

A review of appendotomy in spiders and other arachnids

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Summary

A historical review is presented for appendotomy, a collective term for autotomy, autotilly and autospasy, and examples are given for each category. Autotomy, the instantaneous reflex detachment of an appendage, occurs rarely, if ever, among spiders. Autotilly, the self-removal of an appendage, occurs in most spiders with damaged appendages and in several genera which remove one palp before or both palps after mating. Autospasy is the separation of appendages with the assistance of an outside source. This occurs usually as an abrupt detachment, but takes place slowly in some spiders which do not autospasise readily. It occurs at one of three points or not at all: at the coxa-trochanter joint, the patella-tibia junction, or across the basal part of the patella. The degree of resistance to autospasy varies between families and is not related to slenderness of legs. Hersiliidae are added to the list of spiders in which autospasy occurs at the patella-tibia juncture, and five additional genera of the Agelenidae are reported to show evidence of patella division, *Blabomma*, *Cybaeota*, *Cybaeozyga*, *Ethobuella* and *Yorima*. The 54 families of spiders studied, based on over 100 genera, are arranged in the order of ease with which their legs detach. Selenopidae, Philodromidae and Pholcidae contain the species most susceptible to leg detachment. Seventeen families show little or no sign of autospasy.

A transverse apodeme is described on the trochanter plane and the mechanics involved in the detachment of the coxa and trochanter are redescrbed. Illustrations are provided depicting the types of autospasy and the sclerites involved in coxa-trochanter detachment.

Introduction

A survey of the arachnological literature on appendotomy indicates that many errors and omissions persist for several reasons: inadequate coverage of previous published work, misinterpretation of results by morphologists having little background on spider taxonomy and by researchers having examined too

few genera of spiders for their generalised conclusions. The majority of previous works also showed that detachment of appendages occurred only at the coxa-trochanter joint.

An examination of over 100 genera of spiders in fifty-four families was made to determine if these spiders lose their legs, if so at which point and to determine the ease with which the legs are detached. Both living and preserved spiders were used. The separation of the legs was observed under a low power microscope. Also anaesthetisation of spiders and exposure of spiders to the bites of ambush bugs (*Phymata* sp.) was used to determine whether true autotomy occurs in spiders.

Historical review

The loss of appendages at the coxa-trochanter joint in spiders was first recorded by Lepeletier (1813), and later studied by Heineken (1829a, b), Blackwall (1845, 1848) and Blanchard (1853). In 1883 Frédéricq coined the term "autotomie" for the automatic amputation of legs. Henking first noted the detachment of legs in opilionids in 1888. A series of studies on "autotomy" in spiders after 1883 included those of Parize (1886), Wagner (1887), Frédéricq (1888), Gaubert (1892), Schultz (1898), Friedrich (1906) and Weiss (1907). In 1907 Piéron published the short note, Autotomie et "Autospasie", defined the two terms and pointed out the occurrence of the latter in insects and arachnids. This new term was overlooked or not used by many subsequent workers up to the present time (Foelix, 1982). By 1930, usage had broadened the term autotomy to embrace all examples of appendage detachment.

In 1932 Wood & Wood added the term autotilly to our vocabulary and redefined autotomy and autospasy. Then Woodruff (1937) coined a fourth term, "appendotomy" to include these three phenomena. Excellent reviews on "autotomy" were given by Wood (1926), Bonnet (1930), Wood & Wood (1932) and Bliss (1960). The latter especially reviewed the crustacean literature but also included arachnids.

In 1932 Berland pointed out a "second point of fracture" in spiders, occurring at the juncture between the patella and tibia, and Roth (1981) noted a third area of detachment near the base of the patella in some genera of Agelenidae. A fourth point

of detachment rarely occurs. Bauer (1972) noted that the palpi of some species of *Pardosa* and *Tegenaria* "have their frailest point between the trochanter and femur", but our examination of other species in these genera showed that this weakness is variable. Normally autotilly of the palpi occurs at the coxa-trochanter joint.

In other arachnids, detachment areas are known to occur during autospasy as follows: in some amblypygids at the patella-tibia juncture (Wood, 1926, and pers. obs.); in some long-legged opilionids between the trochanter and femur (*Leuronychus*, *Leiobunum* and *Protolophus*). Although the short-legged *Sclerobunus* species have a strong constriction near the base of the femur, it apparently is seldom used as a detachment point.

In 1926 Wood studied the musculature of five genera in four families of spiders, all of whose appendages separate more or less easily at the coxa-trochanter joint. These few examples prompted her to conclude erroneously that "autotomy" in spiders always occurs between the coxa and trochanter. This statement has been repeated by many researchers up to the present time: Bonnet (1928, 1930) who studied *Dolomedes*; Parry (1957) *Tegenaria* and *Lycosa*; Bauer (1972) *Pardosa*, *Philodromus* and *Tegenaria*, and Randall (1981, 1982) *Latrodectus*, as well as reviewers and writers such as Bliss (1960), Savory (1964), Bonnet (1975) and Foelix (1979, 1982).

Definition of Terms

In the following text the four terms defined below will be used in their restricted sense except when placed in quotes.

APPENDOTOMY — the loss by any means of any appendage or parts thereof, or segments of the abdomen, at a predetermined locus of weakness.

A collective term including autotomy, autotilly and autospasy.

AUTOTOMY — the instantaneous severance or separation of an appendage, body segments or parts thereof by a reflex action at a predetermined locus of weakness, without external assistance or resistance.

AUTOTILLY — the self-removal of an appendage, usually by mouthparts, other appendages, by twisting or other means at a predetermined locus

of weakness.

AUTOSPASY — the separation of appendages, segments, or parts thereof at a predetermined locus of weakness when the appendages or segments are restrained by any external (not self-induced) source. This is usually an abrupt detachment but occurs slowly in some spiders which do not autospasise readily.

