Development of web-building and spinning apparatus in the early ontogeny of *Nephila madagascariensis* (Vinson, 1863) (Araneae: Tetragnathidae)

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Summary

The development of web-building behaviour and spinning apparatus in the first three ontogenetic stages after hatching has been studied in the orb-web spider *Nephila madagascariensis*. The postembryo (first stage) remains in the cocoon after hatching, shows no web-building behaviour, and its spinning apparatus is not developed. The first instar (second stage) leaves the cocoon and, together with its siblings, builds an irregular communal web in which all the spiderlings remain for a considerable period. Only the second instar (third stage) leaves the communal web, disperses and finally builds regular orb-webs. However, when first instars are artificially removed from the cocoon or communal web and put individually on wire frames, they build irregular so-called primary-webs and regular orb-webs. Primary-webs consist of more-or-less radial threads, connected by short, spiral threads, but they lack the geometric regularity of orb-webs. Orbs built by the first and second instar are complete miniature orb-webs and possess a structural as well as a sticky capture spiral. However, only the second instar orb resembles in its appearance the typical *Nephila* web. Consistent with web-building abilities, the external spinning apparatus is well developed in both instars, with a functional triad complex being responsible for the secretion of the sticky capture spiral.

Introduction

Nephiline spiders are widely distributed in the tropics and subtropics. Adult females are well known for their large body and orb-web size. Besides the distinctive golden colour, the orb-webs show some remarkable structural features. First, they are vertically asymmetric in that the lower half of the web is enlarged. Secondly, the structural spiral is, in contrast to the webs of most other Araneidae, not removed in the finished orb, but is retained permanently. Thirdly, numerous branched radii together with the structural and capture spirals contribute to a very fine-meshed web, and the attachment of the structural spiral to the radii over a short distance forms a distinctive zigzag pattern (see Fig. 8). And fourthly, a more or less irregular barrier-web is built in addition to the functional orb-web.

These characteristic web features have evoked a long-lasting discussion about the phylogenetic position of the Nephilinae. According to Kullmann (1958) and Kaston (1964), the nephiline orb-web represents an intermediate step between the "primitive" cyrtophorine web and the orb-web of Araneidae. Eberhard (1982) and Coddington (1986) suggest that the nephiline web has to be considered as a derived orb-web, but with the group placed

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somewhere at the base of all Araneoidea. According to Hormiga *et al.* (1995) and Griswold *et al.* (1998), the Nephilinae are the sister group to all other Tetragnathidae and their orb-webs are derived.

Potential sources of evolutionary information about spider phylogeny are the web structure itself and the ontogeny of web-building behaviour (Eberhard, 1990a). There are several descriptions of adult nephiline orb-webs (see e.g. Wiehle, 1931; Peters, 1953; Robinson & Robinson, 1973), but there is only a little information about their early web ontogeny. Some data are given by Wiehle (1931) and Kullmann & Stern (1981) for *Nephila madagascariensis* (Vinson, 1863). Both authors claim that first-built webs are complete orb-webs. Also only a few studies exist of the early web ontogeny of other orb-weaving spiders. Petrusewiczowa (1938) and Mayer (1952) demonstrated experimentally with *Araneus diadematus* Clerck that orb-web building is innate, and spiderlings build perfect regular orb-webs from the beginning. Peters (1969) showed that *Zygiella* spiderlings build irregular webs when removed from the cocoon at a time when they do not normally construct webs. These irregular webs are interpreted as the result of an incompletely developed central nervous system, spinning apparatus and behavioural pattern.

The present study describes the ontogeny of web-building behaviour and spinning apparatus in the first
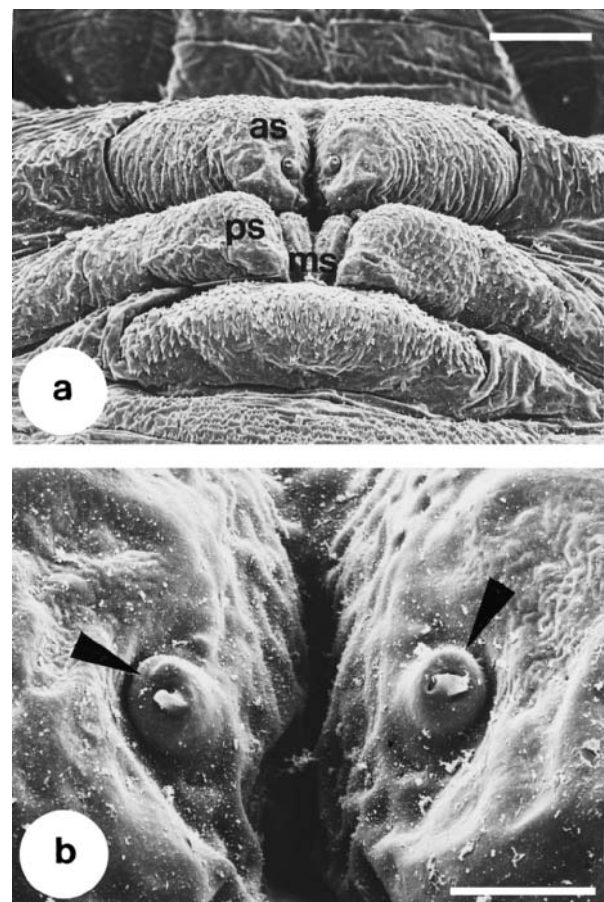

