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ONTOGENETIC CHANGES IN THE SPINNING FIELDS OF *NUCTENEA CORNUTA* AND *NEOSCONA THEISI* (ARANEAE, ARANEIDAE)

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ABSTRACT

The postembryonic development of spinning organs of *Nuctenea cornuta* (Clerck) and *Neoscona theisi* (Walckenaer) (Araneae, Araneidae), was studied with SEM, emphasizing first appearance of, and increase in, spigot and fusule complements. Our results suggest that these species may renew their spinning fields by two distinct methods during their ontogeny: spigots may be merely molted *in situ* like any other cuticular appendage; and/or spigots in one position are lost and "replaced" by an apparently new spigot in a new position. Some or all of each class of fusule (aciniform and pyriform) as well as major and minor ampullate spigots are replaced as well as merely molted. Flagelliform and aggregate spigots seem to be merely molted, never replaced. Evidence for these modes of replacement are the apparently vestigial spinning structures that persist from the previous instar, termed "nubbins" in the case of spigots, and "tartipores" in the case of fusules, as well as patterns in the increase in numbers of fusules and spigots. Spinneret ontogeny confirms Theridiidae and Tetragnathidae as phylogenetically derived taxa relative to Araneidae.

INTRODUCTION

Previous work on spinnerets has concerned histology (see Kovoor 1987 for a review), morphology (Glatz 1967, 1972, 1973; Mikulska 1966, 1967, 1969; Wasowska 1966, 1967, 1970, 1973; Coddington 1989), and function (Peters 1983, 1984; Peters and Kovoor 1980). Relatively few studies, and none using scanning electron microscopy, have described the ontogeny of spinning organs. Mikulska (1966) compared the differences of spinning structures between the adults and subadults of *Nephila clavipes* (L.) but did not know to which instar the subadults belonged. Richter (1970a) presented a very similar work on *Pardosa amentata* (Clerck). Glatz (1972, 1973) compared the spinning structures of first instar to those of adults for several primitive spider groups. Opell (1982) described the ontogeny of only the cribellum of *Hyptiotes cavatus* (Hentz). Works on the entire postembryonic ontogeny were done by Kokocinski (1968) and Wasowska (1977).

Kokocinski used light microscopy to study the changes in the number of external spinning structures in *Agelena labyrinthica* (Clerck). Wasowska used light microscopy to describe the postembryonic morphology of the spinning apparatus in eight species belonging to seven families (Thomisidae, Lycosidae, Agelenidae, Argyronetidae, Theridiidae, Araneidae, Tetragnathidae).

In this study we observed the morphology of each instar with SEM to record detailed characters apparently missed by Kokocinski and Wasowska, who were limited to light microscopy.

For ease of discussion we maintain in this paper the distinction between fusules—multiple spigots serving either aciniform or pyriform glands, and spigots—morphologically singular spigots *per se*. Araneid spiders have five types of spigots (major ampullate, minor ampullate, cylindrical, flagelliform, aggregate) and two types of fusules (piriform, aciniform). All adults have one pair each of major ampullates, minor ampullates and flagelliforms; two pairs of aggregates, and three pairs of cylindricals. The positions of spinning structures and the topographies of adult spinnerets are diagrammed in Coddington (1989).

MATERIALS AND METHODS

Nuctenea cornuta (Clerck) and *Neoscona theisi* (Walckenaer) were studied. Both species are widely distributed in China. The specimens were collected in Wuhan City, China and reared from eggsacs by Jingzhao Zhao, Professor in the Department of Biology, Hubei University. Specimens of each instar were preserved in 75% ethanol. All specimens of one species are from the same egg sac. The number of specimens we used for each instar are given in Table 1. Vouchers are deposited in the National Museum of Natural History (USNM), Smithsonian Institution.

The methods used to prepare specimens generally follow Coddington (1989). The forceps squeeze was only used for third instar or older, as younger instars are too fragile. Younger instars are cleaned and whole abdomens mounted; careful adjustments are needed in the 100% ethanol fixing and mounting steps to ensure visibility of PMS and PLS spinnerets. Ultrasonic cleaning times differed among instars: adults ca. 60 s; fourth or fifth, ca. 30 s; third, ca. 20 s; second, 0-5 s. First instars were mounted without ultrasonic cleaning because their small bodies are easily broken.

