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Review paper

The coevolution of genitalia in Diplopoda Eugnatha

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Summary. The genitalia of Diplopoda, subterclass Eugnatha, are characterised by a remarkably high degree of functional-morphological disparity. The differences between major taxa concern not only a rather superficial 'ornamentation', such as the shape, proportion and number of certain parts, but there are also substantial disparities in the fundamental functional morphology and in the configuration of female and male structures in relation to each other. The evolutionary pathways and selective mechanisms that led to this disparity remain poorly understood. Here, a brief narrative review on the genital mechanics in Eugnatha is provided and differences between major groups are illustrated using simplified diagrams of individual species. Two contrasting hypotheses regarding the genital mechanics of the last common ancestor of Eugnatha are presented. The "telopodite" hypothesis assumes that this ancestor had already fully differentiated the eighth pair of male legs into gonopods, and that it would have transferred sperm with the modified telopodite of these gonopods. In contrast, the "coxal sac" hypothesis assumes that the ancestor would have transferred sperm using the coxal organs of nearly unmodified walking legs. It is currently unclear which of the two narratives is more likely to be true. A comparative approach highlights a particularly striking evolutionary trend, namely a mutual fitting between male and female structures that is made possible by female cooperative structures, complementary to male structures. Female and male structures together stabilise the mutual genital entanglement and increase the chances of successful sperm transfer.

Keywords: cryptic female choice, female cooperative structures, genital mechanics, gonopods, Helminthomorpha, lock and key, receptaculum seminis.

INTRODUCTION

The male secondary genitalia of Diplopoda, subterclass Eugnatha, the gonopods, are located on the seventh body ring. In addition, legs on the sixth or eighth ring may be also modified in some groups. Although the gonopods are modified limbs, they bear almost no resemblance to walking legs (Latzel 1884). As is often the case with genital structures (Eberhard 1985, 1996, 2010), they display an extravagance of forms that could well be described as bizarre for many groups (Verhoeff 1928; Brolemann 1935). Their primary function is, however, rather simple: they receive sperm from the male gonopores which are either on the coxae of leg pair 2 or on the so-called penis behind leg pair 2, and transport it to the openings of the female receptacula seminis located on the paired vulvae (Koch 2015). In Chordeumatida, however, this occurs via a detour, with sperm being temporarily stored in the coxal sacs of the eighth trunk ring (leg pairs 10 and 11) before being transferred to the gonopods (Verhoeff 1928). The vulvae, situated on the third body ring, behind the second pair of legs, are complex ectodermal structures that function not only as copulatory organs, but also ensure the more or less precise deposition of eggs (Brölemann and Lichtenstein 1919; Minelli and Michalik 2015).

Since the seminal works of Wood (1865) and Latzel (1884), the gonopods of Eugnatha have been exploited for taxonomy. In contrast, comparatively little is known about

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the functional morphology and the interaction between male and female structures. But what can already be concluded from the scattered data available so far (see below) is that the interaction between vulvae and gonopods shows an impressively high degree of functional morphological disparity. The term disparity relates here to the fact that the differences between the various groups cannot be seen as variations of a single principle with variations in a kind of "superficial ornamentation". As shown below, the differences between groups often affect the basic mode of operation of the genitalic interaction, and are so pronounced that one could even speak of several different ground plans of genital interaction. This is particularly remarkable given that these animals may have changed comparatively little in terms of their general body structure, lifestyle and ecology since the Palaeozoic era (Edgecombe 2015).

The first goal of this contribution is to illustrate the spectrum of the disparity of eugnathan genital mechanics (i.e. the mechanical correlation between male and female genitalia during copulation). Completeness is thereby not a goal. The aim is to make selected works from different periods and different authors accessible for comparative analysis by presenting them in a simplified and hopefully consistent form.

This leads to the question of to what extent do the genital mechanics of different eugnathan lineages share a common pattern. Did the last common ancestor of Eugnatha already possess significantly modified gonopods which may be identified as a "common denominator" in extant groups? Or did the ancestor still have "protogonopods" similar to walking legs? Although these questions seem far from being solvable at present, in the hope of stimulating further reflection, the corresponding hypotheses are presented and illustrated. In addition, a major trend in the evolution of eugnathan genitalia, i.e., the formation of female cooperative structures, is briefly discussed.

The comparative interpretation of some otherwise promising studies in this field is sometimes complicated by the fact that there is no generally accepted nomenclature for the components of the vulvae in English. Furthermore, excellent older works in languages other than English (in particular Brölemann and Lichtenstein 1919) are sometimes not considered. This is particularly regrettable since recent authors often have access to methods such as μ-CT imaging, which appear to be predestined for such investigations. In order to facilitate the understanding of the following elaborations, an attempt to depict a simplified ground plan and a corresponding nomenclature of the vulvae is given below. However, this must be regarded as a preliminary approach, further comparative investigations and a broader consensus would be beneficial.

METHODS

Diagrams were drawn using the Inkscape (vers. 1.2) vector drawing editor. To designate a specific pair of legs, the number of the body ring is given followed by the leg pair. Thus, leg 7/1 corresponds to the first pair of legs of the seventh body ring, which is leg pair number eight, and is also called „anterior gonopods" in adult eugnathan males.

A GENERALISED DIAGRAM OF THE EUGNATHAN VULVAE

This description is based on Brölemann and Lichtenstein (1919), who refer to the vulvae as ectodermal differentiations that surround the female genital openings. The labelling of the individual parts follows Kurnik (1988), Tadler (1993, 1996), Koch (2015) and Zahnle et al. (2020). The hypothesis developed by Verhoeff (1909, 1928), according to which both diplopodan vulvae and penes are modified limbs ('cyphopods'), is not addressed here. Internal structures of the vulva such as glands are also not considered.

The paired oviducts open behind the coxae of the second pair of legs. The vulvae are built of evaginations and bulges of the integument surrounding these openings. Each vulva (Fig. 1) consists of (1) the bursa, an approximately bulbous evagination behind the oviduct opening, (2) the operculum, a kind of closing lid in front of the opening, and (3) the base that connects these two parts to the surrounding integument of the vulval sac. On the bursa the following sections can be distinguished: the side walls are formed by the two approximately shell-like valves, which are conveniently referred to as the inner and outer valve. Between the valves lies the central area [= cimier sensu Brölemann and Lichtenstein (1919), ventral membrane sensu Zahnle et al. (2020)]. The central area is divided into two halves by the longitudinnally running apodematic groove [= gouttière apodematique sensu Brölemann and Lichtenstein (1919)]. The valve muscles run from the internal face of the apodematic groove to the internal surfaces of the valves. The external face of the apodematic groove forms a covered channel, into which the receptacula seminis open. The receptacula are invaginations of the integument, their number and shape vary greatly among the different groups.

The margin bulge is a thickening of the integument of the bursa located at the border of the oviduct opening. It is divided into two approximately equal halves by a narrow slit. Together with a corresponding thickening on the operculum located in front of the oviduct opening, the margin bulge forms the closing mechanism of the oviduct referred to as "fourches" by Brölemann and Lichtenstein (1919).