Fig. 1: Spinnerets of postembryo of *N. madagascariensis*, ventral view of posterior opisthosoma. **a** Overall view of anterior spinnerets (as), median spinnerets (ms) and posterior spinnerets (ps); **b** Anterior spinnerets, spigot bases of ampullate glands clearly visible (arrows). Scale lines=40 μm (a), 10 μm (b).
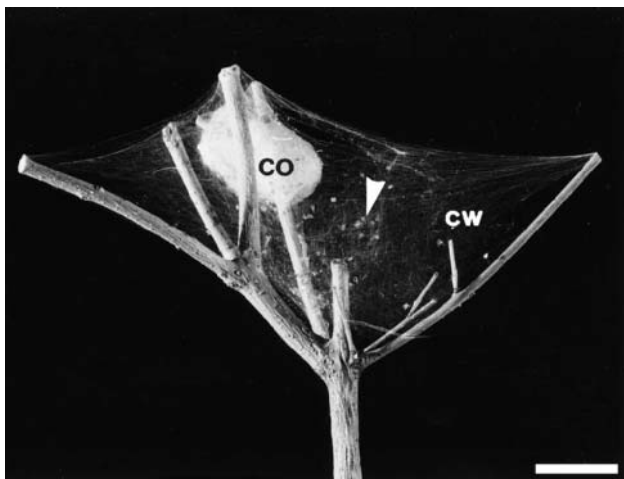
Fig. 2: Irregular communal web (cw) built in the laboratory by first instar spiderlings of *N. madagascariensis*, some exuviae visible (arrow). Spiderlings already dispersed from cocoon (co). Scale line=2 cm.

three stages of *Nephila madagascariensis* after hatching, and thus tries to fill a knowledge gap about this taxon. As ontogenetic changes in web design, with younger spiders usually making less derived designs than older spiders, can be found in many spider groups (see review in Eberhard, 1985), the study of early web-building ontogeny in the Nephilinae may contribute to the discussion of orb-web evolution.

Material and methods

Cocoons of *N. madagascariensis* from Antananarivo, Madagascar, were kept in the laboratory at a temperature of $27 \pm 2°C$, and relative humidity of $75 \pm 15\%$. Cocoons containing eggs were placed in petri dishes, and those with spiderlings were attached to a small branch. First and second instar spiderlings were put individually on circular, vertical wire frames of 7.0 and 12.5 cm diameter respectively. When kept under a reverse day/night rhythm, spiderlings built webs preferably in the early afternoon. When spiderlings built webs, they were shifted to a new frame the next day and lines from the previous day were destroyed after they had been photographed. For photographs of webs the diameter of the extremely fine threads was artificially increased by exposing them to gaseous hydrochloric acid and

ammonia (H. Homann to H. M. Peters, pers. comm.). These substances react to form a very fine suspension of white ammonium chloride particles in the air which precipitate on to the threads. Photographs of the webs were taken by placing them against a black background. Negatives of the photographed orb-webs were projected to measure web parameters. The data were analysed using the computer program JMP (1995). To study the spinnerets and spigots with the scanning electron microscope (SEM), spiderlings were fixed in Carnoy's fluid (Romeis, 1968). Their abdomens were squeezed gently to display the spinnerets. Specimens were then sputtered with gold-palladium.

Results

Postembryo

When hatching, *N. madagascariensis* spiderlings shed their first true integument completely. The following stage is here called the postembryo after Downes (1987) and has only limited ability to move. Therefore, all the postembryos remain in the densely packed cocoon where they sit in a mat of egg-shells, exuviae and strands of silk. In this stage no web structure is built by the spiderlings. The differentiation of the prospective spinnerets is also incomplete, as they can only be seen as slight elevations on the opisthosoma (Fig. 1a). The base of only one spigot is developed on each of the anterior spinnerets, and the opening of this spigot is not clearly identifiable (Fig. 1b). Judging from its location it is the spigot base of a major ampullate gland. Fine silk strands found in the cocoon indicate that the major ampullate gland spigots might be able to secrete at least some silk. Other bases of spigots or fully-developed spigots are not present in this stage (Table 1) and a colulus is lacking.

	Anterior spinneret		Median spinneret			Posterior spinneret		
	ma	pi	mi	tu	ac	tr	tu	ac
Postembryo	1_1	—	—	—	—	—	—	—
First instar	2	8	2	—	2	3_2	—	3
Second instar	2	~34	2	—	2	3_2	—	8

Table 1: Numbers and distribution of spigots on the spinnerets of the postembryo ($n=3$), first instar ($n=2$) and second instar ($n=3$) in *N. madagascariensis*. Numbers correspond to one spinneret. Abbreviations see text. One spigot base developed, probably functional (1_1), triad complex of three spigots developed but spigots at some distance from each other (3_2).
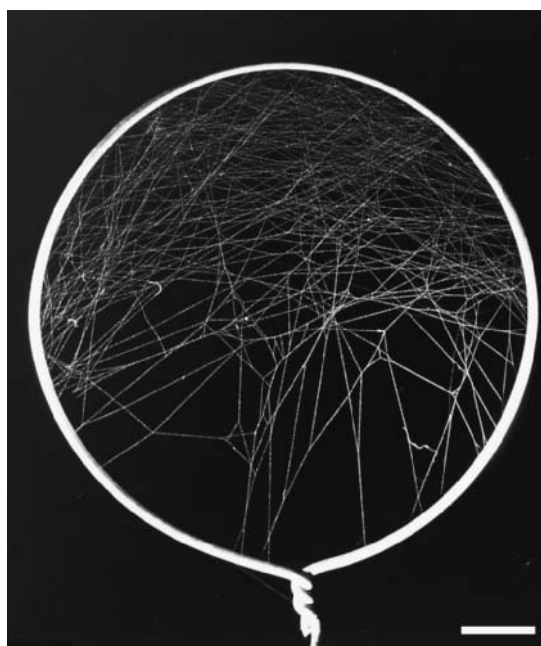

