal part of the anterior chamber and the stalk is formed between the eugenital lips. Here, the stalk-secretion seems to be hardened by oxidation (in Erythraeidae by oxidation of protein-bound sulfhydryl groups to disulfide linkages (WITTE 1975a). An untimely hardening of the secretions in the anterior chamber seems prevented by the oily secretion of the anterior accessory gland, which seals the progenital chamber and may hinder oxygen to enter the ejaculatory complex.

	Origin	Insertion	Function
M1a	lateral arms of operculum	entry of anterior gland into progen. chamber	dilator of opening of anterior accessory gland
M1b	lateral arms of oerpculum	anterior keel, lateral surface	dilator of operculum
M2	apodeme, medial surface of apical portion	distal sclerite	dilator of eugenital opening
M3	apodeme, proximal portion	posterior keel	compressor of central chamber
M4	anterior keel and antero-median sclerite	furca, apical arms	furca protractor, constriction of anterior chamber
M5	posterior keel	proximal chamber sclerite	longitudinal compressor of central chamber
M6			
M7	proximal chamber sclerite	furca, mid-portion	furca retractor, widening of anterior chamber
M8	proximal chamber sclerite	furca, mid-portion	widening of anterior chamber
M9	apodeme, medial surface of proximal portion	distal tip of lateral projections	levator of lateral projections
M10	apodeme, apical tip (left side)	apodeme, apical tip (right side)	compressor of central chamber

M11	lateral arms of operculum, posterior margin	apodeme, lateral surface of apical portion	widening of central chamber
M12	apodeme, medial surface of proximal portion	medial sclerite of lateral projections	
M13	progenital lips	proximal tip of apodeme	protractor of ejaculatory complex
Gen1a	coxa IV	anterior angel of progenital chamber	dilator of progenital chamber
Gen1b	coxa IV	cuticle of progenital chamber (close to anterior genital "papilla")	dilator of progenital chamber
Gen2	dorsal integument	posterior angle of progenital lips	posterior retractor of progenital lips
Gen3			
Gen4a	ventral integument (postero-lateral of progenital lips)	middle region of progenital chamber	dilator of progenital chamber
Gen4b	ventral integument (postero-lateral of progential lips)	integument (lateral of progenital lips)	dilator of progenital chamber
Gen5	latero-ventral integument (close to insertion of Gen 4b)	cuticle of progenital chamber (close to posterior genital "papilla")	dilator of progenital chamber
Gen6	dorsal integument	proximal chamber sclerite	retractor of ejaculatory complex
Ventr.7	anterior angle of progenital lips	endosternite	controll of endosternite position

Tab. 2: Intrinsic and extrinsic muscles of ejaculatory complex of *Fessonia callitricha.*

The spermatophore head is formed in the central chamber of the ejaculatory complex and is probably glued afterwards by means of the secretion of the lateral accessory glands to the tip of the stalk.

If the sheath of the spermatophore droplet is constructed in a similar way as that in *Erythraeus* and *Charletonia* then it would be formed in the central chamber from proteinaceous testes-secretions and only thereafter would the sperm pass into the preformed sheath (WITTE & OLOMSKI, in press).

Discussion

The course of evolutionary change, that has led to the smaridid organization was, on the one hand, surely promoted by selection-mediated adaptation. On the other hand, it was obviously enabled and delimited by inherited developmental at properties, constraints and organismal properties, which have enabled or predisposed particular, subsequent transformation steps. In the discussion I will deal with the role and the interplay of these mechanisms and properties.

Adaptation

Adaptive change in the evolution of the Erythraeoidea and the Smarididae apparently concerned mainly two functional complexes:

1) The protection of the internal milieu from the external.
2) The structure of the gnathosoma and the mode of feeding.

The reconstruction of the course of adaptive transformation was carried out on the basis of the phylogenetic system of the Parasitengonae (compare WITTE 1991b, 1995). The main transformation steps of the gnathosoma are shown in Fig. 12.

Protective structures: In the Parasitengonae and their probable sister group Anystidae the protection of the internal milieu of the animals against external influence was probably originally achieved by means of glands or glandular epithelia, which seal the body by means of secretions (WITTE 1978; OLOMSKI 1995; WITTE & OLOMSKI in press). In the Parasitengonae, the secretions are mainly lipids. In the Erythraeoidea, this type of glands includes: The two-lobed lipid-gland and the distal accessory gland of the female genital tract. The anterior accessory gland and the organa membranoidea of the distal male genital tract. Labial glands (present only in Erythraeidae) and buccal glands in the buccal region. The anal opening, finally, is protected by rectal glands (WITTE 1978). In the larva of the Erythraeoidea, the pathway of sali-

vary secretions along the cervix is protected mainly by oily secretions of the intercheliceral gland and the buccal glands (WITTE 1978). Correlate with development of styliform chelicerae in the deutonymph and the adult, however, the predominant protective apparatus of the salivary secretion pathway obviously changed to structural internalisation. As early as in the common stem lineage of Calyptostomatoidea (VISTORIN-THEIS 1977) and Erythraeoidea (WITTE 1978, 1995) a deep salivary groove evolved. Finally, in the stem lineage of the Erythraeoidea the internalisation of the dorsal surface of the infracapitulum became completed by fusion of the lateral keels above of the chelicerae.

Mouthparts and mode of feeding: The adaptive change from the original type of parasitengone chelicerae to styliform, widely protractable chelicerae took place in the common stem lineage of Calyptostomatoidea and Erythraeoidea (Fig. 12). It was correlated with a series of transformations (WITTE 1995). The articulation of the cheliceral shafts with the sigmoid pieces was abandoned and an elongated cheliceral sheath evolved. This allowed a wide longitudinal mobility of the chelicerae. The cheliceral protractor changed from an indirectly acting muscle (the "sigmoid muscle") to a directly acting muscle, and there evolved a second cheliceral protractor. Protractor and retracor muscles of the chelicerae became considerably elongated.

Further adaptive transformations took place in the stem-lineage of the Erythraeoidea (WITTE 1978, 1995). The movable digit of the chelicera became reduced. The transformation of the dorsal surface of the infracapitulum to an internal canal took place, which not only improved the protection of the salivary pathway and the pharynx-opening, but also effectively guided the chelicerae. The evolution of a longitudinal dovetailing between the chelicerae of the Erythraeoidea, which followed the earlier evolution of an intercheliceral canal, finally integrated both chelicerae to a functional whole. The functional flexibility of the chelicerae became increased by the evolution of a third cheliceral retractor and the evolution of differently elongated protractor- as well as retractor-muscles of the chelicerae.

In regard to the elongated armilla in the Smarididae, which allows a wide protraction of the gnathosoma, one may speculate about an adaptive meaning for preying. It may also be, however, that the main adaptive importance of the armilla is to allow the complete retraction of the gnathosoma and thus to protect it from mechanical injury during locomotion in labyrinthine soil habitats.

Organismal properties determining the course of evolution

In regard to the mechanisms which determine pathways of evolutionary change, STEARNS (1992) pointed out that "constraint and adaptation represent the two ends of a continuum of explanations". Several authors, moreover, have referred to the fact that the course of evolutionary change of organismal patterns can be strongly determined by organismal properties, e.g. RIEDL (1975); GOULD & LEWONTIN (1979); ROTH & WAKE (1985); MCKITRICK (1993). Such organismal properties include:

- Constraints which delimit the potential of the organismal pattern for evolutionary change. RIEDL (1975) has called such constraints the evolutionary burden.
- Developmental properties which have probably enabled complex evolutionary transformations of ontogenetic instars.
- Organismal properties which have been the structural or functional precondition for a subsequent adaptive transformation, or which have predisposed particular transformation steps. MCKITRICK (1993) has called such predisposing properties "key innovations".

