

Leg regeneration in web spiders and its implications for orb weaver phylogeny

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Summary

Many spiders regenerate lost legs. Such regeneration seems to be an ancestral trait. Regenerated legs emerge during a moult and often appear to be poorly- or non-functional until they themselves have moulted at least once more. Some web-building spiders (e.g. *Nephila clavipes* (Linn.), *Zygiella x-notata* (Clerck), *Latrodectus mactans* (Fabr.)) suppress regeneration in the coxa-trochanter joint but retain this faculty in the more distal sections of the leg. Other web-building spiders (e.g. *Araneus diadematus* Clerck, *Argiope argentata* (Fabr.), *Cyrtophora moluccensis* (Doleschall)) regenerate lost legs in the coxa-trochanter joint, as well as further distad. In these latter species regenerated legs or regenerated segments are nearly always fully functional a few hours after their emergence. Regeneration is widespread in arachnids and can be assumed to be a plesiomorphic trait. Inhibition of regeneration localised at a particular articulation is a synapomorphic trait for a few groups of web-building spiders (viz. the Theridiidae, Pholcidae and Tetragnathidae, possibly also the Linyphiidae and Uloboridae). Inhibition of regeneration has heretofore not been used as a taxonomic character. It is an unambiguous trait (with only 2 states: present or absent). I believe that a closer examination of this character might shed light on orb weaver phylogeny.

Introduction

It seems that the ability to regenerate is an ancestral trait for all organisms (Goss, 1969). Among plants and in the more simple animals (like *Hydra*) it is often used for propagation (Barrington, 1967). Among the more advanced animals regeneration serves to replace lost or mutilated parts of the body, generally limbs (Needham, 1965). As such it is widespread in invertebrate groups like Annelida (Morgan, 1902), Crustacea (Heineken, 1829a; Prizibram, 1896; Needham, 1945; Cheung, 1973) and Myriapoda (Cameron, 1927). This faculty also appears in the hemimetabolous insects (Brindlay, 1897; Bordage, 1899), mites (Obenchain & Oliver, 1972) and spiders (Table 1). Among the vertebrates regeneration is rare, although many anurans regenerate legs (Scadding, 1977) and most lizards regenerate tails (Arnold, 1984).

It is commonly thought that all spider species are able to regenerate lost legs (Blackwall, 1873; McCook, 1894; Schultz, 1898; Paulian, 1938; Foelix, 1982). Many species even appendotomise, i.e. detach mutilated or trapped legs at specific articulations (Wood, 1926; Bauer, 1972; Roth & Roth, 1984). Appendotomy may be considered an adaptation against predators, as in the lizards where the shedding and subsequent regeneration of a seized tail has evolved twice

independently (Arnold, 1984). It therefore comes as a surprise that the black widow (*Latrodectus mactans* (Fabr.), Theridiidae) readily appendotomises a leg at the coxa-trochanter articulation but fails to regenerate at that point, although regeneration may occur if a section of leg is forcefully amputated further distad (Randall, 1981). It appears that in *Latrodectus* the faculty of regeneration is suppressed at the articulation of appendotomy, and only there. I shall demonstrate that this feature (inhibition of regeneration at a particular locality) is not limited to the Theridiidae but is also common in some orb weavers, all recently placed in the Tetragnathidae (Levi, 1986). Some orb-weaving genera, however, do not show this trait and regenerate their legs from the coxa-trochanter joint.

Spiders appendotomise (shed) a limb using autotilly or autotomy (for review see Roth & Roth, 1984). In autotilly the animal itself separates leg and body either by rotation in the articulation or by tearing with chelicerae and other legs. In autotomy an internal mechanism is responsible for separating the joints without any external force. It appears to be species specific whether autotilly or autotomy is the mechanism used to shed a leg (Roth & Roth, 1984). Some species, as shown here, do not appendotomise under any circumstances.

Methods

Various methods were used for depriving the spiders under study of their legs. (A) The leg was held by forceps and the animal was free to detach the trapped leg by autotilly or autotomy. (B) Both leg and spider were held with forceps and the leg was pulled lightly. (C) The spider was anaesthetised with CO₂ or restrained without anaesthesia; the leg was severed with a pair of surgeon's scissors, sometimes after applying a tourniquet made from a human hair. Method A was by far the most successful in terms of survivorship, if the animal had the ability to regenerate at the coxa-trochanter articulation. When legs were severed by method C, either at an articulation or in the middle of a segment, a fatal loss of haemolymph often ensued due to the internal fluid pressure. Therefore mortality was high whenever this method was employed. It seemed to make little difference whether a tourniquet was applied or not. Survivorship seemed to increase somewhat when the spiders were anaesthetised and chilled.