Two other similar terms are referred to in the literature but have not been used since. They are autosalizi, credited to Piéron (1924, reference not located) by Savory (1964) who claims that this term is similar to autotilly. Arthreucastie, coined by Piéron (1907) refers to the "fragilité excessive des membres".

No standard term has been used for the predetermined locus of weakness, the region where separation takes place. The marine biological literature contains the following terms: plane of least resistance, preformed breakage plane, predetermined locus of separation and breakage plane (Bliss, 1960), as well as, breaking joint and fracture plane (Wood & Wood, 1932; Bellairs, 1970). In the arachnid literature we find such phrases as predetermined locus of weakness (Gertsch, 1939), appendotomy plane (Randall, 1981), predetermined plane of weakness and autotomic breakage plane (Randall, 1982, autotomy planes (Bliss, 1960), punto de autotomía (Bonnet, 1975), breaking point and cleavage plane (Roth, 1981).

We suggest the following terms for use in discussing appendotomy:

Predetermined locus of weakness — the weakened and specialised area where detachment of an appendage takes place.

Detachment line — a more or less distinct mark visible on the dorsal surface of the patella (Fig. 2) of certain spiders indicating the area of possible division, or a weakening between the proximal trochanter rim and the adjacent sclerotised ring of the intersegmental membrane.

Detachment plane — the transverse surface of segments after separation.

Detachment point — the exact area at which separation starts to take place. In coxa-trochanter autospasy, separation occurs slightly beyond the dorsal end of the oblique sclerite (Fig. 1a or 5f) usually between sclerites d and c (Fig. 5).

Appendotomy

This has been considered as an escape mechanism against predators (Savory, 1964; Etheridge, 1967; Foelix, 1979, 1982; Arnold, 1982); from the female after mating if the embolus of the male spider becomes entangled in the epigynal ducts; from aggressive females during or after courting (especially tarantulas, pers. obs.); or for a release from incomplete moults (Foelix, 1979, 1982). It has been known that the embolus often breaks off after mating in the epigynum of some spiders, especially *Latrodectus* and *Argiope* (Levi, 1970), *Araneus* (Levi, 1975a) and *Larinia* (Levi, 1975b). According to Bonnet (1930) the entangled embolus does not always break free and in such instances the palpus may be detached, allowing the spider to escape, with the palpus still attached to the epigynum.

After an appendage is released there are a few instances in which it can continue to aid in the owner's defence. The claws of some crabs are known to remain clamped to the potential predator after the appendage is released (Bliss, 1960, Robinson *et al.*, 1970). Some nudibranch molluscs, when attacked, will autotomise their papillae which continue to writhe for minutes after detachment. The tails of some lizards and salamanders will jerk for a while after detachment and distract the predator (Edmunds, 1974; Maiorana, 1977; Dial & Fitzpatrick, 1983). This jerking is also true for various arthropods such as scutigermorph centipedes, *Scutigera* spp. (Cloudsley-Thompson, 1958, 1961; Eason, 1964) and the scolopendromorph centipede, *Rhysida naudatogensis* Kräpelin (Cloudsley-Thompson, 1961). As an additional distraction in the latter species its detached limbs continue to stridulate (Cloudsley-Thompson, 1958, 1961). Legs of the long-legged opilionids, *Leiobunum*, *Leuronychus* and *Protolophus*, the long-legged pholcid, *Physocychus tanneri* Chamberlin and the brown spider, *Loxosceles yucatanana* Chamberlin & Ivie twitch for up to sixty seconds (pers. obs.) after detachment but another pholcid, *Psilochorus*, shows no such movements. Miller (1977) reports twitching for as long as an hour or more in the opilionid genera *Oligolophus*, *Phalangium*, *Mitopus* and *Leiobunum* as well as in spiders of the pholcid genera *Smeringopus* and *Crossopriza* from Kenya, but *Pholcus* does not display this phenomenon. This twitching may distract

predators and thus allow the prey to escape. Verbal reports of twitching of detached legs occurring among other spiders could not be confirmed.

Autotomy

This occurs rarely in vertebrates such as some lizards (Bustard, 1967; Bellairs, 1970) and commonly in many non-arthropod invertebrates such as brittle stars, sea cucumbers, marine worms and nudibranch molluscs, and especially in polychaetes and non-arachnid arthropods (Bliss, 1960, contains a good review). The house centipede, *Scutigera* (Cloudsley-Thompson, 1958) loses its legs so easily and rapidly that autotomy appears to occur, but this has not been confirmed.

If autotomy occurs among spiders, it only happens in rare instances and under extreme provocation. J. S. Rovner states (in litt.) that *Heteropoda* (Sparassidae) autotomises its legs while being anaesthetised with CO₂ and F. G. Barth (in litt.) observed the same for *Cupiennius* (Ctenidae).

Personal attempts to induce autotomy by anaesthetising the following spiders with CO₂ failed: *Olios fasciculatus* Simon (Sparassidae), *Selenops actophilus* Chamberlin (Selenopidae), which loses its legs more readily than any other spider, *Physocychus tanneri* Chamberlin (Pholcidae), *Lauricius hooki* Gertsch (Clubionidae), and, not unexpectedly, *Dugesiella* sp. (Theraphosidae).