I will discuss the role of these mechanisms using mainly the evolutionary transformation of the gnathosoma as an example.

Constraints

Rigid fixation of the structural pattern of the erythraeoid gnathosoma by constraints can be assumed, because its basic composition has remained quite stable within the Parasitengonae, although general organization , mode of function and allometric proportions of the various components are strongly transformed in the course of ontogeny (GRANDJEAN 1956, 1959; WITTE 1978), and have changed remarkably in the course of evolution.

Indeed, most of the cuticular structures, muscles and glands of the deutonymphal and adult gnathosoma of the Erythraeoidea may be homologised with corresponding structures of the Trombidioidea and Hydrachnidia (compare Fig. 12, and MITCHELL 1962a, b; WITTE 1995).

The constraints which are responsible for the evolutionary stability of this pattern are probably due to the integration of cuticular structures, muscles, nervous elements and behaviour modes into a functional whole. TYLER (1988) has called this type of constraint "constraint of interaction".

I will point out, regarding the ejaculatory complex of Erythraeoidea, Hydrachnidia and Trombidioidea, that a similar rigid fixation of the pattern by

constraints is likely, because even here most sclerites and many muscles can be homologised (compare WITTE & OLOMSKI in press).

Developmental preconditions

The evolution of calyptostatic proto- and tritonymphs, which took place in the stem lineage of the Parasitengonae, was probably a leading developmental precondition for the evolution of strongly heteromorphic ontogenetic instars in the Erythraeoidea.

Calyptostases seem to enable complex allometric changes of the gnathosoma and the associated muscles in the course of ontogeny, because the time for development of the mobile instars is greatly increased compared to mites which lack calyptostases. Histolytic processes and the differentiation of tissues and organs take place only in the course of metamorphosis of the larva to the calyptostatic protonymph and again when the deutonymph moults to the calyptostatic tritonymph. No histolysis, however, takes place during the subsequent development and final moulting to the deutonymph and adult respectively. Thus, the development of these instars may proceed during the whole previous calyptostatic periods (WITTE 1978). This was already detected by HENKING (1882) in *Allothrombium fuligonosum* and also described by ROBAUX (1974).

In addition, the lack of body openings in the calyptostatic instars probably provided increased protection for the developing mobile instars.

In contrast to the ontogenetic development of the gnathosoma, most internal organs, e.g. gonads, genital ducts, distal genital organs, brain and mid-gut, show fairly continuous development. They undergo no histolysis even during the metamorphose phases. Such histolyses were assumed by GRANDJEAN (1957). However, in erythraeids (*Charletonia cardinalis*), several cells of the ventricle-epithelium are shed and replaced by new ones at the beginning of the calyptostatic phases, when an intense mitotic activity may be observed (unpublished).

Organismal preconditions and predisposing properties in the course of evolution

In an evolutionary sequence of change, transformation steps may be strongly predisposed in regard to structure or function by previously evolved structural properties, and a pathway of evolutionary change may be canalised (ROTH & WAKE 1985; WITTE & DÖRING in press). Previously evolved organismal properties in the evolution of smaridid organization , have obviously

enabled or predisposed subsequent transformation steps in the following ways.

- As structural precondition for subsequent adaptive transformations. E.g. the loss of articulation of the chelicerae with the sigmoid pieces was the structural precondition for the evolution of widely protractable chelicerae.
- The course of adaptive transformation of structures was in particular cases strongly correlated with the transformation of other structures for structural and functional reasons. E.g. the evolution of widely protractable styliform chelicerae obviously was correlated with the evolutionary elongation of the cheliceral sheath, the pro- and retractor muscles of the chelicerae and the cervix.
- Newly evolved structures have induced, in particular cases, the development of new selection pressures, which in turn have mediated adaptive transformations. The evolution of styliform chelicerae and of an elongated cervix obviously engendered a trade off with the reduced protection of the salivary pathway along the cervix. This, in turn, probably produced selective pressure for compensatory protective structures, which has mediated the evolution of a salivary groove in the stem lineage of Calyptostomatoidea and Erythraeoidea (WITTE 1995), and which has mediated the evolution of an internal cervical canal in the stem lineage of the Erythraeoidea.

If I refer again to the sequence of change in the evolution of the smaridid gnathosoma, it may be assumed that it was canalised by organismal properties in the following way. The loss of the articulation of the cheliceral shafts with the sigmoid pieces in the common stem of Calyptostomatoidea and Erythraeoidea was most likely the precondition for the evolutionary change to directly acting cheliceral protraction muscles, and this, in turn, has probably opened the evolutionary window for the development of widely protractable styliform chelicerae. The process of step-wise elongation of the styliform chelicerae, moreover, was probably correlated with the evolution of elongated cheliceral muscles and an elongated cervix. This, finally, has probably induced a selective pressure, which has mediated the evolution of an internal cervical canal in which the chelicerae became effectively guided and in which the pathway of salivary secretions became efficiently protected.

The evolution of widely protractable styliform chelicerae, moreover, has probably favoured the selection for an intercheliceral canal, which evolved in the common stem lineage of the Calyptostomatoidea and the Erythraeoidea. This canal, in turn, has probably predisposed the evolution of longitudinal dovetailing along the middle of the chelicerae of Erythraeoidea, which prevents vertical shifting of the chelicerae relatively to each other. Thus, both

chelicerae have become a functional whole, and the safe transport of salivary secretions and liquid food in the intercheliceral canal is assured.

Summary

In the present paper the structural organization of gnathosoma, female genital organs and male genital system of smaridid mites is described.

The pattern of cuticular structures, muscles and glands of these organ systems is quite similar to that of Erythraeidae. Moreover, the basic structural pattern of these organ systems can still be homologised with the relatively ancestral organization of earlier deviated Parasitengonae, e.g. Hydrachnidia and Trombidioidea. This is remarkable particularly in regard to the gnathosoma, because it has undergone in the course of evolution considerable changes in regard to function, general organization and allometric properties. Styliform, widely protactable chelicerae evolved as early as in the common stem-lineage of Calyptostomatoidea and Erythraeoidea. Thereafter, in the stem-lineage of the Erythraeoidea, the styliform chelicerae became effectively guided in an internal cervical canal. This canal evolved by fusion of the lateral keels above of the chelicerae. The pathway of salivary secretions along the cervix to the mouth opening became efficiently protected due to this internalisation of the dorsal surface of the infracapitulum.

The various body openings of the Smarididae are protected against adverse external influences by lipidaceous secretions produced by glands or glandular epithelia, much as in other Parasitengonae.

The armilla, which allows complete retraction of the gnathosoma into the idiosoma, possibly evolved as an adaptation to prevent mechanical injury to the gnathosoma.

The discussion is concerned with how in the course of evolution the functional character and sequence of the chief transformation steps were controlled by organismal properties and mechanisms. To these belong development via calyptostases, which probably allowed the evolution of strongly heteromorphic active instars, constraints of interaction, which rigidly fixed ancestral character patterns, and newly evolved structural or functional characters, which enabled or predisposed particular, subsequent transformation steps.

