

## Postembryonic development in ten species of neotropical Salticidae (Araneae)

María Elena Galiano

Museo Argentino de Ciencias Naturales "Bernardino Rivadavia",  
Av. Angel Gallardo 470,  
1405 Buenos Aires, R. Argentina

### Summary

The number and characteristics of the instars and the sequence of morphological changes during early development are similar in the ten species studied. There are four postembryonic instars within the cocoon; the first three are embryo-like, with the body bent at the pedicel. The first instar covered by the embryonic cuticle equipped with the egg teeth is intrachorionate and ends at hatching. Hatching occurs with the breaking of the two egg membranes (chorion and vitelline membrane) and the simultaneous splitting (first moult) of the embryonic cuticle. The egg membranes and the embryonic cuticle are later cast together, along with the second moult. The third instar is free. The fourth instar has the cephalothorax and the abdomen in the same plane and is mobile; the cheliceral fangs have no poison gland openings; there are tarsal claws (generally pectinate); setae, trichobothria, tarsal and lyriform organs, and spinning-tubes. In *Lyssomanes pauper* Mello-Leitão and *Thiodina punctulata* Mello-Leitão the spinning-tubes are functional. The appearance in the fourth instar of these species of two of the traits that are supposed to be limited to Spartaecinae is discussed, together with relevant literature.

### Introduction

A growing interest in the early postembryonic development of spiders has resulted in the recent appearance of several publications on the subject. The pioneering work of Holm (1940) demonstrated that, far from being homogeneous, the early development in different groups has particularities whose phylogenetic value has not yet been clarified. After this initial proposal about stages, phases and their nomenclature, several authors presented systems of interpretation, definitions of the stages and new terminologies. The history of this process and discussion of the literature can be read in André & Jocqué (1986) and Canard (1987).

André & Jocqué suggested the convenience of applying to spiders the theory about "l'évolution selon l'âge" of Grandjean (1954, 1957) and his definitions of "stases" and "stades". Canard discussed the approach of André & Jocqué together with those of other arachnologists. In turn, Canard used a new terminology. In 1984 he called the successive instars "pullus", "juvénile" and "pubère" while in 1987 he changed "pullus" to "stade foetal". The terms "prélarve, larve, nymphe" proposed by Vachon (1957) have been considered unsuitable because they are used in entomology for different states of development. On the same grounds it seems necessary to reject the terms postulated by Canard; "stade foetal" because "foetus" is commonly used for unborn Mammalia and "pubère" because it is excessively anthropomorphic.

Vachon (1957, 1958) and Legendre (1958) considered that the first postembryonic stage elapsed between the reversion of the germ band and the

shedding of the embryonic cuticle. Canard (1984) and Downes (1987) defined hatching as the end of the embryonic phase. In Salticidae and Clubionidae, Canard called "premier stade postembryonnaire" (1984) and "premier stade" (1987), the postembryo with egg teeth that appears through the breach of the egg membranes and lasts only some minutes. He divided the development into periods and phases (following in part Vachon, 1957).

Downes (1987) presented his own "proposal for standardization of terms", but did not recognize the embryonic cuticle as a true moult.

Hallas (1988) gave descriptions of the early development of nine species of Salticidae. She wrote: "Establishing how widespread this pattern is among spartaecines and whether it is limited to Spartaecinae will require study of more spartaecine and non-spartaecine salticids".

It is the aim of this paper to describe the development of ten species of neotropical "non-spartaecine" salticids and to compare them with those described by Hallas and other authors, presenting at the same time a discussion about the recent literature on the subject. From the brief account given above the disagreement about terminologies and definitions of the stages is evident. Even if the instars received different names depending on the authors, it is possible to establish an equivalence of terms provided that the descriptions are accurate.

The classification of the Salticidae at the subfamily level is far from being established. Only some isolated subfamilies with peculiar characteristics are accepted (*Lyssomaninae*, *Spartaecinae*). Most of the four hundred or so genera are clustered into groups of no taxonomic category. Of the species dealt with in this paper, *Lyssomanes pauper* Mello-Leitão belongs to the *Lyssomaninae*; the other nine species are placed in groups (*sensu* Simon, 1901-1903), some of them tentatively.