Amputations were performed either at an articulation (coxa-trochanter or tibia-metatarsus) or at the middle of a leg segment (generally the tibia, sometimes the femur). If the species possessed the ability to appendotomise, such mutilated legs were often shed, especially when a tourniquet had been applied. Legs were amputated in a range of instars and periods in the moulting cycle. However, in the analysis only those data were used where the spiders moulted not earlier than 7 days after the operation and had at least two moults to go until maturation. All operated spiders were fed *ad libitum*.

I attempted to study a representative number of

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species from the various families. Nevertheless, some important genera and families are either not at all or are under-represented because of difficulties with obtaining specimens and/or a high mortality associated with the experimental procedure. Only a major investigation (at present impossible for me) will remedy this bias, so I here present my observations and hope that others may add to the data. Most collections contain some individuals with regenerated legs or (unregenerated) leg-stumps. The presence of a regenerated limb shows if the regenerative faculty is present; a healed stump may indicate its absence.

My presentation will rely in part on data gleaned from the literature. As these data often are of an anecdotal nature, hidden among the discussion of other questions, these data have to be taken as indications for a character state, not as proof. This shortcoming, however, does not affect the argument, namely that the two character states, regeneration or inhibition, might be valuable for spider taxonomy. The hypothesis can be formulated as follows: The trait "inhibition of regeneration" is not randomly distributed among spiders; it is

found only in a few groups of web spiders. Most notable is its absence in one family of orb weavers, the Araneidae, and its presence in another family, the Tetragnathidae *sensu* Levi, 1986. The Araneidae contains, e.g., *Araneus*, *Argiope*, *Cyrtophora* and *Mecynogea*, while the Tetragnathidae contains the subfamilies Tetragnathinae (*Tetragnatha*), Metinae (*Metellina*, *Zygiella*) and Nephilinae (*Nephila*).

Results

Literature survey

Table 1 presents the results of a literature survey. It demonstrates convincingly that representatives of the following families regenerate their legs at the articulation of appendotomy: Theraphosidae, Thomisidae, Lycosidae/Pisauridae and Agelenidae. All these families are represented by at least two species or genera and the legs have been appendotomised. The Ctenidae and Anyphaenidae are also likely to show regeneration at the coxa-trochanter articulation of appendotomy. The Philodromidae, Sparassidae,

Species	Family	Author	Regen.	Cut	App.
<i>Dugesia hentzi</i> (Girard)	Theraphosidae	Ruhland, 1976	yes		yes
<i>D. californica</i> (Ausserer)	"	Baerg, 1926	yes		yes
<i>Cupiennius salei</i> (Keyserling)	Ctenidae	E. A. Seyfarth, comm.	yes		yes
<i>Thomisus onustus</i> Walckenaer	Thomisidae	Gabritschevsky, 1930	yes		yes
<i>Misumena vatia</i> (Clerck)	"	Gabritschevsky, 1927	yes		yes
<i>Tibellus oblongus</i> (Walck.)	Philodromidae	C. Bromhall, comm.	yes		yes
<i>Heteropoda venatoria</i> (Linn.)	Sparassidae	McCook, 1894	yes	?	
<i>H. venatoria</i>	"	Bordage, 1901	yes		
<i>Olios fasciculatus</i> Simon	"	Gertsch, 1948	yes		
<i>Anyphaena accentuata</i> (Walck.)	Anyphaenidae	C. Bromhall, comm.	yes		yes
<i>Lycosa</i> sp.	Lycosidae	Heineken, 1829b	yes	yes	
<i>Lycosa singoriensis</i> (Laxmann)	"	Wagner, 1887	yes		yes
<i>Trochosa</i> sp.	"	McCook, 1894	yes		?
<i>Pirata piraticus</i> (Clerck)	"	Heineken, 1829b	yes		
<i>Dolomedes fimbriatus</i> (Clerck)	Pisauridae	Bonnet, 1930	yes		yes
<i>Salticus</i> sp.	Salticidae	Heineken, 1829b	yes	?	
<i>Salticus</i> sp.	"	F. R. Wanless, comm.	yes		?
<i>Metaphidippus aeneolus</i> (Curtis)	"	Banks, 1904	yes	?	
<i>Tegenaria domestica</i> (Clerck)	Agelenidae	Blackwall, 1845, 1848	yes		yes
<i>T. atrica</i> C. L. Koch	"	Mikulska <i>et al.</i> , 1975	yes/no	yes	
<i>Textrix denticulata</i> (Olivier)	"	Blackwall, 1845	yes		?
<i>Agelena labyrinthica</i> (Clerck)	"	Blackwall, 1848	yes		yes
<i>Coelotes terrestris</i> (Wider)	"	Vachon, 1967	yes	?	
<i>Argyroneta aquatica</i> (Clerck)	"	Oppenheim, 1908	yes		yes
<i>A. aquatica</i>	"	Weiss, 1907	yes		yes
<i>Segestria florentina</i> (Rossi)	Segestriidae	Heineken, 1829b	yes	?	
<i>S. senoculata</i> (Linn.)	"	Blackwall, 1845	yes		?
<i>Amaurobius similis</i> (Blackwall)	Amaurobiidae	Blackwall, 1848	yes	?	
<i>A. ferox</i> (Blackwall)	"	Blackwall, 1845	yes		?
<i>A. fenestralis</i> (Stroem)	"	Blackwall, 1845	yes		?
<i>Pholcus phalangioides</i> (Fuessl.)	Pholcidae	Savory, 1936	no	?	
<i>Latrodectus mactans</i> (Fabr.)	Theridiidae	Randall, 1981	no		yes
<i>Enoplognatha ovata</i> (Clerck)	"	Locket, 1936	no		yes
<i>Linyphia marginata</i> C. L. Koch	Linyphiidae	Locket, 1936	no		yes
<i>Microlinyphia impigra</i> (O. P.-C.)	"	Blackwall, 1848	yes/no	?	?
<i>Nuctenea umbratica</i> (Clerck)	Araneidae	Jones, 1984	yes		?
<i>Araneus diadematus</i> Clerck	"	Heineken, 1829b	yes	?	
<i>Tetragnatha extensa</i> (Linn.)	Tetragnathidae	Heineken, 1829b	yes	?	
<i>Metellina merianae</i> (Scopoli)	"	Blackwall, 1848	yes	?	

