

Embryonic and postembryonic morphogenesis of the visual, venom- and silk-gland systems in two species of *Peucetia* (Araneae: Oxyopidae)

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Abstract. Morphogenesis and organogenesis were followed in two oxyopid spiders, from egg to spiderling leaving the egg sac. Attention has been paid especially to development of the visual, venom- and silk-gland systems, given that these three systems are functionally implicated in the behaviour of spiders. Chronology of development differs between systems: at the time of emergence, visual and silk-gland systems seem to be functional, while venom glands, together with the digestive tract, are not. This can be correlated with the positive phototaxis and aggregative behaviour of spiderlings.

INTRODUCTION

Lynx spiders (Oxyopidae) belong to a lineage in which web construction, as a device for capturing prey, has been lost. They live on foliage at the top of bushes or in herbaceous vegetation, where they wait in ambush to catch prey. Visual stimuli seem to play an important role in prey capture and sexual behaviour. The arrangement of the ocular area is a characteristic of the family Oxyopidae, the prosoma of which is very high in front. The eyes are arranged in four rows of two each. The anterior-median pair is very small. The three other, much larger, pairs form a hexagon on the dorsal part of the prosoma.

The classical contribution by Holm (1940) to our knowledge of the early morphogenesis of spiders provides a general scheme of the development of *Oxyopes ramosus* (Martini & Goeze, 1778) from egg-laying to the third postembryonic instar. Apart from the study by Homann (1971) of the comparative ontogenesis of the eyes in spiders belonging to various families, including the oxyopid *Peucetia viridans* (Hentz, 1845), the organogenesis of Oxyopidae is very poorly known.

This study of the morphogenesis of three systems implicated in predatory as well as reproductive behaviour, namely the visual, venom- and silk-gland systems, represents the first contribution to an ongoing research programme on the probable functional relationships between these three systems, and the variation of these interrelationships during the life cycle of oxyopid spiders, in relation to behavioural variations.

MATERIAL AND METHODS

Two *Peucetia* species, *Peucetia cauca* Lourenço, 1990 from Colombia and *P. gerhardi* van Niekerk & Dippenaar, 1994 from Nigeria, were reared in the laboratory at $21 \pm 2^\circ\text{C}$.

Development of eggs was followed from eggsacs of each species, maintained on cotton-wool in small boxes with a water supply (in a separate tube). A small slit opened in the wall of each egg sac allowed several eggs to be taken daily in order to examine their state of development, either under a stereoscopic microscope or in histological sections after fixation with Bouin's fluid, treatment with cellosolve

(Anderson's method, 1964, modified for arachnids) and embedding in paraffin. Sections (5 μm thick) were stained using one-step trichrome (Gabe & Martoja, 1957) or phosphotungstic haematoxylin (Terner et al., 1964). Morphogenesis and organogenesis were studied using serial sections of eggs or individuals throughout the development inside the egg sac, and after emergence.

The terminology of the early instars of spider development is still controversial. We therefore adopted a simple, unequivocal numbering of instars corresponding with the number of moults: the first moult initiates the first instar, and so on.