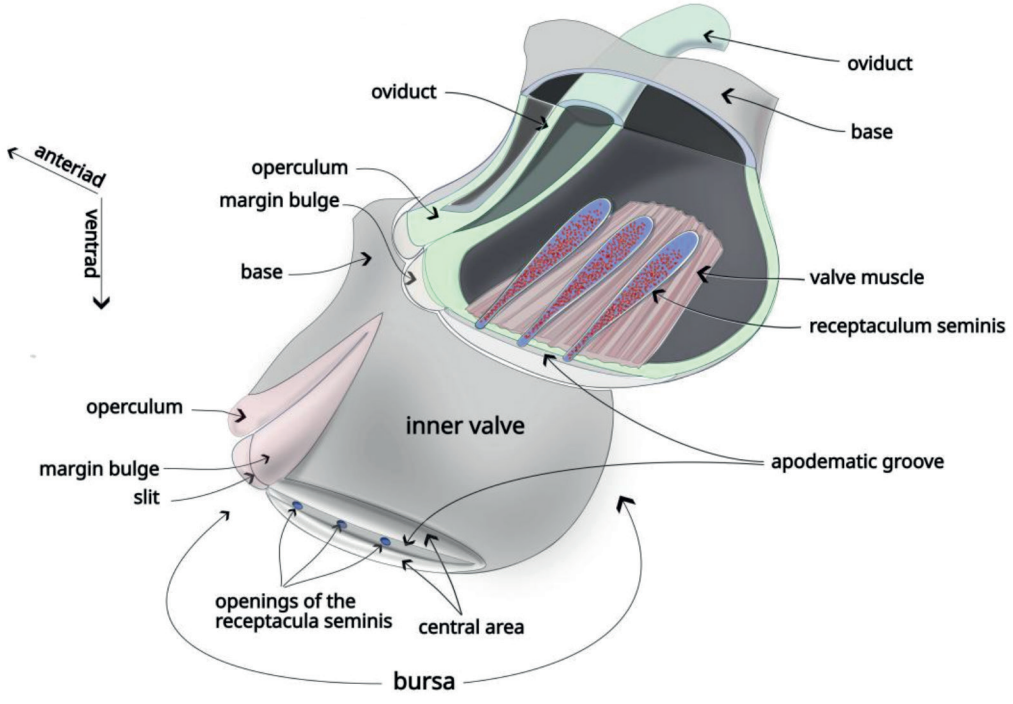

Fig. 1. Generalised diagram of the vulvae of Eugnatha. View from the side and below. The vulval sac is not shown. Left vulva cut open along the apodematic groove. Explanation in text.

GENITAL MECHANICS OF SELECTED DIPLOPODA EUGNATHA

Chordeumatida

A characteristic feature of Chordeumatida is that in adult males, sperm is regularly found in the coxal sacs of the eighth ring. Verhoeff (1900a) therefore referred to this taxon as "Ascospermophora" (~ wineskin sperm carrier). It is assumed that sperm is first transferred from the gonopores to these coxal sacs and then to the gonopods (Verhoeff 1897a, 1910, 1928). The vulvae of female Chordeumatida are not recessed into the body but are freely accessible in shallow vulval sacs (Brolemann 1935).

Mastigophorophyllidae: *Haploporatia eremita* Verhoeff, 1909 and *Mastigona bosniensis* (Verhoeff, 1897) (Figs 2, 3). The main parts of the anterior gonopods (leg pair 7/1) are the slender and more or less backward-curved sickle leaves („Sichelblätter"), which were interpreted by Verhoeff (1897a, 1921, 1928) as telopodites. On the aboral side of each sickle leaf is a sperm canal running from the base to almost the tip. A flagellum inserts into the canal. This flagellum originates basally from a brace-like structure, interpreted by Verhoeff (1897a) as a coxite. The flagellum can apparently be moved up and down by muscles attached to this basal structure. Other remarkable structures of the gonopods of the Mastigophorophyllidae, such as two nested pseudoflagella and the posterior gonopods, are not considered here, as their function is unknown.

The anterior gonopods of the two species presented here, *Haploporatia eremita* Verhoeff, 1909 (Fig. 2) and *Mastigona bosniensis* (Verhoeff, 1897) (Fig. 3) are similar in their ground plan. The functionally most significant differences exist in the shape of the sickle leaf. In *H. eremita*, this part is rather shorter and straighter and there are two approximately triangular projections just before the slender and curved distal end of the telopodite (Fig. 2B). In *M. bosniensis*, the sickle leaf is comparatively longer, curved backwards in a wide arc and flattened distally (Fig. 3B).

Although corresponding to the ground plan presented above, the vulvae show significant functional-morphological differences between these two species. In *H. eremita*, the margin bulge forms two structures similar in shape to the biblical 'tablets of the law' at the front of the bursa (Fig. 2A). The receptacula seminis open between these tablets. In copula sperm transfer is carried out by the aboral side of the tip of the sickle leaf, situated in front of the openings of the receptacula. This is stabilised by the triangular projections which are fitting into grooves between the margin bulge and the bursa (Tadler 1989).

In contrast, the margin bulge of the vulva of *M. bosniensis* is rather inconspicuous and slender, but the base of the vulva is strongly modified (Fig. 3A).

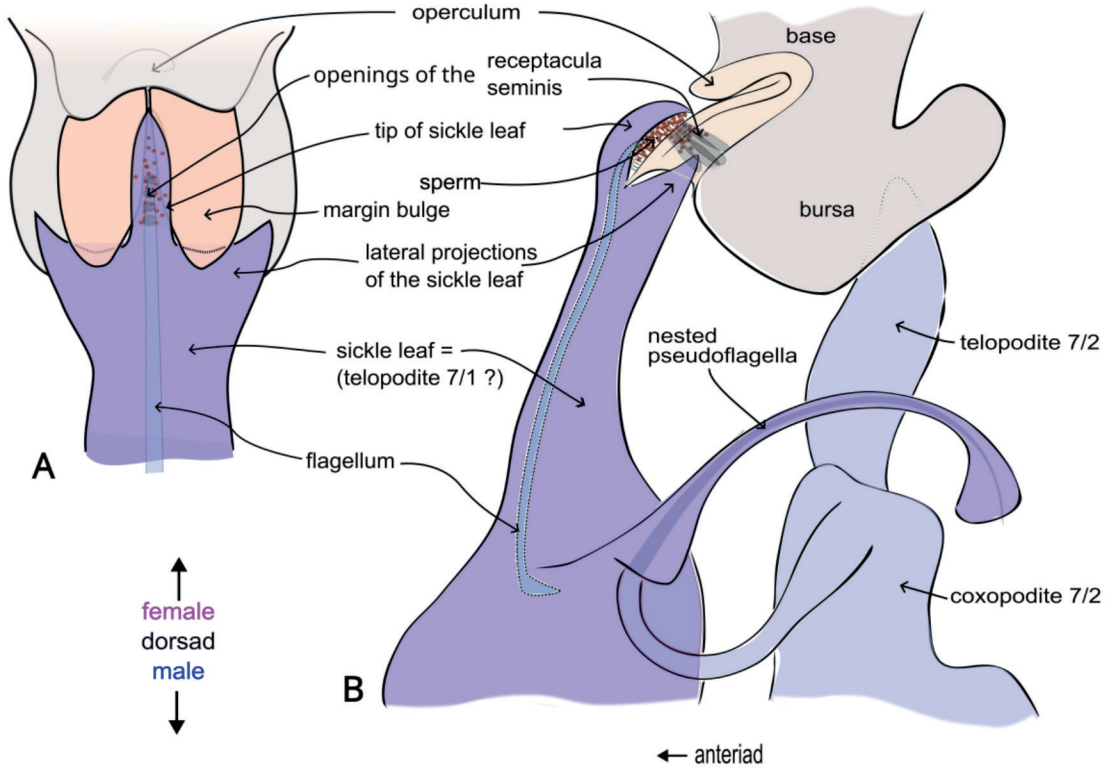

Fig. 2. Simplified diagram of the genital mechanics of *Haploporatia eremita* Verhoeff, 1909 (Chordeumatida, Mastigophorophyllidae). **A**, front view of vulva and distal part of telopodite. **B**, entangled genitalia, lateral view. Adapted from Tadler (1989). Male parts blue. Explanation in text.