It is possible that Lawler's (1972) report on *Mimetus* which "tore off four legs from a victim . . ." was a case of autotomy in the light of reports by Eisner & Camazine (1983). They tested ambush bugs of the genus *Phymata* on spiders of the genus *Argiope*. Detachment occurred in six of seven cases where phymatids seized the spider's leg. In the seventh case the spider died. Seven spiders of the families Salticidae, Thomisidae and Agelenidae lost their legs in response to phymatid "stings" but *Achaearanea tepidariorum* (C. L. Koch) never detached its legs when bitten. Similar tests were made by the author using ambush bugs (*Phymata* sp.) to bite legs of spiders (Agelenidae, *Agelenopsis*, *Hololena*; Araneidae, *Araneus* sp.; Lycosidae, *Lycosa* sp. and Sparassidae, *Olios* sp.). Out of 28 probable bites and injections of venom (indicated by observation of frantic activity by the spider) 15 resulted in no loss of legs and in the spiders' death. Eleven remained alive after the bitten

leg was detached and two remained alive without the loss of a leg. When detachment occurred during the spider's struggle it was not possible to discern which type of appendotomy was taking place. However, several times the leg partially detached and in two cases active movement of the coxa was noted against the resistance provided by the bug or the tweezers. This appeared sufficient for the spider to cause leg detachment by autospasy. Those spiders which did not detach a leg while being manipulated, in most cases removed the leg soon afterwards by grabbing it with their mouthparts (autotilly). Those spiders which died could have autotomised their leg after each bite if they were capable of it, but they did not do so. We conclude therefore that autotomy did not occur among our experimental animals. Our results appear at variance with those of Eisner & Camazine (1983). The reasons could include differences in the venoms of the phymatids used, different species of spiders, different experimental conditions or differences in interpretation of autotomy (no mention was made of the possibilities of autospasy or autotilly occurring).

Autotilly

This is well known in a few families of flying insects which settle down to a terrestrial or aquatic existence and shed their wings by breakage. They include some hippoboscids, ants and termites (Borror *et al.*, 1981), water striders of the genera *Gerris*, *Potamometropsis* (Calabrese, 1980) and *Telmatogetra* and *Trepobates* (Torre-Bueno, 1908). The tungid flea, *Tunga monositus* Barnes & Radovsky, detaches its legs near the base of the tibia after settling down permanently under the skin of its host in its hypertrophied stage (Barnes & Radovsky, 1969).

Among arachnids, autotilly occurs in some spiders which remove a palpus or two, or in some with seriously damaged appendages. In 1934, Chamberlin & Ivie described the genus *Tidarren* (Theridiidae), in which the male in the penultimate stage develops oversized palpi but removes either the left or right palpus shortly after the penultimate moult (Branch, 1942), separating it at the coxa-trochanter joint. After the final moult the coxa has a healed appearance or a hemispherical protuberance, a condition which misled Chamberlin & Ivie (1934) to state incorrectly, "Endite and trochanter of missing palpus

present...". They did comment that the "trochanter" was vestigial. Levi (1981) described a male *Echinotheridion* which has only one enormous palpus, perhaps another case of autotilly.

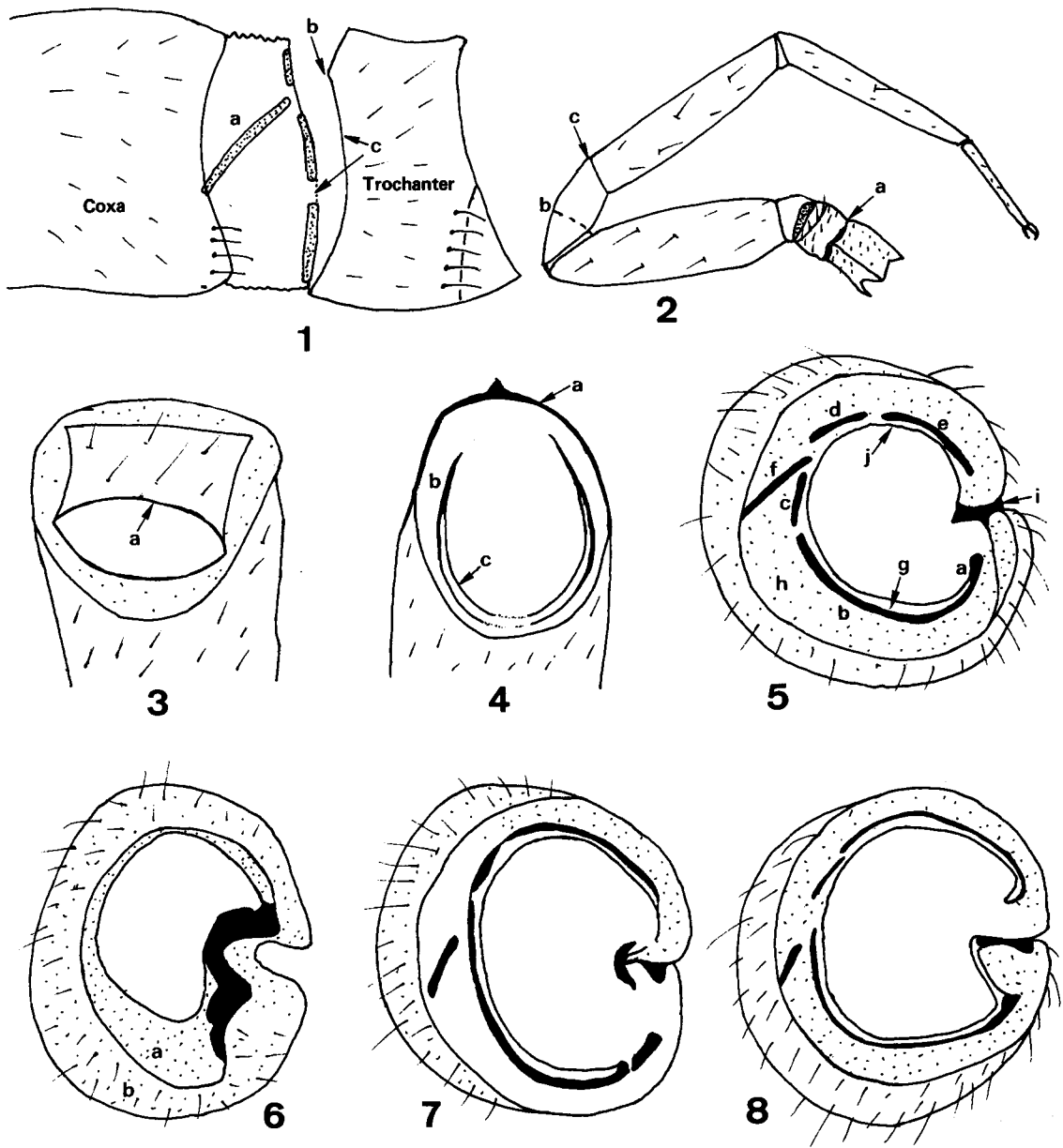
Recently Robinson & Robinson (1978) reported one or both palpi missing in males of species of the orb-weavers *Herennia* and *Nephilengys*, which, after copulation, live in the web where they "fight with other (fertile) males and may drive these off." They observed (1980) a male *Nephilengys* whose embolus was twisted and permanently pointed forward after mating. The spider then "bit" off the palpus.