Fig. 3: Irregular threads laid down by first instar spiderling of *N. madagascariensis* (spiderling 31 days). Scale line=1 cm.
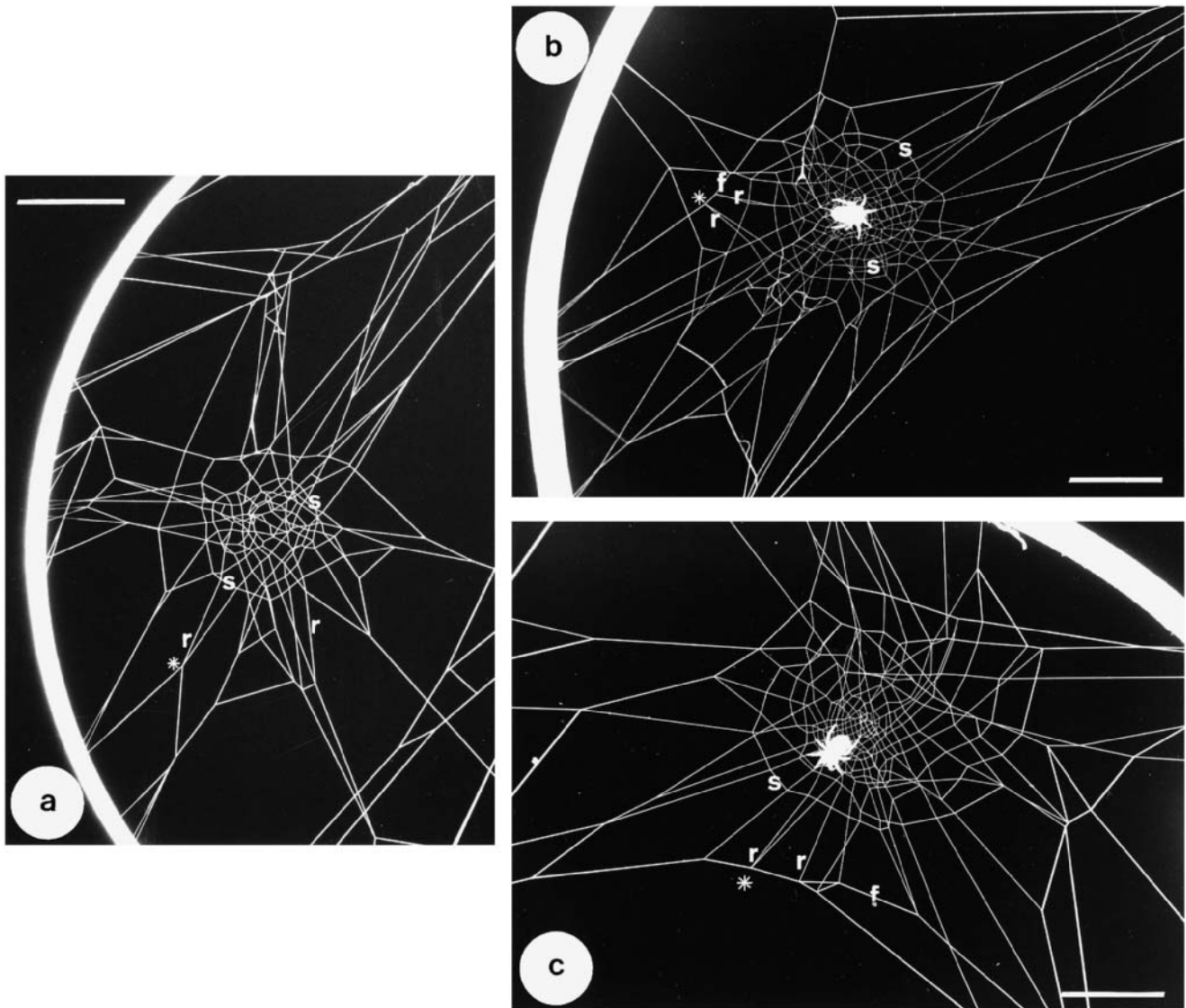
Fig. 4: Primary-webs of first instar spiderlings of *N. madagascariensis*. **a** Primary-web with radial threads (r), some of them converging to a point at the periphery (*), and short, incomplete spiral turns (s) (spiderling 112 days); **b** Primary-web with fine-meshed centre, radial threads (r), with some of them converging to a point at the periphery (*), some frame threads (f) and spiral turns (s) (spiderling 103 days); **c** Primary-web with fine-meshed centre, radial threads (r), with some of them converging to a point at the periphery (*), some frame threads (f) and spiral turns (s) (spiderling 103 days). Scale lines=0.5 cm.

First instar

Two to three days after hatching from the egg-shell and first integument, the postembryo moults into the first instar (term after Downes, 1987). This stage has full ability to move; however, in the laboratory first instars remain inside the cocoon for another 11–18 days, until all spiderlings leave the cocoon to build a communal dense mesh nearby. This web consists of an irregular array of non-sticky threads in which the spiderlings remain in spherical aggregations for a variable time (Fig. 2). When removed artificially from the cocoon or the communal web and put individually on wire frames, first instar spiderlings first build an irregular mesh (Fig. 3). At the age of about 60 days after hatching, however, when artificially removed, they start to build typical web structures, which are called primary-webs and basically serve as resting places for the spiderlings. Typical primary-webs are shown in Fig. 4. Characteristic features are some more or less radial threads (r), originating

from a central area, and sometimes converging in pairs to a point at the periphery (*). Short, incomplete spiral turns (s) connect the radial threads. It was never possible to observe the construction of primary-webs, which suggests that the construction time is very short, or perhaps that the process is not a continual one. Primary-webs showed different levels of structural complexity (Fig. 4). However, the clear separation of radial and spiral elements and the high degree of regularity found in regular orb-webs, is still weakly marked in primary-webs.