Table 1: Compilation from original literature and from communicated observations (comm.) with references to the occurrence of regeneration of limbs at the coxa/trochanter articulation (legs or pedipalps) in spiders. The reported presence or absence of regeneration (**Regen.**) is indicated by a yes (present) or a no (absent). Whenever it is clear from the description whether the legs were appendotomised (**App.**) or cut (**Cut**) this is indicated; if it is unclear but likely a question mark is given in the appropriate column. The species names were generally brought up to present date, for which I thank H. W. Levi.

Salticidae, Segestriidae, Amaurobiidae and Araneidae may show it but the data are insufficient to be sure. It is unlikely that regeneration occurs in the Pholcidae, Theridiidae and Linyphiidae.

Five studies have investigated regeneration of spider legs in considerable detail. Wagner (1887) and Friedrich (1906) discussed the anatomy of regeneration. Bonnet (1930) demonstrated in *Dolomedes fimbriatus* (Clerck) (Pisauridae) the morphology of regeneration in appendotomised and amputated legs. Ruhland (1976) investigated the neuromuscular aspects of regeneration in the mygalomorph *Dugesia hentzi* (Girard). Randall (1981) showed in detail that in *Latrodectus mactans* (*L. variolus* Walck., Theridiidae) regeneration is suppressed at the joint of appendotomy but that legs severed further distad do regenerate.

Experiments: Regeneration or not?

Table 2 shows the results of my own experiments. It appears (Table 2a) that among the spiders which build complex webs the character trait "regeneration at the coxa-trochanter articulation" occurs in the Psecridae and the Araneidae but not in the Theridiidae, Pholcidae and Nephilinae. The trait is also absent in *Zygiella x-notata* (Clerck) and *Phonognatha* sp., both of which I place in the Metinae on account of their web-building behaviour (Vollrath, unpubl.), as would H. W. Levi on account of genitalia structure (pers. comm.). Regeneration at or near the coxa/trochanter articulation is unlikely in the Linyphiidae, Tetragnathidae (Tetragnathinae and Metinae) and Uloboridae.

Nephila and *Zygiella* never regenerate at the coxa-trochanter joint but always regenerate sections of a leg that have been amputated further distad (Table 2b). *Araneus* also regenerates distad amputations. I have no observations on proximal amputations.

I never observed regeneration at the joint of appendotomy in either *Nephila* or *Zygiella* although Weissmann (1987) and I have experimentally induced

the loss of legs in hundreds of individuals of *Nephila* and *Zygiella*. With an equal sample size in *Araneus* there was always regeneration, if not at the first then at least at the second post-amputative moult. Taken together, these observations suggest strongly that we are dealing with an all or none character state, present or absent.

Experiments: Using the regenerate

In 50 *Nephila*, legs were amputated either at the femur (20), the tibia (20) or the metatarsus (10) (Table 2b). In 24 survivors the spiders did not autotillate the remaining stumps (in 10 femur, 10 tibia and 4 metatarsus excisions). With the notable exception of 2 specimens, where the amputation on the femur had been very close to the coxa-trochanter joint, the stumps always regenerated. The observation that legs amputated distad of the coxa-trochanter joint regenerate (if they were not autotillated), was fully repeated in *Zygiella*, where 40 legs were amputated at the tibia, and in *Araneus*, where 10 legs were amputated at the tibia.