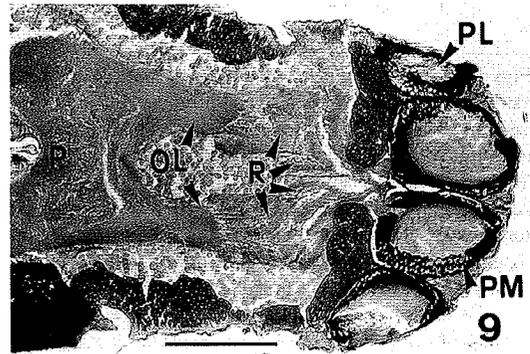
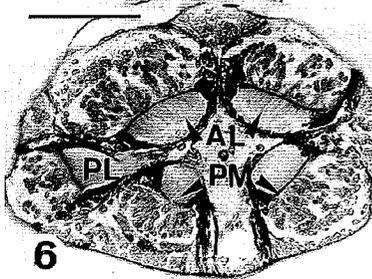
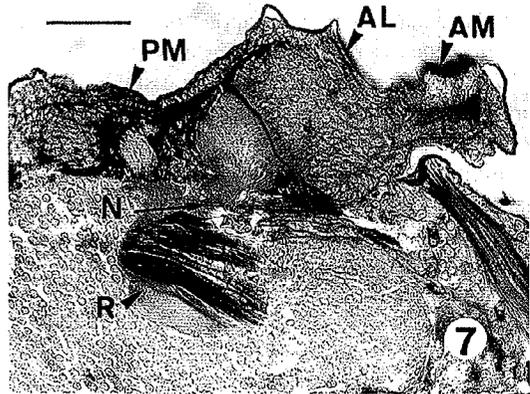
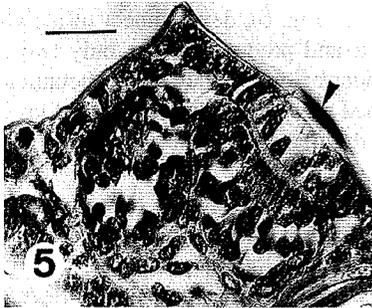
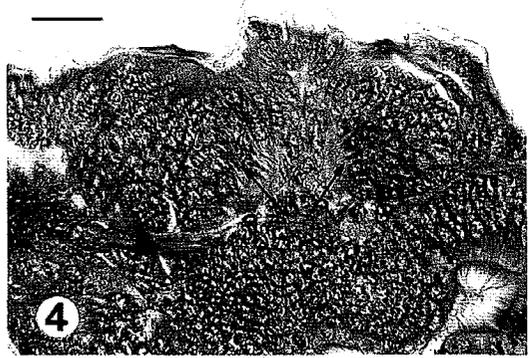
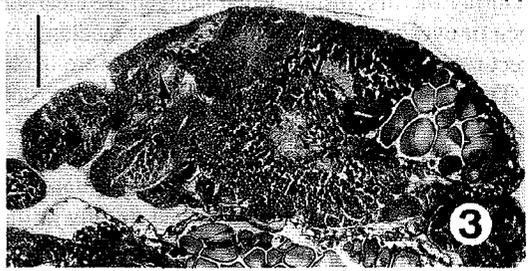
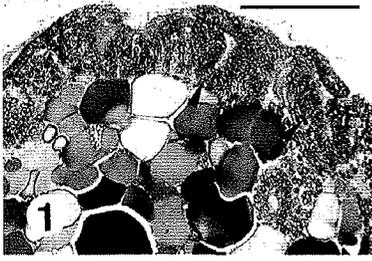
RESULTS

Between 120–160 eggs developed inside each egg sac laid by females of *Peucetia cauca* or *P. fasciventris*. In both species, the females vigilantly guard the egg sacs.

Development inside the egg sac lasted 29 to 32 days. During this period, eggs developed, and young individuals moulted three times. The chorion, vitelline membrane and embryonic cuticle were shed almost simultaneously (hatching) 10 to 12 days after egg-laying; the first instar lasted 3 to 5 days. A second moult took place when first instar juveniles were 15 to 17 days old; 12 to 15 days later, individuals moulted for the third time and emerged from the egg sac. Only minute differences were found in the chronology of the developmental events between the two species studied. The observations described below apply equally to both species.

About three days before hatching, numerous ectodermal invaginations appeared on the dorsal part of the cephalic region of the embryos, two of which were large cerebral vesicles showing intense mitotic activity (Figs 1, 2). Anlagen of optic vesicles began their differentiation from the eighth day (Fig. 2). On the tenth day, a sclerotized thickening of the embryonic integument (egg tooth) appeared at the base of pedipalps. A relatively wide space separated the embryo from the vitelline membrane and chorion (Fig. 3). With the help of its egg tooth, the embryo split these membranes between the 10th and 12th day. At the same time, it shed its own cuticle.