### Material and methods

Eggs were obtained in the laboratory from females of the species listed in Table 1. Some of them have not been systematically revised or are new species. It must be clearly stated that *Evophrys sutrix* Holmberg is not an *Evophrys* but remains in the genus until more studies are done (Galiano, 1963).

Species are referred to in the text by their generic names except when there are two species of the same genus.

The methods for observing and describing the instars are those of previous papers (Galiano, 1967, 1972, 1973a, 1973b). The animal itself between two moults is called an instar and the period, a stage. The shedding of the embryonic cuticle is considered the first true moult and the subsequent moults are numbered successively.

In the present paper it is not considered necessary to apply any special names to instars or stages. The division of the development into periods seems possible at first sight, but for some species (e.g. *Grammostola pulchripes* (Simon) and *G. vachoni* Schiapelli &

Gerschman, Theraphosidae) the definition and inclusion of some instars into the established divisions is very difficult. If it were essential to divide development into periods, the "incomplete" and "complete" periods of Holm (1940) are more clearly defined.

Temperature and photoperiod for all species were 25-35°C, LD 13:11.

One to three eggs of every batch were submerged in Vaseline, and were examined at intervals of three to four hours. When the time of hatching or moulting approached, the observations were continuous even during the night.

Some second and third instars were marked with spots of china ink made with a brush of only one sable-hair (see Table 1).

Living specimens were observed with a stereomicroscope.

Specimens at each of the described postembryonic stages were killed in 60% ethanol and transferred to 70% ethanol four hours later. Dissected anatomical features were mounted on slides, examined using an optical microscope and photographed. Stereoscan micrographs were obtained of exuviae.

The chorion and the vitelline membrane were separated by maceration in lactophenol or 10% potassium hydroxide.

Some abnormal effects may occur during experimentation. (a) Eggs in Vaseline have a short delay in hatching compared with the rest of the batch. It seems that the Vaseline alters the chorion, retarding its breaking. In some cases it is possible to observe the rupture of the embryonic cuticle before that of the chorion and even the sliding of the cuticle from both

sides of the rupture, freeing the chelicerae and bases of the appendages. When the egg hatches in Vaseline, the animal dies. (b) Postembryos submerged in ethanol do not die instantaneously; there are contractions of the body and legs and these may result in tearing of the integument in abnormal places. This tearing may also happen when critical-point drying techniques are used (see Bonaric, 1980; Canard, 1984).

## Results

Hatching, characteristics of the instars, and number of stages and moults are similar in the ten species studied. Specific differences will be mentioned when necessary.

### Egg membranes

There are two: the chorion and the vitelline membrane. They adhere closely, and split and slide together. In eggs in Vaseline, sometimes they come apart after hatching.

### Hatching

Among the eggs from the same egg sac there could be a difference of about twelve hours between the first and the last to hatch. Some ten hours before hatching air spaces appear under the egg membranes; the cephalothorax and appendages become visible. The egg teeth are present at the bases of the palps; their size and colour depend on the species. Before hatching the egg becomes elongated and lines of tension are marked in the chorion; weak contractions of palps occur while the air disappears. In some specimens, one or both egg teeth pierce the egg membranes some time before the

Species	Subfamily or group	Number of egg sacs and individuals	Oviposition to hatching (days)	Marked postembryos		Duration of 2nd stage (hours)	Duration of 3rd stage (hours)	Duration of 4th stage (days)
				2nd	3rd			
<i>Phiale roburifoliata</i> Holmberg	Hylleae	8-145	8-9	9	3	12-19	23-24	10-12
<i>Phiale pantherina</i> Mello-Leitão	Hylleae (?)	2-61	8-9	3	4	24	46	9
<i>Evophrys sutrix</i> Holmberg	Hylleae (?)	3-37	8-9	3	5	11-21	31-35	8-9
<i>Aphirape</i> n. sp.	Evophryidae	2-34	—	5	5	9-11	29-32	8
<i>Sarinda marcosi</i> Piza	Sarindeae	3-11	5-7	2	2	21-23	48-60	11-12
<i>Dendryphantès patagonicus</i> Simon	Dendryphantèae	3-20	6-10	3	3	24-27	153-200	10-11
<i>Tullgrenella serrana</i> Galiano	Aelurilleae	6-91	6-9	4	6	22-28	19-37	9-11
<i>Thiodina punctulata</i> Mello-Leitão	Thiodineae	15-196	4-9	4	7	10-24	17-48	6-8
<i>Cotinusa</i> sp.	Thiodineae	3-15	—	3	2	21	32	—
<i>Lyssomanes pauper</i> Mello-Leitão	Lyssomaninae	5-149	7-8	4	7	16-20	22-32	6-8