Numbers of spigots and fusules in Table 1 are reported for one spinneret of each pair; to calculate total spinning complements, double that number. Occasionally we use this calculated total when discussing our results. When a difference in the number between the two spinnerets was found, both spinnerets of the pair were counted.

Our nomenclature for instars of spiders follows André and Jocqué (1986). We call the stage emerging from the egg the "first" instar, the one emerging from the eggsac the "second" instar, and number succeeding instars consecutively. Individuals of each species matured in either the sixth or the seventh instar. The loss of either spigots or fusules can result in vestigial structures of scars in subsequent instars. To distinguish them we call nubbins resulting from fusules "tartipores" (based on comments in Kovoor (1986) who first noticed the structures), and nubbins resulting from spigots we simply call nubbins. The figures portray either right or left spinnerets, depending on the specimen used.

Abbreviations are: AC, aciniform; AG, aggregate; ALS, anterior lateral spinnerets; CY, cylindrical; FL, flagelliform; MAP, major ampullate; mAP, minor ampullate; Nc, *Nuctenea cornuta*; Nt, *Neoscona theisi*, PI, piriform; PMS, posterior median spinnerets; PLS, posterior lateral spinnerets; tart., tartipores. Throughout the text, these abbreviations are intended to apply to spigots and their distributions only; we have no evidence regarding the ontogeny of the silk glands themselves. To make the figures more easily understandable, each also has a label of the form "Nc ♀ ALS-4." This means, e.g., *Nuctenea cornuta*, female, anterior lateral spinneret, fourth instar. The sex of the earliest instars could not be determined.

RESULTS

Nuctenea cornuta.—First instars have no functional spigots or fusules (Fig. 30). Functional spinning structures first appear in second instars. Although second instars have few fusules (Figs. 1, 7, 13), they have examples of all spigots except CY (Table 1).

From second to fifth instars, two MAP occur on the mesal ALS margin, one anterior and one posterior (Figs. 1, 5). In second and third instars those two MAP are similar in size (Figs. 1, 2). In fourth and fifth instars the hind spigot becomes smaller and finally atrophies to become the ALS MAP spigot "nubbin" in the adult instar (Figs. 4-6).

The PMS mAP develop in a more complex pattern. Second instars have two mAP spigots per PMS (Fig. 7). The posterior spigot apparently disappears in the third and leaves a vestigial "nubbin" in its place (Fig. 8). The posterior position of the nubbin is evidence that it is indeed the posterior mAP spigot that is lost. Third instars also apparently replace the mAP spigot represented by the nubbin with a new mAP spigot between the anterior one and the posterior nubbin. In effect the posterior mAP spigot has "changed places" and left a scar in the old position. The new mAP spigot is generally smaller than the old one. The size differences are clear in fourth and fifth instars (Figs. 9-11). This new mAP spigot, which first appeared in the third instar, also disappears by the adult instar and leaves its own vestigial nubbin on the posterior PMS margin (Fig. 12). In all, 3 mAP appear on the PMS during development but two are lost. Only the most anterior, which first appeared in the second instar, persists as a functional spigot in the adult instar.

One could also interpret the nubbin that appears in the fifth and sixth instars (Figs. 11, 12) as the same, persistent nubbin. This would imply that the second mAP spigot of the fifth instar is lost in the adult instar without a trace, and would therefore propose yet a third method of spigot or fusule renewal. We prefer to think that the nubbin in the adult instar is the scar of the posterior spigot present in the fifth, because then the overall hypothesis for how spiders renew spinning structures remains (relatively) simple.

A small, presumably non-functional PMS CY spigot is first visible in the fourth instar female (Fig. 9), two molts before maturity in the sixth instar.

The development of AG and FL spigots is more stable. They also first appear in the second instar (Fig. 13), as usual grouped in a triad. Once present they never atrophy or leave nubbins (except in adult males), and their number remains the same (Figs. 14-18). They are apparently molted *in situ* like any normal

Table 1.—Number of spigots, fusules, and nubbins on each side of the spinning field in each instar of species studied. A range of values reports variation within or among individuals.

