

Lengthening of embolus and copulatory duct: a review of an evolutionary trend in the spider family Sparassidae (Araneae)

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Dedicated to Dr Manfred Grasshoff on occasion of his 70th anniversary and in memory of his contributions to the functional morphology of the spider family Araneidae

Abstract: The phenomenon of lengthening copulatory structures in the spider family Sparassidae is reviewed. One can distinguish between a diversifying type and a lengthening type, but admitting that there may be combinations and transitions between these cases. Some 55% of 662 species examined show clearly that the embolus and/or copulatory ducts are lengthened in comparison with the ancestral species, whereas only in 8% there is no noteworthy lengthening of these structures. Different types of lengthening are recognised: 'tegular coil', 'distal coil', 'distal screw', the irregular or combination type, and the so-called 'functional lengthening'. In these types uniformity of the copulatory structures prevails, although diversifying elements may occur albeit rarely. Combined morphological changes, occurring in the course of evolutionary lengthening, are considered as being dependent on functional constraints. The position of the embolus' tip may play an important role in this context. Understanding of functional and evolutionary aspects may enlighten possible mechanisms which trigger the phenomenon.

Key words: spider genitalia, copulatory organs, tip of embolus, evolutionary mechanisms, types of lengthening, functional constraints, huntsman spiders

Introduction

In spiders, as in other terrestrial arthropods, copulatory structures have been developed which allow direct sperm transfer (in contrast to indirect sperm transfer in marine or fresh water organisms). Male spiders exhibit copulatory organs on their second pair of appendages: the pedipalpi are modified as gonopods. Females have either rather simple receptacula seminis (Mygalomorphae and haplogyne Araneomorphae) or frequently a complex duct system in front of the genital opening (entelegyne Araneomorphae). Considering the fact that copulatory organs are present only in the last stage of an individual and used for a short time only, and for a restricted purpose, it seems to be most likely that the evolution of these structures may be largely independent from external conditions, e.g. such as climate, habitat, prey animals or others. Both structures in males and females are acting during copulation as one functional unit and are therefore dependent on each other with respect to evolutionary changes of their parts (as in upper and lower jaws in vertebrates) (GRASSHOFF 1975; see also KRAUS 1995, 1998). Apparently, this also seems to be true, if the structures (embolus, copulatory ducts) are in the process of changing their length in the course of evolution, as the lengths of these structures in males and females are changed accordingly. This length-changing occurs, among others, in the spider family Sparassidae, which is represented by about 1000 species worldwide (PLATNICK 2005). Representatives of one subgroup of this family, the Deleninae from the Australasian region, exhibit extremely long emboli and copulatory

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ducts (Figs 1-2). From examination of these copulatory organs, several questions arise, e.g. which mechanisms are responsible for such a trend of lengthening¹, what is the proximate and what the ultimate causation? What advantages or what functional economisation could lengthening genitalia provide for animals of lineages with such an evolutionary trend, such that these have been selected in the evolutionary processes? Have modifications of the mating behaviour been established, as known from e.g. Staphylinidae (GACK, PESCHKE 2005)?

The phenomenon of lengthening genitalia has been addressed only by few authors in the past: COMSTOCK (1910) simply described different types of spider pedipalps and gave standardised names for individual parts. WIEHLE (1961) suggested that for longer female ducts, the emboli would stay for a longer time during the copulation and, by this delay, the transfer of sperm would be secured. Wiehle recognised different types of emboli ('Einführungs-Embolus' and subtypes, 'Anschluss-Embolus') whereas looking for this phenomenon in different spider families. HELSDINGEN (1972) put this subdivision into perspective and considered it an 'oversimplification'. This author dealt with a striking case of lengthening copulatory structures in the family Linyphiidae. He investigated functional aspects of male palp and female epigyne in fixed copulae and used the results for a systematical re-classification of four genera (HELSDINGEN 1965, 1969, 1970). JOCQUÉ (1998) claims that lengthening of the embolus (as described in e.g. JOCQUÉ 1990, JOCQUÉ, BAEHR 1992, JOCQUÉ, SZÜTS 2001, JOCQUÉ, BOSSELAERS 2005) is one of the possibilities for spiders to increase their complexity of the genitalia, in what he calls the "mating module", implying that genital complexity is linked to ecological specialisation.

Before addressing the questions mentioned above, the trend of length-changing genital structures within a particular group (here: Sparassidae) should be investigated for comparison purposes, in order to get an idea of its importance and structural influence on the evolutionary history of the recent species composition.

Material and Methods

During the past ten years, 662 of the 793 Sparassidae species, with male sex known, were examined, i.e. about 83%. Some 546 (69%) with known male sex, have been used here. Legends of drawings or indications in the text should be a sufficient reference. Male and female copulatory organs were investigated and drawn, using stereomicroscopes (Leica MZ 16, Wild M8) and compound microscopes (Zeiss, Leica DMLS), all with camera lucida attachments. Female epigynes were cleared with 96% lactic acid if necessary; epigynes with membranous parts were either cleared very carefully or not treated with lactic acid, since it can change the position of individual parts. Only male copulatory organs were used for taking measurements (length of embolus, position of tip of embolus). Female epigynes are only referred to in a more general manner or in single cases (e.g. *Heteropoda* LATREILLE, 1804). Relative length of emboli and lengthening respectively were measured in comparison to a reference length of an assumingly basal state (short embolus). An arising point in a 6-o'clock-position, for instance, is considered plesiomorphic for many taxa within Sparassidae. To make positions of the embolus' tip comparable, i.e. to compensate for differently shaped pedipalps, the tegulum including all its appendices were fitted into a rectangle as in Fig. 29. The relative position of the tip was calculated with: co-ordinates of the embolus' tip being the relative length and width of the rectangle. Additional measurements were taken from suitable original drawings, i.e. if the cymbium was drawn in a ventral view and the parts were unambiguously identifiable. All measurements were carried out only for those emboli being in the resting position (i.e. bulbs were not expanded). Single females were assigned to one of the

¹ For evidences supporting the hypothesis that copulatory structures lengthen and do not shorten in the process of evolution, see first paragraph of discussion.

categories, when the internal duct system showed evidence of belonging to one of the lengthening types, even though a conspecific male was not known (e.g. in *Heteropoda*).