Figs 1–9. Development of the visual system in *Peucetia cauca* and *P. gerhardi*. 1 – Embryo on 7th day of development. Egg envelopes lie against the epidermis of the embryo which shows numerous invaginations among which cerebral vesicles are distinguishable (arrowheads). Scale bar = 100 μm . 2 – Transverse section of the cephalic region of an embryo on the 8th day. Formation of indirect eye vesicles has started (arrowheads). Cerebral lobes (CV) show numerous mitoses of the cells. Scale bar = 100 μm . 3 – Sagittal section of a 10 day old embryo shortly before hatching. CV = cerebral vesicle; arrowhead points to anlage of the anterior median eye. Scale bar = 100 μm . 4 – In a twelve day old juvenile (first instar) anterior lateral (left) and posterior median (right) eye anlagen have started to develop (arrows). Scale bar = 25 μm . 5 – A fourteen day old juvenile, after the second moult, showing the anterior median eyes with both dioptric and retinal components. A small lens has appeared (arrow head). Scale bar = 25 μm . 6 – The hexagon formed by the eyes with indirect retina, anterior lateral (AL), posterior median (PM) and posterior lateral (PL) eyes, in a juvenile of the same age as in preceding figure. Scale bar = 100 μm . 7 – General side view showing development of the pigmentation in all eyes on 18th day. The nerve (N) of the anterior lateral (AL) eye is connected to the optic lobe of the brain, as the organization of the first synaptic zone (R) begins to take place. AM = anterior median eye; PM = posterior median eye. Scale bar = 50 μm . 8 – Anterior median eyes at emergence (third instar). Scale bar = 25 μm . 9 – Horizontal section of the prosoma of a third instar juvenile at the level of the four posterior eyes (PL, PM) almost completely developed. Differentiation of the central nervous system seems to be complete. OL = optic lobes of brain, P = protocerebron, R = synaptic zones. Bar = 100 μm .



During the first instar, ocularanlagen are clearly differentiated from each other. The anlagen of eyes with direct retina (anterior median) seemed as large as those of eyes with indirect retina, but, in contrast to the latter, were in close contact with cerebral vesicles (Fig. 3). Two layers could be distinguished: an outer one which formed the vitreous body and dioptric apparatus, and an inner one, which developed as the retina. For the other eyes (anterior lateral, posterior median, posterior lateral), development was slower (Fig. 4).

The chelicera of first instar juveniles contained a rudiment of the venom gland in the form of a short tube slightly enlarged distally at the cheliceral base, but not reaching the fang (Fig. 10). Spinnerets differentiated during this instar; they did not bear any spigots, but anlagen of the large (ampullate) silk-gland ducts appeared inside them, together with the first buds of the gland sacs (Fig. 11).

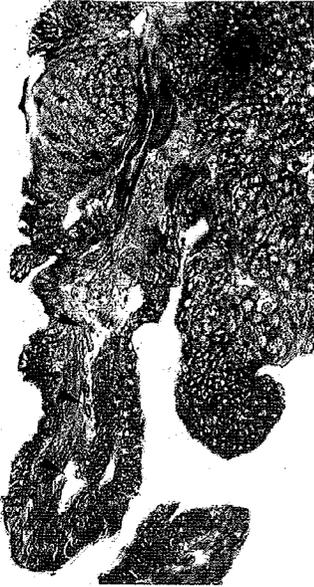
The second instar starts after the second moult. It lasted much longer than the first (12 to 15 days) and represented the most important phase of organogenesis. The visual system developed its sensory and dioptric components and optic ganglia developed in the brain. Retinal cells developed in all ocularanlagen: rhabdomes developed, distal cellular segments lengthened as fibres which joined together to form the optic nerves (Figs 5, 6, 7); pigment cells became progressively loaded with pigment granules (Figs 7, 8). In the anterior median eyes, a flattened lens appeared soon after the second moult (Fig. 5). On the other hand, in the three pairs of eyes with indirect retina (Fig. 6), development of the vitreous body proceeded slowly during the second instar and produced a lens only two or three days before the third moult (Fig. 6). Development of optic lobes was concomitant with that of retinae. Fibres of optic ganglion cells joined the retinal fibres from mid-instar onwards, when the first synaptic zone appeared. On the 25th day from egg-laying, both synaptic zones were in place (Fig. 9).