In addition to primary-webs, first instars also built regular orb-webs in the laboratory. A typical first instar orb-web is shown in Fig. 5. My many observations indicate that there is no one-way development from primary-webs to orb-webs. Some spiderlings built orb-webs first and primary-webs later and vice versa. The first instar orb-web shows simple radii (r), a sticky capture spiral (c) and a structural spiral (s), the latter being a typical structural component of nephiline webs
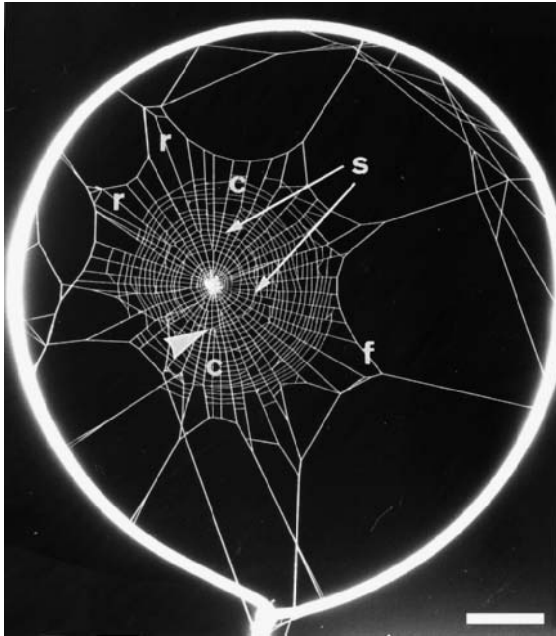
Fig. 5: First instar orb-web of *N. madagascariensis* (spiderling 117 days). Radii (r), structural spiral (s), sticky capture spiral (c), frame threads (f). Short arrow indicates branching of radii. Scale line = 1 cm.

(see Introduction). Table 2 describes various web parameters and gives their median measurements in first instar orb-webs. The median size of a first instar web is about 3.6 cm in height and 3.9 cm in width, and the median capture area, defined as the area enclosed by the innermost and outermost sticky capture spiral, is 6.4 cm^2 (see Table 2). The webs often show a vertical asymmetry in that they are enlarged below the hub. This is reflected in the symmetry index, a ratio of the distance from the centre to the upper and lower web frames, which is 0.6 for first instar webs, and in the number of structural (2 versus 4) as well as capture spiral elements (7 versus 22) above and below the hub. Therefore the structural and capture spirals are often not real spirals, as they swing from one side of the web to the other only. The fine-meshed pattern, with a median mesh size of 1.0 mm^2, results from branched radii which are constructed together with the structural spiral.

The construction of a first instar orb-web takes about 20 to 25 min. Beginning with a thread arrangement of a few radii, more radii are built, each in one behavioural sequence with a frame thread. At the same time, the spider turns at the centre to connect the radii by the first hub loops. After all the frame threads are laid, the spider builds more radii, feeling with the front pair of legs for possible gaps between radii already laid. At the same time, hub loops gradually turn into loops of the structural spiral. As with hub loops, the construction of the structural spiral is also closely connected with the building of more radii. Gaps between radii already laid are recognised by the spider feeling with the first and second leg of the body side moving forward. There are four different methods by which a new radius can be built (Fig. 6). When the spider recognises a gap between two radii during construction of the structural spiral (s), it

draws out one line while moving towards the frame on a radius already present (r), attaches the line to the frame, then draws out a second line while moving back from the frame to the structural spiral along the newly laid radius. The result is a radius of type I (r_1) or II (r_2), each consisting of a double thread. The difference between type I and II is a difference in the branching pattern itself. Radii of type III consist of two single threads (r_3 and r_3,). When moving towards the frame on a radius already present (r) the spider draws out one line (r_3). After fixing that line on the frame, however, the spider continues a little further along the frame to fix a second line (r_3,) and then draws it back to the structural spiral along the newly laid radius (r_3). Radii of types I, II and III are the main types of radii in first instar orbs. Radii of type IV (r_4) consist of two single threads, converging to a point on the frame. This radius type is only occasionally found in orb-webs, but similar "V"-shaped constructions are found in primary-webs. Once the spider reaches the web periphery and the structural spiral is finished, the sticky capture spiral is laid from the periphery to the centre and so the orb-web is completed. Sometimes a barrier-web is built in addition to the orb-web. The barrier-web, a typical feature of nephiline webs, is an irregular-meshed web built near the hub but away from the plane of the orb.
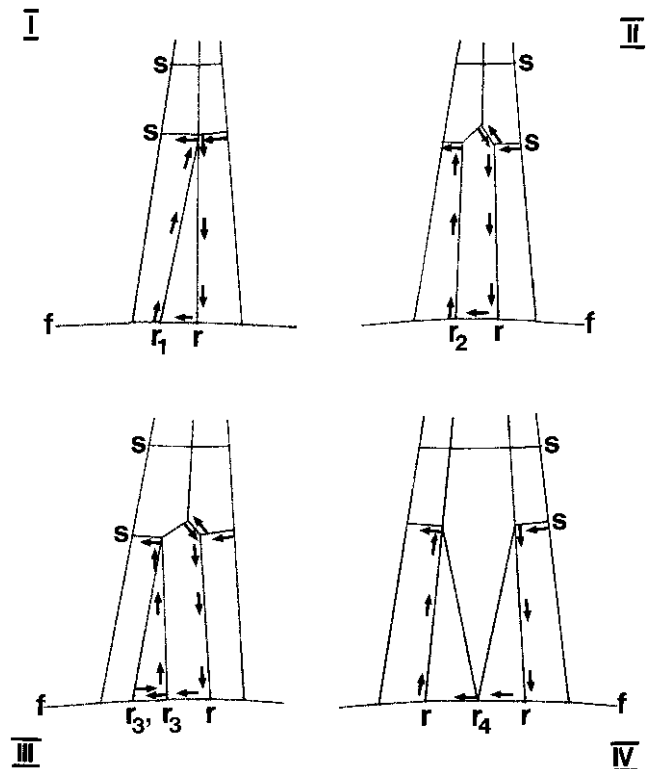