Observations of autotilly to damaged appendages have been made by Friedrich (1906), Wood (1926) and Bonnet (1930). Randall (1981) found that legs with damaged metatarsi or tarsi are usually not removed, whereas ligation, but not amputation, to the tibia or distal half of the femur almost always resulted in autotilly.

Autospasy

This occurs in invertebrates (Bliss, 1960) and vertebrates (Frédéricq, 1893; Hoffstetter & Gasc, 1969). The restrained tails of many species of lizards, the tuatara and some snakes break off easily (Frédéricq, 1893; Smith, 1946; Hoffstetter & Gasc, 1969) as do those of plethodontid salamanders (Wake & Dresner, 1967). When heteromyids, especially white-footed mice and wood rats (Layne, 1972) and kangaroo rats (pers. obs.) are grasped by the tail, the skin will slip off. Among arthropods, only appendages are autospasised. Insects such as grasshoppers, cockroaches and tipulid flies, as well as scolopendromorph and lithobiomorph centipedes, are known to lose legs easily. The latter are seldom found in collections with all their legs intact.

Autospasy occurs in three arachnid orders: In Amblypygi at the patella-tibia juncture, in Opiliones at the trochanter-femur junction or near the base of the femur (*Sclerobunus*, Triaenonychidae) and in Araneae at one of three points (Fig. 2). These three points of detachment are reviewed below. In Araneae autospasy does not occur, or occurs rarely, in most primitive groups, cribellates, most haplogynes (the traditional concept) and many mygalomorphs nor at the coxa-trochanter joint among spiders with patella or patella-tibia detachment points. Uropygi and Palpigradi lose their flagella easily but this is due to



Figs. 1-8: Diagrams showing detachment points, detachment planes, and sclerites. 1 Coxa-trochanter joint showing oblique sclerite (a), detachment point (b) and detachment line (c) with segments beginning to separate. 2 Leg detachment points: (a) coxa-trochanter joint; (b) patella detachment line; (c) patella-tibia juncture. 3 Patella detachment plane (*Calymmaria emertoni* Chamberlin & Ivie) showing detachment line (a). 4 Patella-tibia detachment plane of *Neriene radiata* (Walckenaer) showing the patella rim (a), membrane (b) and tibia ring (c). 5 Coxa detachment plane (*Lycosa santrita* Chamberlin & Ivie) showing sclerites a-e of the ring, oblique sclerite (f), rim of trochanter ring (g), intersegmental membrane (h), coxa apodeme (i) and the detachment line (j). 6 Trochanter detachment plane (*Lycosa santrita* Chamberlin & Ivie) showing the transverse invagination of the trochanter (a) and the detachment line (b). 7 Coxa detachment plane (*Olios fasciculatus* Simon) with ring of four sclerites. 8 Same, (*Selenops actophilus* Chamberlin) with ring of three sclerites.

the fragility of the appendage, rather than a function of defence.

Patella separation

This results in a separation of the patella into two parts at a detachment line (Figs. 2b, 3a) near its base. After autospasy occurs, the proximal wedge-shaped part of the patella folds back (Fig. 3) against the femur, somewhat closing the opening. This type of separation has been reported in two genera of Agelenidae, *Willisus* and *Calymmaria* (Roth, 1981) and observed in the genera *Blabomma*, *Cybaeota*, *Cybaeozyga*, *Ethobuella* (whose legs occasionally part at the coxa-trochanter joint) and *Yorima* (John Heiss in litt., and pers. obs.).

Patella-tibia detachment

This is the separation between the patella and tibia. Nothing has been reported on the mechanism operating to prevent the loss of haemolymph after separation. The patella detachment plane of the linyphiid *Neriere radiata* (Walckenaer) shows a narrow sclerotised rim (Fig. 4a). The intersegmental membrane (Fig. 4b) is encircled by a sclerotised ring (Fig. 4c) which is open dorsally, weakened ventrally, and which separates from the rim of the tibia. This type of autospasy occurs in the families Linyphiidae (including Erigoninae), Filistatidae, Leptonetidae (Berland, 1932) and Hersiliidae (pers. obs.). *Leptoneta* and *Filistatoides* show a tendency toward palpal separation at the patella-tibia joint, and some genera in the Clubionidae (*Agroeca*, *Castianeira*, *Lauricius* and *Scotinella*) and Philodromidae (*Philodromus*, one example) occasionally show a tendency to autospasise at this junction as well as at the coxa-trochanter joint. This is not surprising since Bauer (1972) showed that the patella-tibia joint was the second weakest one of the *Philodromus* leg after the coxa-trochanter joint, the latter separating after a pull of 2.8 g vs. 11.0 g at the patella-tibia junction. Contrary to these results Wood (1926) showed that in *Lycosa*, which has no indication of a weak patella-tibia juncture, it took a pull of 14 g to separate the coxa-trochanter joint but 220 g for the next weakest, at the metatarsus-tarsus joint.