It is possible that the factor suppressing regeneration is carried in the haemolymph. To test this hypothesis I induced in 5 *Nephila*, immediately following tibial amputation of one leg, the autotilly of a neighbouring leg at the coxa/trochanter. Two of these 5 specimens shortly afterwards autotillated the tibial stumps as well. In the other 3 cases the tibial stumps regenerated. This suggests that the suppressing factor is not carried in the haemolymph, at least not from one leg to another.

Legs of *Araneus* which have been regenerated at the coxa-trochanter are much smaller but remarkably well proportioned (Fig. 1). The proportions of the different leg segments are similar to those of a normal leg (Table 3) although regenerates are relatively thicker (Vollrath, 1989, in prep.). However, the emergent regenerate has

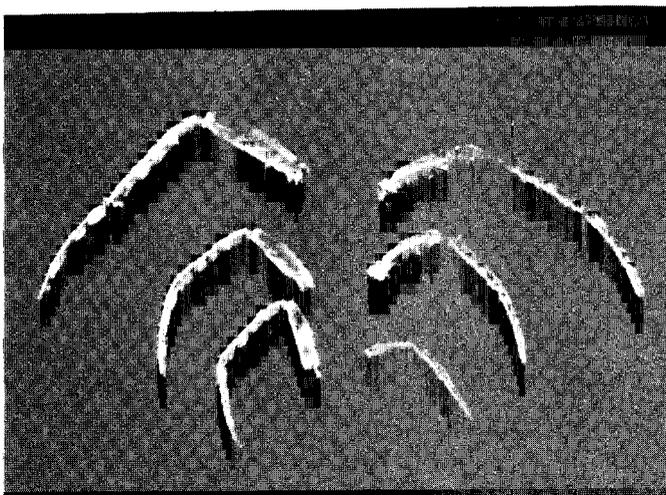


Fig. 1: Regeneration of a first leg in *Araneus diadematus* (left) and *Nephila clavipes* (right). In *Araneus* the leg was autotillated, in *Nephila* it was amputated at the femur. Each photograph shows the subsequent stages (going up) of the regenerating and the normal leg. For *Araneus* the exuviae of 3 moults following appendotomy are shown, and for *Nephila* those of the stadium at the operation as well as the 3 following moults.

fewer sensory hairs, and abnormal lyriform organs as well as a thinner cuticle (Vollrath, 1989, in prep.). With additional moults the leg rapidly approaches normality in absolute size (Table 4), proportion and sensory complement (Vollrath, in prep.). In *Araneus* the regenerated tarsus/metatarsus after a tibial amputation resembles the regenerated tarsus/metatarsus after regeneration at the coxa-trochanter autotilly. *Araneus* may use either regenerate (be it caused by autotilly or amputation) shortly after its emergence. If and how much the leg is used, depends on the importance of the leg in the behaviour sequence (Vollrath, 1987b, 1988, and unpubl.). A newly moulted pair of first legs is used within 24 hours after emergence. If the second pair of legs is missing, the first pair will be used both in web building and prey capture. If the second pair is present, the regenerated first legs are likely to be used in web building but not in prey capture. Webs built with such

newly regenerated legs can be very regular structures yet betray in their geometry the use of regenerated legs. Rarely indeed (3 out of *c.* 100 observations) is an emergent regenerate in *Araneus* a non-functional 'stump' without articulation or claws.

In *Zygiella* and *Nephila* newly regenerated legs are always non-functional. A newly regenerated section of a leg in *Nephila* is very different both from the comparable section of a normal leg in the same species and from a comparable leg regenerate in *Araneus* (Fig. 1). As a rule the new regenerate of *Nephila* and *Zygiella* lacks articulation, claws and sensory organs. It is not used but instead is held away from the body more or less rigidly. With increasing additional moults it slowly approaches normal morphology (Table 4) and normal usage. In *Nephila* none of the 22 emergent regenerates possessed a claw. This only appeared after a second ($n=12$) or third moult ($n=10$) (see also Fig. 1).