A species was identified as belonging to the lengthening type, when either the gradual character states of the embolus or of the copulatory ducts with respect to their length in different, related species appeared (Fig. 1), or if in a single species a distinctly elongated embolus pointed to a derived state. In contrast, emboli with different shapes or with new features such as apophyses and without any evidence of lengthening, were assigned to a so-called diversifying type (Figs 3-6). These assignments are partly supported by females with copulatory ducts of the same or of a similar length. Species without characters of one or other group were noted as questionable.

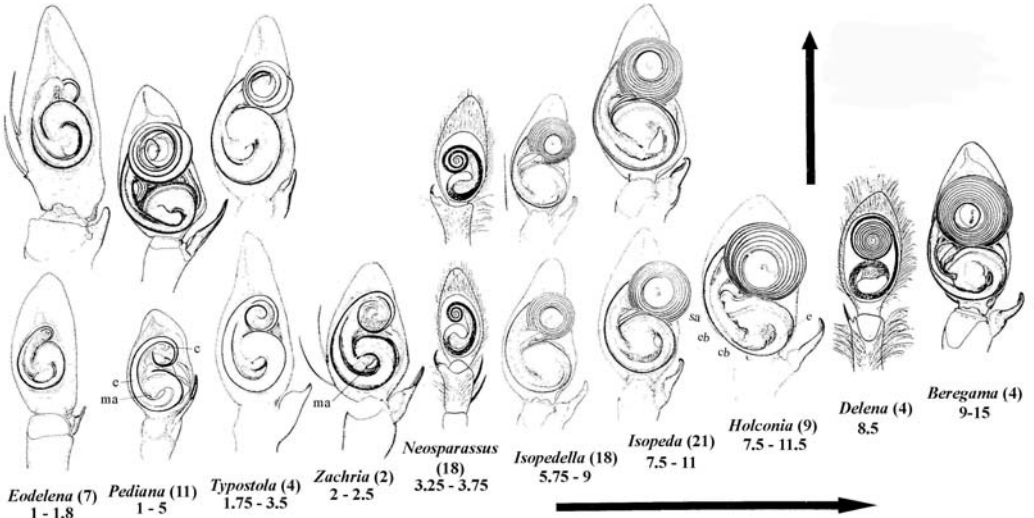


Fig. 1. Male pedipalps of different species of the subfamily Deleninae from Australia, showing different lengths of distal coils of the embolus, here interpreted as 'lengthening type'. All illustrations by HIRST (1989, 1990, 1991a, 1991b, 1992, 1993, 1995, 1997, 1999), exception: *Neosparassus* and *Delena* (by HICKMANN 1967). Arrows point to lengthening within the subfamily (horizontal) and within the particular genus (vertical), but are not interpreted as direct detector of phylogenetic relationship. Numbers in parentheses behind genus names indicate species numbers, ranges below genus names number of coils observed within the particular genus.

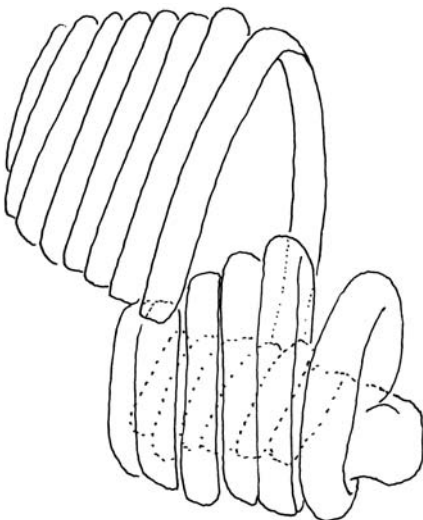
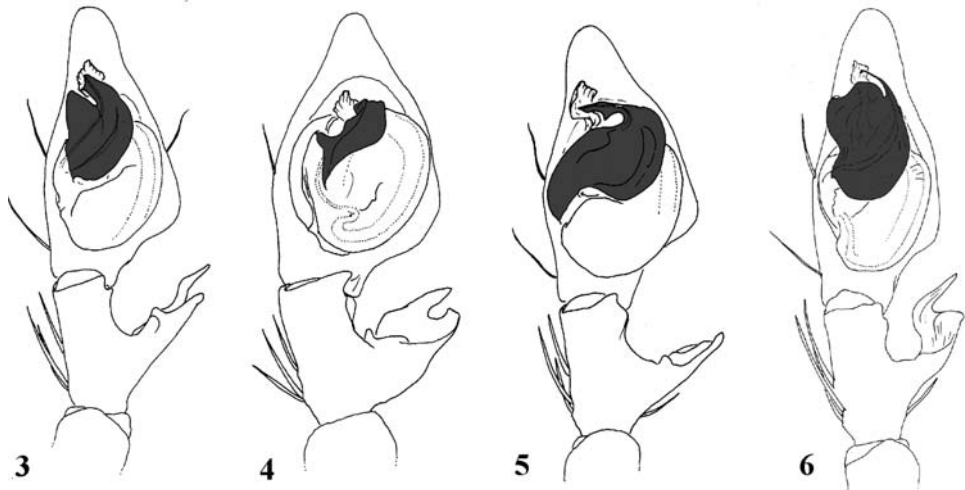


Fig. 2. Distal coils of the embolus of an undescribed *Neosparassus* sp., lateral view, showing organisation of the twenty coils in three spirals. The outer coil was compassed to make inner coils visible.