Table 1: Postembryonic development in Salticidae. Number of egg sacs, individuals and marked postembryos; duration of the periods.

latter break. The rupture of the membranes occurs near one of the egg teeth, the line of rupture runs quickly back following the edge of the cephalothorax, turns round the fourth coxae, continues along the fourth legs and stops at some point in their middle. Through the slit appear the chelicerae, and the bases of the legs and palps. After a short pause, the body straightens a little and the egg membranes slide backwards uncovering the anterior half of the cephalothorax but generally passing over the pedicel and stopping at the dorsum of the abdomen.

#### *Embryonic cuticle*

This is the chitinous external cover of the first intrachorionate instar and is equipped with the egg teeth; it has no hairs or spicules. It covers the body and each of the appendages independently. Generally the embryonic cuticle splits simultaneously with the egg membranes, but in some eggs of every batch the rupture takes place seconds after the splitting of the egg membranes. In eggs submerged in Vaseline, sometimes the embryonic cuticle splits before the chorion.

The embryonic cuticle breaks at the anterior edge of the cephalothorax and the rupture progresses backwards. The covering of the cephalothorax is connected above the pedicel to that of the abdomen; the sheaths of the appendages remain attached to the covering of the sternum and mouthparts. The cover of the cephalothorax slides backwards together with the egg membranes, while the lower edge of the rupture stays at about the level of the coxae. The shedding of the embryonic cuticle occurs in the same way and with the same characteristics as any other moult of the animal. It is possible to observe the movements of the palps, stretching and extending inside their sheaths. Deciduous teeth were never observed.

Some special cases: (1) *Tullgrenella serrana* Galiano. One egg in Vaseline remained adhered to an air bubble. When the egg membranes split the air entered through the rupture and produced the total shedding of the swollen egg membranes and embryonic cuticle. The latter floated in the Vaseline, totally expanded; the circular "lid" of the cephalothorax was united to the partially wrinkled cover of the abdomen which in turn was attached to the cover of the sternum from which the appendages spread out (legs, palps with egg teeth, labium, maxillae and chelicerae).

(2) *Lyssomanes pauper*. As above, except that the separation of the membranes and the embryonic cuticle occurred without the assistance of an air bubble. Although they remained crumpled, the sheaths of the legs were distinct.

(3) *Evophrys sutrix*. In one egg in Vaseline the embryonic cuticle broke before the egg membranes. The lower border of the rupture travelled down a little and the chelicerae were freed. After another two hours the egg membranes split.

#### *First postembryonic instar*

Equivalences: A of Holm; prélarve 1 of Vachon; pullus 1 (P1) of Canard, 1984; stade foetal 1 (F1) of

Canard, 1987.

The body is strongly bent; the legs are parallel, close to the sides of the body. The chelicerae have rounded apices. The instar is covered by the embryonic cuticle with egg teeth. The stage is intrachorionate.

#### *Second postembryonic instar*

Equivalences: B of Holm; prélarve 2 of Vachon; pullus 2 (P2) of Canard, 1984; stade foetal 2 (F2) of Canard, 1987.

This instar appears after the splitting of the embryonic cuticle. It remains partially covered by the cuticle and the egg membranes that break at the same time but are not discarded. The only visible parts are the dorsal surface of the cephalothorax, part of the dorsal surface of the abdomen, the chelicerae and the bases of the legs and palps. The chelicerae are similar to those of the first instar. The integument is smooth but anteriorly, at the bases of the chelicerae and palps, there are small granules which are probably the result of the pressure against the second instar integument of the spicules of the third instar, already formed.

In *Sarinda* a faint pigmentation appears by the end of this stage at the position of the anterior median eyes. *Lyssomanes* shows the beginning of the retinal pigmentation of the lateral eyes 16 hours after hatching.