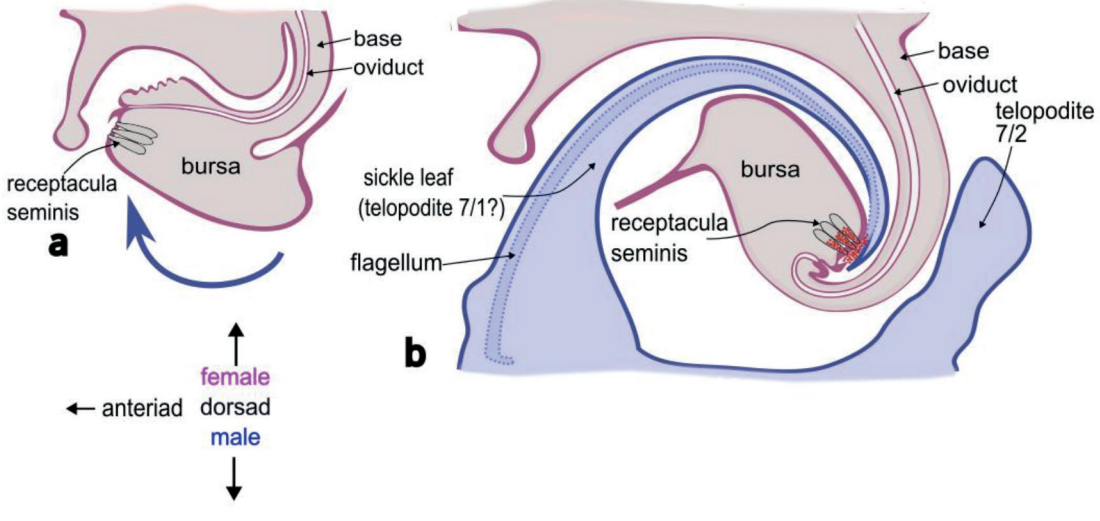

Fig. 3. Schematic longitudinal (parasagittal) section of the genital mechanics of *Mastigona bosniensis* (Verhoeff, 1897) (Chordeumatida, Mastigophorophyllidae). **A**, Vulva in resting position. The arrow indicates the rotation direction of the bursa in copula. **B**, Entangled genitalia. Adapted from Tadler (1989). Male parts blue. Explanation in text.

During copulation the bursa is rotated by more than 180 degrees around the transverse axis, and thereby together with the sickle leaf wrapped into its own base. The sperm transmitting distal part of the sickle leaf is pressed against the bursa so that the distal opening of the sperm canal with the tip of the flagellum is fixed against the central area (Tadler 1989).

Craspedosomatidae: *Craspedosoma raulinsii* Leach, 1816 (Fig. 4). Detailed descriptions of the gonopods of *Craspedosoma* Leach, 1816 can be found in Wernitzsch (1910), Verhoeff (1928) and Tadler (1993). Following the comparative anatomical considerations of Verhoeff (1900b, 1928), the telopodites of the leg pair 7/1 are fused with the tracheal pouches forming the so called cheirites ("Greifhaken" = clasping hooks). In *C. raulinsii* each cheirite is equipped with a dorsally and a ventrally directed projection. Between the cheirites lies the syncoxite, i.e. the fused and strongly modified coxopodites, which in turn form a fixed unit with the modified sternite. The syncoxite is jointedly connected to the cheirites, which are moved by particularly large muscles running from the tracheal pouches to the modified sternites.

At the posterior side of the syncoxite are invaginations ("sperm vesicles"), laterally on both sides are brush-like structures, and at the anterior side a pair of pseudoflagella. On the posterior gonopods (leg pair 7/2), the coxopodites are fused with the sternite building a uniform structure with six appendages, called podosternite. The telopodites of 7/2 have largely disappeared.

During copulation (Fig. 4), the bursa is lifted away from the operculum, the mouth of the oviduct is thereby opened wide, and the projections of the cheirite insert into corresponding pockets in the area of the oviduct mouth. The bursa is further stabilised by the outer anterior processes of the podosternite, which insert into corresponding grooves in the central area. Sperm is transferred to the openings of the receptacula seminis via the brush structures of the syncoxite.

Chordeumidae: *Chordeuma sylvestre* C. L. Koch, 1847. The gonopods of *Chordeuma sylvestre* C.L. Koch, 1847 belong to the most complex genitalia among all diplopods, in that modified legs from three body rings (6, 7, 8) are included. This may be related to the fact that males use them to produce elaborated cap-shaped secreted structures ["Kappenspermatophoren" sensu Verhoeff (1910)].

The copulation of *C. sylvestre* was described by Haacker (1971a, b). After a remarkable gustatory courtship, involving also drum beats with the male head, the anterior gonopods (leg pair 7/1) hook onto the front wall of the vulval pouch and pull it forward, creating a wide opening into which the posterior gonopods (leg pair 7/2) are inserted. The posterior gonopods then perform rhythmic movements within the vulval sac and withdraw after about 50 min. Thereafter sperm is transferred by the coxal sacs of the modified leg pair 8/2 ("hintere Nebengonopoden" = posterior paragonopods). How the secretion cups are applied still doesn't seem to be entirely clear. However, if the vulvae are covered by

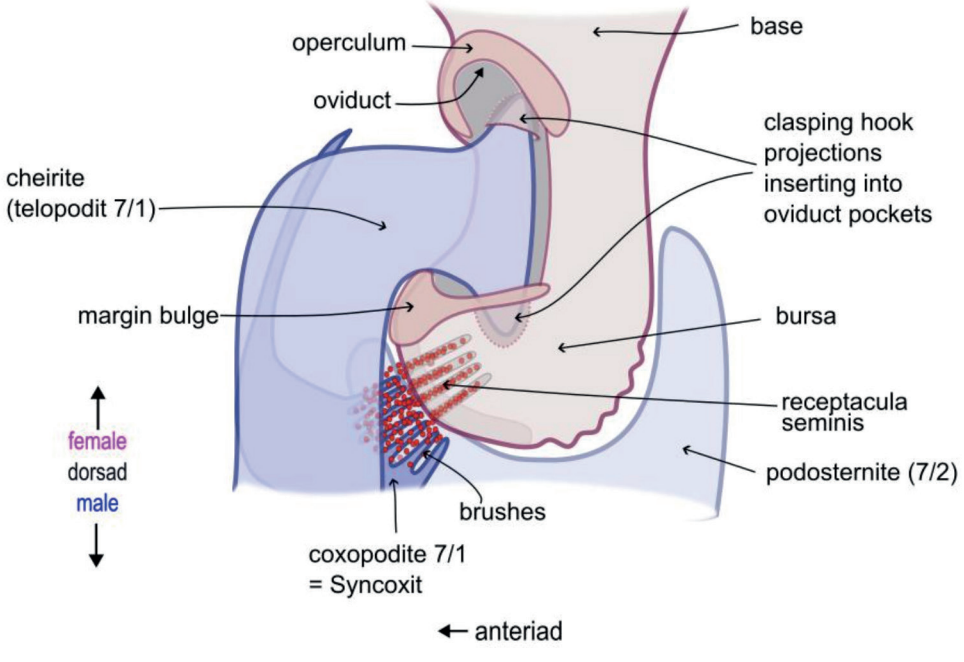

Fig. 4. Simplified diagram of the genital mechanics of *Craspedosoma raulinsii* Leach, 1816 (Chordeumatida, Craspedosomatidae). Lateral view. Sperm bubbles and pseudoflagella not shown. Adapted from Tadler (1993). Male parts blue. Explanation in text.

the secretion caps, further insertions of the gonopods are prevented (Haacker 1971b).