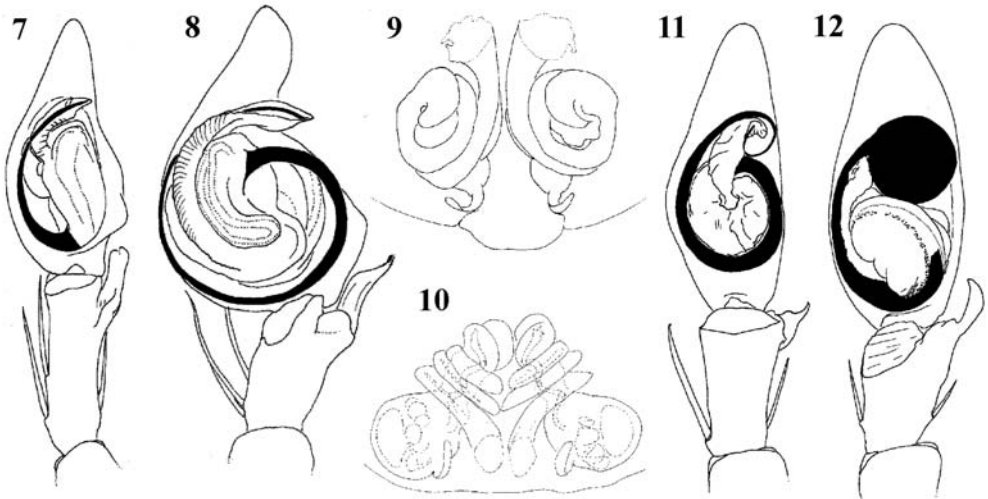
Figs 3-6. Male pedipalps of different undescribed *Pseudopoda* species from Yunnan, showing different shapes and sizes of emboli, here interpreted as 'diversifying type'. Emboli shaded.

Results

In total 364 species (55%) of 662 species examined were considered belonging to a lengthening type of copulatory structures. In contrast only 54 species (8%) exhibit a clearly diversifying type of emboli (e.g. *Pseudopoda* JÄGER, 2000 cf. Figs 3-6, *Anaptomecus* SIMON, 1903, *Sparianthina* BANKS, 1929, *Prusias* O.-P. CAMBRIDGE, 1892 ad part., *Olios* WALCKENAER, 1837 ad part.). Two hundred forty-five species could not be assigned to one of the two categories and remain questionable until further work. Generally, lengthening can take place at the tip (e.g. in *Holconia* THORELL, 1877) or at the base (e.g. in *Heteropoda*) of the embolus. Moreover, both types can occur together (e.g. in *Pandercetes* L. KOCH, 1875; compare JÄGER 2002: fig. 173). Beside these, different types of lengthening were also recognised.

Different types of lengthening

In the '**tegular coil**'- type the base of the embolus is shifted in the course of evolution around the tegulum, the tip of the embolus remains almost in the same position (Figs 7-8). This type occurs in *Heteropoda* (180 species), *Barylestis* SIMON, 1910 (9), *Yinthe* DAVIES, 1994 (8), *Polybetes* SIMON, 1897 ad part. (8), *Damastes* SIMON, 1880 (17), *Gnathopalystes* RAINBOW, 1899 ad part. (7), *Tychicus* SIMON, 1880 (5) and *Prychia* L. KOCH, 1875 (4) (total number of species: 238). Maximal lengthening of the embolus constitutes 200% additional length. The '**distal coil**'- type is characterised by a lengthening at the tip of the embolus, which during the process remains in almost the same position, with the embolus tightly circling around a central point (Figs 11-12). It is realised in the Deleninae (11 genera, 105 species), *Clastes* WALCKENAER, 1837 (1), *Palystes* L. KOCH, 1875 ad part. (6), *Remmius* SIMON, 1897 (5), *Rhitymna* SIMON, 1897 ad part. (10), *Sarotesius* POCOCK, 1898 (1) (total number of species: 128). Emboli exhibit a maximal lengthening of 900%. Representatives of one genus (*Olios* ad part., i.e. former *Pelmopoda* KARSCH, 1879 spp.; 10 species) exhibit a **distal screw** with a maximum of 120% additional length (Figs 14-15). The embolus' tip is circling around its straight length axis and the embolus is lengthened at its tip retrolaterad. In *Pseudopoda* ad part. (20), *Pandercetes* (18), *Olios* ad part. (10), *Palystella* LAWRENCE, 1928 (4), *Microrchestris* LAWRENCE, 1962 (2), *Cebrennus* SIMON, 1880 (13) the embolus is lengthened at the base and at its tip **irregularly** (i.e. with no distinct shape, such as a circle, spiral, etc.) or **in combination** (Figs 18-19; total species number: 67; maximal lengthening: 350 % additional length).



Figs 7-12. 7-8 - Male pedipalps of *Heteropoda* species representing the ‘tegular coil’ type; 7 - *Heteropoda* sp., 8 - *Heteropoda cyperusiria* BARRION, LITSINGER, 1995. 9-10 Female internal duct systems of *Heteropoda* species belonging to the same lengthening type of males (tegular coil) but show different pattern of lengthening: 9 - *Heteropoda lumula* (DOLESCHALL, 1857), 10 - *Heteropoda cyperusiria* BARRION, LITSINGER, 1995. 11-12 Male pedipalps of Deleninae species representing the ‘distal coil’ type: 11 - ‘*Olios*’ *coccineiventris* (SIMON, 1880), syntype, 12 - *Deleninae* sp. Note the shorter tibia in males with longer embolus in both types and the shape of cymbium changed in *Heteropoda cyperusiria*. Emboli shaded. 8, 10 from JÄGER, BARRION (2001).

