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Evolutionary Transformation From Muscular to Hydraulic Movements in Spider (Arachnida, Araneae) Genitalia: a Study Based on Histological Serial Sections

Bernhard A. Huber*

Zoological Research Institute and Museum Alexander Koenig, 53113 Bonn, Germany

ABSTRACT The male genitalia of 107 spider species representing 73 families were serially sectioned and studied with an emphasis on muscles moving the genital bulb. As a rule, most non-Entelegynae have two bulbal muscles, most Entelegyne have none, but many exceptions occur. Variation also occurs with regard to origin and attachment of bulbal muscles. There appears to be a trend towards a shift of the origin from proximal (*Liphistius, Atypus*) to more distal palpal segments (Haplogynae). In most Entelegynae the muscular movement is replaced by hydraulic movement caused by expanding membranes (hematodochae). Hematodochae probably permit increased bulbal rotation and movements of higher complexity. New evidence is presented arguing against Palpimanidae being representatives of Entelegynae. Bulbal glands other than those discharging into the sperm duct (previously known in Amaurobiidae and Dictynidae only) are described in several entelegyne families. J. Morphol. 261:364–376, 2004. © 2004 Wiley-Liss, Inc.

KEY WORDS: spider genitalia; hydraulic movements; muscles; glands; Palpimanoidea

Many spider movements are heavily dependent on hydraulics. It has long been known that certain leg joints are not provided with extensor muscles and that leg extension is accomplished by hydraulic pressure (Ellis, 1944; Frank, 1957; Parry and Brown, 1959). In many spiders, hydraulics are also involved in the movements of the male copulatory organs, the genital bulbs on the pedipalps (e.g., van Helsdingen, 1965; Grasshoff, 1973; Lamoral, 1973; Loerbroks, 1984; Huber, 1993; Eberhard and Huber, 1998). However, in contrast to leg extension, there is considerable variation in the way genital bulbs are moved: muscular, hydraulic, or both (Cooke, 1970; Haupt, 1979; Huber, 1994). This provides an opportunity to study the evolutionary transformation of muscular to hydraulic movement.

Male spider genital bulbs are ontogenetically derived from cells of the pedipalpal "claw fundament" (review: Coddington, 1990). These epidermal cells also secrete the tendons of two muscles (m29 and m30 following the terminology of Ruhland and Rathmayer, 1978) that move the genital bulbs prior and during intromission. In most "primitive" (non-Entelegynae) spiders, both muscles are present in adult males. They play an important role both in directing the genital bulb into the female copulatory opening and in putative courtship during copulation by rhythmical movements (Harm, 1931; Cooke, 1966; Haupt, 1979; Huber and Eberhard, 1997). In "higher" spiders (Entelegynae), these muscles have long been thought to be absent (Cooke, 1970). In these spiders, bulbal movements result from the expansion of folded membranes connecting the various sclerites as well as from the elasticity of certain components (van Helsdingen, 1965; Grasshoff, 1973; Loerbroks, 1984; Huber, 1993; Eberhard and Huber, 1998). The membranes (hematodochae) are expanded by hydraulics, i.e., by pressure increase generated primarily in the prosoma (Anderson and Prestwich, 1975). Different types of movements (rotation, expansion, tilt) are generated by the specific way in which the hematodochae are folded at rest.

The present study aims at providing an overview of the morphological basis of genital bulb movements and attempts to answer when, how often, and why muscular movements were replaced by hydraulic movements in spider evolution.

MATERIALS AND METHODS

This study is based on histological serial sections of the male pedipalps of 107 species representing 73 spider families. The Appendix lists the species studied. Most of the material was fixed and preserved in ethanol, 70–80%, which does not result in brilliant sections but was both unavoidable and sufficient in the present case. The pedipalps were usually cut in the patella area, dehydrated, embedded in Spurr's medium (ERL epoxy resin) after vacuum impregnation, serially sectioned with a Microm HM 350 rotation microtome (1 μm) using a diamond knife, and stained with a mixture of azur II (1%) and methylene blue (1%) in an aqueous borax solution (1%) at 70°C for about 20 sec. Photos

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*Correspondence to: B.A. Huber, Zoological Research Institute and Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany. E-mail: b.huber.zfmk@uni-bonn.de

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were made with a Nikon Coolpix 995 digital camera (2048 × 1536 pixels) mounted on a Leitz Dialux 20 compound microscope. In total, about 40,000 sections were produced, of which about 10,000 were saved and mounted on slides.

The term "hematodocha" has been used ambiguously (Huber, 2002). I will emphasize the aspect of homology and use the term for any membrane that allows or actively produces movement of the bulb or of parts of it. Most important in the present context is the membrane connecting the genital bulb to the tarsus, the basal hematodocha. Pedipalps are shown with distal ends toward the left and ventral sides up unless indicated otherwise.

RESULTS

There is a striking basic agreement between certain taxonomic units and the morphology of the genital bulb. Therefore, the results are presented in four sections, corresponding to successive branches of the phylogeny of spiders (Coddington and Levi, 1991): 1) *Liphistius* represents the most basal branch, the Mesothelae, believed to show plesiomorphic conditions in many characters; 2) Mygalomorphae, the sister group of higher (araneomorph) spiders; 3) "non-entelegyne araneomorphs," a paraphyletic group including the Palaeocribellatae, the Austrochiloidea, and the Haplogynae; and finally, 4) the Entelegynae. Palpimanoids (including Palpimanidae) are included in Entelegynae because cladistic analysis has not yet suggested otherwise (Platnick et al., 1991; but see Discussion section).

Liphistiidae

Liphistius bristowei has the plesiomorphic pair of muscles, but these muscles originate more proximally than in any other spider studied. The m29 originates in the patella and tibia, the m30 in the tibia (Fig. 1). A similar situation (with no muscle originating in the tarsus) was only found in *Atypus* (see below). Haupt (1983) reported a different situation for *Heptathela kimurai*, but it is not clear whether he specifically studied the points of origin or simply assumed that they would be identical to those reported for *Aphonopelma hentzi* (as *Dugesiella h.*) by Ruhland and Rathmayer (1978).

Both muscles attach to the bulb via tendons. The tendon of m29 winds around the basal sclerite of the bulb (Fig. 1), while the tendon of m30 attaches to this same sclerite without winding around it. Attachment data thus agree with those reported by Haupt (1978, 1979, 1983) for *Heptathela kimurai* and *H. nishihirai*.

The basal hematodocha of *Liphistius bristowei* is weakly folded (Fig. 1), comparable to the membranes of leg joints and between bulbal sclerites. In *Heptathela nishihirai*, the basal hematodocha supposedly aids the muscles in moving the genital bulb (Haupt, 1979).

Mygalomorphae

All mygalomorphs studied have both muscles, but there is variation with respect to the origins. In *Atypus affinis*, both muscles originate in the tibia (Figs. 3, 4). In no other spider except *Liphistius* and *Atypus* was the origin of m30 restricted to the tibia. Two *Atypus* palps were sectioned and both show the m30 to originate in the tibia and not in the tarsus as illustrated by Heimer (1990: fig. 21). Two species, *Hadronyche* sp. and *Missulena bradleyi*, are unique in having a split m30: most of it originates in the tarsus, but a smaller part originates in the tibia (Fig. 7). In all other mygalomorphs (and araneomorphs with muscles), the m30 is restricted to the tarsus (Figs. 2, 5; cf. Barrows, 1925 on "*Eurypelma californica* Ausserer").