Two days after the second moult a small, glandular sac appeared above each chelicera, representing the venom gland, the duct of which ran along the whole chelicera, although not yet opening at the tip of the latter (Fig. 12). Shortly after the second moult, the four ampullate glands (the largest silk glands of *Peucetia*) started to develop (Fig. 13). Several smaller glands (aciniform glands) subsequently appeared in the posterior third of the abdomen (Fig. 14); and finally piriform glands (the smallest) differentiated (Fig. 14). The corresponding spigots were distinguishable on the different spinnerets (Fig. 15). The silk-gland system seemed ready to function from the end of the second instar, even before the third moult.

* Terminology: eyes with direct retina = principal eyes (Hauptaugen) = anterior median eyes; eyes with indirect retina = secondary eyes (Nebenaugen) = anterior lateral + posterior median + posterior lateral eyes.

Figs 10–15. Development of the venom- and silk-gland systems. 10 – Sagittal section of a chelicera in a first instar juvenile. Arrowheads point to the anlage of the venom gland. Scale bar = 50 μm . 11 – Sagittal section of the distal part of the abdomen showing anterior lateral (ALS) and posterior lateral (PLS) spinnerets. Arrowheads point to the anlage of a silk gland in a first instar juvenile. Scale bar = 50 μm . 12 – Frontal section of chelicerae of a juvenile during the second instar (18th day). A small, glandular sac has developed following the duct (arrowheads), which does not yet open outside. Scale bar = 100 μm . 13 – Horizontal section of the abdomen on the 13th day, showing two ampullate gland sacs (arrowheads) at the beginning of their development in the anterior dorsal region. Scale bar = 100 μm . 14 – Two types of small silk glands are present in the posterior part of the abdomen on the 19th day of development: aciniform (AC) and piriform (PI) glands. Scale bar = 50 μm . 15 – On the anterior spinnerets, two types of spigots are developed on the 19th day. Scale bar = 100 μm .

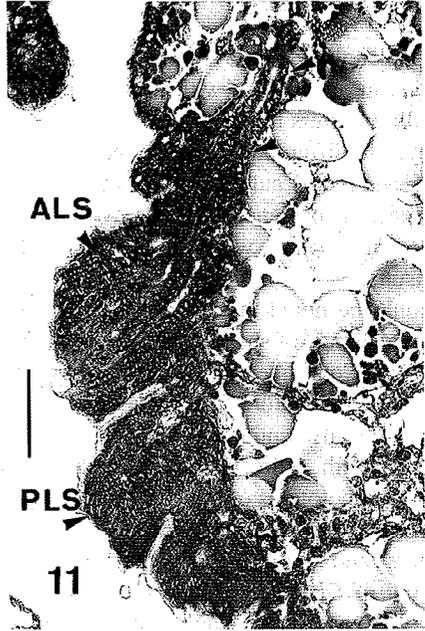
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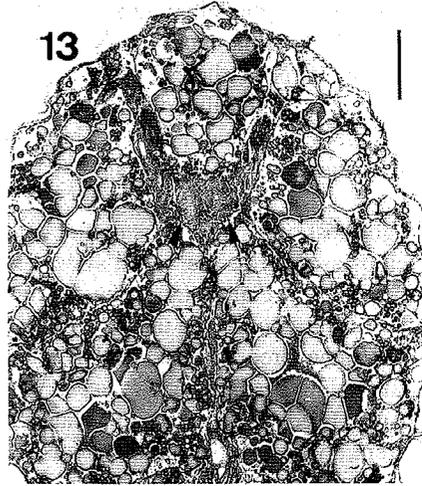
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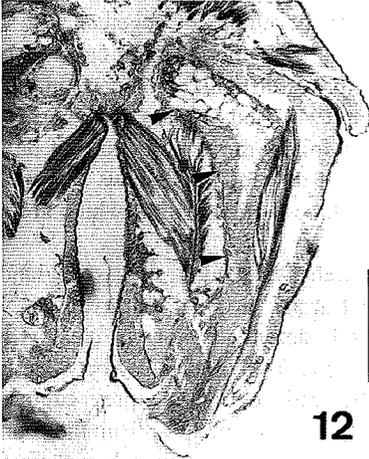
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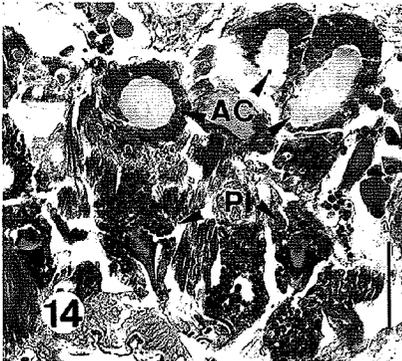
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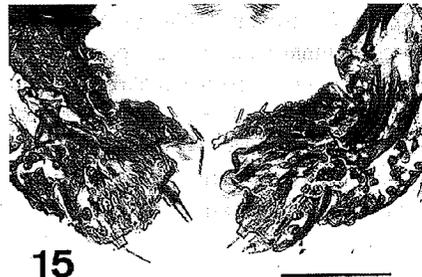
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The chronology of development established from our observations on two *Peuceitia* species is in accordance with Holm's results (1940) for *Oxyopes ramosus*, although his terminology differs from ours. Studies by Homann (1971) on the comparative organogenesis of eyes in different families of spiders have been useful in comparing the three *Peuceitia* species. As this author pointed out in the case of *Peuceitia viridans* (the only oxyopid he studied), the presence of a cell layer in the indirect retinae, which might be assigned to a developing tapetum, was not detected at all in *P. cauca* or in *P. gerhardi* during the first three instars.