Polydesmida

Polydesmidae: *Acanthotarsius edentulus* (C.L. Koch, 1847) and *Pseudopolydesmus serratus (Say, 1821)* (Fig. 5). The following is based on the excellent descriptions of the genital mechanics of the European *Acanthotarsius edentulus* (C.L. Koch, 1847) by Seifert (1932) (sub *Polydesmus e.*) and the American *Pseudopolydesmus serratus* (Say, 1821) by Zahnle et al. (2020). The two species are quite similar in this respect and are therefore here presented together in a highly simplified form.

Only leg pair 7/1 of the males is transformed into gonopods. The gonopods consist of coxopodites and the clearly separated approximately hook-shaped telopodites. Each coxopodite is equipped with a cannula, a movable, horn-like structure which inserts into the funnel-shaped proximal end of the seminal canal of the telopodite. When at rest, the vulvae are largely recessed inside the body. In copula they are rotated around the transverse axis, thereby turned out of the vulval pouch [see Zahnle et al. (2020) for a detailed description of this rotation], so that the aboral side of the telopodite lies opposite the vulval central area with the opening of the receptacle. Between the telopodite of the gonopods and the central area of the vulva is a large secreted droplet from which the spermatozoa apparently may migrate into the receptaculum. In *P. serratus*, an extension of the telopodite (pulvillus) is inserted into the opening of the receptaculum in order to keep it open (Zahnle et al. 2020).

Paradoxosomatidae: *Antichiropus variabilis* Attems, 1911. Wojcieszek et al. (2012) used μ-CT equipment to examine the copulation mechanics of *A. variabilis* Attems, 1911. They show that almost the entire telopodite (7/1) is inserted "into the female", and claim that the solenomere 'inserts fully into the receptaculum'. However, this cannot be verified with certainty based on their illustrations. It seems possible that the structure labelled as 'receptaculum' is in fact the bursa + operculum and the part referred to as the 'vulva' would be the vulval sac. If so, the arched solenomere would probably fit onto the central area of the vulva, but would not penetrate the receptaculum itself.

Xystodesmidae: *Parafontaria* sp. Verhoeff, 1936. Tanabe and Sota (2008) report on the copulation mechanics of *Parafontaria* Verhoeff, 1936. The pig-tail-like curled distal part of the telopodite 7/1 is introduced into the vulval sac ("deep into the female genitalia"). Based on the illustrations given by Tanabe and Sota (2008) it seems that the telopodite is somehow wrapped around the bursa and the operculum ("the tibiotarsus and tibiotarsal process of the male gonopods coupled with the female valvae and receptacle"). Tanabe and Sota (2008) claim that the "tip of the tibiotarsus" (telopodite 7/1) is thereby "inserted into a slit of the valvae and receptacle which is the female genital opening". However, from Tanabe and Sota (2008: fig. 1), it seems most likely that the

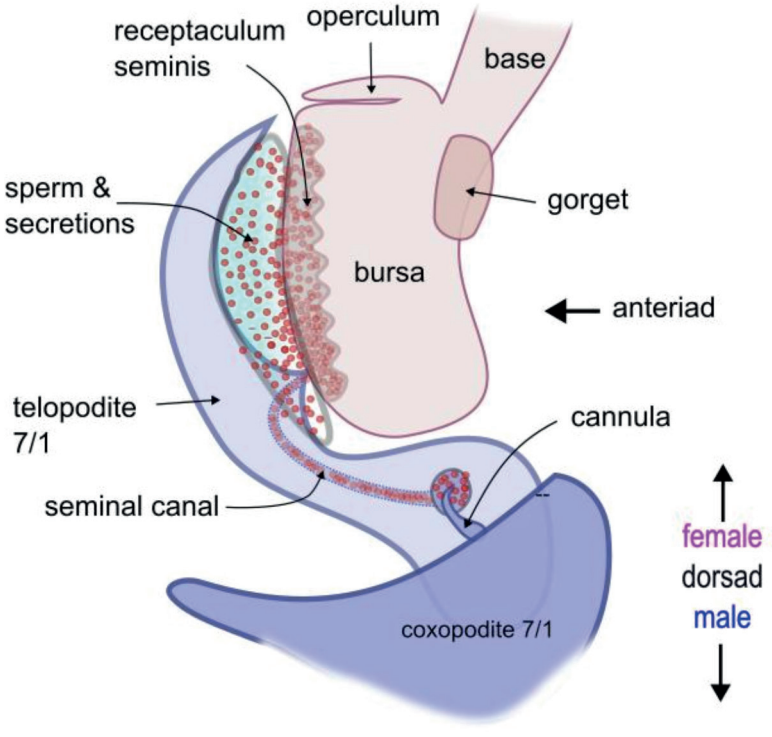

Fig. 5. Simplified diagram of the genital mechanics of *Acanthotarsius edentulus* (C.L. Koch, 1847) and *Pseudopolydesmus serratus* (Say, 1821) (Polydesmida, Polydesmidae). Lateral view. Adapted from Zahnle et al. (2020) and Seifert (1932). Male parts blue. Explanation in text.

structure labelled as "receptacle" is the operculum and the "genital opening" is the central area of the vulva. In this case, the topology of *Parafontaria*'s genital mechanics would correspond to the other examples presented above and below, where the aboral side of the telopodite faces the central area of the vulva.

Spirostreptidea

The gonopods of the Spirostreptidea correspond to the modified leg pair 7/1 (Brolemann 1920). The elongated telopodite, which in many species is intricately twisted and subdivided, is passed through by a sperm canal which ends on a solenomere. A projection formed by the coxopodite (stylet prostatique) protrudes into the proximal part of the canal (Démange 1959). Parts of the coxopodite form a tubular structure, into which the proximal sections of the telopodite are enclosed (Brolemann 1920; Barnett 1997; Brandt et al. 2024). On the vulvae, the central area forms a cleft-shaped depression, a "deep furrow" (Brandt et al. 2024) or "dépression très profonde" (Brölemann and Lichtenstein 1919). The openings of the receptacula are located at the bottom of this cleft (Brölemann and Lichtenstein 1919).

Spirostreptidae: *Archispirostreptus tumuliporus* (Karsch, 1881) (Fig. 6). The following greatly simplified description is based on Démange's (1959) paper on the copulation of *A. tumuliporus* (Karsch, 1881). The impressive complexity of spirostreptid genitalia is described in more detail in Barnett et al. (1993, 1995), Barnett and Telford (1994), Barnett (1997) and Brandt et al. (2024). In copula the vulvae remain located deep in the vulval sac and are rotated forward so that the opercula are approximately dorsal to the bursa. The gonopods are inserted into the vulval sac so that the solenomere is situated above the central area of the vulva (Démange 1959).

Julida

Nemasomatidae: *Nemasoma varicorne* C.L. Koch, 1847 (Fig. 7A); **Julidae: *Brachyiulus lusitanus* Verhoeff, 1898** (Fig. 7B); ***Cylindroiulus boleti* (C.L. Koch, 1847)** (Fig. 8B), ***Unciger transsilvanicus* (Verhoeff, 1899)** (Fig. 8A). The following descriptions and the corresponding illustrations are based on Haacker and Fuchs (1970) and Tadler (1996). The representatives of the Order Julida discussed here are opisthospermophorous, which means that the sperm is transferred by the posterior gonopods (leg pair 7/2). On the anterior gonopods (leg pair 7/1), the coxopodites are transformed into the so-called promerites. The main parts of the posterior gonopods are the opisthomerites. Flagella which can be moved due to muscles at their base arise from the proximal part of the promerite. These flagella insert into sperm canals on the opisthomerites.