Species	Family/Subfamily	<i>n</i>	Surv.	Aut.	Reg.	Not	Regen.
A							
<i>Psechrus argentatus</i> (Doleschall)	Psechridae	4	4	yes	4	0	yes
<i>Fecenia ochracea</i> (Doleschall)	"	3	3	yes	3	0	yes
<i>Uloborus plumipes</i> Lucas	Uloboridae	2	1	no	0	1	no
<i>U. walckenaerius</i> Latreille	"	30	1	no	0	1	no
<i>Miagrammopes</i> sp.	"	10	0	no	—	—	
<i>Theridiosoma</i> sp.	Theridiosomatidae	5	0	no	—	—	
<i>Theridiosoma gemmosum</i> (L. Koch)	"	2	0	no	—	—	
<i>Symphytognatha</i> sp.	Symphytognathidae	5	0	no	—	—	
<i>Tetragnatha extensa</i> (Linn.)	Tetragnathidae	20	2	no	0	2	no
<i>T. montana</i> Simon	"	5	0	no	—	—	
<i>T. maxillosa</i> Thorell	"	5	0	no	—	—	
<i>Metellina segmentata</i> (Clerck)	"	25	1	no	0	1	no
<i>Leucauge</i> sp.	"	10	0	no	—	—	
<i>Nephila clavipes</i> (Linn.)	"	>50	all	yes	0	all	no
<i>N. maculata</i> (Fabr.)	"	2	2	yes	0	2	no
<i>Zygiella x-notata</i> (Clerck)	"	>50	all	yes	0	all	no
<i>Phonognatha</i> sp.	"	5	2	yes	0	2	no
<i>Mecynogea lemniscata</i> (Walck.)	Araneinae	?	3	likely	3	0	yes
<i>Cyrtophora moluccensis</i> (Doleschall)	"	1	1	yes	1	0	yes
<i>Araneus diadematus</i> Clerck	"	>50	all	yes	all	0	yes
<i>Nuctenea umbratica</i> (Clerck)	"	2	2	yes	2	0	yes
<i>Eriovixia laglaizei</i> (Simon)	"	1	1	yes	1	0	yes
<i>Neoscona theisi</i> (Walck.)?	"	5	4	yes	4	0	yes
<i>N. theisi</i> (Walck.)	"	3	3	yes	3	0	yes
<i>Araniella cucurbitina</i> (Clerck)	"	10	6	yes	6	0	yes
<i>Argiope argentata</i> (Fabr.)	"	4	4	yes	4	0	yes
<i>A. trifasciata</i> (Forskål)	"	2	2	yes	2	0	yes
<i>Gea spinipes</i> C. L. Koch?	"	1	1	yes	1	0	yes
<i>Acusilas coccineus</i> Simon	?	10	0	yes	—	—	
<i>Cyclosa insulana</i> (Costa)	?	1	0	yes	—	—	
<i>Gasteracantha taeniata</i> (Walck.)	?	10	0	no	—	—	
<i>Tidarren</i> sp.	Theridiidae	2	2	yes	0	2	no
<i>Linyphia triangularis</i> (Clerck)	Linyphiidae	15	2	no	0	2	no
<i>Pholcus phalangioides</i> (Fuesslin)	Pholcidae	6	6	yes	0	6	no
<i>Oxyopes</i> sp.	Oxyopidae	1	1	yes	1	0	yes
<i>Salticus scenicus</i> (Clerck)	Salticidae	?	1	likely	1	0	yes
B							
<i>Nephila clavipes</i> (Linn.)	Tetragnathidae	50	24	amp.	22	2	no
<i>Zygiella x-notata</i> (Clerck)	"	40	15	amp.	15	0	no
<i>Araneus diadematus</i> Clerck	Araneidae	10	5	amp.	5	0	yes

Table 2: Results of my experiments and observations on regeneration of legs. All spiders shown had either (i) regenerated after the first moult or (ii) moulted at least twice after the operation with or without regeneration. A: Legs were removed entirely at the coxa-trochanter joint, either by autotomy (Aut. — yes) or by amputation if the spider did not autotomise (Aut. — no). It is indicated for each species whether the legs regenerate at the coxa-trochanter joint. B: Legs were amputated (amp.) at either the femur, tibia or metatarsus (see text). *n* indicates the total sample size (a question mark indicates that individuals with missing legs were collected in the field), *Surv.* indicates the number of survivors, *Reg.* are those that regenerated (not at coxa-trochanter joint in B), *Not* are those that did not regenerate, *Regen.* indicates whether it is likely that the species has the faculty of regeneration at the coxa-trochanter joint (yes) or suppression (no).

Segment	Leg I			Leg II			Leg III			Leg IV		
	Norm.	Reg.	%	Norm.	Reg.	%	Norm.	Reg.	%	Norm.	Reg.	%
Tarsus	6	3	50	5	2.5	50	4	2	50	4.5	2.5	56
Metatarsus	12	7.5	63	10	7.5	75	7	4	57	10	6.5	65
Patella-tibia	20	11	55	18	9	50	11	6	55	16.5	8.5	52
Femur	17	12	71	15	10	67	11	8.5	77	16.5	10	61

Table 3: Comparison of length of normal (Norm.) and newly regenerated (Reg.) legs in *Araneus diadematus*. In the spider shown here all legs on the left side had been autotillated and all regenerated together. The measurements of the various segments of each leg are given in units (10 units = 1.4mm), and the proportional length of the regenerates in relation to the normal leg is given in %.