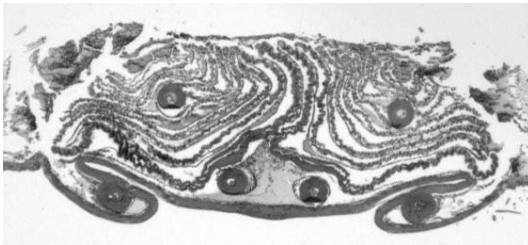
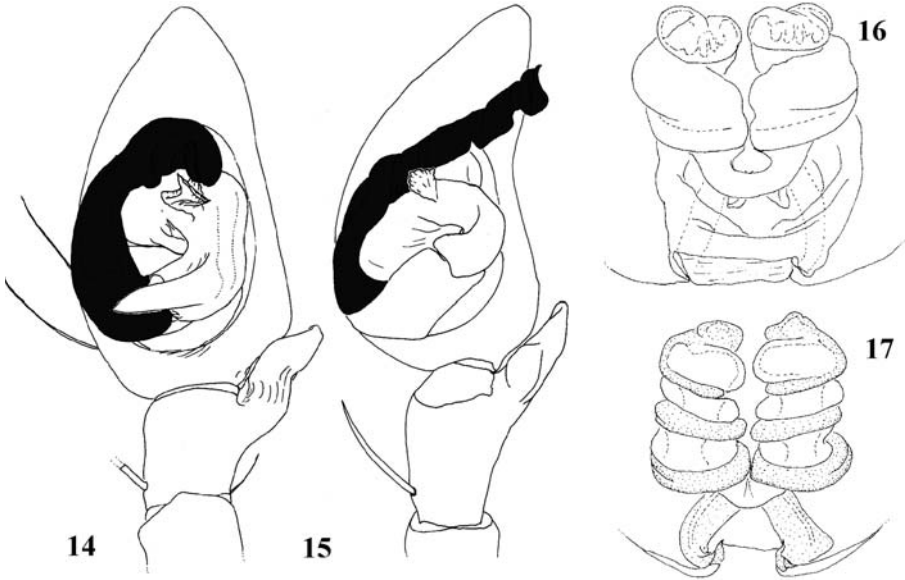


Fig. 13. Cross section through female copulatory organ of *Holconia* sp. from Australia (stained with Azan-Heidenhain, 8µm) showing space saving type of windings in membranous copulatory ducts (ducts arranged in tiers partly folded). Preparation and photo by M. Reinke.

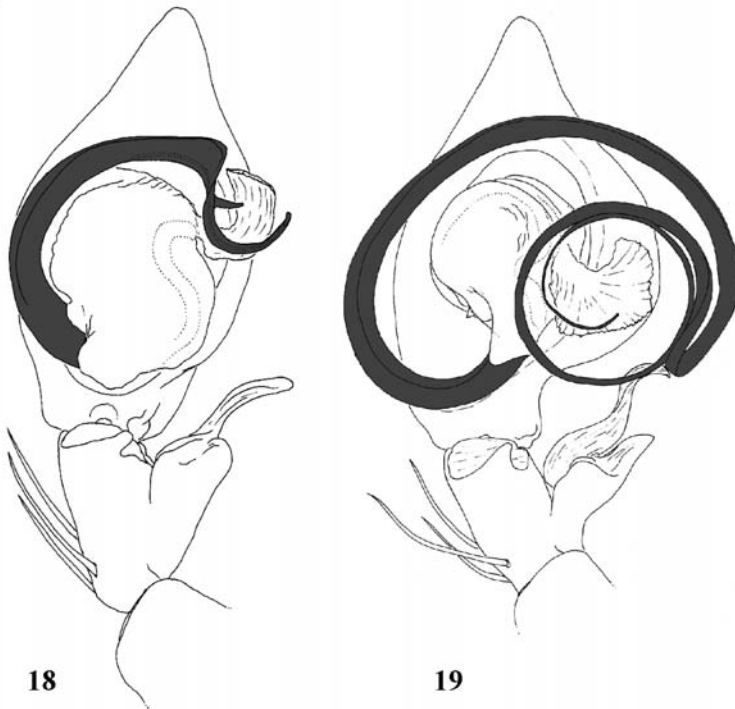
A special type of lengthening occurs in the *okinawana*-group of the genus *Sinopoda* JÄGER, 1999: the embolus is reduced in its width, the embolic apophysis is reduced and the shape of the embolus changes from an ‘S’ to a semi-circle (Figs 20-24). Since it is assumed that the reduction of hindering parts (i.e. broad base, distal embolic apophysis, S-shaped tip) allows an insertion of longer parts, this type is called **functional lengthening**. This assumption is slightly supported by the internal duct system of the female spiders: in the species with functionally longer emboli the ducts are more strongly bent to the dorsal

side (Figs 25-26), which could be explained as a better accommodating the longer emboli. However, this group exhibits some apomorphies (reduced ventral part of RTA, distinct brush of hairs at the base of RTA, body size reduction; JÄGER, ONO 2002) which polarise the gradual change in direction to the reduced embolus and thus an assumed functional lengthening. Species with assumed derived structures occur in the most eastern part of the distribution range (Japan) of this species-group (see also legend of Figs 22-26).