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Abbreviations of figures

Gnathosoma

AM	articulation membrane
arm.	armilla
AS	arcal sclerite
asp.G	aspidosomal gland
b.c.	buccal cavity
BG	buccal gland
Ch	chelicera
Cm	crista metopica
CvC	cervical canal
CvS	cervical sclerite
Cx I	coxa I
Cx II	coxa II
d.PG	duct of pharyngeal gland
dil.phar.	dilator of pharynx
flex.phar.	flexor of pharynx
ic.C	intercheliceral canal
l.L	lateral lips
La	labrum
Lcr	latero-coxal region of pedipalp, posterior elongation
LP	lateral phragma
Oe	oesophagus
PG	pharyngeal gland
Ph	pharynx
Pp	pedipalpus
protr.cap.1	dorsal protractor of gnathosoma
protr.cap.2	ventral protractor of gnathosoma
protr.chel.1	short protractor of chelicera
protr.chel.2	elongated protractor of chelicera
Pt	peritreme
retr.cap.1	posterior retractor of gnathosoma
retr.cap.2	anterior retractor of gnathosoma
retr.cap.3, d.	ventral retractor of gnathosoma, dorsal ramus
retr.cap.3, v.	ventral retractor of gnathosoma, ventral ramus
retr.chel.1	anterior retractor of chelicera
retr.chel.2	posterior retractor of chelicera
retr.chel.3	intrinsic retractor of chelicera
SaG	salivary groove
Tb	trichobothrium
Tr	tracheal trunk
TvP	transversal phragma

Female genital organs

cu.S	cuticular strengthening
dG	dorsal accessory gland
di.G	distal accessory gland
e.p.	egg-pouch
ec	egg cell

g.p.	genital papilla
lG	vaginal lipid gland
Mu	muscle cells
n.c.	nurse cell
Ov	ovary
pO	paired oviduct
pr.l.	progenital lips
pr.p.	progenital pouch
R.s.	receptaculum seminis
uO	unpaired oviduct
V	vagina

Male genital organs

alv.gen.pap.	alveolarous genital papillae
AmdScl	anteromedial sclerite
ant.acc.gl.	anterior accessory gland
ant.org.membr.	anterior organa membranoidea
AntCmb	anterior chamber
AntKl	anterior keel
AntPrj	anterior projection
Apd	apodeme
CentCmb	central chamber
cu.S.	cuticular strengthening
DisSc	distal sclerite
eu.l.	eugenital lips
Frc	furca
Gen 1 - Gen 6	extrinsic genital muscles of male
HypApd	hypapodeme
lat.acc.gl.	lateral accessory gland
LatCmb	lateral chamber
LatPrj	lateral projection
M1 - M13	intrinsic genital muscles of male
mC	mucous cells
MdScl	medial sclerit
Opc	operculum
PosKl	posterior keel
post.org.membr.	posterior organa membranoidea
pr.l.	progenital lips
PrgCmb	progenital chamber
PrxCmb	proximal chamber
PrxCmbScl	proximal chamber sclerite
Ventr. 7	anterior extrinsic genital muscle of male

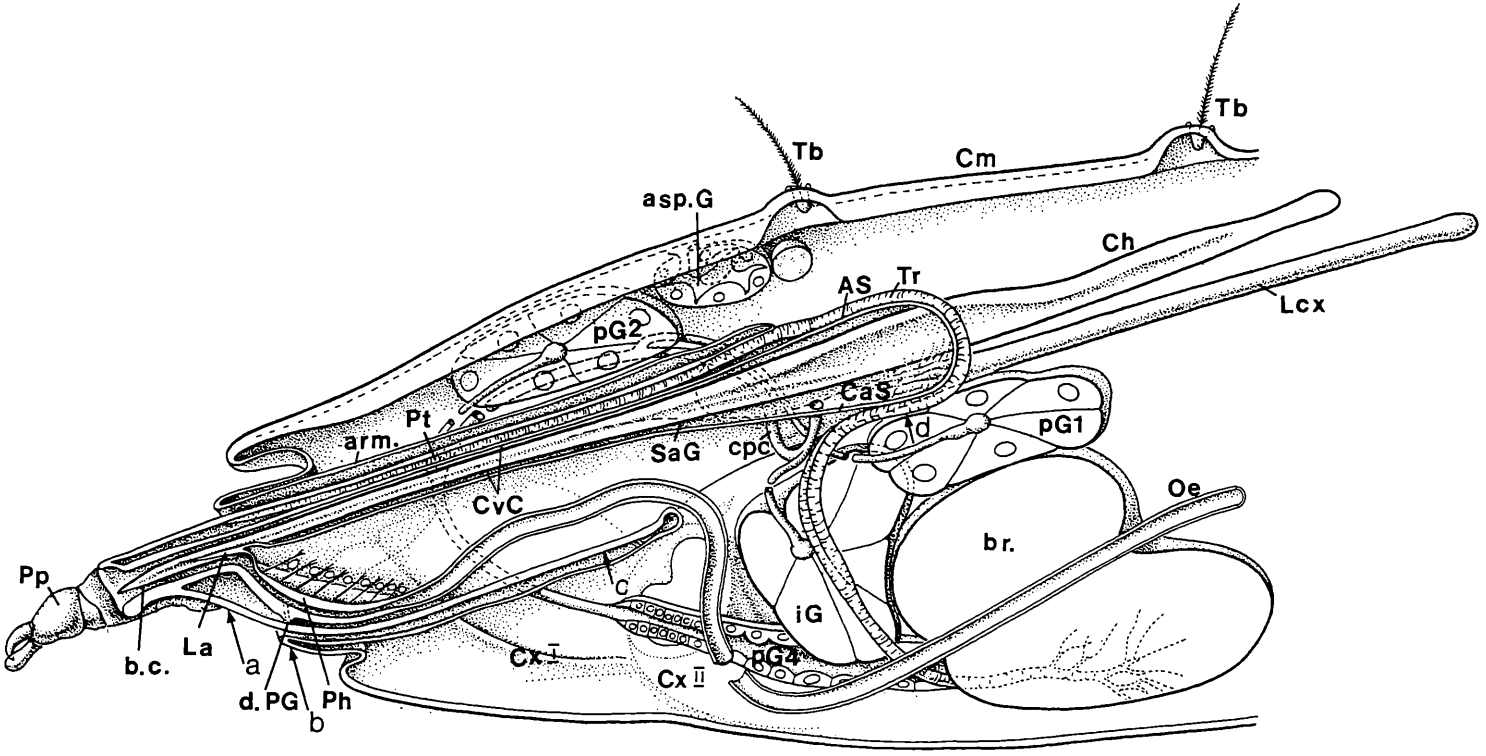


Fig. 1: *Fessonia callitricha*. Median sagittal section of gnathosoma and prosoma showing glands and cuticular structures.