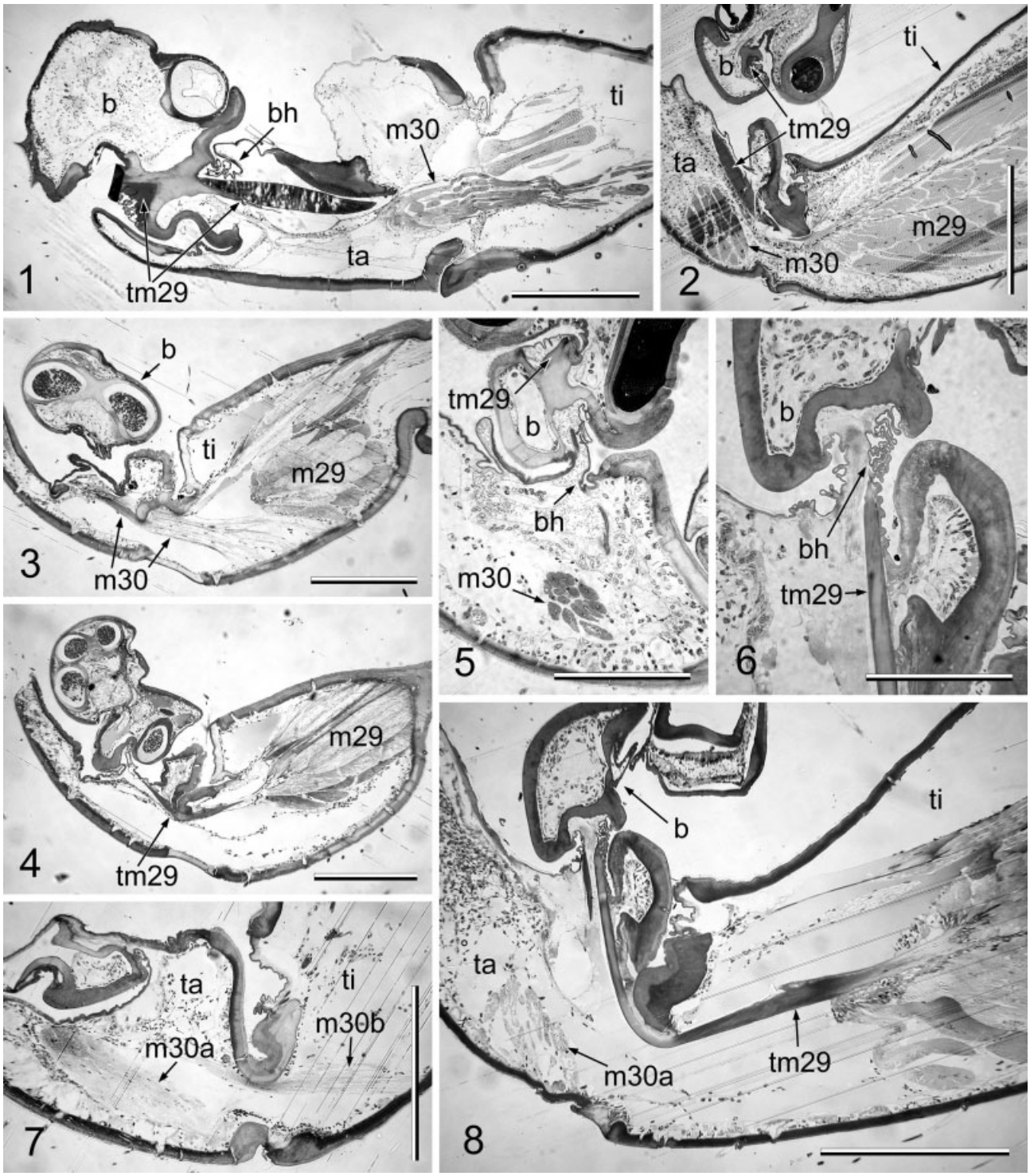
A similar degree of variation occurs in the origin of m29. In some mygalomorphs there is clearly a part that originates in the patella (*Hadronyche, Chenistonia, Homostola*), in others it is clearly restricted to the tibia (*Masteria, Atypus*; Barrows, 1925: "*Eurypelma c.*"), in some it could not be determined if it reaches back to the patella or not because the patella was not sectioned (*Bymainiella, Australothele, Namirea, Aname, Seqocrypta, Missulena*).

The m29 enters the tarsus as a tendon and attaches to the basal sclerite of the bulb winding around it (Fig. 2). The m30 may be provided with a tendon (*Australothele*: ~10% of total length; *Atypus*: very short) or attach to the distal rim of the basal bulbal sclerite without a tendon. As in *Liphistius*, it does not wind around the basal bulbal sclerite. Basal hematodochae were poorly developed in all cases, resembling the joint membranes of flexed legs (Figs. 5, 6).