	(*n*)	MAP	mAP	AG	FL	CY	PI	PI tart.	PMS-AC	PLS-AC
N. cornuta										
1st	(15)	0	0	0	0	0	0	0	0	0
2nd	(4)	2	2	2	1	0	8-9	0	2	3
3rd	(4)	2	2	2	1	0	15-17	5-7	6	7-8
4th	(2)	2	2	2	1	3	41,47	20,24	7,10	27,29
5th	(2)	2	2	2	1	3	61,74	26,27	12,15	42,43
6th (adult)	(1)	1	1	2	1	3	110	60	21	59
7th (adult)	(1)	1	1	2	1	3	124	60	20	71
N. theisi										
1st	(4)	?	?	?	?	?	?	?	?	?
2nd	(6)	2	2	2	1	0	5-9	0	2	3
3rd	(4)	2	2	2	1	0	5-17	3-6	4-8	7-13
4th	(3)	2	2	2	1	0	17-31	5-18	10-26	10-23
5th	(3)	—	—	—	—	—	40-45	22-23	42	29-30
6th (adult)	(2)	2	1	2	1	3	58,72	?	59,72	51,57
7th (adult)	(2)	—	—	—	—	—	69,79	?	78	50

interpret these and other tartipores as vestiges left over from fusules functional in the previous instar. If these tartipores are counted, interesting trends appear (Table 1). In third, fourth and fifth instars, the range of tartipores present in an instar is roughly equivalent to the range of piriform fusules in the previous instar. The second instar PI persist only for this instar because their number (16-18) is roughly equal to the number of tartipores in the third instar (10-14; difference probably due to individual variation). A similar pattern of total replacement probably also occurs in the third instar PI because their number (30-34) roughly equals that of tartipores in fourth instars (40-48). However, we cannot be certain that all fourth instar tartipores can be construed as remnants of third instar PI, because it is possible, although unlikely, that some third instar tartipores persist into the fourth instar. If they do, then some functional third instar PI fusules also persist. The numbers are not exact. Judging from the mAP spigot evidence, however, nubbins themselves can disappear in the course of postembryonic development (the nubbin of the first mAP spigot to atrophy is a example). During young instars therefore, the entire complement of PI fusules may be replaced at each molt.

The development of aciniforms is roughly the same, though not so regular. No tartipores are found in third instars and relatively few are found in subsequent instars. AC fusules apparently function and are molted *in situ* through more molts than PI fusules. Nevertheless, the presence of sparse tartipores from at least the fourth instar on suggests that some AC fusules do atrophy during development, and are "replaced" by new fusules in new positions.

The distribution of ALS and PMS spigots and fusules remains more or less constant during development. The PLS distribution changes the most from third to fourth instars, when the spinneret tip and especially the AC spinning field elongates (Figs. 14, 15). Fourth instar PLS already have the basic topography of the adult.

Neoscona theisi.—The basic pattern of postembryonic growth of spinning structures in this species is similar to *N. cornuta*, and so we only note features that seem particularly significant. However, we illustrate *N. theisi* comprehensively to emphasize that the patterns hold across these genera (Figs. 19-23; 25-35). This consistency argues that individual variation or interspecific variation is unimportant at the level at which we are comparing patterns.

Again, spigots probably first appear in the second instar (Figs. 19, 25, 31). Although all our preparations of first instars failed, this can be inferred from the few spinning structures in second instars, a condition similar to second instar *N. cornuta* (compare Figs. 1 and 19; 7 and 25; 13 and 31, numbers in Table 1).