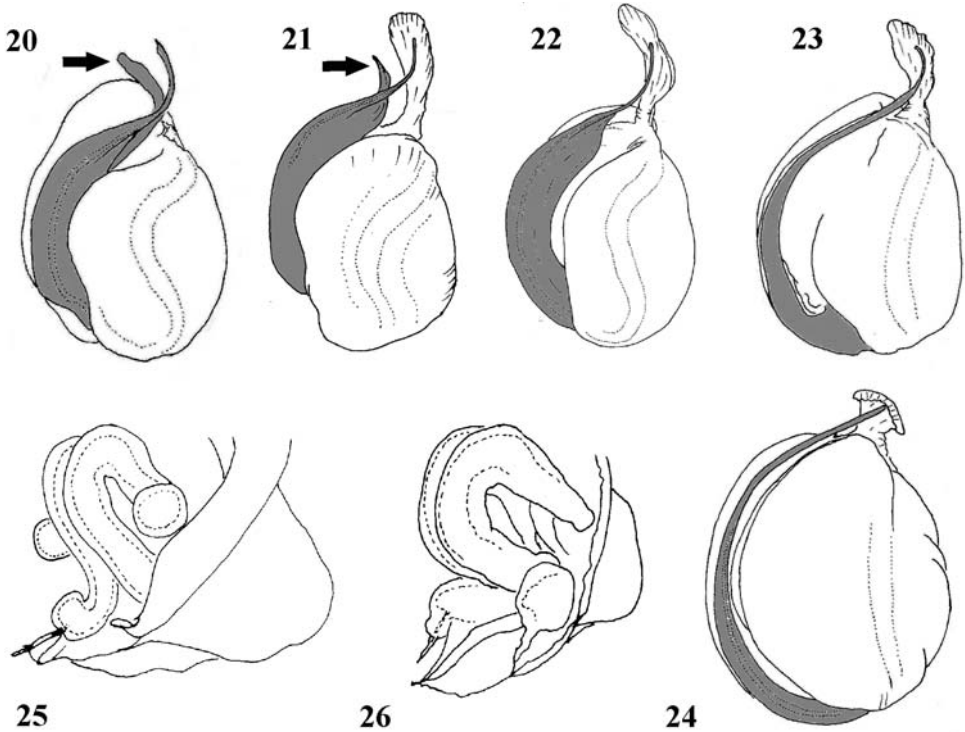
Lengthening may occur in a group exhibiting generally diversifying copulatory structures as e.g. in the genus *Pseudopoda* (Figs 3-6). In this case only parts of the embolus are lengthened (e.g. *Pseudopoda martensi*-group, see JÄGER 2001: 124, fig. 84) and it is called here **secondary lengthening**.



Figs 14-17. 14-15 - Male pedipalps of *Olios* species representing the 'distal screw' type: 14 - *Olios* sp., 15 - *Olios punctipes* SIMON, 1884; 16-17 - Female internal duct systems of *Olios* species belonging to the same lengthening type: 16 - *Olios nigrifrons* (SIMON, 1897), 17 - *Olios* sp. Note that a straight (functionable) screw is only realisable in the distal part of the pedipalp. Emboli shaded.



Figs 18-19. Male pedipalps of *Pseudopoda* spp. from Japan representing an irregular type of lengthening: 18 - *Pseudopoda kasariana* JÄGER, ONO, 2002; 19 - *P. spirembolus* JÄGER, ONO, 2002. Emboli shaded. 18-19 after JÄGER, ONO (2002).

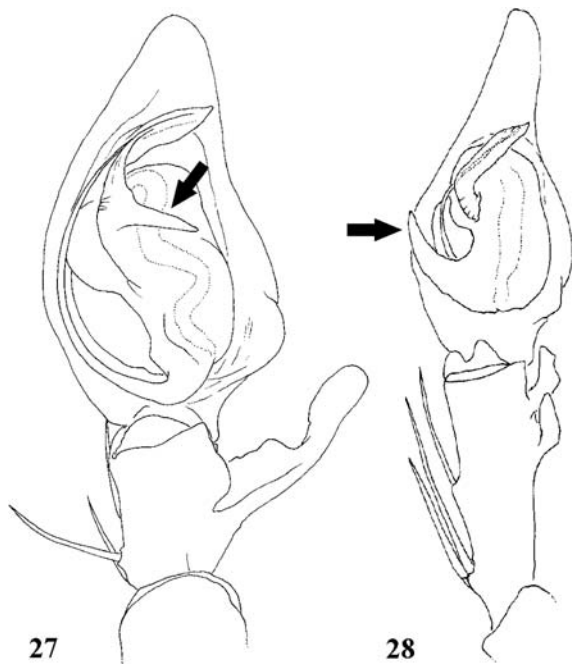


Figs 20-26. 20-24 - Male tegula with appendices of *Sinopoda* species of the *okinawana*-group representing the 'functional lengthening' type: 20 - *S. hamata* (FOX, 1937), holotype from Sichuan Prov. (China), conductor omitted, 21 - *S. fasciculata* JÄGER, GAO, FEI, 2002, holotype from Guizhou Prov. (China), 22 - *S. wangi* SONG, ZHU, 1999, syntype from Jiangxi Prov. (China), 23 - *S. albofasciata* JÄGER, ONO, 2002, holotype from Tokashiki Isl. (Japan), 24 - *S. derivata* JÄGER, ONO, 2002, holotype from Tokara Isl. (Japan). Note that embolic apophysis (arrows) and basal width of embolus are reduced and shape of embolus is changed from *s*-shaped to semi-circular, and note the geographic gradient (reduction from West to East). Emboli shaded. 25-26 - Female internal duct system of *Sinopoda* spp. of the *okinawana*-group: 25 - *S. hamata* (FOX, 1937), 26 - *S. tanikawai* JÄGER, ONO, 2000. Note that the right vulva is more strongly bent and could accommodate theoretically a longer embolus inserted. 21-22 after JÄGER *et al.* (2002), 23-24, 26 after JÄGER, ONO (2002).

Uniformity within one type

Within one type of lengthening the copulatory organs appear rather uniform, i.e. without diversifying elements. Only in relatively rare cases are new structures found, such as new apophyses at the tegulum, conductor or embolus. One such example occurs in the genus *Heteropoda*: *H. javana* SIMON, 1880 and some related species (Fig. 27; JÄGER 2002: fig. 61), which exhibit an apophysis arising from the conductor in conjunction with an unusually shaped RTA (in comparison with the common form of the RTA in *Heteropoda* spp. which is supposed to be plesiomorphic for this genus). Other examples occur in *Heteropoda boiei* (DOLESCHALL, 1859) with an additional tegular apophysis (Fig. 28), and the different genera of the Deleninae in Australia, which are distinguished among other characters by their differently shaped tegular apophyses and embolic sclerites (HIRST 1990).