Non-Entelegyne Araneomorphae

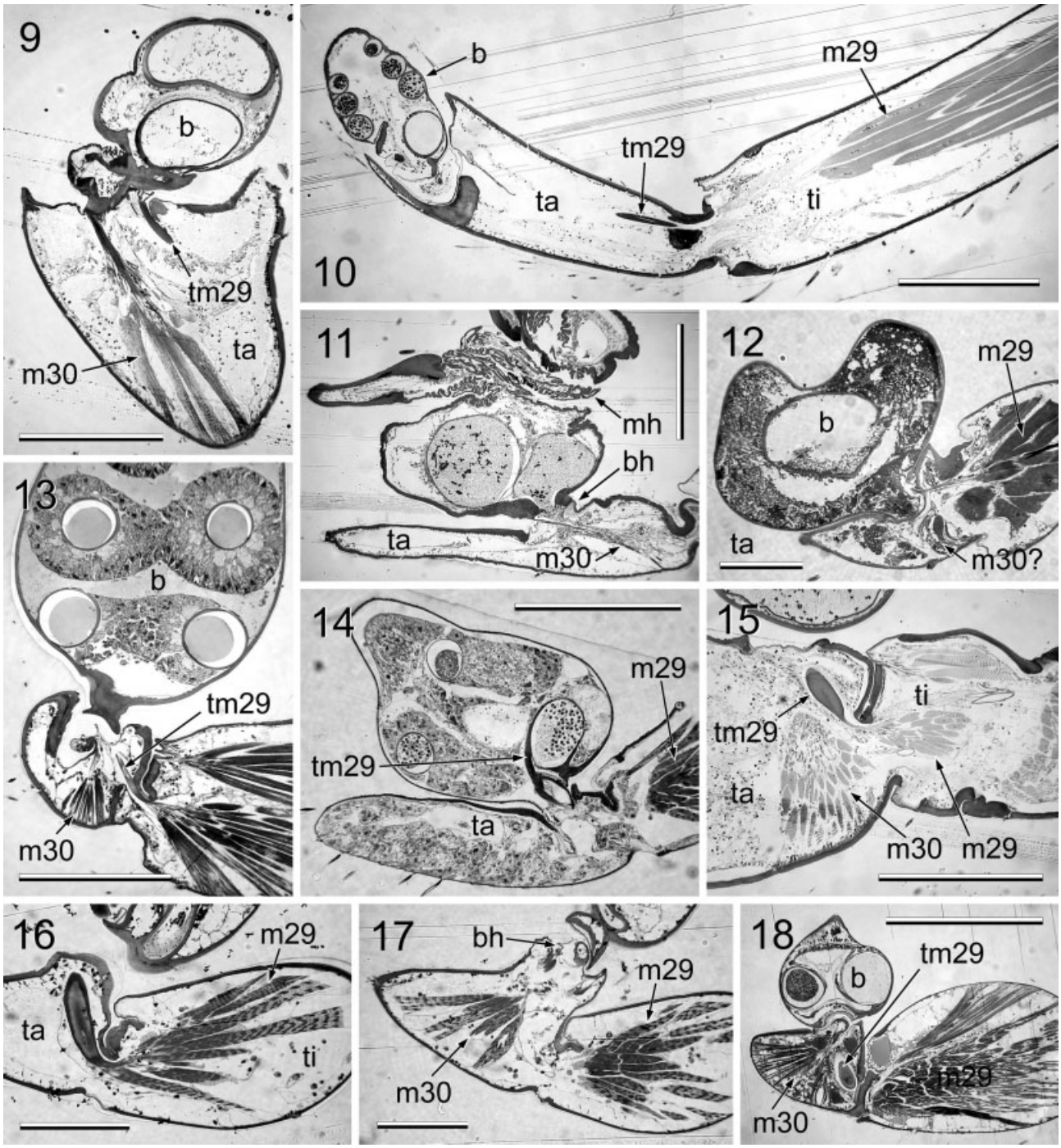
In representatives of this large paraphyletic group both muscles are usually present. The m29 usually originates in the tibia, the m30 in the tarsus. Exceptions occur in *Hypochilus*, in filistatids, and in oonopids. In *Hypochilus* (Fig. 9), the m29 partly originates in the patella, comparable to *Liphistius* and some mygalomorphs. In Filistatidae (Fig. 10) there is no m30. In the unidentified oonopid, the bulb is fused to the tarsus and both muscles are absent. In *Oonops pulcher*, the m29 is present but the m30 is either absent or reduced to connective fibers with very thin striated muscle fibers among them (Fig. 12). If these fibers are correctly identified, the muscles are composed of no more than about four sarcomeres. Heimer (1989) reported both muscles present in *O. pulcher*.

As in *Liphistius* and mygalomorphs, the m29 enters the tarsus as a tendon. Its mode of attachment could not be clearly resolved in all cases. Only in *Hypochilus* and *Caponia* it appeared to wind around



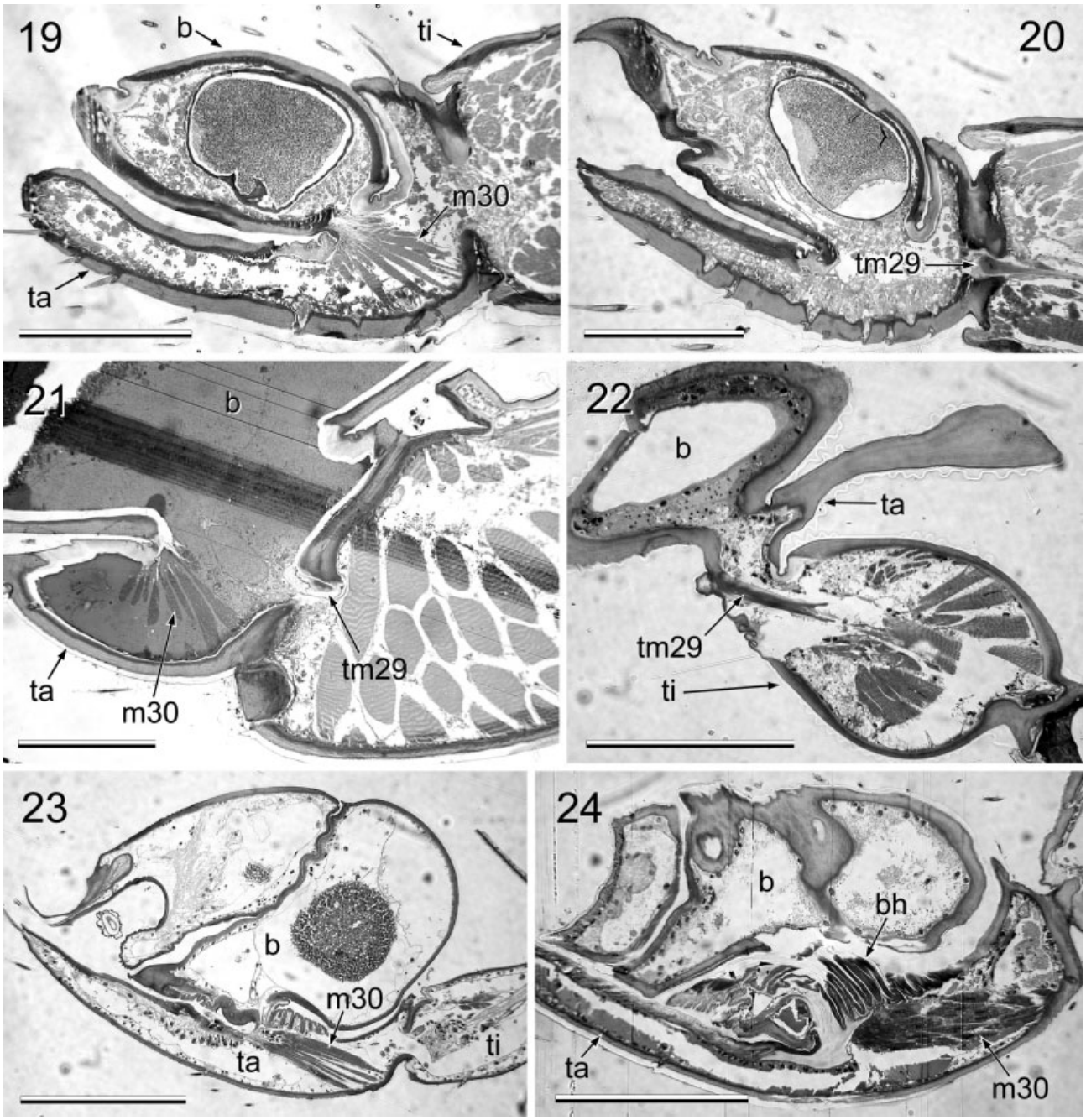
Figs. 1–8. Mesothelae and Mygalomorphae. 1: *Liphistius bristowei*. 2: *Homostola* sp. 3–4: *Atypus affinis*. 5: *Bymainiella terraereginae*. 6–8: *Hadonyche* sp. b, genital bulb; bh, basal hematodocha; m29/30, genital bulb muscles m29 and m30; ta, tarsus; ti, tibia; tm29, tendon of m29. Scale lines: 0.2 mm (5, 6), 0.3 mm (3, 4), 0.5 mm (1, 2, 7, 8).

the basal bulbal sclerite, much as in *Liphistius* and mygalomorphs (Fig. 9). In all other species the tendon rather seems attached to the inside of the basal bulbal sclerite. Only in some species (*Wiltonia, Oonops, Dysdera*), the tendon continues towards the sperm duct (Fig. 14; cf. Cooke, 1966 on *Dysdera crocata*; Harm, 1931 on *Segestria bavarica*; Heimer, 1990, fig. 29 on *Scytodes longipes*).