Discussion

Regenerate growth

Regenerated legs are shorter (Fig. 1; Tables 3, 4) but the segments regenerated at the coxa-trochanter have the same proportions as normal legs (Ausserer, 1867). This is true for web-less hunting spiders like *Dolomedes* and *Dugesiella* (Bonnet, 1930; Ruhland, 1976). It is also true for all the web-building spiders I examined which regenerate appendotomised legs (e.g. representatives of the genera *Argiope*, *Araneus*, *Mecynogea*, *Cyrtophora* (Araneidae), *Psechrus*, *Fecenia* (Psechridae) and others, see Tables 3 and 4). In these species legs regenerate proportional to their intact counterparts, although the total length seems to depend on the nutritional state of the individual and the time elapsed between the loss of a leg and the subsequent moult (Bonnet, 1930). In *Araneus* and *Dolomedes* regeneration after appendectomy creates legs which are about half normal size at their emergence, and which will be of near normal size after another two moults (Table 4). In contrast the regenerates of *Nephila* and *Zygiella* only reach a reasonable degree of functionality after about three moults, when the regenerated segments are still not even half normal size. This cannot be a result of amputation (as opposed to appendotomy) because in *Araneus* as well as in *Dolomedes* (Bonnet, 1930) most

amputated segments of legs emerge already functional and well-proportioned. In Bonnet's experiments 34 *Dolomedes* survived the amputation of various segments and moulted twice afterwards. Of these 34 animals all but 2 regenerated well-proportioned and apparently functional legs. I observed the same for 10 cases of segment regeneration in *Araneus*. This contrasts with my observations on *Nephila* ($n=22$) and *Zygiella* ($n=15$), where none of the regenerating segments had proportional regeneration. In *Nephila* not one of the emergent segment regenerates had even a claw. All of them were non-functional and became functional only after three moults and then still looking like regenerated legs. At this stage *Araneus* segment regenerates as well as full-length regenerates were indistinguishable from normal legs.

Why regenerate?

During its lifetime any spider may experience the loss of a leg. Oppenheim (1908) estimated that up to 70% of hunting spiders lose a leg during their lifetime. Friedrich (1906) noted in his spider collection that 30% had lost a leg (neither sample size nor species are given); it is possible that some individuals might have lost legs in transit (O. Kraus, pers. comm.). Bauer (1972) carefully noted missing legs in the spiders he collected (April-October 1966/67 in Erlangen, West

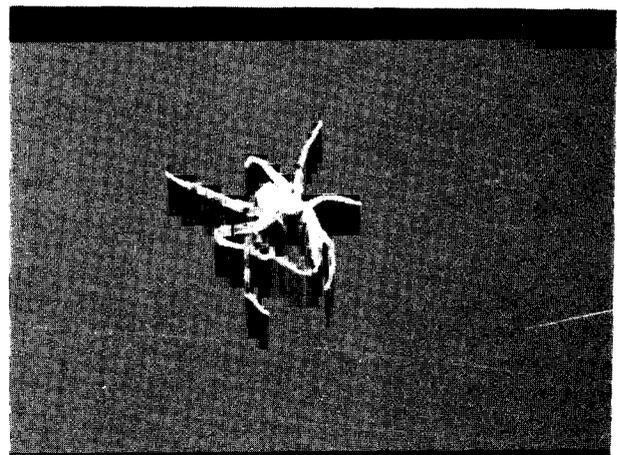
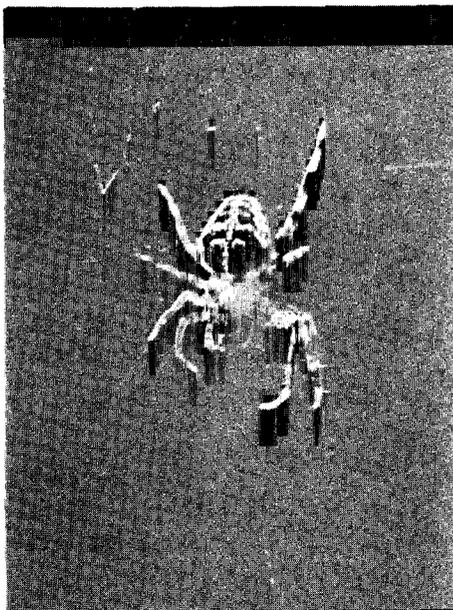


Fig. 2: Left — *Araneus diadematus* with all legs on its right side newly regenerated. Right — The same spider building a web 24 hours after the regenerating moult, and already using the regenerated legs in co-ordination with the normal legs. For a photograph of such a web see Vollrath (1988).

concentrated on the orb weavers, where accuracy of limb co-ordination is paramount and can be analysed in the geometry of the web. All web spiders (except *Tetragnatha* and *Metellina* which appear to die rather than lose a leg) must be able to cope when legs are missing. They must still be able to build webs that are functional. The probability of losing a leg or two is sufficiently high (5 to 20% at least) to favour the evolution of such a trait, i.e. a behaviour pattern that leads to a functional web even when legs are missing. All the spiders that Weissmann (1987) and I (Vollrath, unpubl.) examined can build functional webs when one or two legs are missing. *Nephila*, for example, still builds a remarkably regular web with only three legs (Vollrath, unpubl.), and consistently builds functional webs with only four legs! (Weissmann, 1987).