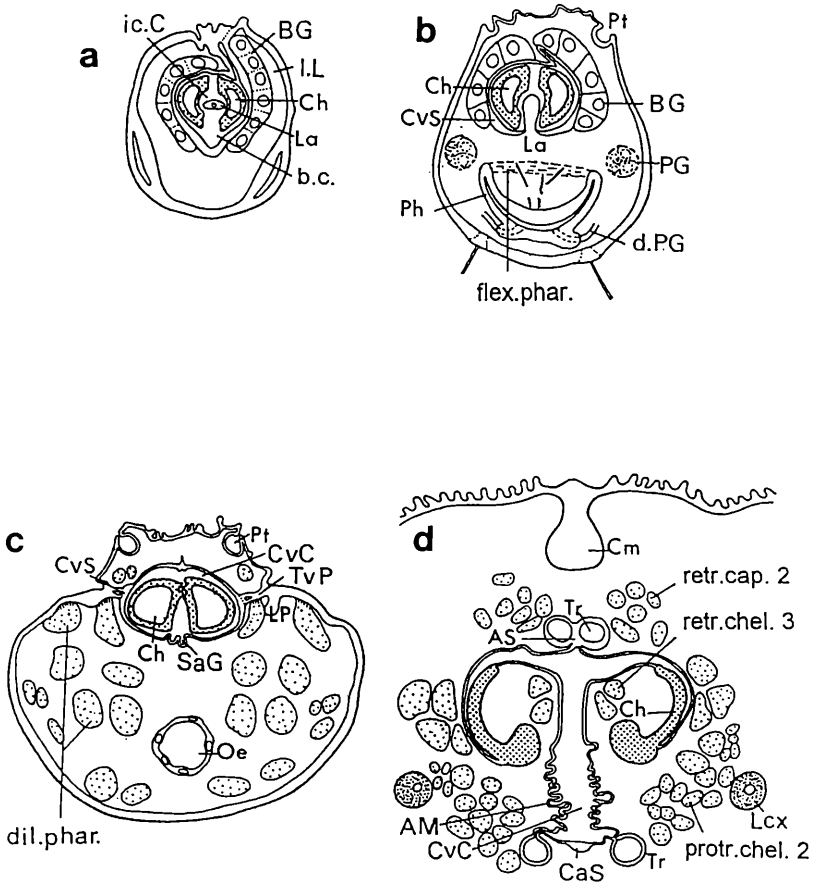


Fig. 2: *Fessonia callitricha*. Cross sections of gnathosoma at the levels indicated by arrows in Fig. 1.

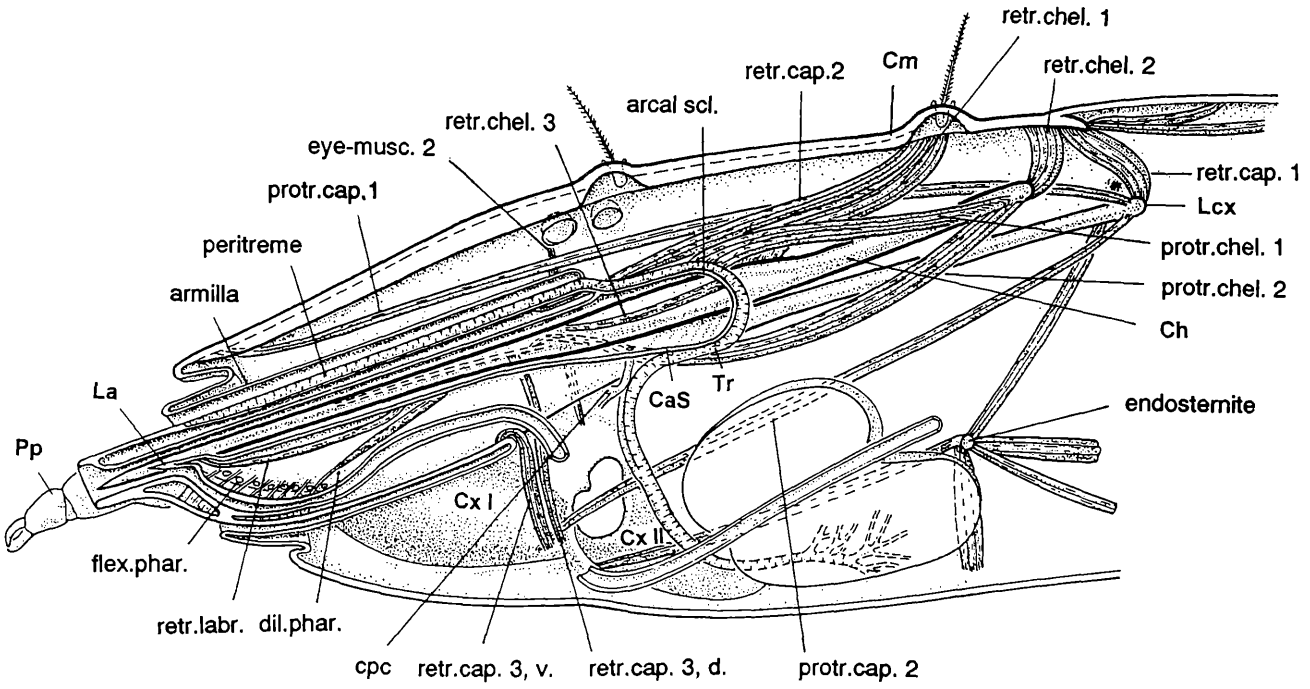


Fig. 3: *Fessonia callitricha*. Median sagittal section of gnathosoma and prosoma showing intrinsic and extrinsic muscles.