The legs are close to the body which is strongly bent at the pedicel, with the mouthparts near the anal tubercle. Four to five hours before the second moult, lines of tension extend between the cephalothorax and the abdomen, principally towards the front. The tension increases and the integument bursts at the anterior margin; the rupture runs backwards on each side and stops near the fourth coxae. After a pause of one or two minutes, a sudden movement widens the space between the cephalothorax and abdomen and causes the breaking of all the membranes that were still connecting these parts behind the fourth legs. The cover of the cephalothorax slides backwards, passes over the pedicel and stops at the dorsal base of the abdomen. The legs and palps stretch and extend inside their sheaths and the basal parts become free. At this moment, the abdomen begins the movements that will result in the total rejection of the membranes: the dorsal side of the abdomen contracts and shortens, the furrows (remains of the embryonic segmentation) become deeper and the anal tubercle rises dorsally. Then, the abdomen extends its dorsal side, the furrows widen, and the anal tubercle bends ventrally and pulls all the membranes towards the apex of the abdomen. These alternate movements are repeated and the four membranes (chorion, vitelline membrane, embryonic cuticle and second exuviae) reach the apex and remain there crumpled or fall off. Even after the end of the moult, the movements of the abdomen continue for some minutes more. The entire moulting process lasts five minutes.

*Observations:* Specimens of second instars of the studied species were marked with ink as indicated in Table 1. The direct observation of the moult allows the observer to follow the track of the spot on the thin

integument. When it reaches the apex of the abdomen, the spot may stop dorsal to the anal tubercle or advance until disappearing inside the other membranes. All the species behave in the same way. In one specimen of *Thiodina*, the ink slid from the dorsum to the margin of the cephalothorax. At the moult, it acted as a glue, and the integument broke at the posterior margin of the cephalothorax, cutting its connection with the pedicel. The cover of the cephalothorax remained attached to those of the legs and they did not come off.

#### *Third postembryonic instar*

Equivalences: C of Holm; pullus 3 (P3) of Canard, 1984; stade foetal 3 (F3) of Canard, 1987; second prelarva, "shiny stage" of Hallas.

This appears after the shedding of the second exuviae and the rejection of the other covers. It is completely free. The body is bent at 90°; the legs are longer than in the previous instar and are extended close to the sides of the body. The segmentation is present, except at the metatarsal-tarsal joint. The chelicerae have a short conical terminal portion with a blunt tip, weakly sclerotized. The abdomen is elongated, with six or seven transverse furrows in the dorsal apical half. There are two conical tubercles on the dorsal abdominal base and two smaller ones on the posterior margin of the cephalothorax. The function of these tubercles is unknown. The anal tubercle is large; the spinnerets are represented by four blunt structures. The integument has spicules, spinules and granules. The cephalothoracic cuticular microsculptures form a raised reticulated surface (Fig. 5). The tarsal claws are represented by two small conical tubercles (Figs. 13, 15:a). A short spinule is in a subapical position on the tarsi (Fig. 15:b) (also shown in *Thomisus onustus* Walck. by Canard (1984: pl. 26, fig. 7)). Tarsal and lyriform organs, trichobothria, setae and spinning tubes are absent.

Through the integument it is possible to follow the development of the integumental derivatives of the fourth instar. The deposit of visual pigments is also visible. *Lyssomanes* shows, 7-10 h after the second moult, two longitudinal blackish discontinuous lines in the cephalic region. They are formed by the visual pigments of the anterior lateral, posterior median and posterior lateral eyes. Some time later, patches of brown pigment appear at the site of the anterior median eyes. In the other species studied, the patches of the anterior median eyes were formed before those of the other eyes.

The moulting of this instar (third moult) occurs with characteristics similar to previous moults as it was observed in the marked specimens (Table 1).

#### *Fourth postembryonic instar*

Equivalences: D of Holm; prénymphe of Vachon; préjuvénile (Ji 1) of Canard; larva, "setose stage" of Hallas.