Nemasoma varicorne C.L. Koch, 1847 has club-shaped telopodites on the anterior gonopods, whereas the telopodites of the anterior gonopods are reduced in the other three species. In *Cylindroiulus boleti* (C.L. Koch, 1847) and *Unciger transsilvanicus* (Verhoeff, 1899), a split-off part of the

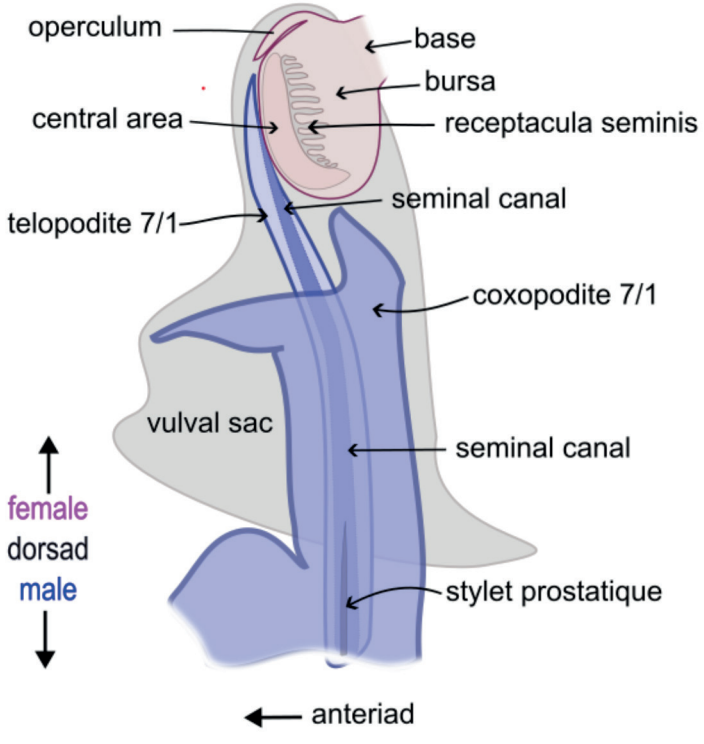

Fig. 6. Simplified diagram of the genital mechanics of *Archispirostreptus tumuliporus* (Karsch, 1881) (Spirostreptidae). Lateral view. Adapted from Démange (1959). Male parts blue. Explanation in text.

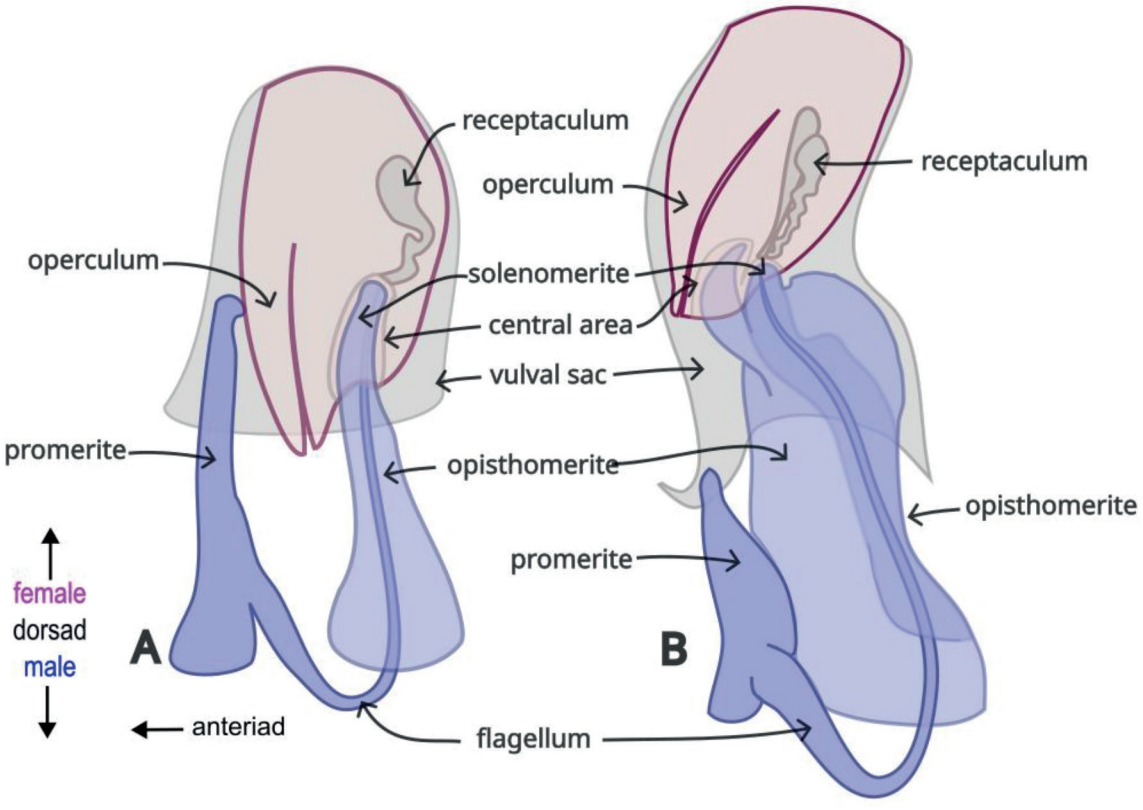

Fig. 7. Simplified diagram of the genital mechanics of **A**, *Nemasoma varicorne* C. L. Koch, 1847 (Nemasomatidae) and **B**, *Brachyiulus lusitanus* Verhoeff, 1898 (Julidae). Lateral view. Adapted from Tadler (1996). Male parts blue. Explanation in text.

posterior gonopods (7/2), the so-called mesomerite, forms together with the promerite a forceps-like structure. This forceps is powered by large muscles attached to tracheal pouches which are connected to the promerite and the mesomerite. The comparative anatomy of the meso- and opisthomerite, was discussed controversially by Verhoeff (1928) and Attems (1939), but still has not yet been satisfactorily clarified.

The vulvae of the julidan species presented here appear elongated in the dorsoventral direction and remain at rest deeply retracted into the body. In *N. varicorne* and *B. lusitanus*, the central area of the vulvae forms a funnel-like structure. During copulation, the vulvae of these species remain in their vulval sacs where the gonopods are inserted (Fig. 7). In both species the sperm-transferring projections of the opisthomerite (solenomerite) insert into the funnel-shaped central areas of the vulvae. In *B. lusitanus* an extension of the opisthomerite in front of the solenomerite contributes to the stabilisation of sperm transfer by being inserted into a slit formed by the central area. In *N. varicorne*, the long, slender promerite is located in front of the operculum of the vulva, apparently stabilising the sperm-transferring parts. In contrast, the promerite of *B. lusitanus* is quite short and does not penetrate the vulval sac.

In *U. transsilvanicus* and *C. boleti* (Fig. 8) the function of the pro/mesomerite forceps [first described by Haacker and Fuchs (1970)] is to grasp the vulvae on the opercula, pull them out of the vulval sacs and hold them during copulation. In *U. transsilvanicus* the promerite fits thereby into a corresponding depression of the operculum while pulling the operculum slightly forward. The solenomerite attaches to the slit-shaped central area; in *C. boleti*, the solenomerite is stabilised by a projection ("brachite") that inserts into a slot between the valves. In *U. transsilvanicus*, the connection between the solenomerite and the central area is less stable, and the solenomerite performs movements of unknown function within the elongated central area (Tadler 1996).