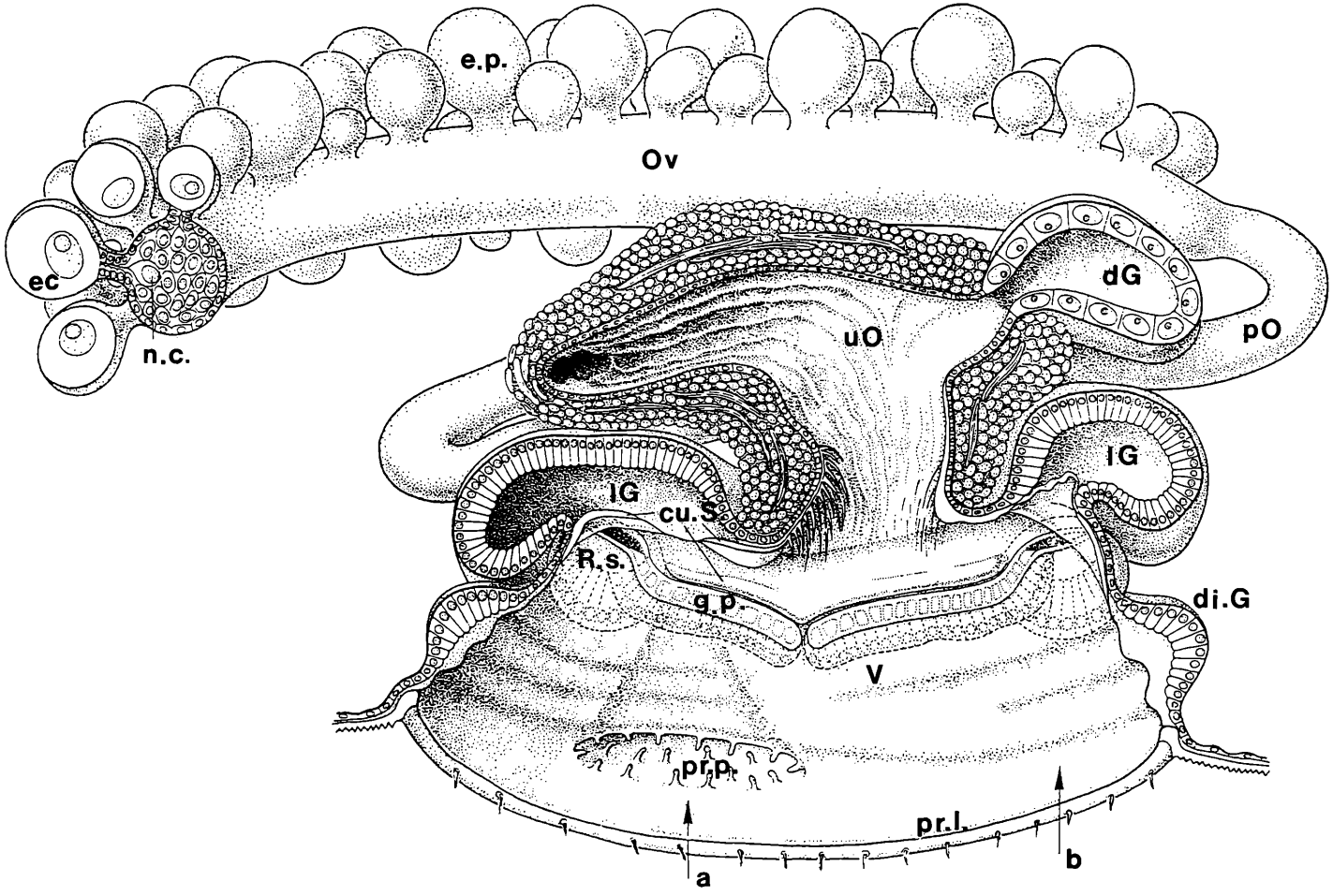


Fig. 4: *Fessonia callitricha*. Median sagittal section of the female genital system.

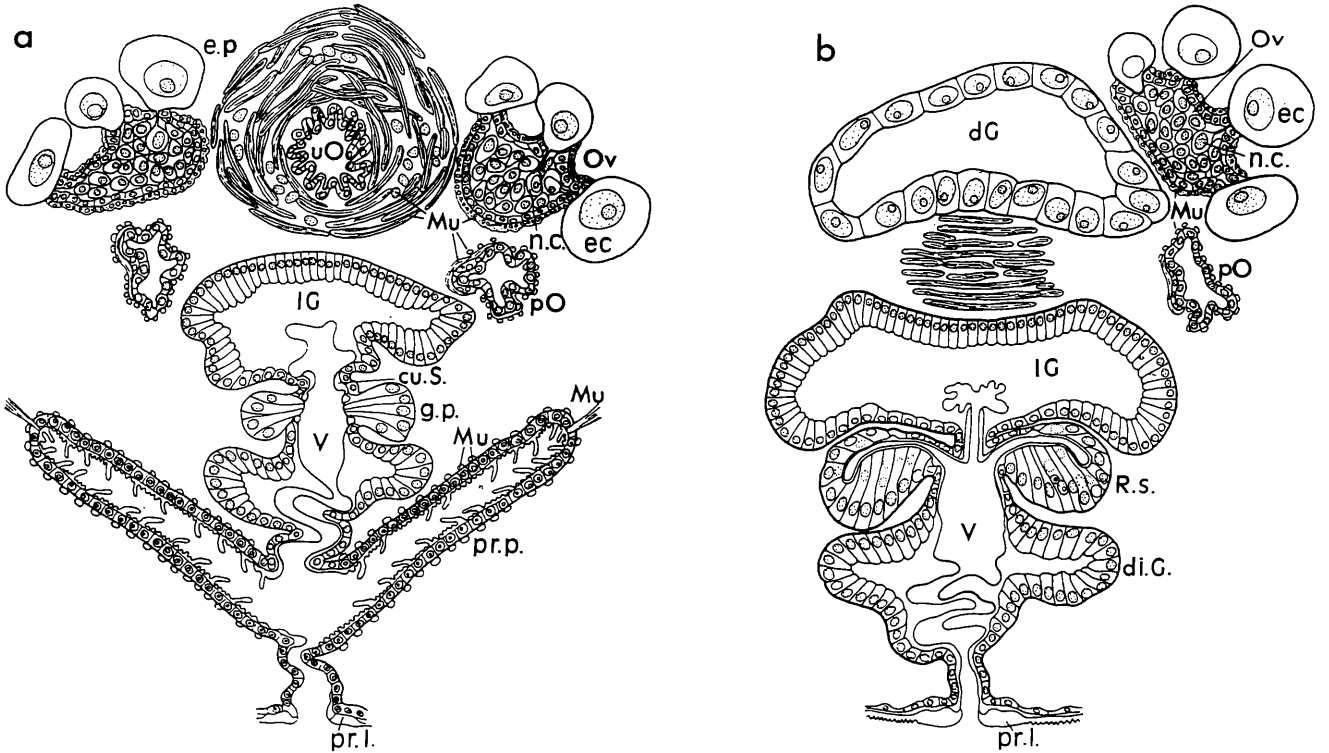


Fig. 5: Cross sections of the female genital system at the levels indicated by arrows in Fig. 4.

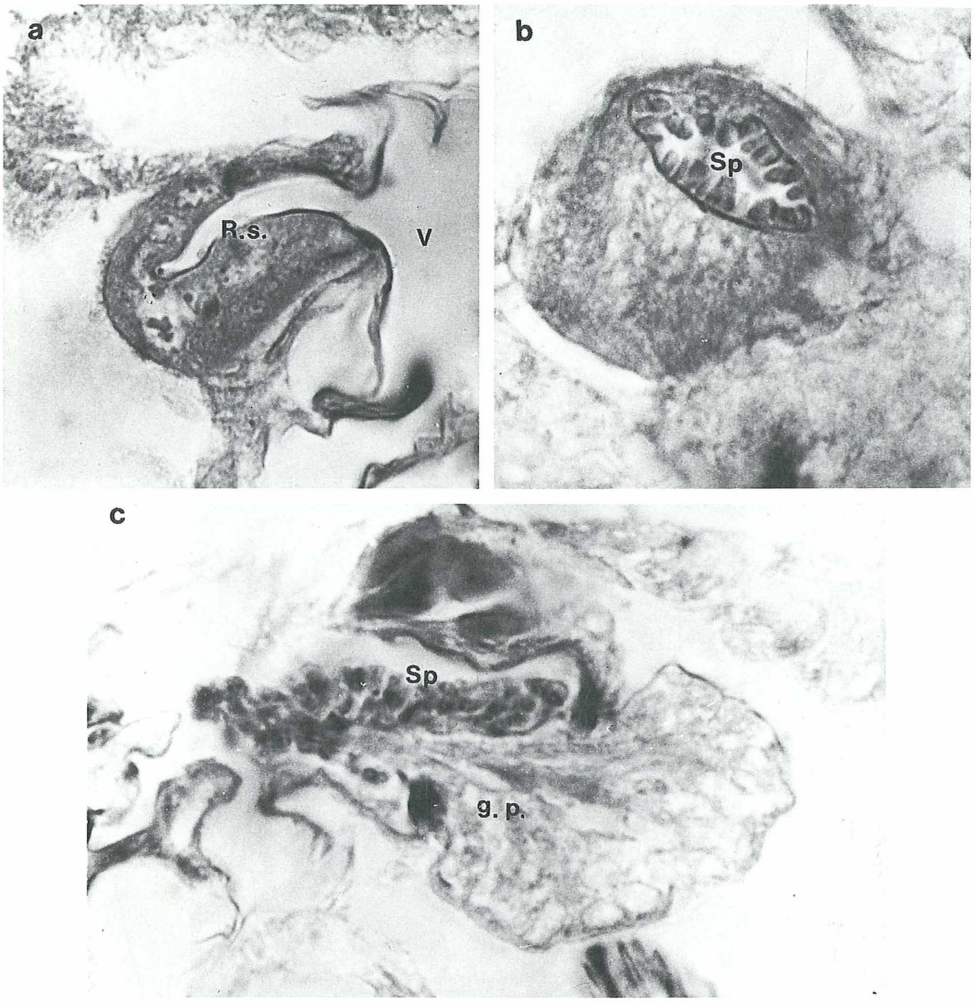


Fig. 6: Seminal receptacles in female Smarididae. a, *Fessonia callitricha*, cross section of the distal genital tract showing receptaculum seminis located in alveolareous part of the genital papillae. b, *Fessonia callitricha*, sagittal section of a receptaculum seminis showing numerous sperm cells in close contact to the surface of the receptaculum. c, *Hirstiosoma* sp. cross section of a genital papilla showing sperm cells densely arranged on the surface of the organ.