Adult specimens have one MAP spigot and one mAP spigot with accompanying nubbins as in *N. cornuta* (Figs. 23, 24, 29). One mAP spigot of the second instar also atrophies by the third instar (Fig. 26). The same pattern may occur in the ALS MAP spigot as well in *N. theisi*. If the ALS MAP area in third instars is carefully examined, one possible nubbin can be observed at the inner margin of the posterior MAP spigot (Fig. 20). Like the nubbin near third instar PMS mAP spigot, this appears to be an atrophied MAP spigot which only functioned during the second instar. From the MAP spigot distribution in second and third instars we infer that the third instar posterior MAP spigot is new, and so the nubbin came from the posterior MAP spigot in the second instar. This new MAP spigot also atrophies by the sixth instar. Evidence for a similar process of ALS MAP spigot replacement in third instars of *N. cornuta* is negative or equivocal (Fig. 2).

Fusule number varies more within an instar in this species than in *N. cornuta*. The instar in which the largest number of fusules is gained is difficult to determine, because fusule number seems to increase evenly in each instar.

As in *N. cornuta*, the number of fusules in a fourth instar male and female are very similar (Figs. 33, 34). The same holds true for other spinnerets (male, Figs. 22, 28; female not illustrated). Unlike *N. cornuta*, *N. theisi* fourth and fifth instar females lack rudimentary CY spigots (Figs. 27, 33, 35).

Third instars have many ALS tartipores (Table 1 and Fig. 20). The number of tartipores counted for *N. theisi* is not as accurate as that for *N. cornuta* because piriforms in this species are too densely packed. Tartipores in third and fourth instars can still be easily counted. In Table 1 tartipore numbers in one instar match better fusule numbers in the previous instar than in *N. cornuta*.

The development of the shapes of spinning fields in *N. theisi* is almost the same as that in *N. cornuta* except that the inner margin of the PLS of *N. theisi* are more depressed and it is more difficult to see the whole spinning PLS field. The biggest difference between the adults of the two species is PMS AC fusule number. In *N. cornuta*, the PMS have the fewest fusules among three pairs of the spinnerets, totalling only about 45 (Fig. 12). But *N. theisi* PMS AC fusules total about 150 (Fig. 29).

DISCUSSION

The evidence presented here suggests two different modes in which these species of spiders rejuvenate their spinning fields from one molt to the next. First, spigots and or fusules can be simply molted *in situ*. Presumably these structures are

replaced in the same way that spiders replace their exoskeleton with its associated structures.

Second, an existing fusule or spigot may disappear from one instar to the next, leaving behind a scar of the old spigot or fusule base (either tartipore or nubbin). In the case of spigots, this mode of jettisoning old structures seems usually to be accompanied by the appearance of a new spigot adjacent to the scar. This may also be consistently the case for fusules, but the evidence is strong only for the earliest instars.

Flagelliform and aggregate spigots may be unique in being rejuvenated exclusively by the first mode. Piriform fusules in the third instar, and perhaps subsequently, may be rejuvenated exclusively by the second mode. Aciniform fusules, minor ampullate spigots, and perhaps the primary major ampullate spigot apparently undergo both modes of replacement during their functional lives.

The appearance of CY spigots in *N. cornuta* two instars before maturity is startling, as CY spigots typically appear only in adults (Kovoor 1987). We found no trace of these spigots in *N. theisi* before the adult molt. Perhaps *Nuctenea* is phylogenetically derived in this respect.

Because we did not attempt to describe the spinning complement of an individual through successive molts but instead compared cohorts of individuals from the same eggsac, the variation between individuals weakens the evidence for some of these inferences. We can not be sure that piriforms fail to persist from one molt ot the next, or that major ampullates are routinely replaced by the second mode, i.e., the production of nubbins. Many spigots, as opposed to fusules, do persist from one molt to the next.

Our interpretations also depend on the inference that the nubbins and tartipores are in fact vestigial. To some extent, we are merely extending the accepted explanation for spigot nubbins, at least in the case of the ALS major ampullate spigot, to explain structures associated with fusules. These structures have also been interpreted as sensory organs ("petits organes vraisemables sensoriels," Kovoor 1986, p. 19). Similar structures have been found in most families of spiders excepting mesotheles (Shear et al. 1989). Our interpretation of the PI and AC tartipores as vestigial scars of previous fusules is new. Sectioning of the structures might decide the issue if one assumes that the enervation and secretory connection to the old spigot should also be vestigial, if not absent altogether. Because we did not section nubbins or tartipores, we cannot comment on a possibly sensory role. Evidence at the cellular level on how the molting process affects silk glands is also lacking.