Cephalothorax and abdomen in the same plane; legs segmented, spread out; chelicera with an apical

articulated segment with a short curved fang which does not have a poison gland opening. At the posterior edge, the fang has a "lamella" the form of which differs according to the species. The basal segment of the chelicera has one promarginal tooth, sometimes accompanied by one or two low tubercles (Figs. 11, 12). There are filamentous and whorled setae, trichobothria, spinules, spicules, tarsal claws, tarsal and lyriform organs. The maxillae have spicules and spinules. The spicules are more abundant near the outer distal corner (*Tullgrenella*, *Phiale roburifoliata* Holmberg, *P. pantherina* Mello-Leitão, *Cotinusa* sp.) or form a serrula-like structure (*Thiodina*, *Evophrys*, *Aphirape* n. sp., *Dendryphantes*). In *Lyssomanes* and *Sarinda*, the thorns are bigger than the other spicules and are arranged in a single line at the border (Figs. 1, 3). They form a true serrula, though different from that of the following instar (Figs. 2, 4). The two tarsal claws are asymmetrically pectinated in all species except *Phiale pantherina* which has simple claws. There are small differences in size and shape depending on the species. Generally the anterior claw has 3-4 teeth and the posterior 0-2 teeth (Fig. 16), except in *Lyssomanes* which has 7 or 8 teeth on the anterior claw and 6 on the posterior (Fig. 14).

There are no claw tufts. The posterior spinnerets have the outline of the segmentation, visible also in the lines of setae. The spinning-tubes are present, but are fewer and smaller than in the following instar (Figs. 7-10). The integument of the cephalothorax has microsculptures (Fig. 6). At the site of the corneae, the integument is uneven and rippled (Figs. 17, 18: a). The lenses of the eyes are not formed (Hallas, 1988: fig. 4). During this stage, the progress of development of the eye capsules and corneae of the fifth instar can be seen under the integument. By the end of the stage and under a strong light, *Lyssomanes* shows horizontal displacements of the anterior median eye capsules. These movements were observed by Land (1969) in *Metaphidippus harfordi* (Peckham). He wrote "Spontaneous activity . . . also seen in juvenile spiders before their second moult - i.e. before the corneae and lenses are fully formed."

In the first days of this stage locomotory ability is poorly developed. In the laboratory dishes, the animals stay upside-down with the legs moving feebly. Even if they are righted they fall again. But by the middle of the stage they are better balanced and more agile, and by the end of the period they walk and even do short runs. They have a strong tendency to cluster. One specimen of *Thiodina* and two of *Evophrys* were found near collapsed eggs with their abdomens very dilated. It is believed that they had eaten from these eggs (see Galiano, 1967; Schick, 1972). About three days before the next moult, *Evophrys* and *Phiale roburifoliata* accomplish all the movements related to spinning: the abdomen descends and the anterior spinnerets rotate, but they do not produce silk. *Thiodina* and *Lyssomanes*, however, are able to produce silk, spinning draglines and attachment discs.