Fig. 6: Types of radii in first and second instar orb-webs of *N. madagascariensis*. **I** The newly built radius r_1 consists of a double thread; **II** The newly built radius r_2 consists of a double thread; **III** The two newly built radii r_3 and r_3, each consist of a single thread; **IV** The newly built radius r_4 consists of two single threads converging to one point at the periphery. The spider's path when laying the new radius is indicated by small arrows; arrows originating from a line indicate that lines were attached by the spider. Structural spiral (s), already existent radius (r), newly built radii (r_{1-4}), frame thread (f).

Although first instar webs are complete miniature orb-webs, showing some typical nephiline web features like an intact structural spiral, branched radii, a fine-meshed pattern and a barrier-web, they differ from the adult *Nephila* orb-web in some other features. The structural spiral in most first instar webs lacks the characteristic zigzag attachment (see Fig. 8) at the radii (only 2 out of 20 webs with some characteristic attachments) and, as indicated by the structural spiral index (Table 2), it does not extend as far towards the web frame as in webs of later stages.

Together with the ability to construct complete orb-webs, first instars have a well developed spinning apparatus (Fig. 7, Table 1). On the anterior spinnerets eight

small piriform gland spigots (pi) are found in a crescent-shaped area, with the posterior spigots being smaller than the anterior ones (Fig. 7a). Two large major ampullate gland spigots (ma) are located in a median depression, the posterior one being smaller. On the median spinnerets two aciniform gland spigots (ac) and two minor ampullate gland spigots (mi) stand one behind the other (Fig. 7b). Spigots of the ampullate glands of the anterior and median spinnerets are similar in size. On the posterior spinnerets three small aciniform gland spigots (ac) stand in a line (Fig. 7c). Three other spigots in one functional unit (one flagelliform gland spigot and two aggregate gland spigots) represent the triad complex (tr). Even though these three spigots are

Parameter	Description	First instar	Second instar	z	p
height (cm)	distance from lower to upper web frame	n=26 M=3.6 q_1=3.1 q_3=4.5	n=26 M=6.6 q_1=5.0 q_3=7.9	5.10	***
width (cm)	distance from right to left web frame	n=26 M=3.9 q_1=3.0 q_3=4.5	n=26 M=6.4 q_1=5.4 q_3=7.4	5.33	***
capture area (cm²)	area enclosed by inner- and outermost capture spiral	n=21 M=6.4 q_1=4.7 q_3=11.0	n=22 M=25.2 q^1=16.5 q_3=26.5	−4.8	***
vertical symmetry index	ratio of distance from centre to upper and from centre to lower web frame	n=26 M=0.6 q_1=0.5 q_3=0.7	n=26 M=0.7 q_1=0.6 q_3=0.9	1.67	n.s.
# radii	total number of radii at frame	n=26 M=57.5 q_1=49.0 q_3=71.3	n=27 M=89.0 q_1=76.0 q_3=113.0	−4.43	***
# s-spirals above hub	number of structural spiral turns above hub	n=26 M=2.0 q_1=2.0 q_3=2.0	n=26 M=4.0 q_1=3.0 q_3=4.0	−3.23	**
# s-spirals below hub	number of structural spiral turns below hub	n=26 M=4.0 q_1=5.0 q_3=3.0	n=26 M=7.0 q_1=5.0 q_3=4.0	2.89	**
s-spiral index	ratio of distance from last s-spiral turn to web frame and from centre to lower web frame	n=16 M=0.31 q_1=0.25 q_3=0.41	n=21 M=0.2 q_1=0.15 q_3=0.24	2.95	**
# c-spirals above hub	number of capture spiral turns in capture area above hub	n=23 M=7.0 q_1=4.0 q_3=13.0	n=25 M=25.0 q_1=16.0 q_3=31.0	−4.28	***
# c-spirals below hub	number of capture spiral turns in capture area below hub	n=23 M=22.0 q_1=14.0 q_3=30.0	n=25 M=36.0 q_1=31.0 q_3=49.0	−4.53	***
mesh size (mm²)	area enclosed by 2 radii and 2 capture spiral threads, calculated by mean mesh length and width	n=18 M=1.0 q_1=0.7 q_3=1.1	n=21 M=1.2 q_1=1.0 q_3=1.4	−2.07	*