Berland's (1932) observation that this break occurs especially among species with long slender legs was based upon observations of only a few

species and not long-legged spiders such as species of Pholcidae whose legs readily separate at the coxa-trochanter joint and long-legged dinopids, tetragrathids and hypochilids which do not autospasise. Bauer's (1972) conclusion that "A directly proportional relation between the length of the extremities and the frequency of their amputation was to be found" was based upon an examination and comparison of species of only three genera, *Pardosa*, *Tegenaria* and *Philodromus*, all with similar autospasy. Our survey of over 100 genera of spiders showed that resistance to detachment is not related to slenderness, stoutness nor length of leg.

Coxa-trochanter detachment

This occurs between the coxa and trochanter. When the femur is restrained in some manner the coxa is jerked abruptly upwards against the relatively immobile trochanter, thus putting stress on the detachment point (Fig. 1b) and separating the two segments along the detachment line (Fig. 1c). The coxal opening is then closed by a constriction of muscles attached to the ring of the intersegmental membrane (Figs. 5, 7, 8).

The ease with which spiders lose their legs at the coxa-trochanter joint varies from the extreme case of *Selenops*, whose legs seem to be shed at the slightest touch, to those families in which no autospasy occurs. Spiders whose legs are more necessary for the capture of prey, for mating (males) or for jumping, show less tendency to lose legs. These include Dinopidae, Salticidae, Thomisidae, Mimetidae and Uloboridae, as well as many Araneidae, including Tetragnathinae, and Theridiidae (spiders which wrap their prey with the hind legs). These spiders can, however, detach a leg through autotilly or by twisting around until the leg breaks free. For instance, tarantulas (*Aphonopelma*, Theraphosidae) do not lose legs easily but we observed two examples where these spiders used the twisting method. After the femur of one was grasped, the spider twisted around till the leg detached at the coxa-trochanter joint. The other example was observed after mating, when the male twisted his leg free from a female when she caught it in her chelicerae.

Living spiders (whose legs easily detach at the coxa-trochanter joint) will exhibit autospasy readily if the leg is grasped by or immobilised at the tibia or

femur segments, but it takes considerable pulling force to separate the segments (Wood, 1926; Bauer, 1972) because the coxa cannot move upwards to detach the leg (see: *Mechanics of Separation*). Merely pulling the leg seldom results in autospasy. For instance, by pulling the front legs of *Physocyclus* (Pholcidae) in opposite directions the cephalothorax flattens from the tension before the segments separate, whereas the slightest grasp of a tibia or femur results in autospasy. In this latter example the mechanism for autospasy can operate freely.

When autospasy occurs in living spiders, or when legs are detached from preserved spiders, there is usually a clean break between the detached parts from which little or no broken muscle tissue extrudes. A healed surface across the coxa detachment plane can be seen in specimens where a leg was missing before the spider was preserved. When preservation is poor or spiders are handled roughly, legs can become separated between any segments, but these abnormal detachments can be recognised by the irregular breaks or by extruding muscle tissue across the detachment plane.

If autospasy occurs in the living spider a similar break will occur with preserved specimens. For this reason, most of the 102 genera in 54 families we studied were from preserved material. The families of spiders studied are arranged below in the order of ease with which their legs detach at the coxa-trochanter joint. When five or more preserved specimens were available for examination, the average number of legs missing was determined and multiplied by 100. A value of 100 indicates one leg missing per spider examined. Within the parentheses following this value are two figures, the first indicating the number of genera examined (often several species are included) and after the slash, the number of specimens involved. These families are: Selenopidae (400, 1/7), Philodromidae (305, 4/18), Pholcidae (216, 2/12), Homalonychidae (200, 1/8), Oonopidae (200, 4/7), Anyphaenidae (182, 3/11), Dipluridae (170, 2/10), Gnaphosidae (130, 8/30), Sparassidae (127, 1/11), Araneidae (*Mangora*, 120, 1/5), Dysderidae – Segestriinae (100, 2/17), Barychelidae (100, 1/6), Clubionidae (94, 6/17), Thomisidae (90, 5/22), Lycosidae (68, 4/134), Oxyopidae (60, 2/5), Nesticidae (48, 1/25), Ctenidae (45, 1/11), Agelenidae (41, 6/24, except genera

whose patella breaks), Loxoscelidae (40, 1/25), Mecicobothriidae (40, 2/20) and Theridiidae (37, 10/43).

The following families showed a much lesser degree of coxa-trochanter detachment: Amphinec-tidae, Argyronetidae, Dictynidae, Diguettidae, Dysderidae (Dysderinae), Mysmenidae, Ochyroceratidae, Pisauridae, Salticidae, Scytodidae, Tengellidae and Theraphosidae. A missing leg does not necessarily indicate autospasy but may show evidence of autotilly as shown by Weiss (1907) and Oppenheim (1908, 1913) in *Argyroneta*.

The remaining families studied showed no evidence of coxa-trochanter detachment: Anapidae, Antrodiaetidae, Ctenizidae, Amaurobiidae, Araneidae (most genera, including those of Tetragnathinae), Caponiidae, Desidae, Dinopidae, Eresidae, Hahniidae, Hypochilidae, Mimetidae, Miturgidae, Oecobiidae, Palpimanidae, Plectreuridae, Uloboridae and Zodariidae, as well as those whose legs detach at the patella-tibia joint or whose patella breaks.