Figs. 9–18. Non-entelegyne Araneomorphae. 9: *Hypochilus pococki*. 10: *Kukulcania hibernalis*. 11: *Thaida peculiaris*. 12: *Oonops pulcher*. 13: *Segestria senoculata*. 14: *Wiltonia graminicola*. 15: *Caponia* sp. 16–17: *Ochyrocera* sp. 18: *Loxosceles rufescens*. b, genital bulb; bh, basal hematodocha; m29/30, genital bulb muscles m29 and m30; mh, median hematodocha; ta, tarsus; ti, tibia; tm29, tendon of m29. Scale lines: 0.05 mm (12), 0.1 mm (16, 17), 0.2 mm (14), 0.3 mm (9, 13), 0.5 mm (10, 11, 15, 18).

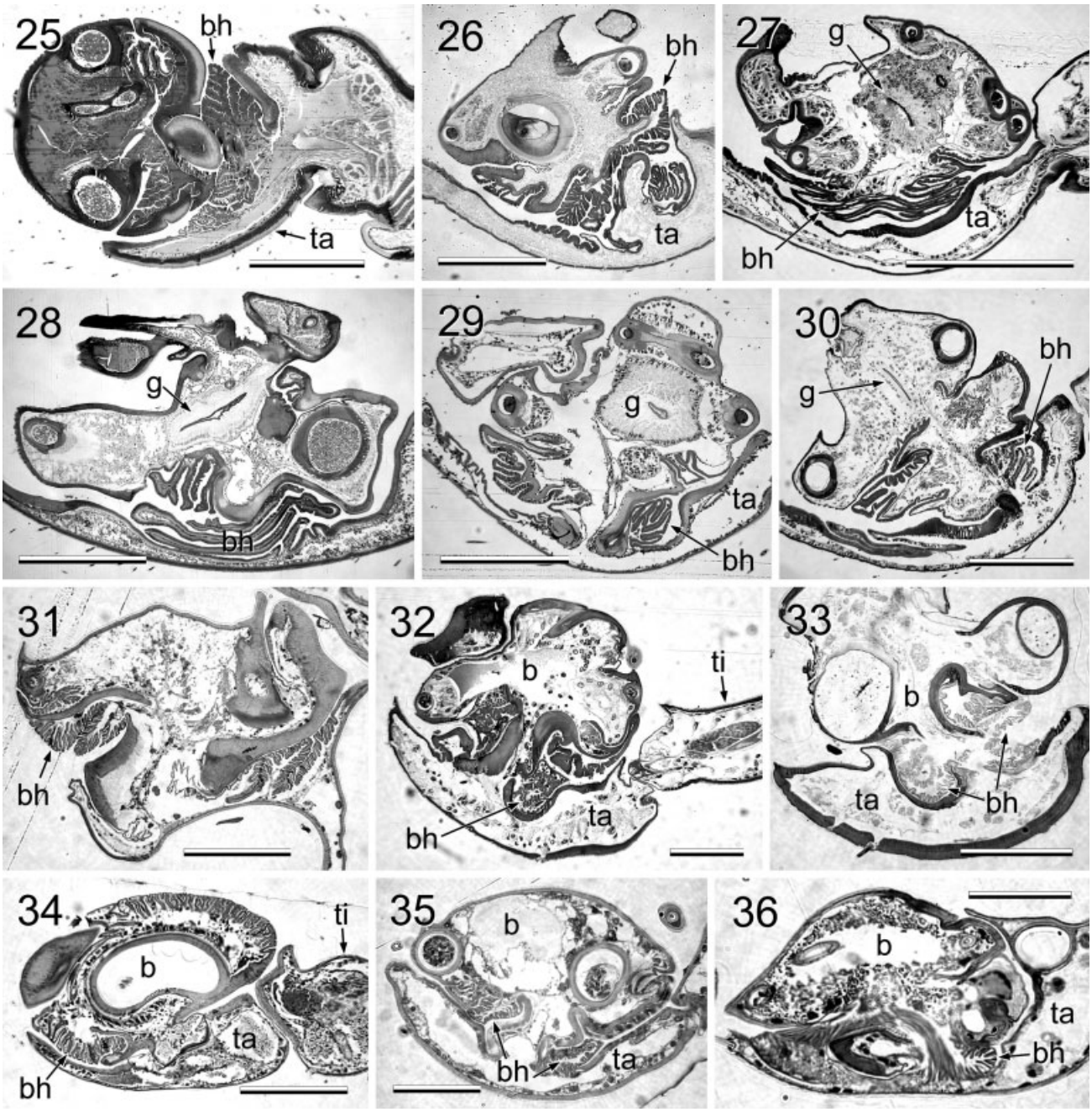
The m30 usually attaches to the basal bulbal sclerite without winding around it; either via a distinct tendon (*Hypochilus*, Fig. 9), a short tendon (*Caponia, Wiltonia, Segestria, Ochyrocera, Proleptoneta, Scytodes*) or without tendon. Basal hematodochae are poorly developed, much as in *Liphistius* and in mygalomorphs (Figs. 10, 11, 12, 14, 17, 18). The median hematodocha of *Thaida* is remarkably well developed (Fig. 11), comparable to that of *Grandungula* (cf. Huber, 1994, figs. 1, 2).



Figs. 19–24. Palpimanidae and Mecysmaucheniidae. 19–20: *Palpimanus* sp. 21: *Anisaedus pellucidas*. 22: *Otiothops atlanticus*. 23: *Aotearoa* sp. 24: *Mecysmauchenius segmentatus*. b, genital bulb; bh, basal hematodocha; m29, genital bulb muscle m29; ta, tarsus; ti, tibia; tm29, tendon of m29. All scale lines 0.2 mm.

Entelegynae

Most entelegynes studied have no bulbal muscles and are provided with a strongly developed basal hematodocha (Figs. 25–36). Exceptions occur as follows: 1) In *Tama* and *Hersilia* (but not in *Tamopsis*) and in *Uroecobius* (but not in *Oecobius* and *Uroctea*) the m30 is present in the tarsus (Huber, 1994) and the basal hematodocha is poorly (*Uroecobius, Tama*) to well (*Hersilia*) developed. 2) In Palpimanidae, both muscles are present in *Palpimanus* and *Anisaedus* (Figs. 19–21), while only m29 is present in *Otiothops* (Fig. 22). In all three species the basal hematodocha is very poorly developed, comparable to non-entelegynes. 3) In Mecysmaucheniidae (Figs. 23, 24), *Argyroneta aquatica*, and *Deinopis* sp., the m30 is present (in the tarsus), and the basal hema-



Figs. 25–36. Entelegynae. 25: *Eresus cinnaberinus* (horizontal). 26: *Megadictyna thilenii*. 27: Cycloctenidae gen. sp. indet. 28: *Uliodon tarantulinus*. 29: *Stiphidion facetum*. 30: *Maniho ngaitaho*. 31: *Mysmenopsis tengellacompa* (horizontal). 32: *Ero canionis*. 33: *Chilenodes australis*. 34: *Miagrammopes animotus*. 35: *Sofanapis antillanca*. 36: *Symphytognatha picta*. b, genital bulb; bh, basal hematodocha; g, gland; ta, tarsus; ti, tibia. Scale lines: 0.05 mm (35, 36), 0.1 mm (31–34), 0.3 mm (25, 27, 28, 29), 0.5 mm (26).

todocha is very well developed (slightly less in *Aotearoa*: Fig. 23).