Table 2: Parameters (and their description) of orb-webs of first and second instar spiderlings in *N. madagascariensis*, with medians (M), 25% (q_1) and 75% (q_3) quartiles, z (Wilcoxon test) and p values. ***$p<0.001$, **$p<0.01$, *$p<0.05$, n.s. no significant difference.
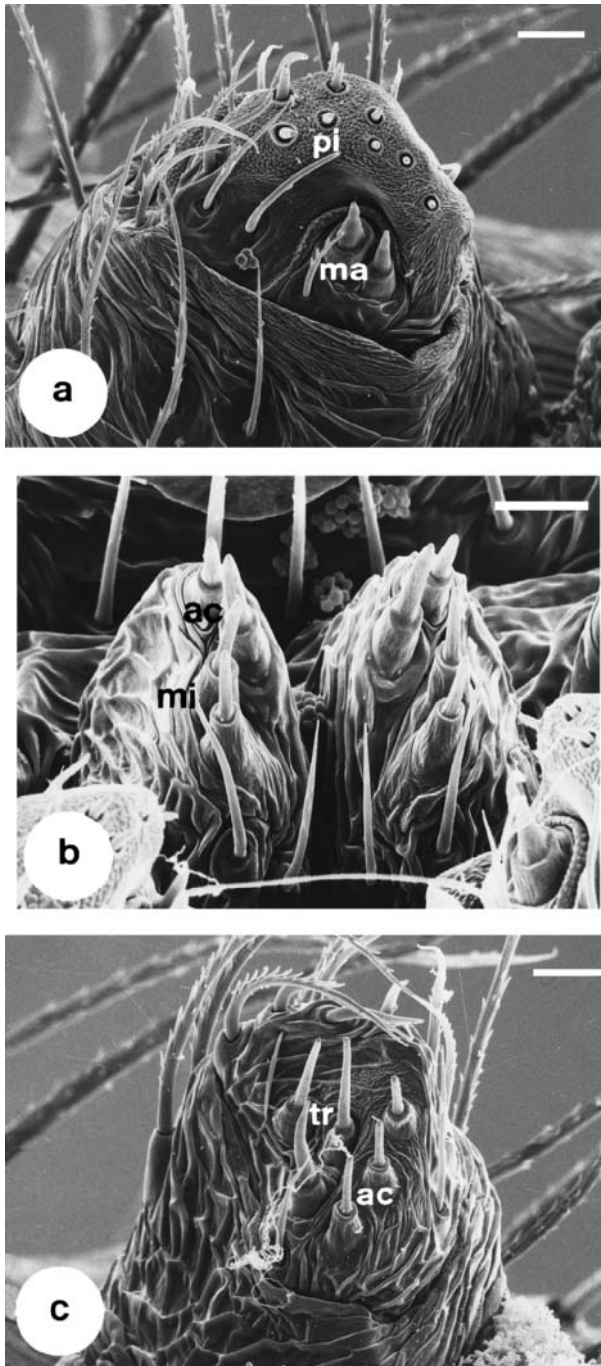
Fig. 7: Spinnerets of first instar spiderling of *N. madagascariensis*. **a** Anterior spinneret of left side; **b** Median spinnerets; **c** Posterior spinneret of left side. Spigots of major ampullate glands (ma), spigots of minor ampullate glands (mi), spigots of piriform glands (pi), spigots of aciniform glands (ac), triad spigots (tr). Scale lines = 10 μm.

situated at some distance from each other, sticky capture threads can be produced. Only spigots of tubuliform glands are lacking in this stage. A colulus is present anterior to the spinnerets.

Second instar

After a variable time from 14 to over 100 days after leaving the cocoon, the spiderling moults again into the second instar (term after Downes, 1987). Spiders in this stage finally leave the communal web and build individ-

ual orb-webs, but never primary-webs. Second instar orb-webs are similar to first instar orbs in having simple radii (r), a sticky capture spiral (c), an intact structural spiral (s) and a fine-meshed structure (Fig. 8). Table 2 gives medians of various second instar orb-web parameters and compares them with measurements of first instar orbs. With a median web size of about 6.6 cm in height and 6.4 cm in width, and a capture area of 25.2 cm^2, second instar orbs are considerably larger than those of the preceding stage, but the mesh size of 1.2 mm^2 is only slightly larger (Table 2). Vertical asymmetry was not, however, significantly different from that of first instar orbs. Radius construction behaviour of types I, II and III occurred, but type IV was missing (29 webs observed). Web-building behaviour is the same as already described for first instar orbs. A barrier-web is also built by this stage (Fig. 9).

In addition to the web features already shown by first instars, second instar orbs resemble more closely the typical *Nephila* web of adult females in that the structural spiral shows the typical attachment pattern at the radii much more frequently (19 out of 22 webs with many typical attachments at the radii) (Fig. 8, short arrows). Moreover, the structural spiral is less restricted to the centre of the web but extends further towards the periphery (s-spiral index, see Table 2).

The external spinning apparatus of second instars shows the same types of spigots as that of first instars (Fig. 10, Table 1). Differences from first instar spinnerets are the greater numbers of piriform and aciniform gland spigots (Table 1). As in first instars, the triad spigots (tr) on the posterior spinnerets are also located at some distance from each other (Fig. 10c). A colulus was also present anterior to the spinnerets.
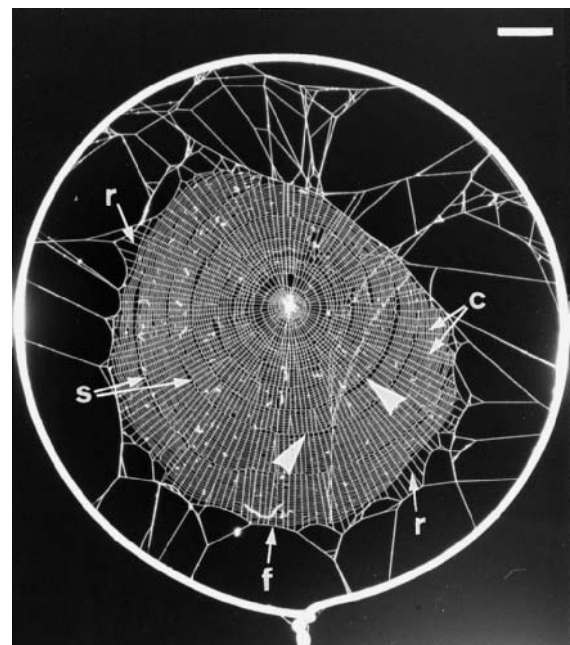

Fig. 8: Second instar orb-web of *N. madagascariensis* (spiderling 64 days). Radius (r), structural spiral (s), sticky capture spiral (c), frame threads (f). Short arrows indicate typical attachment of structural spiral at radii. Scale line = 1 cm.