Mechanics of separation of appendages at the coxa-trochanter joint

The first speculation on the mechanics of separation of spider appendages was made by Friedrich (1906) who suggested a cutting device occurring within the trochanter, "... an der Unterseite des Trochanter hat sich der Chitinfortsatz gebildet, der weit ins Innere des Beines vorspringt und die Weichteile bei der Autotomie durchschneidet". A detailed study of arachnid leg musculature and exoskeleton by Wood (1926) showed that no such cutting device existed, but that separation of appendages occurred at a definite weakened line encircling the coxa-trochanter joint.

Our examination of the rim of the trochanter detachment plane of *Lycosa santrita* Chamberlin & Ivie shows a relatively large transverse invagination (Fig. 6a), the trochanter apodeme, extending into the cavity of the trochanter. This is the "cutting device" noted by Friedrich (1906: 501). This apodeme is easily visible in other large spiders which autospasise at the coxa-trochanter joint but the distal part of the ring retains a narrow clear chitinous rim after detachment (Fig. 5g), evidently the transverse section which is attached to the trochanter rim (Fig. 6a).

Only one small muscle, the levator longus femoris of Wood (1926) or muscle 9 of Parry (1957), extend through the trochanter from the coxa to the femur. This muscle breaks readily in spiders which autospasise their legs. Unfortunately, all of the subsequent studies on spider musculature and autospasy included *only* those species which autospasise more or less readily at this joint (Bonnet, 1930; Parry, 1957; Bauer, 1972). Their conclusions that spiders autospasise only at the coxa-trochanter joint could have been anticipated. These workers agree that seven of the eight coxal muscles are attached to the proximal rim of the trochanter. Actually the attachment points of these muscles on the ring or its sclerites, are either embedded in or are part of the intersegmental membrane which is attached to the proximal rim. These sclerites form an incomplete, segmented or unsegmented, ring of one to four and possibly five parts (Figs. 5a-e, 7, 8), which is fixed solidly or variably weakened along the detachment line depending upon the ease with which the spider autospasises. The detachment line (Fig. 1c) between the trochanter rim and the ring forms an incomplete circle which is open below the indentation of the coxa apodeme (Fig. 5i). Below here, the membrane and ring are attached firmly and during autospasy sometimes sclerite a (Fig. 5) separates from the ring as the leg tears loose (Fig. 7). Sclerites a-e may be more or less fused (Fig. 7) in *O. fasciculatus* Simon (Sparassidae), divided into three parts (Fig. 8) in *S. actophilus* Chamberlin (Selenopidae) or divided into four parts (Fig. 5) in *L. santrita* Chamberlin. Sclerites d and e of some species are thickened and are separated slightly from the ring at the detachment point (*Brachypelma smithi* F. Pickard-Cambridge (Theraphosidae)).

The intersegmental membrane between the coxa and trochanter of all spiders studied bears an oblique sclerite (Figs. 1a, 5f). It is located at an angle across the posterior dorsal face of the intersegmental membrane and varies in size and shape, being short and slender in *S. actophilus* Chamberlin (Fig. 8) or very stout and knobbed distally in *B. smithi* F. Pickard-Cambridge. It acts as a pivot point opposite the coxa apodeme and apparently strengthens the membrane at a point where detachment begins.

Bauer (1972) gives an excellent account of autospasy of an appendage at the coxa-trochanter joint

(with a summary in English). When the femur is sufficiently restrained, the coxa is raised, stressing the membranous area between the coxa and trochanter, whereby the oblique sclerite apparently transfers the strain to the detachment point (Fig. 1b) and begins to separate the ring or its fragments from the trochanter along the detachment line.

After detachment of the appendage, the tension of the coxal muscles then gradually closes the wound, as has been well illustrated by Bonnet (1930, fig. 76, 1975, fig. 4), Parry (1957, fig. 3) and Bauer (1972, figs. 15-18) and observed repeatedly under a microscope during our studies.

Discussion

Autotomy, as defined in this paper, doubtfully or rarely occurs among spiders. Reports by F. G. Barth (in litt.), Eisner & Camazine (1983), and J. S. Rovner (in litt.) have not considered the possibility of autospasy or autotilly, nor have they described the specific action that takes place with the loss of an appendage. In tests conducted by the authors, appendages never clearly detached except when they were restrained in some way, either by the spider or by the experimenter. More detailed examinations are necessary to determine the mechanisms involved in appendotomy.

Appendotomy among spiders provides additional taxonomic characters useful, in some instances, for family separation or for determining relationships between genera. It appears to be consistent at the family level except in Agelenidae and Araneidae. Examination of other genera and families not reviewed should be undertaken to determine what, if any, types of autospasy occur. This review corrects many errors in the literature and points out the shortcomings of our present state of knowledge. In most research, the end result often generates more questions than answers, which is clearly the case with this study. What is the muscle arrangement that occurs across the patella-tibia junction that allows for detachment at this point among certain families? Does the patella musculature differ to allow for a patella separation? What is the mechanism that stops the haemolymph from escaping after the above type of autospasy? Also, comparative and morphological studies should be made of the sclerites involved at the coxa-trochanter detachment line.

It is known that regeneration of appendages commonly occurs among spiders but does it happen with spiders in which autospasy does not or seldom occurs (Randall, 1981)? These questions and others are left unanswered but posed for future studies.