This discussion deals with orb spiders but it must be remembered that the Pholcidae and Theridiidae also inhibit regeneration. The Theridiidae may be descendants of orb weaving stock (Levi, 1980; Coddington, 1986, 1989) and are therefore a specialised group. The Pholcidae are web spiders with exceptionally long legs. The speed at which long thin appendages can grow is limited (Majorana, 1979). Therefore regrowing a lost leg to full size or nearly full size may require too many moults to be practical for a pholcid. Clearly there is scope for future research.

The ability to co-ordinate accurately the much shorter regenerates with the normal legs is altogether another matter from making do when legs are missing (Vollrath, 1987b). Depending on the complexity of the behaviour pattern and its central nervous control, special provisions would have to evolve along with the behaviour to incorporate the regenerated, and therefore abnormal, legs (Vollrath, 1989). On the one hand, the sensory and motor complement of the regenerated leg has to be sufficiently complex to allow accurate control. On the other hand, the inherited rules which control and co-ordinate the movements and activities of the legs have to incorporate procedures which make allowance for the abnormal length of any leg. In this context it is relevant (Vollrath, unpubl.) that neither *Nephila* nor *Zygiella* uses legs which carry recently regenerated segments. *Araneus*, on the other hand, does so and without it showing in the geometry of the web. *Nephila* and *Zygiella* may begin to use such legs after 2 or 3 moults, when the regenerated segments are a good deal longer and more developed.

I suggest (without at present being able to test this hypothesis) that the inhibition of leg regeneration at the articulation of appendotomy is an adaptation to prevent the emergence of leg regenerates which, for several moults, cannot be used profitably during web construction. These regenerates cannot be used because the spider lacks the ability to control their movement accurately. Such accuracy of control is required during the construction of an orb web whose effectiveness relies on geometric regularity (Eberhard, 1986). Comparable accuracy seems unnecessary in hunting spiders which during locomotion often drag a new regenerate along rather than use it actively (Ruhland, 1976). During the construction of an orb

web a useless leg can get in the way, as witnessed by the fresh femoral regenerates in *Nephila* that are held away stiffly but still often catch on the sticky capture threads.

Thus we can imagine two possible pathways to deal with leg loss during the emergence of highly geometric webs with sticky threads (i.e. orb webs): (1) the evolution of a high degree of accuracy in the control of movement of regenerates, and (2) the suppression of regenerates through the inhibition of regeneration. This dichotomy renders the trait highly significant for spider evolutionary taxonomy. It is unlikely that inhibition would or could have been reversed as this would involve selection to improve the action of a leg that is absent (having been suppressed). On the other hand, it seems equally unlikely that the spider would give up such a beneficial trait as being able to replace fully a lost leg, especially since the loss of a leg is likely and bears a high cost in reproductive fitness (Vollrath, 1980, 1987a). This provides independent evidence that Levi's (1986) placing of *Nephila* and *Zygiella* with the metines in the Tetragnathidae and removing them from the Araneidae is correct. Moreover, it provides a good synapomorphic character for the family Tetragnathidae as defined by Levi (1986). Information about regeneration in the Uloboridae would help to understand the phylogeny of the orb weaving spiders.

A better understanding of the selection pressures responsible for the inhibition of regeneration in araneids might even shed light on a truth much closer to home: that regeneration, although present in the more ancestral vertebrates, like salamanders, is suppressed in the more derived vertebrates, like man. Curiously, the phenomenon of suppression is rarely discussed from an evolutionary point of view, even within single phyla (Scadding, 1977; Arnold, 1984). The observation of this trait in the araneids may provide a rare insight into regeneration, its mechanism as well as its function.

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Germany): 12% of *Philodromus* spp. ($n=452$), 18% of *Lycosa* spp. ($n=400$) and 2% of *Tegenaria domestica* (Clerck) ($n=320$) had lost one or more legs; the first two genera are hunting spiders, the third is a funnel-web spider. Oppenheim (1908) found in the water spider *Argyroneta aquatica* (Clerck) that 4% had lost a limb ($n=80$). In one sampled population of *Araneus diadematus* ($n=100$, September 1984, Isles of Scilly, England) 10% were individuals which had lost one or two legs (Vollrath, pers. obs.). In *Nephila clavipes* this proportion was 21% ($n=78$, January 1981, Cerro Galera, Panama, Vollrath, pers. obs.). Both *Nephila* and *Araneus* are orb weavers which occupy the centre of the web, exposed to predators. *Metellina [Meta] segmentata* (Clerck) and most *Tetragnatha* spp. also stay in the centre of their web but I never found an individual with an incomplete set of legs ($n>500$, September 1985/86, Wick Copse, Oxford, Vollrath, pers. obs.). *Zygiella* is an orb weaver which retires into a retreat during the day. A population of *Zygiella x-notata* (University Parks, Oxford, Weissmann, 1987) showed that 5% of the individuals were missing one or two legs in the summer ($n=594$, August 1985). Four months later this figure had increased to 8% ($n=100$, December 1985).