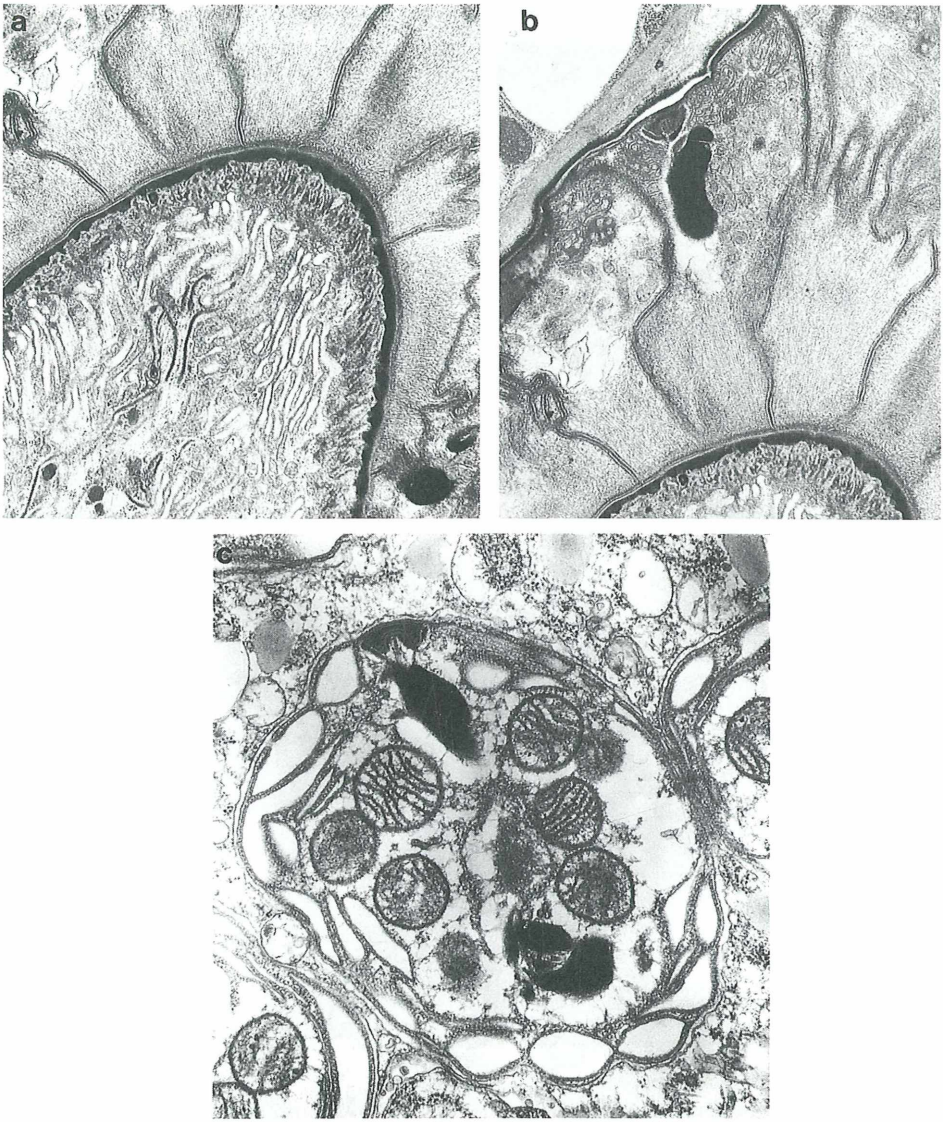


Fig. 7: a, *Hirstiosoma* sp., apical region of cells of a female genital papilla and layer of capacitating sperm cells. b, *Hirstiosoma* sp., capacitating sperm cells on the surface of a genital papilla of the female. c, *Hirstiosoma* sp., non-capacitated sperm cell in the germinal part of testis.

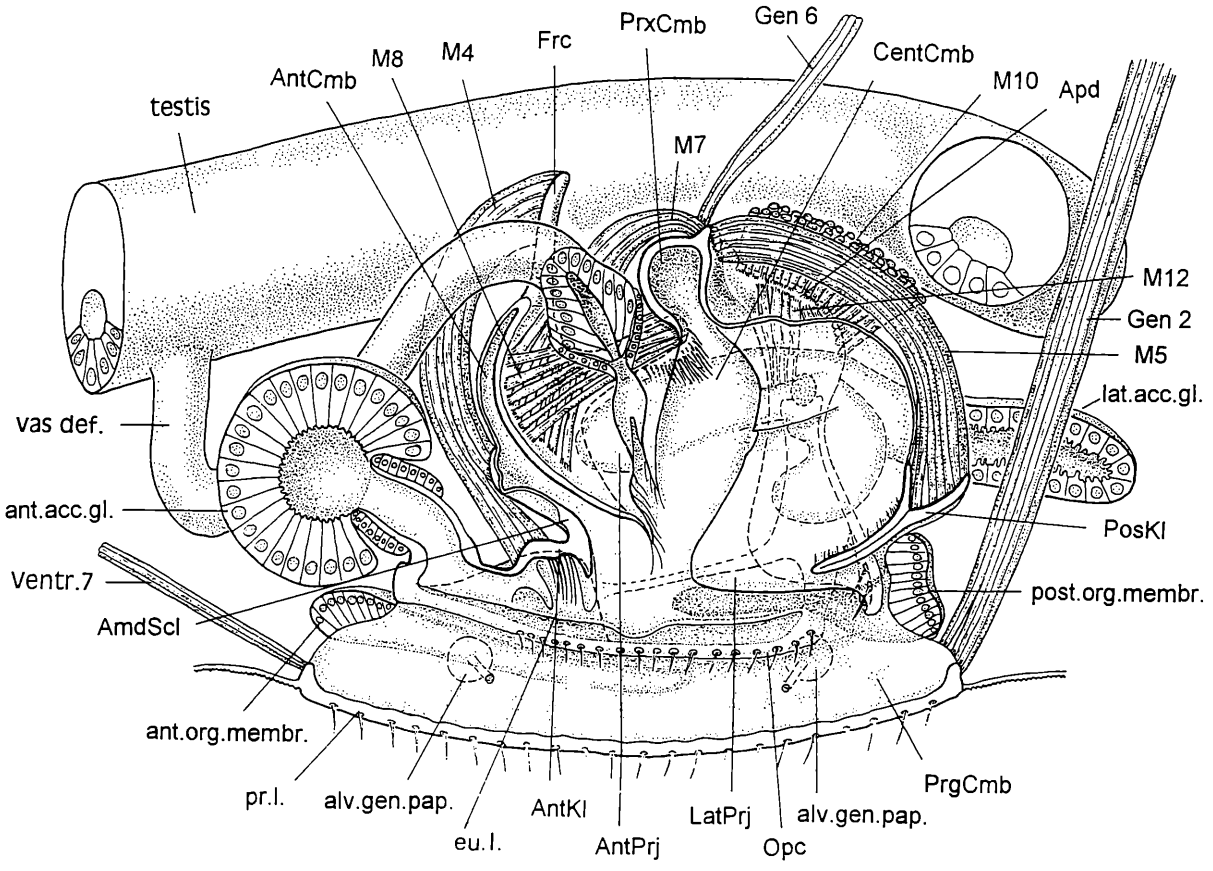


Fig. 8: *Fessonia callitricha.* Median sagittal section of the male genital system showing, in particular, spatial structures, accessory organs, muscles and sclerites of the ejaculatory complex.