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References

- ARNOLD, S. J. 1982: A quantitative approach to anti-predator performance: salamander defense against snake attack. *Copeia* 1982(2): 247-253.
- BARNES, A. M. & RADOVSKY, F. J. 1969: A new *Tunga* (Siphonaptera) from the Nearctic region with description of all stages. *J.med.Entomol.* 6(1): 19-36.
- BAUER, K. H. 1972: Funktionsmechanismus der Autotomie bei Spinnen (Araneae) und seine morphologischen Voraussetzungen. *Z.Morph.Tiere* 72(3): 173-202.
- BELLAIRS, A. 1970: *The life of reptiles*. Vol. II. Universe Books, New York City.
- BERLAND, L. 1932: *Les Arachnides*. 1-485. Encyclopédie Entomologique, Paris.
- BLACKWALL, J. 1845: Report on some recent researches into the structure, functions and economy of the Araneida made in Great Britain. *Rep.Br.Ass.Advmt Sci.* 14: 62-79; and *Ann.Mag.nat.Hist.* 15: 221-241.
- BLACKWALL, J. 1848: Researches having for their object the elucidation of certain phenomena in the physiology of the Araneida. *Ann.Mag.nat.Hist.* (2)1: 173-180.
- BLANCHARD, E. 1853: Sur les mouvements du fluide nourricier chez les arachnides pulmonaires. *C.r.hebd. Séanc.Acad.Sci., Paris* 36: 1079-1081.
- BLISS, D. E. 1960: Autotomy and regeneration. Chapter 17: 561-589 in Waterman, T. H. et al. *The physiology of Crustacea* 1: 1-670.
- BONNET, P. 1928: Note préliminaire sur les phénomènes de la mue, de l'autotomie et de la régénération chez les araneides. *C.r.Séanc.Soc.Biol.* 99(35): 1711-1713.
- BONNET, P. 1930: La mue, l'autotomie et la régénération chez les araignées avec une étude des Dolomèdes d'Europe. *Bull.Soc.Hist.nat.Toulouse* 59: 237-700.
- BONNET, P. 1975: Las arañas. *Graellsia* 29: 183-200.
- BORROR, D. J., deLONG, D. M. & TRIPLEHORN, C. A. 1981: *An introduction to the study of insects*. Fifth ed. 1-827. Saunders College Publishing Co.
- BRANCH, J. H. 1942: Notes on California spiders. *Bull.Sth. Calif.Acad.Sci.* 4: 138-140.
- BUSTARD, R. H. 1967: A mechanism for greater predator survival during cold torpor in gekkonid lizards. *Br.J. Herpet.* 4(1): 7-8.
- CALABRESE, D. M. 1980: Zoogeography and cladistic analysis of the Gerridae (Hemiptera: Heteroptera). *Misc.Publs ent.Soc.Am.* 11(5): 1-119.
- CHAMBERLIN, R. V. & IVIE, W. 1934: A new genus of theridiid spiders in which the male develops only one palpus. *Bull.Univ.Utah* 24(4): 1-18.
- CLOUDSLEY-THOMPSON, J. L. 1958: Spiders, scorpions, centipedes and mites. 1-228. Pergamon Press, New York.
- CLOUDSLEY-THOMPSON, J. L. 1961: A new sound-producing mechanism in centipedes. *Entomologist's mon.Mag.* 96: 110-113.
- DIAL, B. E. & FITZPATRICK, L. C. 1983: Lizard tail autotomy: Function and energetics of postautotomy tail movement in *Scincella lateralis*. *Science, N.Y.* 219: 391-393.
- EASON, E. H. 1964: *Centipedes of the British Isles*. 1-294. Frederick Warne & Co., New York.
- EDMUNDS, M. 1974: *Defence in animals*. 1-357. Longman, Essex.
- EISNER, T. & CAMAZINE, S. 1983: Spider leg autotomy induced by prey venom injection: An adaptive response to "pain"? *Proc.natn.Acad.Sci.U.S.A.* 80(11): 3382-3385.
- ETHERIDGE, R. 1967: Lizard caudal vertebrae. *Copeia* 1967(4): 699-721.
- FOELIX, R. F. 1979: *Biologie der Spinnen*. 1-258. Georg Thieme Verlag, Stuttgart.
- FOELIX, R. F. 1982: *Biology of spiders*. 1-306. Harvard Univ. Press, Cambridge, Mass.
- FRÉDÉRICQ, L. 1883: Sur l'autotomie ou mutilation par voie réflexe comme moyen de défense chez les animaux. *Archs Zool.exp.gén.* (2)1: 413-426.
- FRÉDÉRICQ, L. 1888: L'autotomie ou la mutilation active. *Trav.Lab.Physiol.L.Frédéricq* 2: 201-221.
- FRÉDÉRICQ, L. 1893: L'autotomie ou la mutilation active dans le regne animal. *Bull.Acad.r.Belg.* 26: 758-772.
- FRIEDRICH, P. 1906: Regeneration der Beine und Autotomie bei Spinnen. *Arch.EntwMech.Org.* 20: 469-506.
- GAUBERT, P. 1892: Autotomie chez les pycnogonides. *Bull.Soc.zool.Fr.* 17(8): 224-225.
- GERTSCH, W. J. 1939: A revision of the typical crab-spiders (Misumeninae) of America north of Mexico. *Bull.Am. Mus.nat.Hist.* 76(7): 277-442.