It should be noted that morphogenetic movements at the end of the second instar resulted in a change of shape of the prosoma, the anterior part of which became much higher than before. Consequently, the optic nerves, which initially had an undulating appearance became stretched before the third moult.

The initial differentiation of the anterior median eyes seemed to occur earlier than that of the eyes with indirect retina. This chronology of eye development might be related to the positive phototaxis of *Peuceitia* spiderlings immediately after emergence.

From bibliographical data (Holm, 1940; Vachon, 1959, 1965; Vachon & Hubert, 1971; and others) and an original scanning electron microscopic study of the postembryonic development of *Cheiracanthium virescens* (Sundevall, 1883) (Clubionidae), Canard (1987) tentatively suggested a general interpretation of spider development, together with a new terminology. The methodology used by Canard and other authors, which consists of observations of the external morphology of juveniles, makes difficult a comparison with our histological study. Nevertheless, according to Holm (1940) and Vachon & Hubert (1971), it seems that clubionid, salticid, and oxyopid spiders follow the same pattern of development (cf. table V in Canard, 1987). This similarity of development shows a remarkable parallel with the reduction in web spinning in these three families, all of which are active hunters.

Although most oxyopid spiders do not construct webs when adult, their silk-gland system develops as early as the visual system. It is not at all "residual" in juveniles, which spin silk during several instars. The function of this activity is not yet clear (Kaston, 1972), but it can be suggested that silk spinning favours a kind of sociality between juveniles of the same brood, since we have often observed cooperative prey capture and communal feeding among young *Peuceitia* individuals of different ages, from the fourth instar onwards. Feeding behaviour only appears after the fourth moult, when the venom-gland system, the last of the three systems to form, and the digestive tract are sufficiently developed. Social behaviour has been discovered and studied in other oxyopid spiders (genus *Tapinillus* Simon, 1898) by Mora (1986) and Avilés (1994). Individuals share an irregular communal web, and cooperate in prey capture and feeding. On the other hand, spiders of the genus *Oxyopes* make very little use of silk and, as far as we know, do not tolerate the proximity of other congeners after their dispersion. As a continuation of this first study on Oxyopidae, we will follow the variations of the visual, silk- and venom-gland systems during the life span of *Peuceitia gerhardi*, in relation to predatory and sexual behaviour. A comparative study will be also undertaken on *Oxyopes lineatus* Latreille, 1806.

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