Some previous mentions of muscles in entelegyne spider bulbs are clearly erroneous (Billaudelle, 1957, on *Dictyna*; Haupt, 1983, fig. 1a on *Nuctenea*; Heimer, 1989, on various families).

A secondary result of this study is the discovery of presumably glandular tissue in addition to the usual sperm duct glands in the bulbs of some entelegyne spiders. Figures 27–30 show four examples (representatives of Cycloctenidae, Miturgidae, Stiphidiidae, Amphinectidae), and similar tissue occurs in the tegulum of *Pisaura mirabilis*. Such glands have previously been known from *Amaurobius* and *Dictyna* only (Suhm et al., 1995; Huber, 1995), but are apparently widespread.

DISCUSSION

Homologies: Muscles, Entelegyne Hematodochae, and Sperm Ducts

The terminology above implies that the bulbal muscles are homologs of the claw flexors (m29) and extensors (m30) in the walking legs (Ruhland and Rathmayer, 1978). In walking legs, the m29 originates either in patella and tibia (*Aphonopelma*: Ruhland and Rathmayer, 1978), in the tibia (*Zygiella*: Frank, 1957), in tibia and basitarsus (*Latrodectus*: Whitehead and Rempel, 1959), or in the basitarsus (*Gasteracantha*: Emerit, 1972). This is a similar degree of variation as described herein for pedipalps (assuming that the thin patellar component has not been overlooked in some previous studies using gross dissection). Much the same occurs with leg muscle m30: it may originate in tibia and basitarsus (*Latrodectus*: Whitehead and Rempel, 1959), or in the basitarsus only (*Aphonopelma, Zygiella, Gasteracantha*). In no spider leg is it known to originate entirely in the tibia, like in *Liphistius* and *Atypus* pedipalps, but it may well do so in these and other unstudied taxa. The most parsimonious solution is that the longer bulbal muscle is homologous to the longer claw muscle, i.e., to the walking leg muscle m29.

Another problem is the nomenclature in species that have only one bulbal muscle. Considering the variability in origins, it is the attachment that provides confirmatory evidence. There is a significant difference in the attachment mode between the two muscles in most spiders. The m29 winds around the basal sclerite of the bulb or enters the bulb, while the m30 attaches to the basal sclerite without winding around it. This confirms that the single muscle in filistatids and in *Otiothops* is m29, while the single muscle in certain hersiliids, *Uroecobius*, mecysmaucheniids, *Argyroneta*, and *Deinopis* is indeed m30 (and not m29 whose origin has moved into the tarsus).

The highly expandable basal hematodochae of entelegynes are clearly derived from the simple membranes connecting tarsus and bulb in more primitive spiders. Interestingly, variation has been reported regarding the direction of movement of the expanding hematodocha: in most entelegyne spiders studied, the left bulb moves clockwise when seen in ventral view (Loerbroks, 1983, 1984: *Heriaeus, Misumena*; Sierwald, 1987: *Thalassius*; Eberhard and Huber, 1998: *Leucauge*; Kropf, 1990: *Comaroma*; Lamoral, 1973: *Palystes*; Melchers, 1963: *Cupiennius*; Blest and Pomeroy, 1978: *Mynoglenes*; van Helsdingen, 1969: *Neriene*; Osterloh, 1922: *Linyphia, Agelena*). This is the same direction as observed for muscular movement in more primitive spiders (Kraus, 1984: *Heptathela*; Huber and Eberhard, 1997: *Physocyclus*). However, in some it moves counterclockwise (Dondale, 1986: Lycosidae, some Pisauridae; van Helsdingen, 1965: *Lepthyphantes*). The taxonomic distribution of character states suggests that counterclockwise movement has repeatedly evolved from clockwise movement, rather than that highly expandable basal hematodochae have originated more than once.

Cooke (1970) proposed the idea that sperm ducts of Haplogynae and Mygalomorphae may not be homologous, arguing with different muscular attachment sites. Such differences do occur indeed. In *Liphistius*, Mygalomorphae and a few basal Araneomorphae (*Hypochilus, Caponia*), the tendon of m29 winds around the basal sclerite of the bulb (Figs. 1, 2, 5, 9). In all other Araneomorphae with m29 present the tendon either enters the bulb and continues to the sperm duct (*Wiltonia*, Fig. 14), attaches to the basal sclerite on the inside (*Otiothops*, Fig. 22), or attaches to the thickened basal hematodocha (*Palpimanus, Anisaedus*). Character mapping on the cladogram of Coddington and Levi (1991) suggests that the situation in *Liphistius*, Mygalomorphae, and *Hypochilus* is plesiomorphic, and that other attachment modes are derived. However, the details of attachment were often difficult to observe on the sections and the topic warrants further investigation.

Potential Selective Advantage of Hydraulics

Spiders evolved two major innovations concerning bulbal movement: 1) the transformation of the hinge movement of claws to a rotating movement of the bulb caused by changes in the attachment mode of m29; and 2) the transformation of predominantly muscular to predominantly hydraulic movement by expansion of specifically folded membranes. The first transformation occurred before the evolution of the most primitive extant spiders, the second at the base of entelegyne spiders. I hypothesize that both transformations may have been driven by similar selective forces, i.e., to evolve, maintain, or improve on the mobility of the genital bulb. The question of why complex movements are advantageous is a different issue. It may be for the simple mechanical reason that complex movements may improve the lock between male and female structures during sperm transfer. It may also be that more complex movements trigger female responses that are advantageous for the male in a sexual selection context.

Whatever the ultimate reason, muscular movement appears limited for several reasons: first, the length of the muscle determines the degree of movement (maximum reported rotation in muscular bulbs is 300°: Huber and Eberhard, 1997); second, depending on the complexity of the joints, the resulting movement is more or less limited to one plane, i.e., two-dimensional; third, structures cannot be moved away by muscles unless a lever system be integrated. All these limitations do not apply for hematodochae. Expanding hematodochae may rotate the bulb to considerable degrees (430° in *Cupiennius* [Melchers, 1963], 500° in *Agelenopsis* [Gering, 1953], 540° in *Tapinocyba* [Martin, 1981]), and

depending on how the hematodocha is folded at rest, it may unfold in a complex way, often including rotation, tilt, and expansion that moves structures away.

In sum, hematodochae improve bulbal mobility and produce movements of higher complexity, movements that are not easily generated with one pair of muscles.