Parajulidae: *Aniulus garius* (Chamberlin, 1912). In *Aniulus garius* (Chamberlin, 1912), as described by Mathews and Bultman (1993) (sub *A. bollmanni*), both the anterior and the posterior gonopods are involved in the manipulation of a spermatophore. The spermatophore is first taken up by the telopodite of the anterior gonopods (7/1) and brought to the basal part of the syncoxite 7/1, while the distal part of the syncoxite is inserted into the vulval sac ["cyphopode openings" sensu Mathews and Bultman (1993)]. The distal parts of the posterior gonopods (7/2) are then introduced into the

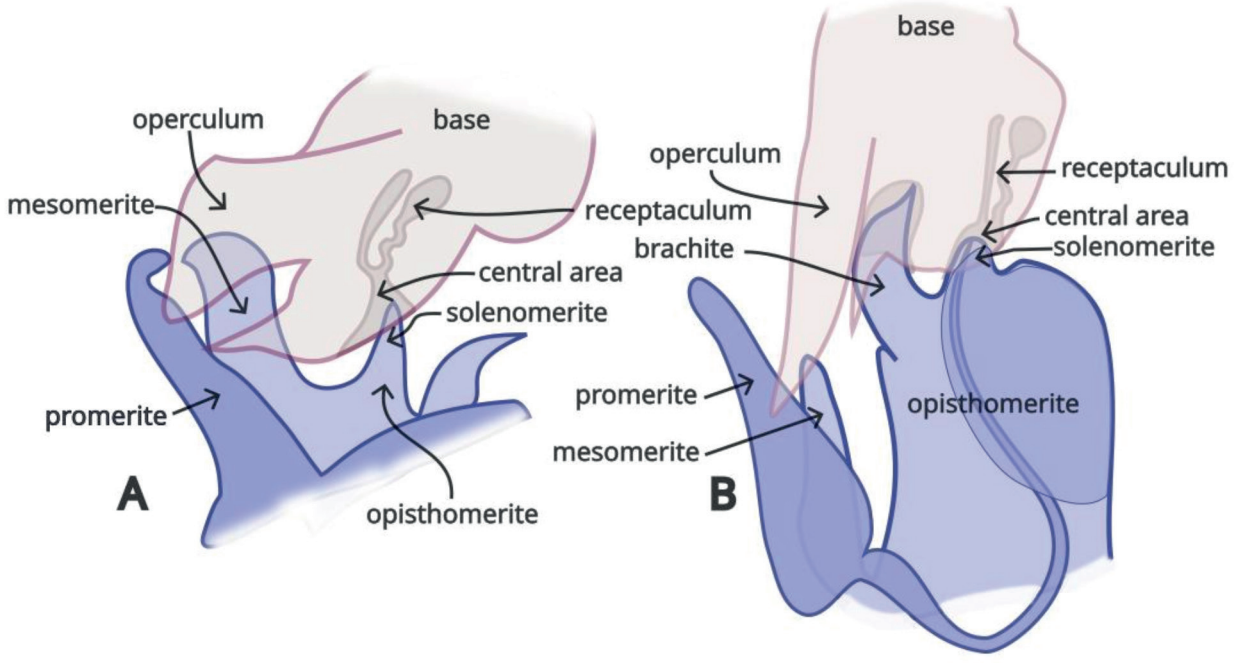

Fig. 8. Simplified diagram of the genital mechanics of **A**, *Unciger transsilvanicus* (Verhoeff, 1899) and **B**, *Cylindroiulus boleti* (C.L. Koch, 1847) (both Julidae). Lateral view. Male parts blue. Flagellum of *Unciger* omitted. Adapted from Tadler (1996). Male parts blue. Explanation in text.

vulval sac, whereas the proximal parts make the spermatophore burst and cause the sperm "to spread in all directions". Then, the prefemoral processes of the posterior gonopods that remain outside the vulval sac collect sperm secretion, which is then taken up into the sperm canal of the posterior gonopods and most probably transported onto the vulvae (Mathews and Bultman 1993).

Blaniulidae: *Blaniulus guttulatus* (Fabricius, 1798). The copulation of *Blaniulus guttulatus* (Fabricius, 1798) was described by Kinkel (1953, 1955). The vulvae remain in the particularly deep vulval sacs during copulation. The sperm is pushed from the "Mittelblatt" (apparently the elongated syncoxite of the anterior gonopods) into the "vulva" (= vulval sac). Kinkel (1953, 1955) could also observe the transfer of sperm from the penis to the "Mittelblatt" and using heat-fixed preparations he was able to detect sperm here. He also mentions that the long and slender posterior gonopods (leg pair 7/2) with their antler-like appendages are not introduced but clasp the female's trunk from the outside. If this could be confirmed, *B. guttulatus* may be classified as proterospermophorous, since it transfers sperm using the anterior gonopods (leg pair 7/1).

Blaniulidae: *Blaniulus lorifer* (Brolemann, 1921). Mauriès (1969) observed in the cave-dwelling blaniulid *Blaniulus lorifer* (Brolemann, 1921) the insertion of the syncoxite of the anterior gonopods ('prolongement impair du peltogonopode') into the vulval sac and emphasised its important role in sperm transfer. However, he also observed that the posterior gonopods (7/2) thereby cling closely to the syncoxite, so that they also become inserted. Mauriès (1969) did not carry out histological examinations, so it remains unclear which parts, the syncoxite 7/1 or the posterior gonopods, transfer sperm to the vulvae.

DISCUSSION

As is the case with many other animal groups (e.g. Ah-King et al. 2014), the female copulatory structures of Diplopoda have received somewhat less attention by taxonomists than male structures. For instance, spirostreptid vulvae have even been regarded as undifferentiated soft-skinned sacs by recognised specialists (Kraus 1968). However, repeated efforts have been made to take female structures into account from a morphological (Brölemann and Lichtenstein 1919; Zahnle et al. 2020) as well as from a taxonomic perspective (e.g. Brolemann 1935; Kurnik 1987, 1988; Tadler and Thaler 1993; Enghoff 2016). The results reviewed above demonstrate that eugnathan vulvae show very pronounced and functionally significant differences between individual groups. The vulvae of the relatively closely related species, *Mastigona bosniensis* and *Haploporatia eremita* differ in functional terms to a far

greater extent than the gonopods. Consequently, it appears to be rather futile to attempt to study the function and evolution of gonopods without taking the actual relation to their female counterparts into account. Thereby only data based on actual *in vivo* observations and preparations should be considered to be reliable. Attempts to reconstruct gonopod function based on the morphology of the gonopods alone may lead to erroneous assumptions (e.g. Verhoeff 1910 vs. Haacker 1971b).

Two hypotheses about genital coupling in the last common ancestor of Eugnatha

The telopodite hypothesis (Fig. 9). As shown above, some representatives of all three major groups of Eugnatha (i.e. Merochaeta, Nematophora, and Juliformia) share a common pattern. The following features presented here may be common to the species of Mastigophorophyllidae, Polydesmidae and Spirostreptidae:

(1) Sperm transfer occurs via the single-articulated telopodite of leg pair 7/1.

(2) A folding of the integument of telopodite 7/1 forms a "seminal canal". The seminal canal begins basally close to the coxopodite and ends on the aboral side of the telopodite, either on the main surface of the telopodite or on a projection (solenomerite).

Remark: The term 'seminal canal' is used here because it has become established in the literature; it is not proven that sperm is transported through this canal in all taxa.

(3) An apophysis of the coxopodite, here tentatively designated as "panflagellum", is basally connected to muscles. It is proximally inserted into the seminal canal. The term panflagellum should include not only the sickle-leaf flagella of the Mastigophorophyllidae, the cannula of the Polydesmida and the stylet prostatique of the Spirostreptida, but also the flagella of the Julida (see discussions below).