All of these studies show that the loss of one or several legs is not a rare event for a spider. Hunting spiders and exposed web spinners seem more at risk than the secretive web spinners hiding in a retreat. The lack of even a single individual with a lost or regenerated leg in the exposed orb weavers *Metellina* and *Tetragnatha* suggests that representatives of these genera may not survive the loss of a leg. The alternative hypothesis, that these genera experience fewer attacks by predators, seems unlikely. It is curious (and at present I cannot explain it) that representatives of both these genera do not autotomise their legs.

Loss of a leg, not surprisingly, seems to affect the efficiency of prey capture. Weissmann (1987) found that "incomplete" *Zygiella* and *Nephila* built functional webs but nevertheless had a lower rate of prey capture than "complete" controls. This was due only partly to increased irregularities in web geometry. More importantly, the spiders without a full complement of legs had longer reaction times because of difficulties in locating prey, even when the spiders were placed on a normal web (Weissmann, 1987). Thus the absence of a leg carries a cost.

It also seems that neither regeneration nor its inhibi-

tion are correlated with any obvious parameters of the animal's habits. *Nephila clavipes* (which inhibits leg regeneration) is a large orb weaver, with an active life span of up to a year. It occupies the hub day and night. Leg loss is a frequent occurrence in *Nephila* (21%). In *Nephila* the loss of one or more legs leads to greatly reduced reproductive fitness, especially in the males (Vollrath, 1980, 1987a). *Araneus diadematus* (which regenerates legs) is also a large orb weaver, with an active life span of up to a year (we may discount hibernation as a period of inactivity). In its predatory behaviour *Araneus* resembles *Nephila*, and leg loss is similarly quite common (with 10% probability). *Araneus* generally occupies the hub and rarely hides in a retreat during the day (Vollrath, pers. obs.). *Zygiella x-notata* (which has inhibition) is much smaller than *Nephila* and even smaller than *Araneus*. Its active life span is 6 months at the most. Although *Zygiella* will catch prey during the day, it always spends nearly all of the daylight hours in the safety of a retreat, only to leave it at night for the hub. Nevertheless, for *Zygiella*, too, leg loss is a frequent event (c.7%). It is curious that these obvious differences between *Nephila*, *Zygiella* and *Araneus* in body size, longevity and activity pattern do not seem to correlate with either the ability to appendotomise or the ability to regenerate.

More examples support this statement. *Argiope* and *Cyrtophora* occur syntopically with *Nephila*; are not much smaller and have a similar life history (e.g. Robinson, Lubin & Robinson, 1974). Yet *Argiope* and *Cyrtophora* regenerate like *Araneus*. The tropical sham-orb weaver *Fecenia* (Psecridae), which resembles *Zygiella* in size and in its habit of spending the day in a retreat (Robinson & Lubin, 1979), nevertheless regenerates its legs. Its syntopic, exposed and much larger confamilial *Psecchus* also regenerates. Both species readily appendotomise.

It is unlikely that parameters of the spiders' habits and/or life history have caused the observed selection for inhibition of regeneration. As inhibition is not an inconsequential step, it is unlikely to be the result of random drift. Thus we will have to seek the selective advantage associated with the trait or, at least, be able to point towards the ghost of past selection. A comparative study might make this possible.

It seems that the presence or absence of regeneration might be associated with the ability to use the regenerated leg (within the limits of accuracy of control required) during web construction. My studies have

Species	Stump	M1	M2	M3	n	Reference
<i>Dugesiella hentzi</i>	0	61-71%	76-85%	83-90%	22	Ruhland, 1976
<i>Dolomedes fimbriatus</i>	0	67-79%	86-91%	96-98%	4	Bonnet, 1930
<i>Araneus diadematus</i>	0	57-64%	69-82%	84-94%	4	Experiment
<i>Nephila clavipes</i>	15-52%	18-56%	30-72%	47-88%	4	Experiment

Table 4: Regeneration in proportion to the normal opposite leg. Legs were either autotomised at the coxa-trochanter joint (Stump = 0) or amputated at the femur or tibia (proportion of stump given). M1-M3 indicates the sequence of moults after the amputation. Measurements were either gleaned from the literature or taken from experimental animals (Reference). Note that as *Nephila* has a sizeable stump to begin with, the relative size of its leg regenerates cannot be compared directly with those of the other species.

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