Systematic Implications: the "Palpimanoidea"

Forster and Platnick (1984) created the superfamily Palpimanoidea to include both haplogyne (e.g., Palpimanidae) and entelegyne (e.g., Mimetidae) families. The monophyly of Palpimanoidea was supported by the cladistic analysis of Platnick et al. (1991) that placed the superfamily within the clade "Higher Entelegynes." This view was adopted by Coddington and Levi (1991), but not by others (e.g., Wunderlich, 1986; Lehtinen, 1996). It was Schütt (2000, 2003) who provided strong evidence against it, moving several "palpimanoid" families to the Araneoidea. However, some "palpimanoid" families, like Palpimanidae and Mecysmaucheniidae, were not treated by Schütt (2000, 2003) nor by Griswold et al. (1999), even though the latter were specifically concerned with Entelegynae. I propose that palpimanid bulbal muscles argue for a much more basal position of palpimanids, not within "Higher Entelegynae" but at their base, or even outside Entelegynae.

Haplogyne female genitalia occur in several families within Entelegynae (e.g., Uloboridae, Tetragnathidae, Anapidae), and are easily explained by the secondary loss of the copulatory ducts. The occurrence of "haplogyne" male genitalia (defined here as genitalia with both bulbal muscles present) within Entelegynae is not that easily explained. While it does not necessarily imply regaining of a lost structure (the muscles may have been retained in juveniles; cf. Szombathy, 1915; Barrows, 1925; Harm, 1935; Bhatnagar and Rempel, 1962; Sadana, 1971; but see Gassmann, 1926), it is hard to imagine the palpimanid bulb derived from an entelegyne bulb without muscles and well-developed basal hematodocha. The apparently simultaneous reversal in females also to a haplogyne condition makes it all the more improbable. Therefore, I rather agree with Platnick's (1975, p. 2) former conclusion that "it is far more likely that the palpimanids share a common ancestor with one or more of the other haplogyne families." Future data matrices for phylogenetic reconstruction will have to include both bulbal muscles and will show whether it is the male bulb and female haplogyne genitalia or the canoe tapetum (Homann, 1971) that is homoplastic and misleading.

Open Questions

The hemolymph pressure needed for leg extension and hematodochal expansion is generated primarily in the prosoma (Wilson, 1970; Anderson and Prestwich, 1975), resulting in a general increase of pressure in the spider's body rather than in a localized increase at specific joints or at the bulb in use. In legs, extension can be inhibited by the flexor muscles, but it is not clear how in genital bulbs without muscles one hematodocha remains collapsed while the other is expanding. Rovner (1975) and Rovner and Wright (1975) hypothesized a valve in the palp that is opened by muscles but closed during most of the spider's life. This may explain the observation that genital bulbs are often difficult to infiltrate even with low viscosity resins. More specifically, in the present study it usually was the tibia-tarsus joint that separated the well fixed and well infiltrated tissue from the poorly fixed and poorly infiltrated one. A similar position of the valve is suggested by Knoflach's (2002) findings on *Echinotheridion gibberosum*. In this species, the male autotomizes the palp at the tibia-cymbium joint and the expanded hematodocha remains expanded, probably due to the valve being closed. Whatever the details, some sort of valve must exist, but the constructional details remain to be established. Moreover, Rovner's hypothesis raises the question of how the area distal of the valve is supplied with hemolymph.

Kraus (1984) distinguished between hydraulic and glandular genital bulbs (admitting "intergrading stages"), arguing with differences in the mode of sperm ejaculation. However, with the exception of Liphistiidae, and maybe a few other spiders (cf. Kraus, 1978; Lopez and Juberthie-Jupeau, 1985; Lopez, 1987), all genital bulbs studied herein seem to have glands that secrete into the sperm duct (cf. Lopez, 1977, 1987; Juberthie-Jupeau and Lopez, 1981; Lopez and Juberthie-Jupeau, 1982, 1985; Suhm et al., 1995), and some hydraulic mechanism seems to be involved in most if not all bulbs. This makes a distinction of glandular vs. hydraulic problematic. The temporal coincidence between hematodochal expansion and ejaculation has lead to the belief that the two are causally related, but experimental and morphological evidence argues against it (Cooke, 1966; Huber and Eberhard, 1997). Obviously, the exact mechanism of gland activation for sperm ejaculation (and induction) is still poorly understood (Cooke, 1966; Lamoral, 1973). Therefore, I propose a distinction between hydraulic and muscular genital bulbs, emphasizing the undisputed key role of hydraulics in bulbal mobility rather than in sperm ejaculation.

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APPENDIX

Taxa studied, listed according to Coddington and Levi (1991). Asterisks indicate specimens that were taken from the Vienna University students' collection and whose collection data were unknown.

Liphistiidae
Liphistius bristowei Platnick and Sedgwick, 1984
Thailand: Doi Suthep, 1290 m, 9.x.1986 (P. Schwendinger)

Hexathelidae
Hadronyche sp. (sp. 19: Gray 1987)
Australia: SEQ, Mt. Superbus (28°14′S, 152°29′E), 9.ii.-12.iii.1990 (G. Monteith, G. Thompson, T. Churchill), QM S21246
Bymainiella terraereginae (Raven, 1976)
Australia: SEQ, Lamington N.P., O'Reillys (28°14′S, 153°08′E), iv.-vi.1982 (G. Monteith); QM S11080

Dipluridae
Masteria toddae Raven, 1979
Australia: NEQ, Cape Tribulation, 2.5 km W, site 5 (16°05′S, 145°27′E), 23.ix.-7.x.1982 (G. Monteith, D. Yeates, G. Thompson), QM S8141
Australothele jamiesoni Raven, 1984
Australia: SEQ, Numinbah Valley (28°12′S, 153°13′E), x.1989 (R. Fleay-Thompson); QM S15925
Namirea planipes Raven, 1984
Australia: SEQ, Brisbane, Mt. Coot-tha (27°29′S, 152°57′E), 14.xii.1979 (R.J. Raven); QM S 9790

Nemesiidae
Chenistonia earthwatchorum (Raven, 1984)
Australia: NEQ, Upper Gayundah Creek, Hinchinbrook (18°22′S, 146°13′E), 9-11.xi.1984 (G. Monteith, D. Cook); QM S 21249
Aname pallida L. Koch, 1873
Australia: SEQ, Biloela (24°24′S, 150°31′E), 14.x.1987 (D.P.I.), inside house; QM S3170

Barychelidae
Seqocrypta jakara Raven, 1994
Australia: SEQ, Brisbane, Fig Tree Pocket (27°28′S, 153°03′E), 22.vii.1973 (V.E. Davies); QM S6627

Atypidae
Atypus affinis Eichwald, 1830*

Cyrtaucheniidae
Homostola sp.
Swaziland: Mlilwane Game Reserve, 31.iii.2001 (K. Schütt), in ZFMK

Actinopodidae
Missulena bradleyi Rainbow, 1914
Australia: New South Wales, Murwillumbah (28°20′S, 153°24′E), 1.iii.1975 (D. Ball, in swimming pool); QM S21245

Hypochilidae
Hypochilus pococki Platnick, 1987
USA: North Carolina, Jackson Co., Caney Fork Rd., 1.2 mi N intersec. with Johns Cr. Rd., 2350 ft elev., 8.ix.1994 (F. Coyle), on boulders; det. F. Coyle 1994

Gradungulidae
Gradungula sorenseni Forster, 1955
New Zealand: Fiordland, Secretary Is., pitfall, iii.1984 (C.F. Butcher)

Austrochilidae
Thaida peculiaris Karsch, 1880
Chile: Llanquihue; Salto Petrohue, V. Perez N.P., mixed moist forest, 23.xii.1984-4.ii.1985 (S. and J. Peck), in AMNH

Filistatidae
Kukulcania hibernalis (Hentz, 1842)
Costa Rica: San Jose, on building, 1995 (B.A. Huber)
Filistata insidiatrix (Forskål, 1775)
Italy: Sicily, Taormina, 29.viii.1993 (B.A. Huber)

Caponiidae
Caponia sp.