Discussion

First instar spiderlings of *N. madagascariensis* or other *Nephila* species have never previously been reported building orb-webs. At this stage, they normally remain in the communal web together with their siblings for a considerable time before moulting again and dispersing (Robinson & Robinson, 1973; Austin & Anderson, 1978). Climatic factors (Lowry, in McKeown, 1952) or physiological constraints (Peters, 1969; Austin & Anderson, 1978) have been proposed as reasons for their stay. In this study, however, first instars built primary-webs and orb-webs. The irregular primary-webs differ considerably from the regular and highly symmetrical orb-webs and have not previously been described. Personal observations of *N. senegalensis* (Walckenaer) in the Ivory Coast indicate that first instar spiderlings construct primary-webs in the field as well. The fact that younger spiders spin more generalised webs than adults has been reported for several species (see review in Eberhard, 1985). The atypical first-built webs of *Uloborus* spiderlings (and mature males) result from a lack of morphological structures necessary to produce the silk used by older individuals and mature females (Szlep, 1960). However, the present study of the external spinning apparatus shows that the spigots necessary for orb-web construction are already well developed in first instars of *N. madagascariensis*. The distribution of spigots on the spinnerets closely corresponds to the adult nephiline pattern (Peters, 1955). Differences lie in the lower number of piriform and aciniform gland spigots, and in the lack of tubuliform gland spigots which normally develop at a later stage as they are used only for cocoon construction. The fact that there are two functional major ampullate gland spigots on each of the anterior spinnerets and two minor ampullate gland spigots on each of the median spinnerets, in contrast to the spinnerets of adult *Nephila* females which have only one functional spigot each, has already been reported (Peters, 1955; Sekiguchi, 1955; Mikulska, 1966). This reduction occurs during the maturation moult and is known in the Nephilinae, Araneidae,
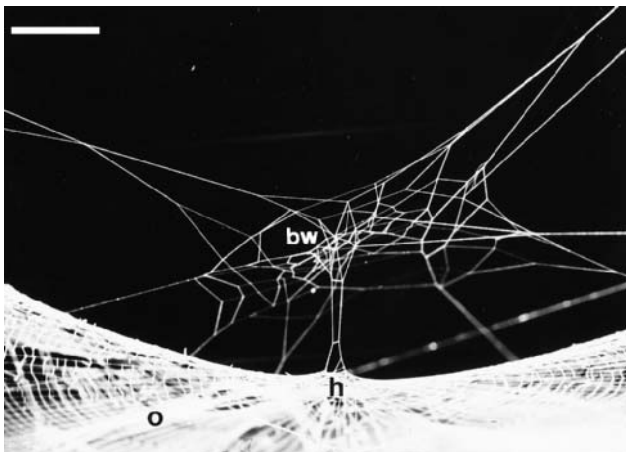

Fig. 9: Barrier-web (bw) built by a second instar spiderling of *N. madagascariensis* additionally to orb-web (o), as seen from above (spiderling 95 days). Hub where the spider normally sits (h). Scale line=0.5 cm.
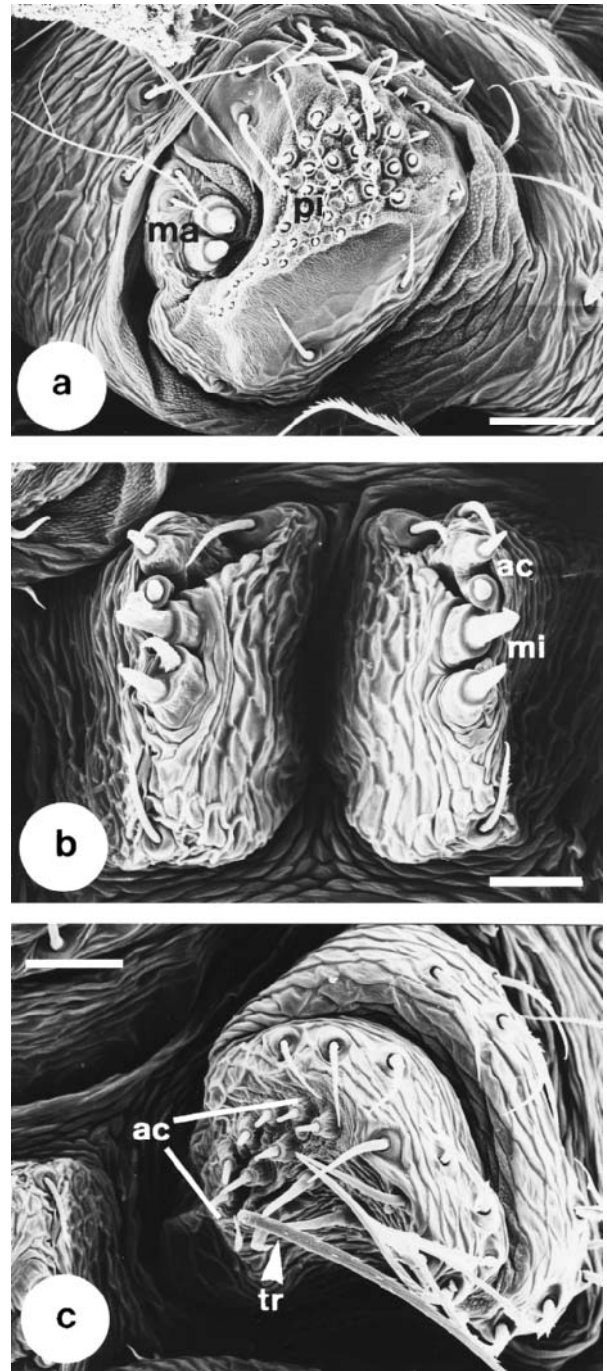

Fig. 10: Spinnerets of second instar spiderling of *N. madagascariensis*. **a** Anterior spinneret of left side; **b** Median spinnerets; **c** Posterior spinneret of right side. Spigots of major ampullate glands (ma), spigots of minor ampullate glands (mi), spigots of piriform glands (pi), spigots of aciniform glands (ac), triad spigots (tr). Scale lines=20 μm.