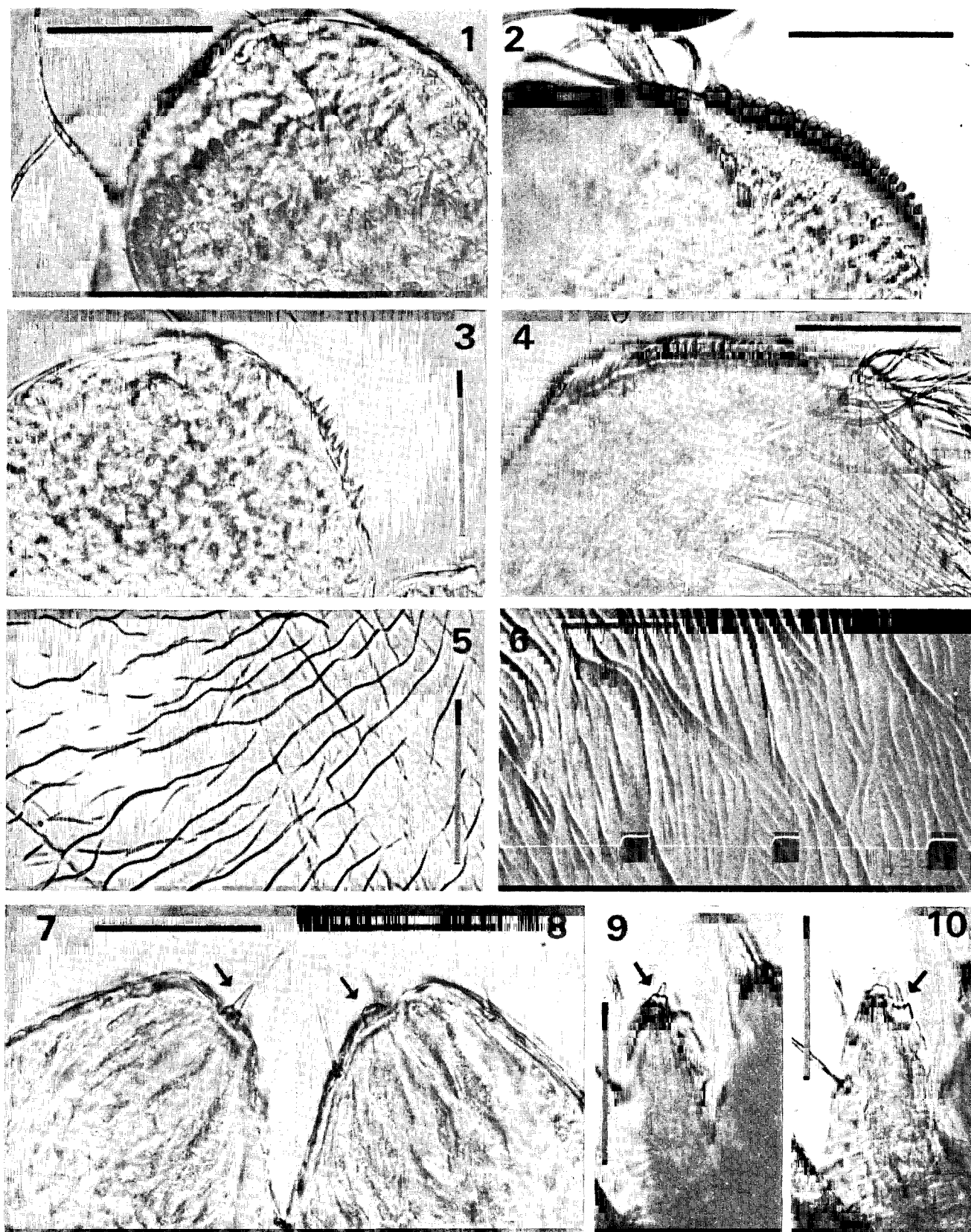
The threads form a mesh where the spiders cluster. *Sarinda* does not produce silk. Some elements of the

morphology of *Sarinda* (swollen palps, constricted abdomen) and its behaviour (continuous tremble of the abdomen, elevation for seconds of the first legs) are related to its myrmecomorphy.

*Fifth instar*

Equivalences: Complete instar I of Holm; première nymphe of Vachon; juvénile (J2) of Canard.

This is the first "complete" postembryonic instar and



Figs. 1-10: 1-4 Maxillary serrulae. 1 *Sarinda marcosi*, fourth instar; 2 *S. marcosi*, fifth instar; 3 *Lyssomanes pauper*, fourth instar; 4 *L. pauper*, fifth instar. 5, 6 Cephalothoracic integument. 5 *Tullgrenella serrana*, third instar; 6 *Thiodina punctulata*, fourth instar. 7-10 Fourth instar anterior spinnerets (arrows indicate spinning-tubes). 7, 8 *Thiodina punctulata*; 9, 10 *Sarinda marcosi*. Scale lines = 0.05mm (1-5, 7-10), 0.01mm (6).



resembles closely the adult of the species, except for the colour that sometimes is different. *Thiodina* has two pairs of bulbous setae on tibia I; *Sarinda* has swollen palps with black hairs, a constricted abdomen and black stripes on the transparent legs; *Lyssomanes* is pale green with some black spots on the abdomen. In all the species the eyes are well developed, the serrula is as in the adults (Figs. 2, 4), the fangs have poison gland openings, and the margins of the chelicerae have more teeth. The spinnerets have more and bigger spinning-tubes and produce silk. During this stage they disperse and feed actively.