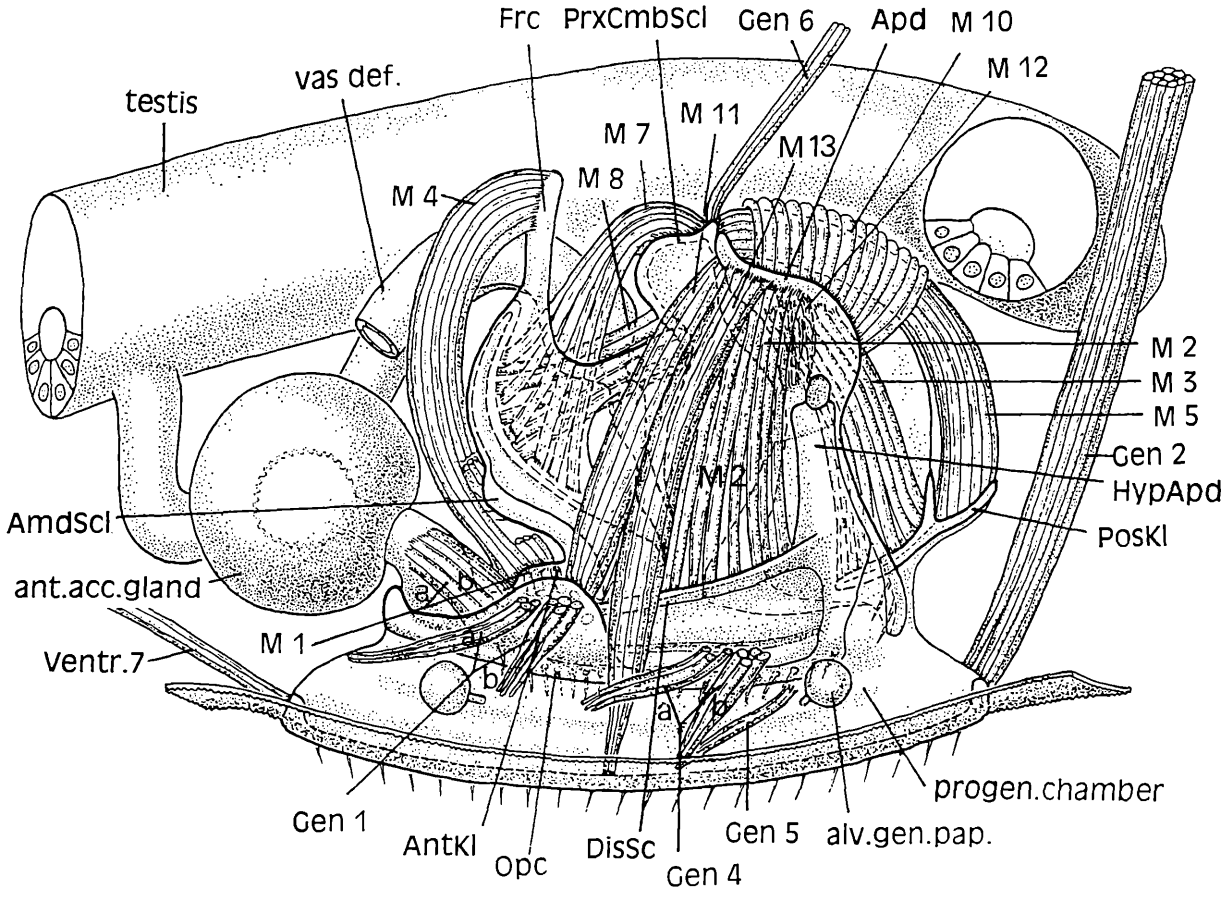


Fig. 9: *Fessonia callitricha.* Lateral aspect of the male genital system showing intrinsic and extrinsic muscles and sclerites of the ejaculatory complex.

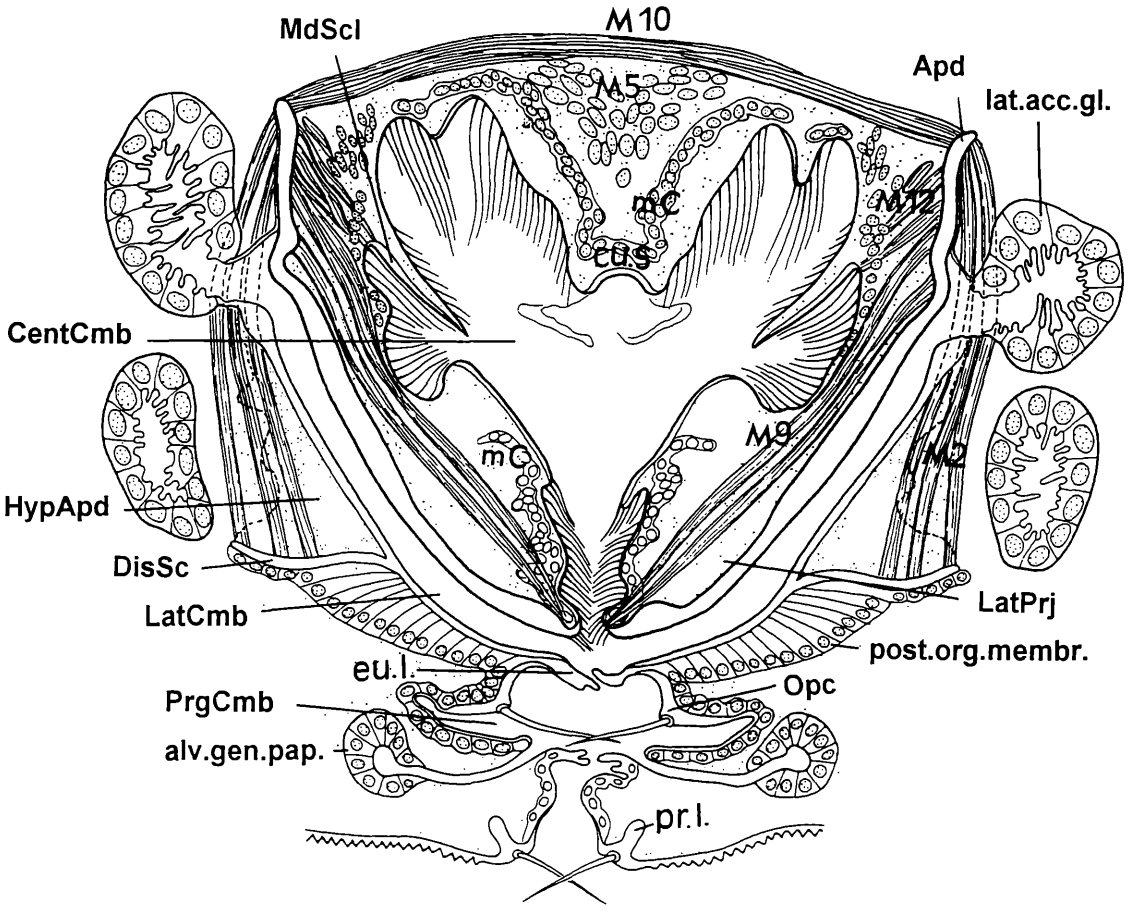


Fig. 10: *Fessonia callitricha.* Cross section of the ejaculatory complex at the level of the posterior alveolareous genital papillae.