Linyphiidae and Tetragnathidae (Sekiguchi, 1955; Peters & Kovoor, 1991; Townley *et al.*, 1991; Peters, 1993). The triad complex, responsible for the production of the sticky capture spiral in orb-webs, is already developed in the spinning apparatus of first instars, which holds for araneids generally (Peters, 1993). In adult females of Nephilinae and Araneidae the three triad spigots are in close functional contact, i.e. the distal ends of the aggregate gland spigots embrace the distal ends of the flagelliform gland spigots, whereas in all other groups they stand apart from each other (Hormiga *et al.*, 1995).

In first and second instars of *N. madagascariensis*, however, the three triad spigots are situated at some distance from each other, as has also been reported for subadult Araneidae, both female and male (Peters & Kovoor, 1991). Apart from these minor differences in the spinning apparatus, the morphological structures and behavioural patterns for building orb-webs are already developed in first instar spiderlings. Developmental constraints can therefore not be seen as the answer to the question why first instars also build irregular webs.

Orb-webs built by the first instars of *N. madagascariensis* in the present study were complete regular orbs. However, in some aspects they lacked the typical *Nephila* appearance and can therefore be interpreted as somewhat more generalised orbs when compared with the adult nephiline orb-web. Such ontogenetic changes are widespread among Nephilinae. Webs of young *Nephila maculata* (Fabricius) (Robinson & Robinson, 1973), *Herennia ornatissima* (Doleschall) (Robinson & Lubin, 1979), *Nephilia clavata* L. Koch (Shinkai, 1985) and *Nephilengys cruentata* (Fabricius) (Japyassú & Ades, 1998) are more similar to a typical orb-web than are those of adults. First instar orbs of *N. madagascariensis* already show both a vertical orientation and a vertical asymmetry, but the latter is not as marked as in adult webs. These observations are not in accordance with the findings of Kullmann & Stern (1981), who reported that *N. madagascariensis* spiderlings built horizontal circular webs where the spider represented the centre. However, Japyassú & Ades (1998) showed in *Nephilengys cruentata* that orb-web inclination in first stages can be quite variable compared with orbs of later stages. Because of the horizontal webs built by *N. madagascariensis* in early stages, Kullmann & Stern (1981) considered the *Nephila* web as an intermediate step between the horizontal cyrtophorine web and the vertical orb-web of Araneidae. Subsequent data, however, indicate that cyrtophorine webs are secondarily derived from orb-webs (Peters, 1993), as also are nephiline webs (Hormiga *et al.*, 1995; Griswold *et al.*, 1998). Coddington (1990), Hormiga *et al.* (1995) and Griswold *et al.* (1998) confirmed that the Nephilinae are the sister group of the remaining Tetragnathidae.

Some specialisations in nephiline web-building behaviour and web architecture have probably evolved in close association with their sexual size dimorphism (Hormiga *et al.*, 1995), e.g. the attachment of the radii twice at the frame (Eberhard, 1982: character F2; Hormiga *et al.*, 1995: character 48; Griswold *et al.*, 1998: character 83). This radius type corresponds to type III in the present study and is seen as a synapomorphy of the Nephilinae (Eberhard, 1982; Coddington, 1986; Hormiga *et al.*, 1995; Griswold *et al.*, 1998). First and second instar orb-webs of *N. madagascariensis*, however, also possess radii of type I (Eberhard, 1982: character F3), which are generally known from webs of juvenile and adult *N. madagascariensis* (Wiehle, 1931), *N. clavata* (Shinkai, 1985) and *N. maculata* (Robinson & Robinson, 1973; Shinkai, 1985) and from early orb-webs of *Nephila clavipes* (Linn.) (Eberhard, 1990b). Further-

more, "V"-shaped radii of type IV were occasionally found in primary-webs and orb-webs in the present study and have also been reported for adult *N. clavata* orb-webs, *N. maculata* barrier-webs (Shinkai, 1985) and *Cyrtophora* orb-webs (Peters, 1937, 1993). If we assume that the way orb-weavers lay and connect radii is phylogenetically informative (Coddington, 1990; Hormiga *et al.*, 1995), radius type III is a synapomorphic character for the Nephilinae and radius types I and IV could be plesiomorphic states which Nephilinae have in common with other groups.

The persistence of the structural spiral is probably a nephiline specialisation which preceded female giantism (Hormiga *et al.*, 1995: character 50; Griswold *et al.*, 1998: character 86). The typical zigzag attachment of the structural spiral at the radii also contributes to strength in larger webs. The persistence of a structural spiral and the occurrence of female giantism are both seen as synapomorphies of the Nephilinae (Griswold *et al.*, 1998). As the structural spiral is a continuation of the hub loops and in early stages of *N. madagascariensis* is more restricted to the inner web area, we can assume that the nephiline web is derived from the normal symmetrical orb-web which lacks a remaining structural spiral.

In cladistic analysis mostly adult characters have been considered so far. However, as the present study demonstrates, early ontogenetic stages often exhibit the plesiomorphic behaviour of a group (Hormiga *et al.*, 1995). Therefore, further studies on web-building behaviour and spinning apparatus should also include early ontogenetic stages.

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