(4) During copulation, the distal opening of the seminal canal is located approximately opposite the openings of the receptacula seminis. Sperm is thereby deposited on and around the openings of the receptacula.

The resulting reconstruction of the genital mechanics of the last common ancestor of the Eugnatha is shown in Fig. 9. The homology of the respective elements involved (i.e. coxopodite, telopodite, sperm canal, panflagellum) is supported by the topological correspondence between the included species. Even if the shape and proportions of individual parts change dramatically, their numbers and their connections to each other remain unchanged, which complies with the homology criterion of position ["Lageähnlichkeit im Gefüge" sensu Remane (1952)]. In this case, however not only connections between parts within an individuum, but also between male and female structures are considered.

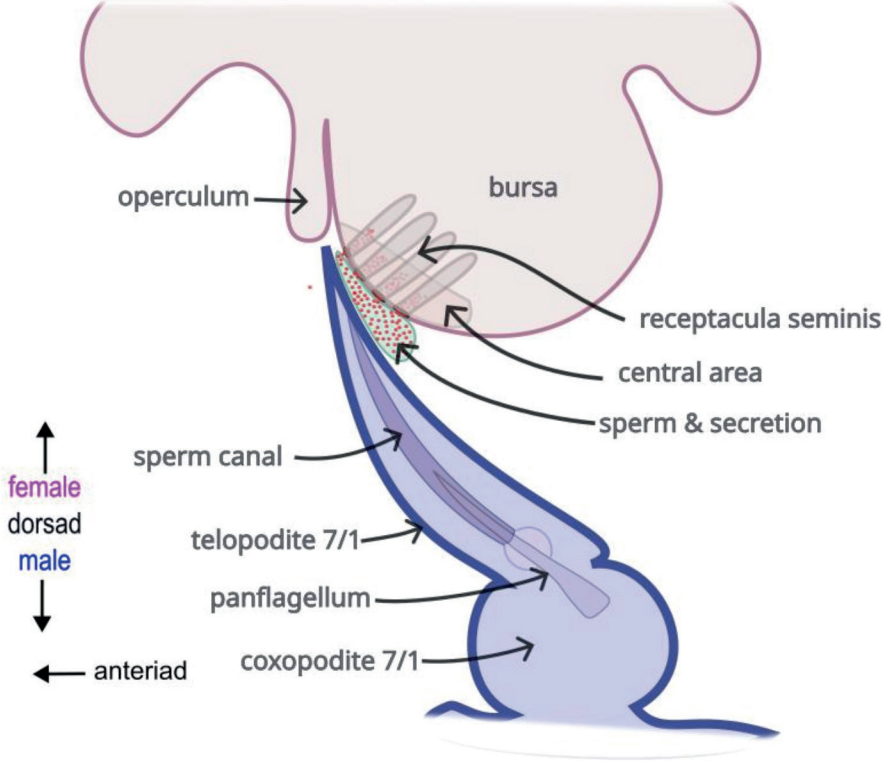

Fig. 9. Hypothetical genital mechanics of the last common ancestor of the Diplopoda Eugnatha according to the telopodite hypothesis. Male parts blue. Explanation in text.

However, due to the lack of data, these homologies and the corresponding reconstruction can be seen only as a possible scenario. Despite a debate that has been ongoing for at least 130 years, there is still no general consensus on the homologies within eugnathan gonopods. This concerns here in particular the putative telopodites of the anterior gonopods and the structures which are summarised here as panflagella.

Regarding the telopodite Shear (2000) almost categorically denies the existence of a telopodite of the anterior gonopods in Chordeumatida. Démange (1967) assumes that the "so-called telopodite" of the Spirostreptida consists of components of both the coxopodite and the telopodite. A completely different interpretation regarding the homologisations in the gonopods of Spirostreptida (Jeekel 1985) is too complex to be elaborated here.

The homology between the polydesmid cannula and the flagella of the Julida has already been proposed by Verhoeff (1901) and was extended by Démange (1967) to include the spirostreptid stylet prostatique. The assumption behind this is that these structures originally developed from coxal sacs and may constitute a synapomorphy of the Eugnatha (Enghoff 1984a). Here, the homology of the sickle-leaf flagellum of the Mastigophorophyllidae with these structures is suggested. However, Verhoeff (1897a, 1928) consistently referred to the sickle-leaf flagellum of the Mastigophorophyllidae as 'pseudoflagellum', even though it meets his own (Verhoeff 1897b) definition of a true flagellum, as it is movable by basal muscles ("Geißelbildung mit Grundmusculatur = Flagella"). Likewise, Verhoeff (1900b) strongly rejected the homology of the sperm canal of the Mastigophorophyllidae with other sperm canals. At present, it seems that these diverging opinions cannot be conclusively judged. It should be considered that most of the related data is based on unstained light microscopic total preparations. Further studies using state-of-the-art morphological and developmental genetic methods may be helpful.

Another question that cannot currently be answered in the context of the telopodite hypothesis is the evolution of sperm transfer via the posterior gonopods in Julida and Spirobolida ("Opisthospermophora"). If the telopodite hypothesis outlined above is correct, there must have been, or perhaps still be, proterospermophorous and intermediate "amphispermophorous" (Jeekel 1985) stages. Proterospermophorous Julida may include *B. guttulatus* (Kinkel 1953, 1955) as well as the Zosteractinidae, where the posterior gonopods are reduced and the flagella run through the telopodites of the anterior gonopods (Enghoff 1982; Enghoff pers. com. 2026). It is possible therefore that also extant intermediary stages may still exist. A definitive proof of sperm transfer via the anterior gonopods as well as a functional explanation of intermediate stages would help to understand the transition from anterior to posterior gonopods and may support the telopodite hypothesis.

The coxal sac hypothesis (Fig. 10). There are good reasons to believe that, as has already been suggested by Verhoeff (1900b), "gonopodisation" started with sperm transfer via the coxal sacs of unmodified walking legs in stem group Helminthomorpha. Assuming that ancestral Helminthomorpha had a similar ventral vs. ventral copulation position as their present-day descendants, the telopodites of unmodified walking legs are thereby rather inadequate for sperm transfer. Because of their laterad/ventrad orientation, they can hardly reach the vulvae and they are not equipped with structures for the uptake, short-term storage and transfer of sperm. Coxae are, due to their position opposite to the vulvae, better suited, and coxal sacs which are likely to belong to the ground plan of the Diplopoda Chilognatha (Enghoff 1990) may be predisposed to the uptake and transfer of sperm (Verhoeff 1900b). Sperm transfer via coxal sacs seems feasible even with unmodified walking legs, provided a certain amount of female cooperation. Such cooperation may include that females actively protrude their vulvae and pick up sperm from the male coxal sacs.

The two hypotheses outlined above are insofar compatible as it is possible that sperm transfer via the coxal sac represents an earlier stage, which may have been already replaced by telopodite sperm transfer in the common ancestor of the Eugnatha. So, it is likely that "gonopodisation" of walking legs started with coxal sperm-transfer, but it is unclear at which phylogenetic node this occurred. Thus, it does not seem possible to decide today which of the two hypotheses is true. The parsimony principle makes the coxal sac hypothesis less probable. On the other hand, the coxal sac hypothesis may avoid the "Opisthospermophora" problem, since it is conceivable that sperm transfer in Julida and Spirobolida was primarily carried out via the leg pair 7/2 so that there would be no transition of sperm transfer from the anterior to the posterior gonopods.