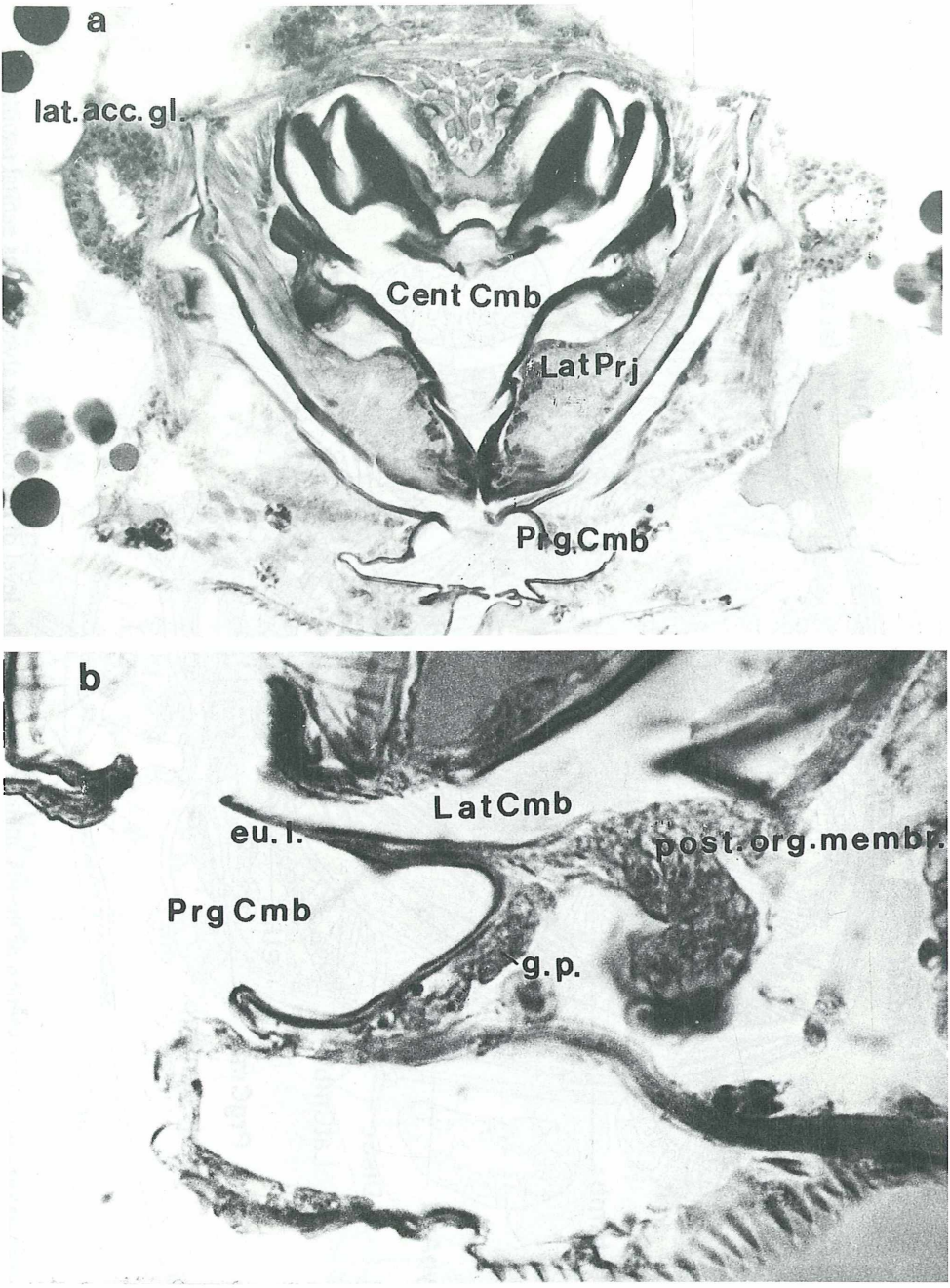
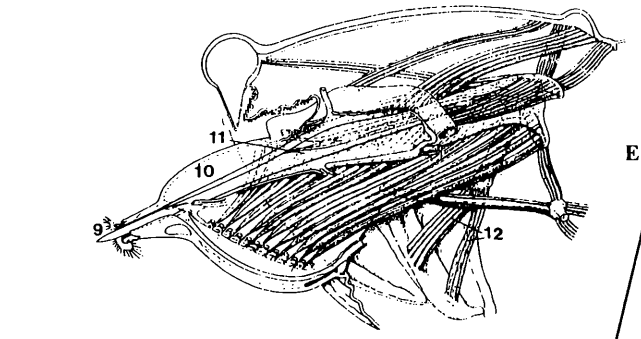
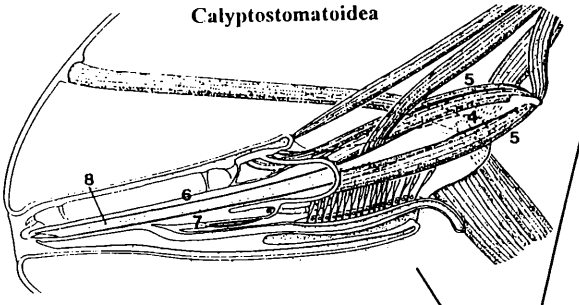


Fig. 11: a, *Fessonia callitricha*, cross section of the male ejaculatory complex at the level of the lateral projections. b, *Hirstiosoma* sp., cross section of the distal male genital organs showing their posterior organa membranoidea and a genital papilla (for explanation, compare text).



Erythraeoidea

Calyptostomatoidea



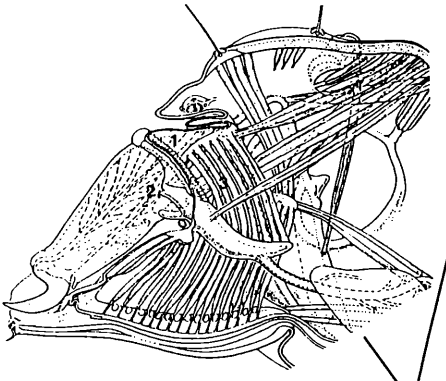
loss of digitus mobilis of styliform chelicera (9)

internalization of dorsal surface of gnathosoma (protection of salivary pathway, guiding of chelicerae) (10)

chelicerae with longitudinal dovetailing (11)

capitulum protractor 2 (12)

Trombidioidea



elongated styliform chelicerae (4)

direct protraction of chelicerae (protractor muscles 1 and 2) (5)

elongation of cervix (guiding of chelicerae) (6)

salivary groove (protection of pathway of salivary secretions) (7)

intercheliceral canal (8)

posteriorly elongated cheliceral shafts (1)

articulation of chelicera with sigmoid piece (2)

indirect protraction of chelicerae (cheliceral protractor 1) (3)

Fig. 12: Main adaptive transformations in evolution of the erythraeoid gnathosoma. The figured species are *Johnstoniana ventripilosa* (Trombidioidea), *Calyptostoma velutinus* (Calyptostomatoidea) and *Erythraeus regalis* (Erythraeoidea). Characters are indicated by numbers.