## Discussion

### Egg membranes

Balbani (1873) and Wagner (1888) described two covers of the egg: the chorion and the vitelline membrane. Wagner found that by the end of the embryonic period the vitelline membrane separated from the chorion and covered the body and legs of the spider as a sheath, the same as the old integument will do at the following moults of the animal.

Taylor & Peck (1975) and Peaslee & Peck (1983) described the egg teeth as placed on the vitelline membrane in *Phidippus audax* (Hentz) (Salticidae) and *Octonoba octonarius* (Muma) (Uloboridae). Peck & Whitcomb (1970) studying *Chiracanthium inclusum* (Hentz) (Clubionidae) described the splitting of the chorion at hatching, but the vitelline membrane covered the body 36 h longer. Hite *et al.* (1966) mentioned that in *Loxosceles reclusa* Gertsch & Mulaik (Scytodidae) after the bursting of the chorion "it was evident that a transparent membrane covered the entire postembryo confining the pedipalps and legs and holding them close to the body". Galiano (1967) found that in *Loxosceles laeta* (Nicolet) the two egg membranes split simultaneously, the first postembryo is covered by the embryonic cuticle with egg teeth, and has the appendages independently covered.

Downes (1987) published a schematic representation of the "process of transition from embryo to first instar" taken from fourteen investigators. In his categories VII, VIII and IX he mentioned species that shed the chorion separately from the vitelline membrane. Apart from the authors mentioned above, Downes also referred to Schick and Galiano. But Schick (1972), describing the development of *Misumenops* (Thomisidae), never mentioned the separation of the egg membranes, and Galiano (1969a), studying *Diguetia catamarquensis* (Mello-Leitão) (Diguetidae), observed the shedding and total rejection of the two egg membranes at hatching, and a first postembryo covered by the embryonic cuticle with egg teeth.

Downes also misinterpreted the development of species of *Polybetes* described by Galiano (1971). The correct description is: chorion and vitelline membrane shed together but not rejected. Two to twelve hours later the embryonic cuticle splits (first moult), but neither it nor the egg membranes are rejected. The subsequent second moult is cast along with the egg

membranes and the embryonic cuticle, producing a free instar.

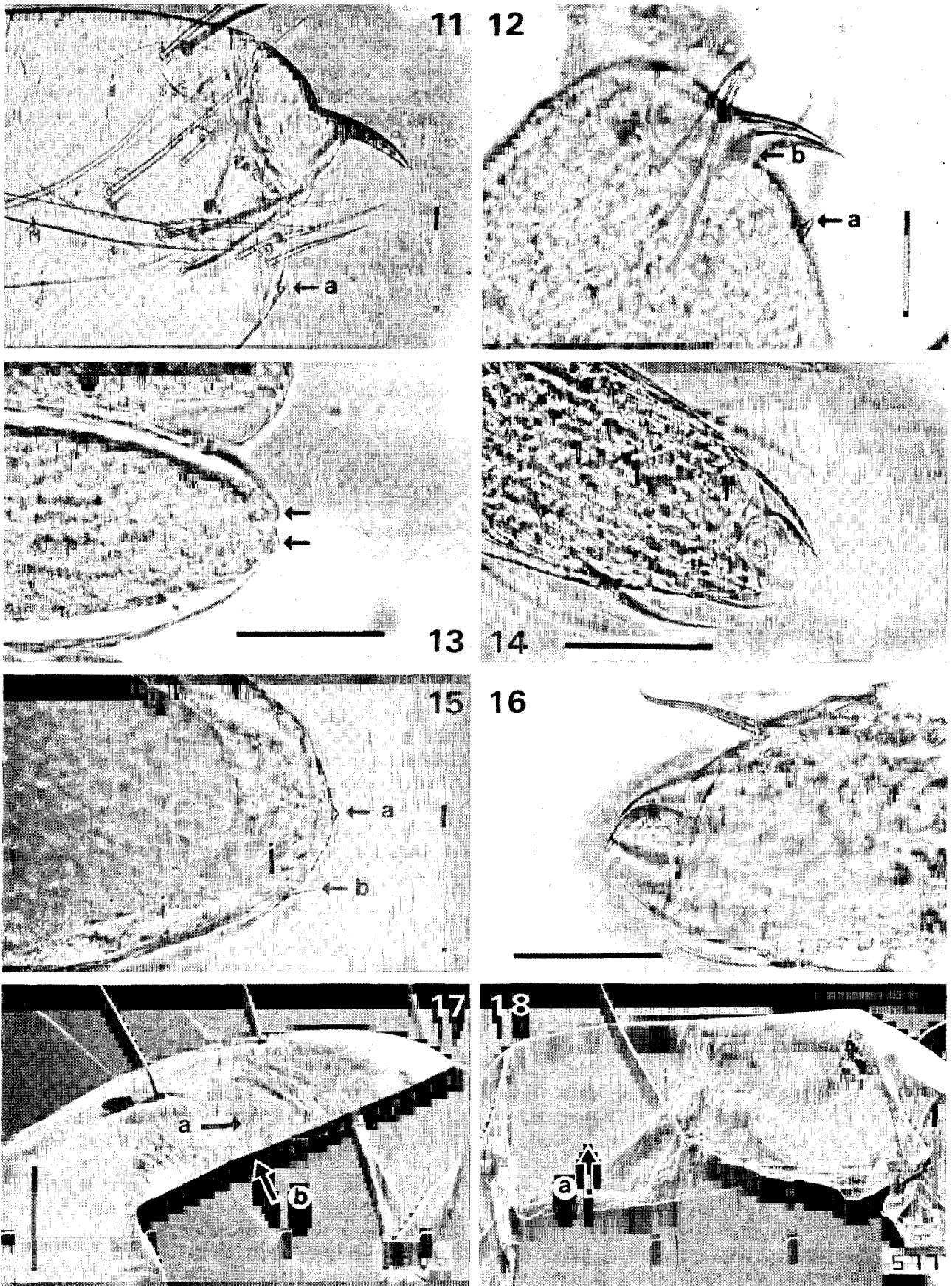
Holm (1940, 1954), Vachon (1957), Legendre (1958), Canard (1984, 1987), Hallas (1988), and Galiano (1967, 1969a, 1969b, 1971, 1972, 1973a, 1973b and this paper) described two egg membranes that split, slide and are rejected together.