South Africa: Northern Prov., near Pietersburg, 26.viii.1974 (E. Kullmann), in ZFMK

Orsolobidae
Wiltonia graminicola Forster and Platnick, 1985
New Zealand: Otago, Flagstaff, in tussock, 9.iii.1982 (R.R. Forster)

Oonopidae
Gen. sp.
Costa Rica: Heredia, La Selva, near Pto. Viejo de Sarapiqui, 20 m, 1995 (G. Delgado), in ZFMK
Oonops pulcher Templeton, 1835
Germany: Bonn, Plittersdorf (~50°42′N, 7°09′E), in house, 2.x.2002 (B.A. Huber)

Dysderidae
Dysdera ninnii Canestrini, 1868*
Harpactea rubicunda (C.L. Koch, 1838)
Austria: Vienna, Prater (~48°13′N, 16°24′E), 28.iii.1992 (B.A. Huber)

Segestriidae
Segestria senoculata (Linnaeus, 1758)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), 8.iii.1992 (B.A. Huber)

Pholcidae
Pholcus phalangioides (Fuesslin, 1775)
Germany: Denzlingen (near Freiburg), in house, 16.ii.1992 (B.A. Huber)
Metagonia mariguitarensis (González-Sponga, 1998)
Venezuela: Estado Sucre, Marigüitar (10°26.5′N, 63°54.5′W), ~30 m a.s.l., 29.xi.2002 (B.A. Huber)

Diguetidae
Diguetia sp.
USA: California, San Benito Co., Clear Creek, 10 mi S Idra, 15.viii.1969 (M.M. Bentzien), in AMNH

Plectreuridae
Plectreuris tristis Simon, 1893
USA: California, San Bernardino Co., Pisgah Lava Flow, station 24, 18.iv.1959 (B. Banta)

Ochyroceratidae
Ochyrocera sp.
Costa Rica: San Jose Prov., San Antonio de Escazu, xi.1995 (B.A. Huber), in ZFMK

Leptonetidae
Proleptoneta sp. [cf. *italica* (Simon, 1970)]
Italy: Udine Prov., Bordano, 260 m, 12.vi.1991 (F. Gasparo)

Sicariidae
Loxosceles rufescens (Dufour, 1820)
Italy: Sicily, Taormina, 29.viii.1993 (B.A. Huber)

Scytodidae
Scytodes thoracica (Latreille, 1802)
Austria: Vienna, in house, 1.vii.1992 (B.A. Huber)

Oecobiidae
Uroctea durandi (Latreille, 1809)*
Oecobius cellariorum (Dugès, 1836)
Italy: Trieste, in house, 3.iv.1993 (F. Gasparo)
Uroecobius ecribellatus Kullmann and Zimmermann, 1976
South Africa: North West Prov., Broederstroom (25°45′S, 27°52′E), 21.vii.1986 (A.S. Dippenaar-Schoeman)

Hersiliidae
Hersilia sp.
South Africa: KwaZulu Natal, farm Vergeval, district Ngotsche near Pongola (27°29′S, 31°40′E), 2.v.1967 (A.S. Dippenaar-Schoeman)
Tama sp.
South Africa: KwaZulu Natal, farm Vergeval, district Ngotsche near Pongola (27°29′S, 31°40′E), 27.vi.1968 (H. v. Ark)
Tamopsis parthensis Baehr and Baehr, 1987
Collection data unknown (probably Perth, Australia; B. Baehr, pers. commun.)

Eresidae
Eresus cinnaberinus (Olivier, 1789)*

Nicodamidae
Megadictyna thilenii Dahl, 1906
New Zealand: Orongoronga, 1.iii.1992 (M. Fitzgerald)

Cycloctenidae
gen. sp.
Australia: Tasmania, Florentine Valley, 29.2 km WNW Maydena, on Eleven Rd., 460 m, 6.ii.1980 (A. Newton, M. Thayer), det. D. Silva, AMNH

Zodariidae
Zodarion germanicum (C.L. Koch, 1837)*

Miturgidae
Uliodon tarantulinus (L. Koch, 1873)
Australia: SCQ, Mt. Moffatt N.P., Dargonelly Rock Holes (25°01′S, 147°57′E), 20-27.ix.1986 (M. Bennie); QM S15981

Homalonychidae
Homalonychus theologus Chamberlin, 1924
USA: California, San Bernardino Co., Pisgah Lava Flow, station 11, 17.iv.1959 (B. Banta)

Mimetidae
Ero canionis Chamberlin and Ivie, 1935
USA: Idaho, NE Fruitland, 116.55′W, 44.01′N, 10-25.ix.1943 (W. Ivie)
Gnolus cordiformis (Nicolet, 1849)
Chile: Cautin: Chacamo, NW of Nueva Imperial and W of Temuco, 16-24.ii.1981 (L.E. Peña)

Malkaridae
Chilenodes australis Platnick and Forster, 1987
Chile: Cautin, 9 km S Pucon Volcan Villarrica Nat. Pk., 900 m elev., 15.xii.1984-10.ii.1985 (S. and J. Peck)

Palpimanidae
Palpimanus sp.
Greece: S-Peloponnese, Areopoli-Vahos, near coast, ~50-100 m elev., under stones, 1995 (K. Thaler, B. Knoflach)
Otiothops atlanticus Platnick, Grismado and Ramirez, 1999
Brazil: Bahia, Itabuna, abandoned cocoa plantation, 100 m elev., 14.38′S, 39.18′W, 26.i.1995 (D. Agosti)
Anisaedus pellucidas Platnick, 1975
Chile: Antofagasta, 6 km E Paposo, 480 m elev., 12.x.1992 (N. Platnick, K. Catley, P. Goloboff)

Micropholcommatidae
Teutoniella cekalovici Platnick and Forster, 1986
Chile: Concepcion: Parque Hualpen, 10.xii.1971 (T. Cekalocic) "TC-36"

Mecysmaucheniidae
Mecysmauchenius segmentatus Simon, 1884
Argentina: Río Negro, El Bolsón, Cerro Piltriquitron, 3-4.ii.1985 (M. Ramirez)
Aotearoa sp.
New Zealand: South Island, Fiordland, Eglinton Valley, The Divide, 27.iii.1987 (N. Platnick, R. Forster), in AMNH

Dictynidae
Dictyna uncinata Thorell, 1856
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), 6.iv.1992 (B.A. Huber)