The most striking functional trend in the evolution of eugnathan genitalia

In the examples presented above, the sperm is not actively brought into the female receptacles by the males and there seems to be no pressurised injection. Sperm together with glandular secretions is applied outside of the receptacula, onto and around their openings. Reports of sperm deposition within the receptacula seem often to be based on the obvious confusion of the vulvae with the vulval sacs (Barnett 1997). This suggests that although the mechanisms are not yet fully understood, sperm intake into

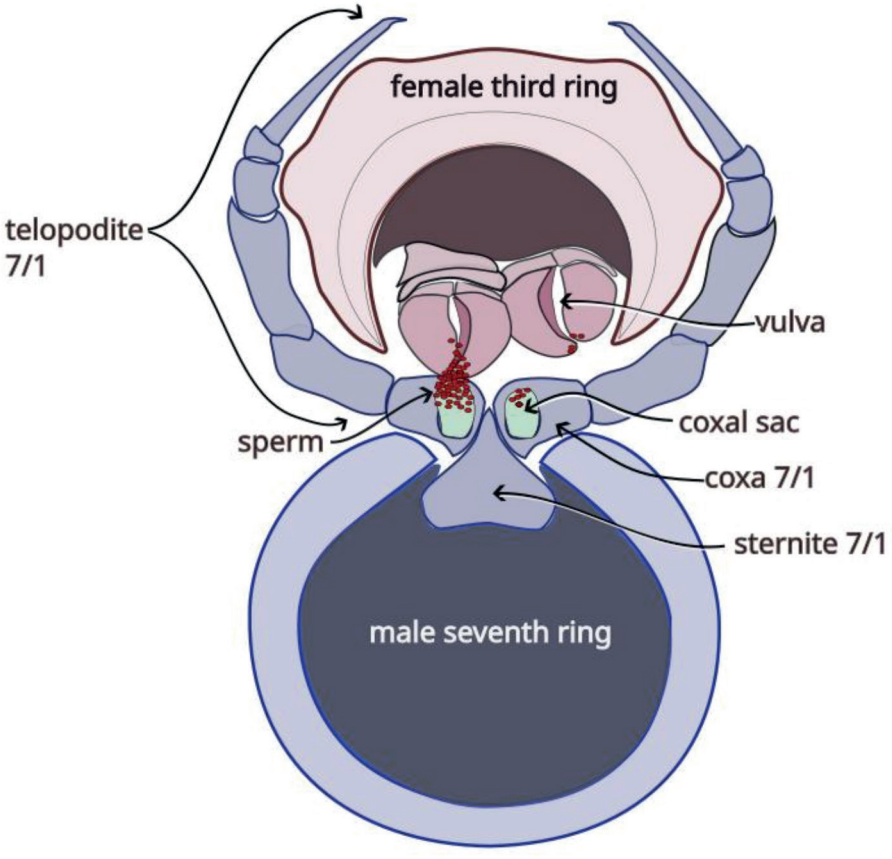

Fig. 10. A model of sperm transfer in stem-group Eugnatha according to the coxal sac hypothesis. Frontal view (based on the third female ring and the eighth male ring of *Craspedosoma raulinsii*). Compared with systems involving more elaborate gonopods, this would obviously require a higher degree of female cooperation in sperm uptake.

the receptacula would be mainly controlled by females.

Assuming that as in most terrestrial arthropods, the original form of sperm transfer in stem-group diplopods was indirect (Schaller 1971), a female-controlled sperm intake is likely to be phylogenetically older than gonopods. Indirect sperm transfer still exists today in the Pselaphognatha, where a spermatophore is deposited by the male on the ground and then actively picked up by the female with the vulva (Schömann 1956). Therefore, it seems likely that, as outlined above such an actively female-controlled sperm uptake from the male coxal sacs was the starting point of gonopodisation.

Then, the most general trend in the evolution of eugnathan gonopods appears to be towards enhanced male control over the transfer and protection of sperm. This leads to the evolution of more or less elaborated stabilisation systems that fix the male sperm-transferring parts in the central area of the vulvae and may allow the males to protect the sperm there and prevent it from being removed or eaten by the females. In several lineages the stabilisation system also allows the use of flagella and brushes, which may remove hardened layers of secretion sealing the receptacula. As shown above, in some taxa (e.g. *C. raulinsii*, *M. bosniensis*) the stabilisation system provides a particularly firm mutual interlocking of genitalia that secures the females in the copulation position against the obvious resistance of the females (Tadler 1989, 1993; Eberhard 1996).

Female resistance is probably widespread in Eugnatha including the Chordeumatida *H. eremita, M. bosniensis and C. raulinsii* (Tadler 1989, 1993), the spirobolid *Centrobolus* Cook, 1897 (Cooper and Telford 2000) the odontopygid spirostreptidean *Spinotarsus* Attems, 1909 (Brandt et al. 2024), whereas the copulation initiation appears to be somewhat more peaceful in *C. sylvestre* (Haacker 1971b) and *Julus scandinavius* Latzel, 1884 (Haacker 1969) in which the males try to win over the females by means of a gustatory courtship.

At first glance, it seems obvious to explain these male-female struggles and the corresponding ability of the males to fix the females with their gonopods within

the framework of the sexually antagonistic coevolution hypothesis. This hypothesis explains the evolution of complex genital structures through a conflict in which males attempt to increase their chances of fertilisation to the disadvantage of females, triggering thereby an arms race between male persistence and female resistance traits (e.g. Eberhard 2010; Perry and Rowe 2012; Simmons 2014). Thus, the sexual conflict hypothesis predicts the evolution of female "antigrasping traits" to decrease mating frequency (Perry and Rowe 2015). This is however in stark contrast with the most striking trend in the evolution of eugnathan copulatory mechanics, which is the formation of female "cooperative structures" (Eberhard 1996) that obviously stabilise the interlocking of genitalia and increase thereby the probability of an effective sperm transfer. As shown above, this is achieved in the different groups via totally different mechanisms, including the pockets in the oviduct of *C. raulinsii*, the modified margin bulge of *H. eremita*, the rotation-vulva of *M. bosniensis* or the pockets and slits in the bursa of some Julidae. Such "cooperative structures" may also involve non-genital structures, as in the blaniulid *Choneiulus subterraneus* (Silvestri 1903) in which some females have a rather modified second antennomere which would facilitate the grip by the male's parrot-bill like mandibles during copulation (Enghoff 1984b; Enghoff pers. comm. 2026).

These cooperative female structures are clearly incompatible with a sexual conflict arms race. The main selective principle of diplopod genital evolution seems to be rather a co-evolution between male traits and female preference within the framework of the cryptic female choice concept (Eberhard 1985). Thereby the female preferences are determined by the cooperative structures via a "selective surrender" tactic, whereby only males with precisely adapted gonopods are successful against female resistance (Eberhard 1996). In other words: if one wishes to test the precision of the fit and strength of a connection, one may shake and pull on it.

However, one cannot expect to explain all phenomena of the evolution of the genitals of Eugnatha by a single selective principle. There are gonopods whose complexity seems to be primarily related to male competition. These may include the Spirostreptida, for which no specific "cooperative structures" have been described to date. The often surprisingly complicated ramifications, bends and twists of spirostreptid gonopods probably serve to clear the vulva sacs of sperm from competing males (Barnett et al. 1993, 1995; Barnett and Telford 1994; Barnett 1997; Brandt et al. 2024). Likewise, the extreme complexity of the gonopods of the Chordeumatidae may be partly related to "male competition" whereby males prevent successful copulation by other males by covering the vulvae with secretion cups (Haacker 1971b).

Finally, it must be reiterated that only a few small fragments of the vast and wild world of eugnathan genital mechanics are known to date. Only preliminary assumptions can be made regarding the evolution and selective mechanisms that have led to the disparity and extravagances of these structures and a plethora of fascinating phenomena are still waiting to be discovered.

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