If our inferences are correct, the second mode of renewal would seem to make continuity of silk production through the molting process difficult. Appearance of nubbins or tartipores implies either that the silk gland and duct serving that structure also atrophies, or that the spider somehow connects the old system to the new spigot or fusule in a rather short time. It would be interesting to know if spiders cease using their piriform or aciniform glands in advance of a molt, and if so, how long before. Which spigots make molting cells or chambers? If spiders do switch the connection of ducts at the time of the molt, the process must be complex. The other explanation-that they replace substantial numbers of secretory systems at each molt-also seems somewhat bizarre.

In *N. theisi* and possibly *N. cornuta* one pair of MAP appears to atrophy in the third instar, and another pair appears to compensate for the absent spigot,

thus restoring the status quo for juvenile araneoids. Replacement of one ALS MAP spigot by another in juvenile instars has not been reported previously in araneoid spiders.

Replacement of the ALS ampullate spigot in the third instar is rendered more plausible by the obvious replacement of the ampullate that takes place on the PMS. The ontogenetic patterns are similar. Surprisingly, three pairs of mAP appear during development: two appear in the second instar and one at the third. Two of these disappear before the adult stage. New spigots always seem to emerge posterior to existing ones. This pattern may have been misunderstood by Wasowska (1977) who reported that only one pair of mAP is atrophied before maturity in *Araneus diadematus* Clerck. Perhaps *A. diadematus* shows a different pattern.

Wasowska (1977) reported that spinning structures also appear in the "first" instar in *A. diadematus*, but that AG and FL exist only from the "second" instar; in *Metellina segmentata* (Clerck), spinning structures appear also in "first" instars. Our results agree in part, because Wasowska numbered instars differently, counting the first eclosed stage as first instar, whereas we count it as the second. However, our results also differ in that we found all classes of spinning structures on the second instar. The pattern we found makes more biological sense, because second instars are fully equipped to make viscid catching webs.

The increase in number of PI and AC differs slightly between species. In *N. cornuta* fourth and sixth instars gain the most, but in *N. theisi* the gain between instars is more or less the same. Wasowska (1977) reported that all species studied by her gained the most at the third instar. Our results again differ. Opell (1982) found that the number of fusules in the cribellum of *Hyptiotes cavatus* (Hentz) increased most from the third to fourth, and evenly from the fourth to the sixth instar. This is similar to the ontogeny of *N. theisi*. The gain in number of fusules probably differs between taxa; only more studies will resolve the issue.

Based on the results both from this study and existing papers (Mikulska 1966; Wasowska 1977), all araneid adults examined thus far (and all araneoids) have only one functional pair of ALS MAP spigots, whereas they have two pairs of MAP in some earlier instars. On the other hand, *Metellina segmentata* has two pairs of MAP only in "first" instars; the other four instars have just one pair of MAP (Wasowska 1977). *Metellina segmentata* MAP spigot ontogeny thus seems accelerated relative to the rest of the spinning structures. If true of other tetragnathids, this ontogenetic pattern supports the inference that metines and other tetragnathids are derived araneoids rather than primitive (Coddington 1986, 1989).

The ontogeny of mAP is further evidence for the same inference. According to Wasowska (1977), *Metellina segmentata* and *Enoplognatha ovata* (Clerck) both have just a single mAP during juvenile instars, as opposed to the two mAP characteristic of araneids. By ontogenetic criteria the araneid condition is primitive and thus this evidence confirms both theridiids and tetragnathids as derived ananeoids relative to araneids (Coddington 1989, 1990).

ALS MAP nubbins near the functional MAP are also found in adult uloborids and in *Deinopis* (the latter have numerous ALS MAP). These nubbins apparently reflect MAP existing in younger instars (Coddington 1989). Both deinopoids and araneoids seem to lose the posterior member of the pair. Deinopoids, araneoids

and possibly some dictynids are unique as far as we know in having persistent ALS MAP nubbin(s) in the adult stage (Coddington in press).

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