Desidae
Otagoa nova Forster, 1970

New Zealand: Canterbury, Kaikoura, under stones on beach, 15.iii.1969 (R.R. Forster)

Cybaeidae
Argyroneta aquatica (Clerck, 1757)*

Hahniidae
Hahnia pusilla C.L. Koch, 1841
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), 8.iii.1992 (B.A. Huber)

Neolanidae
Neolana dalmasi (Marples, 1959)
New Zealand: Vinegar Hill Reserve (39°57′S, 175°39′E), 6.i.1967 (R.R. Forster)

Corinnidae
Cetonana laticeps (Canestrini, 1868)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), forest, 4.viii.2003 (B.A. Huber)

Liocranidae
Agroeca brunnea (Blackwall, 1833)*

Lamponidae
Lampona cylindrata (L. Koch, 1866)
New Zealand: Christchurch (43°33′S, 172°38′E), no date (C. Vink)

Gnaphosidae
Gnaphosa nigerrima L. Koch, 1877*

Clubionidae
Clubiona pallidula (Clerck, 1757)
Austria: Vienna, Prater (~48°13′N, 16°24′E), 29.i.1992 (B.A. Huber)
Clubiona lutescens Westring, 1851
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), Toter Grund, 4.i.1992 (B.A. Huber)

Anyphaenidae
Anyphaena accentuata (Walckenaer, 1802)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), iii.1993 (B.A. Huber)
Patrera procera (Keyserling, 1891)
Argentina: Misiones, Santa Ana, 16.vii.1986 (M. Ramirez)
Wulfila albus (Mello-Leitão, 1945)
Argentina: Misiones, San Antonio, vi.1970 (M.E. Galiano)

Salticidae
Pseudeuophrys lanigera (Simon, 1871)
Austria: Vienna, v.1992 (B.A. Huber)
Myrmarachne formicaria (DeGeer, 1778)
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), 6.v.1992 (B.A. Huber)
Synageles venator (Lucas, 1836)
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), 6.v.1992 (B.A. Huber)

Thomisidae
Xysticus cristatus (Clerck, 1757)*
Ozyptila simplex (O.P.-Cambridge, 1862)*
Misumenops tricuspidatus (Fabricius, 1775)
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), 14.v.1993 (B.A. Huber)

Sparassidae
Barylestis montandoni (Lessert, 1929)
Uganda: Semliki Forest (0°48′N, 30°08′E), 5-12.ii.1997 (T. Wagner)

Selenopidae
Anyphops sp.
South Africa: KZN, Bonamanzi Reserve, 1.iv.2001 (B.A. Huber), in ZFMK

Zoridae
Zora spinimana (Sundevall, 1833)
Germany: Bonn, forest W Heiderhof (50°39,5′N, 7°09′E), 29.ix.2002 (B.A. Huber)

Philodromidae
Philodromus dispar Walckenaer, 1826
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), xii.1991 (B.A. Huber)

Amaurobiidae
Amaurobius fenestralis (Ström, 1768)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), forest, 6-9.iii.1992 (B.A. Huber)

Agelenidae
Agelena gracilens C.L. Koch, 1841
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), 25.vii.1993 (B.A. Huber)
Histopona torpida (C.L. Koch, 1837)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), 17.vi.1993 (B.A. Huber)
Textrix denticulata (Olivier, 1789)
Austria: Vienna, Prater (~48°13′N, 16°24′E), 2.iv.1993 (B.A. Huber)

Amphinectidae
Maniho ngaitaho Forster and Wilton, 1973
New Zealand: Canterbury, Kaituna Valley, 13.iv.1964 (R.R. Forster)

Ctenidae
Cupiennius salei (Keyserling, 1877)
Austria: Vienna University laboratory population, 1993

Pisauridae
Pisaura mirabilis (Clerck, 1757)*

Lycosidae
Aulonia albimana (Walckenaer, 1805)*

Stiphidiidae
Stiphidion facetum Simon, 1902
New Zealand: Ohope Beach, 1.x.1969 (C.L. Wilton)

Deinopidae
Deinopis sp.
Australia: SEQ, Brisbane (27°28′S, 153°01′E), no further data; QM S21247

Uloboridae
Hyptiotes paradoxus (C.L. Koch, 1834)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), vii.1992 (B.A. Huber)
Philoponella sp.
Costa Rica: San Jose Prov., 1995 (R.L. Rodriguez-Sevilla)
Waitkera waitakerensis (Chamberlain, 1946)
New Zealand: Whangarei, 5.ii.1991 (B. Opell)
Miagrammopes animotus Chickering, 1968
Puerto Rico: Loquillo National Forest (B. Opell)
Miagrammopes sp.
Costa Rica: La Selva, 27.vi.1985 (B. Opell)

Araneidae
Nuctenea umbratica (Clerck, 1757)*

Linyphiidae
Linyphia triangularis (Clerck, 1757)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), vii.1993 (B.A. Huber)
Neriene montana (Clerck, 1757)
Austria: Vienna, Prater (~48°13′N, 16°24′E), iv.1993 (B.A. Huber)

Cyatholipidae
Wanzia fako Griswold, 1998
Cameroon: NW Prov., Menchum Div., forest nr. Lake Oku

(6°12′N, 10°27′E), 2150 m, 7.-13.ii.1992 (C. Griswold and C. Wanzie)

Synotaxidae
Chileotaxus sans Platnick, 1990
Chile: Chiloé, 15 km S Chepu, 3.ii.1991 (M. Ramirez)

Nesticidae
Nesticus cellulanus (Clerck, 1757)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), xi.1992 (B.A. Huber)

Theridiidae
Enoplognatha ovata (Clerck, 1757)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), 7.vi.1992 (B.A. Huber)
Tidarren chevalieri (Berland, 1936)
Cape Verde Islands: Santiago, "Tarratal," 10.ii.1992 (G. Schmidt)

Tetragnathidae
Tetragnatha extensa (Linnaeus, 1758)
Austria: Vienna, Donauinsel (~48°15′N, 16°24′E), v.1992 (B.A. Huber)
Metellina mengei (Blackwall, 1870)
Austria: Upper Austria, Walding (~48°21′N, 14°12′E), xii.1991 (B.A. Huber)
Leucauge mariana (Taczanowski, 1881)
Costa Rica: San Jose, Ciudad Universitaria, 1995 (B.A. Huber)

Mysmenidae
Mysmenopsis tengellacompa Platnick, 1993
Costa Rica: Heredia, La Selva, nr. Puerto Viejo, ~100 m, on webs of *Tengella radiata*, 1983 (W. Eberhard)

Anapidae
Sofanapis antillanca Platnick and Forster, 1989
Chile: Llanquihue, Caleta, La Arena, 30.i.1991 (M. Ramirez)
Minanapis talinay Platnick and Forster, 1989
Chile: Concepcion, Camino a Ramuntcho, 8.xii.1981 (T. Cecalovic) "TC-107"

Symphytognathidae
Symphytognatha picta Harvey, 1992
Australia: WA: Tall Tingle Tree Path, Wqalpole-Nornalup Nat. Pk., 13.vi.1987 (N.I. Platnick, R.J. Raven)