In females, usually the same type of lengthening of copulatory ducts were observed within one type of lengthening of the corresponding embolus (e.g. *Olios* spp., Figs 16-17). Only within *Heteropoda* were different types recognised (Figs 9-10). Thus, females apparently may provide a morphological basis for recognising subgroups (sublineages) within one trend of lengthening emboli of males.



Figs 27-28. Male pedipalps of *Heteropoda* spp. showing diversifying elements within the otherwise uniformly developed bulbs of the ‘tegular coil’-type: 27 - *Heteropoda dagmarae* JÄGER, VEDEL, 2005, holotype, with apophysis at the base of the conductor (arrow), from JÄGER, VEDEL 2005; 28 - *Heteropoda boiei* (DOLESCHALL, 1859) with a tegular apophysis (arrow), from JÄGER 2001.

tip distad (e.g. Deleninae, Figs 11-12; *Cebrennus rungsi* JÄGER, 2000, *C. aethiopicus* SIMON, 1880, see JÄGER 2000: figs 34, 49). Furthermore, in few cases, the membranous part of the tibia-tarsus joint is extended more onto the tibia part (Deleninae: *Eodelena* HOGG, 1902 => *Beregama* HIRST, 1990, Figs 11-12, *Heteropoda*, Figs 7-8, *Olios* ad part., Figs 14-15).

Position of embolus’ tip

In male copulatory organs the position of the embolus’ tip appears, in many lineages, to be strikingly constant. To check this first impression, the position of this tip in different species ($n = 546$) within the Sparassidae, were measured. Results are shown in Figs 29-30. The tip of the embolus is situated, in most cases (95.4%) in the distal half of the constructed rectangle, and also in most species (72%), is situated in the retrolateral distal quarter (e.g. in *Heteropoda*). In contrast, there are only 4.6% of the species with the embolus ending in the basal half, and just 0.4% in the pro-lateral basal quarter. In fact, in the latter case there is a large area, in which no tip of an embolus was situated, i.e. in general the emboli end more to the distal or retrolateral directions.

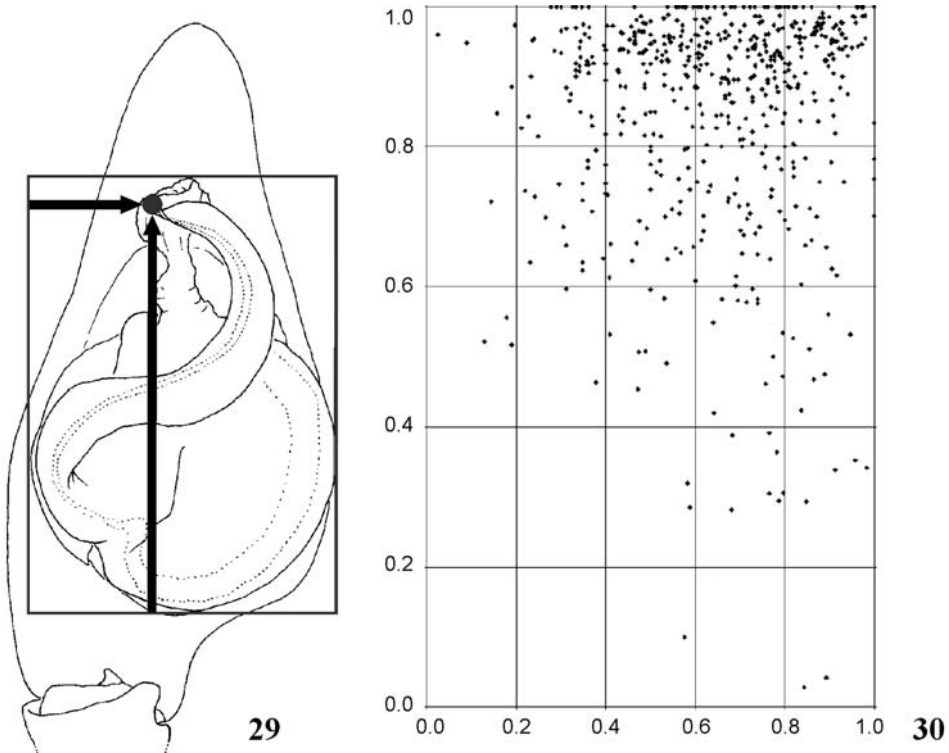
Discussion

In the opinion of the author copulatory structures are lengthening in the process of evolution. It arises the question, why it should not run the opposite way, i.e. evolve from long to short. Here, some evidences are listed, which support the ‘lengthening-hypothesis’. One of the main arguments is that it seems unlikely that species in different (sub)lineages (e.g. in the Deleninae, Fig. 1) with

Combined morphological changes

Within a certain lineage, species with longer emboli exhibit additional morphological features which changed either in size or shape. In several cases the tibia is often shorter than in species with longer emboli (*Heteropoda* spp., Figs 7-8; Deleninae, Figs 11-12; *Pseudopoda* spp., Figs 18-19). Moreover the shape of the cymbium also changed, e.g. is transformed from having more straight or slight concave retrolateral margins, to having strongly concave retrolateral margins in a ventral view for *Heteropoda* species (Figs 7-8). When the embolus is lengthened and requires more space, the tegulum is reduced or shifted mostly in direction of the basal half of the palp (Deleninae, Figs 11-12). The latter phenomenon may also occur in cases of species with a diversifying type of embolus (*Bhutaniella*, JÄGER 2001: fig. 54b; *Sparianthina* spp., unpubl. observations).