- HEINEKEN, C. 1829a: Experiments and observations on the casting off and reproduction of the legs in crabs and spiders. *Zool.J.* **4**: 284-294.
- HEINEKEN, C. 1829b: Observations on the reproduction of the members in spiders and insects. *Zool.J.* **4**: 422-432.
- HENKING, H. 1888: Biologische Beobachtungen an Phalangiden. *Zool.Jb.* **3**: 319-335.
- HOFFSTETTER, R. & GASC, J. P. 1969: Vertebrae and ribs of modern reptiles, Chapter 5: 201-310 in Gans, C. (ed.), *Biology of the Reptilia* **1**: 1-373. Academic Press.
- LAWLER, N. 1972: Notes on the biology and behavior of *Mimetus eutypus* Chamberlin and Ivie (Araneae: Mimetidae). *Notes Arachnol.Southwest* **3**: 7-10.
- LAYNE, J. N. 1972: Tail autotomy in the Florida mouse, *Peromyscus floridanus*. *J.Mammal.* **53**(1): 62-71.
- LEPELETIER, M. 1813: Extrait d'un mémoire sur les araignées. *Nouv.Bull.Soc.philom.Paris* **3**: 254-258.
- LEVI, H. W. 1970: Problems in the reproductive physiology of the spider palpus. *Bull.Mus.natn.Hist.nat., Paris* (2) **41**(1): 108-111.
- LEVI, H. W. 1975a: Mating behavior and presence of embolus cap in male Araneidae. *Int.Congr.Arachn.* **6**: 49-50.
- LEVI, H. W. 1975b: The American orb-weaver genera *Larinia*, *Cercidia* and *Mangora* north of Mexico (Araneae, Araneidae). *Bull.Mus.comp.Zool.Harv.* **147**(3): 101-135.
- LEVI, H. W. 1981: The male of *Echinotheridion* (Araneae: Theridiidae). *Psyche, Camb.* **87**(3-4): 177-179.
- MAIORANA, V. C. 1977: Tail autotomy, function conflicts and their resolution by a salamander. *Nature, Lond.* **265**(5594): 533-535.
- MILLER, P. L. 1977: Neurogenic pacemakers in the legs of Opiliones. *Physiol.Entomol.* **2**: 213-224.
- OPPENHEIM, S. 1908: Regeneration und Autotomie bei Spinnen. *Zool.Anz.* **33**: 56-60.
- OPPENHEIM, S. 1913: Autotomie und Regeneration bei Ephemeren Larven (*Chleon dipterum*) and Wasser-spinnen (*Argyroneta aquatica*). *Diss.Marburg-Fulda* 1-68.
- PARIZE, P. 1886: L'amputation réflexe des pattes de crustacés. *Revue scient., Paris* **1886**(2): 379.
- PARRY, D. A. 1957: Spider leg-muscles and the autotomy mechanism. *Q.Jl microsc.Sci.* **98**(3): 331-340.
- PIÉRON, H. 1907: Autotomie et "Autospasie". *C.r.Séanc. Soc.Biol.* **63**: 427.
- RANDALL, J. B. 1981: Regeneration and autotomy exhibited by the black widow spider, *Latrodectus variolus* Walckenaer. *Wilhelm Roux Arch.EntwMech. Org.* **190**: 230-232.
- RANDALL, J. B. 1982: Coxal relocation following the loss of an adjacent coxa in *Latrodectus variolus* Walckenaer. *J.Arachnol.* **10**: 247-250.
- ROBINSON, M. H., ABELE, L. G. & ROBINSON, B. 1970: Attack autotomy: A defence against predators. *Science, N.Y.* **169**: 300-301.
- ROBINSON, M. H. & ROBINSON, B. 1978: The evolution of courtship systems in tropical araneid spiders. *Symp.zool.Soc.Lond.* **42**: 17-29.
- ROBINSON, M. H. & ROBINSON, B. 1980: Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac.Insects Monogr.* **36**: 1-218.
- ROTH, V. D. 1981: A new genus of spider (Agelenidae) from California exhibiting a third type of leg autospasy. *Bull.Am.Mus.nat.Hist.* **170**(1): 101-105.
- SAVORY, T. H. 1964: *Arachnida*. 1-291. Academic Press, London.
- SAVORY, T. H. 1977: *Ibid.*, 2nd ed. 1-340.
- SCHULTZ, E. 1898: Über die Regeneration von Spinnenfüssen. *Trudy imp.S.-Peterb.Obshch.Estest.* **29**(1): 94-101.
- SMITH, H. M. 1946: *Handbook of lizards*. 1-557. Comstock Publ.Co., Ithaca, N.Y.
- TORRE-BUENO, J. R. de la 1908: The broken hemelytra in certain Halobatinae. *Ohio Nat.* **9**(1): 389-390.
- WAGNER, W. A. 1887: La régénération des organes perdus chez les araignées. *Bull.Soc.Nat.Moscou* **1887**(4): 871-900.
- WAKE, D. B. & DRESNER, I. G. 1967: Functional morphology and evolution of tail autotomy in salamanders. *J.Morph.* **122**: 265-306.
- WEISS, O. 1907: Regeneration und Autotomie bei der Wasserspinne (*Argyroneta aquatica* Cl.). *Arch.Entw-Mech.Org.* **23**: 643-645.
- WOOD, F. D. 1926: Autotomy in Arachnida. *J.Morph.* **42**(1): 143-195.
- WOOD, F. D. & WOOD, H. E. 1932: Autotomy in decapod Crustacea. *J.exp.Zool.* **62**: 1-55.
- WOODRUFF, L. 1937: Autospasy and regeneration in the roach, *Blatella germanica* (Linn.) *J.Kans.ent.Soc.* **10**(1): 1-9.

Addendum

The unpublished thesis of Christa Wasgestian-Schaller was brought to our attention recently by Dr J. Cokendolpher. This is an excellent study of "autotomy" in the Opiliones with a literature review. Remarks made in our paper about opiliones are confirmed and more genera showing autospasy are added, mostly in the Eupnoi and a few in the Dyspnoi of the Palpatores. She shows that opiliones whose legs twitch after detachment always have accessory tibial spiracles which provide oxygen to activate the muscles used in twitching.

Reference

- WASGESTIAN-SCHALLER, C. 1967: Die Autotomie-Mechanismen an den Laufbeinen der Weberknechte (Arachnida, Opiliones). 1-77. Dissertation, Johann-Wolfgang-Goethe-Universität, Frankfurt am Main.