In a few cases the RTA becomes longer in species with longer emboli, either by shifting the RTA base proximad, or by increasing the length at the



Figs 29-30. 29 - Rectangle constructed for measuring position of embolus' tip; 30 - Position of embolus' tip from 546 species of Sparassidae (of 793 with males known). Prolateral half 130 spp. (24%), retrolateral half 416 spp. (76%), basal half 25 (4.6%), distal half 521 (95.4%); Basal prolateral quarter 2 spp. (0.4%), basal retrolateral quarter 23 spp. (4.2%), distal prolateral quarter 128 spp. (23.4%), distal retrolateral quarter 393 spp. (72.0%).

long emboli and long copulatory ducts have evolved independently and then have been shortened and resulted by chance in species with very similar, convergently developed short structures. In contrast, it seems more likely that those species with shorter structures are derivatives of one stem species and represent the initial point for lengthening in different lineages. There exist more such examples from further subfamilies, e.g. Heteropodinae, and Sparassinae. Another example, supporting the idea of lengthening copulatory structures, is the *Sinopoda okinawana*-group (for details see paragraph 'functional lengthening' in subchapter 'Different types of lengthening'). A further strong argument is of more hypothetical nature: considering the high percentage of species with long copulatory structures, it seems likely that there are mechanisms - yet unknown - triggering this kind of evolutionary process. If so, it would wonder, when this process could be reversed by the same mechanisms. One could ask, why species with short emboli are still present in the recent fauna, if the trend of lengthening and its mechanisms are so strong. But species composition is not a question of evolution alone, but also of post-evolutionary, ecological mechanisms, e.g. such as competition. However, for most of the aspects and thoughts presented here, it does not matter, whether the embolus and the copulatory ducts are lengthening or shortening in the evolution. For instance, the assumed combined morphological changes seem to be present anyway, no matter whether structures have been lengthened or shortened, and should be considered in future research, e.g. in phylogenetic analyses.

When considering the more derived states, i.e. those with a definitely long embolus and copulatory ducts, e.g. in the Deleninae, it is surprising that so little attention has been paid to this

striking phenomenon. No attempt has been made as yet, to explain the mechanisms behind the trend, either by looking for immediate or long-term causes. Although the present paper cannot provide any explanations in this respect, it does bring the phenomenon into sharp focus. The simple recognition of the trend is important for taxonomic descriptions, systematic sorting as well as for phylogenetic analyses, regarding the secondary effects it might have (see under ‘combined morphological changes’).

Because the phenomenon occurs in different spider families, the results obtained in the Sparassidae may serve as an example and may help to understand evolutionary mechanisms in these other families. I do not think that the results of one analysis may apply to all spider families as was done by WIEHLE (1961), as longer emboli and the corresponding structures in female spiders may have different causations. It may be useful for an organism to shift the spermathecae away from the close contact with the outside environment as it occurs in some Mygalomorphae, to prevent dehydration, bacteria infection or simply leakage. However, it is not likely that the same cause can be called upon to explain the development of more than 10 coils as is the case in the Deleninae. Moreover, it makes more sense to look at causal effects within one group with a large range of embolus types (here: Sparassidae), since the same structures may be used differently in non-related groups (RTA anchored in epigastric furrow in Sparassidae, but in epigyne in Gnaphosidae; pers. observ., SENGLLET 2004).

Different types of lengthening

Different types of lengthening structures which occur in different, but not closely related taxa, may point to general constraints, which, in the course of evolution, are effective and stabilise such a type of “increasing complexity” (sensu JOUQUÉ 1998). Apparent differences in species numbers and maximal lengthening of copulatory structures among the Sparassidae, lead to the question, whether the recent diversity of this family can be explained by this phenomenon? The example of the distal screw may show that, at least, part explanations can be found looking for functional constraints of the different types: the screw of *Olios* species is lengthened by circling around its length axis and by extending the length of the embolus in a retrolateral direction. The space for doing so is limited to the dorsal half of the bulb, as the embolus length axis has to remain straight, as only then a screw is functionable. According to the females’ genitalia, the male screw is indeed screwed into the copulatory ducts of the female. In this case a bent screw could not work, neither for a real screw, nor for a screw in spiders’ copulatory organs. We can presume that the bauplan of the ancestors of copulatory structures - once established in the course of evolution of a spider - restricts the subsequent evolutionary events in their evolutionary changes. Even if there was a strong evolutionary pressure for long copulatory structures in these *Olios* species-group, the development of a screw cannot be reversed. Thus, the development of a screw in the copulatory organ of this species group delimits its relative evolutionary output - i.e. results a fewer number of species – in comparison with other lineages without such (morphological) restrictions, e.g. with a distal coil and a higher maximal lengthening as e.g. in Deleninae.

The maximum length of a male embolus can also be delimited by restrictions in the particular female: a male embolus with a potential of maximal lengthening of for instance 200%, cannot lengthen further if the female duct system is restricted to 100% and could not accommodate the additional lengthened structures of the male. On the other hand, one explanation for the strongly lengthened emboli and ducts in the Deleninae may be a combination of two different factors: 1. the male distal coil of the embolus provides a system of lengthening which has no strong structural restrictions (i.e. tip of the embolus remains almost in the same position, while evolutionary lengthening and space saving type of coiling, backed up by the similar-shaped conductor, allow for a high number of coils; in comparison with the distal screw of *Olios* spp., the distal coil is

also restricted in its shape [only a circular coil is insertable in the case of several windings]. But this restriction does not decrease but increase the output with respect to the number of possible coils). 2. Additionally, the female duct system represents the rare case of being membranous and thus space saving, facilitating strong coiling within a restricted space (Fig. 13). The same number of coils would need a lot more space in the sclerotised form as in e.g. *Heteropoda* spp., as these cannot be folded, apart from the fact that sclerotised coils have thicker walls per se.

Uniformity within one type

Within one type of lengthening, the copulatory organs were distinctly uniform (e.g. Deleninae, *Heteropoda*). Diversifying appears, but apparently in fewer cases in comparison with lengthening events. In Deleninae, genera are distinguished by the shape of the tegular apophysis and the basally situated embolic sclerite (e.g. HIRST 1990). Based on the fact that Hirst distinguished genera by means of these diversifying elements, a ratio of about 1:10 is observed (11 genera, 105 species). This means that lengthening events occur 10 times more frequently than diversifying ones. A similar ratio is present in *Heteropoda*: from the total number of species (n=180) less than 10% (n=14) show diversifying elements, i.e. tegular apophyses, conductor apophyses or embolus modifications. A scenario which would explain this ratio is that the lengthening type develops faster than the diversifying one, i.e. produces more functionable variants within a specified time period. The apparent higher degree of freedom with respect to evolutionary changes in the copulatory traits in females of *Heteropoda* species, may be explainable by proximate causations of the individual development of these structures in the ontogeny. Investigations in this field would be interesting, but may be also complex to carry out.

Combined morphological changes

The observed morphological changes, in combination with an elongation of an embolus, may be explained by functional constraints based on copulatory mechanics. No investigations were conducted, so far, for this topic in the Sparassidae, whereas results of ‘frozen copulations’ were described in Gnaphosidae (SENGLET 2004) and Pholcidae (UHL *et al.* 1995, SENGLER 2001, HUBER 2002). In the latter cases investigated, exclusively diversifying types were present, i.e. no conclusions about the phenomenon on lengthening can be drawn. In respect of combined changes in tibia length, or different cymbium shapes, the observations made in the Sparassidae are backed up by observations in e.g. Zodariidae (*Palfuria panner* JOCQUÉ, 1991, *P. spirembolus* SZÜTS, JOCQUÉ, 2001: SZÜTS, JOCQUÉ 2001a; *Australutica moreton* JOCQUÉ, 1995, *A. quaerens* JOCQUÉ, 1995: JOCQUÉ 1995), Salticidae (*Bacelarella tentativa* SZÜTS, JOCQUÉ, 2001, *B. tanohi* SZÜTS, JOCQUÉ, 2001: SZÜTS, JOCQUÉ 2001b, JOCQUÉ, SZÜTS 2001) and Lamponidae (*Asadipus humptydoo* PLATNICK, 2000, *A. yundamindra* PLATNICK, 2000: PLATNICK 2000). Although a thorough analysis for each family or genus or even species group would be necessary for making statements, the examples may be seen as evidence for this trend of combined changes in other families (at least within the RTA-clade). However, the results shown here for the Sparassidae indicate that similar combined changes found in other taxa and their utilisation for systematical purposes may be viewed in a different perspective.

Position of embolus’ tip

A similar position for the embolus’ tip within one type of lengthening, and also among less closely related taxa, may point to a functional constraint, which inhibits a considerable shifting of the tip, since the behavioural, as well as morphological changes, to accommodate this shifting may be too intricate. Distinctly different positions within an assumed monophyletic lineage (e.g. in the subfamily Sparianthinae) on the other hand may point to a polyphyly or to different sublineages. The

position of the tip is considered here as just providing indications for further investigations.

A similar result, in respect of the position of the embolus' tip, is observed in other spider families, especially those from the RTA-clade: Philodromidae, Gnaphosidae, Lamponidae, Thomisidae, Salticidae, Corinnidae, etc. Constraints, in respect to functional morphology of the particular pedipalps or copulatory mechanics in male-female interaction, may explain why an embolus tip obviously cannot be situated in certain positions. It may have something to do with the fact that the RTA is fixed during the copulation and subsequent movements are possible only in a mechanically restricted frame, due to the automatic haemolymph pressure driven expansion of the haematodochae (as described in HUBER 2004). The typical embolus tip position for particular taxa, may act as additional diagnostic character, e.g. in *Sinopoda* and *Pseudopoda*, mostly in the prolateral distal quarter of cymbium, in *Heteropoda*, Deleninae, etc. in the retrolateral distal quarter of cymbium and so on. Once recognised as typical for a group an unusual position of an embolus tip can indicate a special systematic position for a particular species, e.g. basal or derived within the stem group.

Future studies should focus on a broad-range comparison within the family, i.e. to fix couples during copulation, and to show where the spermatophor opening is situated during copulation, which glandular parts of the female duct system are secreting to which part of the copula, and where the sperm mass is deposited. Results may enlighten mechanisms in the course of the evolution which are responsible for the process of lengthening, described above, and, partly, for the recent composition of species.

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Удължаване на емболуса и копулаторния канал: преглед на еволюционна тенденция при паяците от семейство Sparassidae (Araneae)

П. Йегер

(Резюме)

Разгледан е феноменът на удължаване на копулаторните структури при паяците от семейство Sparassidae. Определени са различни типове на модифициране и на удължаване, но се допускат и комбинации и преходи между тях. При 55% от изследваните 662 вида ясно се вижда, че емболусът и/или копулаторните канали са удължени в сравнение с прародителските видове, докато само при 8% не е установена елонгация на тези структури. Разграничени са следните типове на удължаване: “тегуларна спирала”, “дистална спирала”, “дистално витло”, неправилен или комбиниран тип, и така нареченото “функционално удължаване”. Комбинираните морфологични изменения, ставащи в процеса на еволюционното нарастване, вероятно зависят от функционалните ограничения. В тази връзка, положението на края на емболуса може да играе важна роля. Изясняването на функционалните и еволюционни аспекти на разглеждания феномен може да разкрие механизмите, които го отключват.