### Embryonic cuticle and egg teeth

Legendre (1958) studied the development of *Dolomedes* (Pisauridae), showing the cytological changes of the hypoderm of the first prelarva (between the reversion of the germ band and the moult). On the 20th day of development, the hypoderm had become enlarged and was covered by a chitinous layer, the "cuticle prélarvaire". At hatching, this cuticle separated from the hypoderm which retained its thickness. Legendre wrote (1958: 70): "cette première mue a absolument la même valeur que les autres". The egg teeth were on the chitinous layer of the prelarva on the 20th day (*op. cit.*, fig. 3).

Holm (1940) supposed that in Argiopiiformia the egg teeth were formed independently of the cuticle because when the egg membranes split, they often came loose.

Canard (1984) described deciduous teeth in the araneomorphs *Pellenes tripunctatus* (Walck.), *Evophrys petrensis* C. L. Koch, *Phlegra v-insignita* (Clerck), *Sitticus floricola* (C. L. Koch) (Salticidae), *Chiracanthium pennatum* Simon and *C. virescens* (Sundevall) (Clubionidae) (1987). About *Dysdera crocata* C. L. Koch and *D. erythrina* (Walck.) (Dysderidae), Canard (1984: 71) said: "des dents d'éclosion . . . se prolongent latéralement par un cordon plus ou moins large (figs. 2, 3). Ce cordon contourne toutes les pattes, mais pas les chélicères (fig. 1), il se prolonge sur la face ventrale des pattes et émettrait peut-être entre chacune des ramifications qui se rejoindraient ventralement (fig. 4)". In the mygalomorph *Atypus affinis* Eichwald (Atypidae), Canard (1984) described an intrachorionate first postembryo that has egg teeth on a smooth integument (*op. cit.*, pl. IV, figs. 1, 2). These teeth are shown in a "lambeau de tégument" that indicates a torn cuticle. But here he did not say that the teeth are deciduous. When he referred to the species of *Grammostola* (Theraphosidae) studied by Galiano (1969b, 1973a), Canard (1987: 102) said: "des dents d'éclosion, même lorsque le tégument portant ces organites se limite à une bandelette et n'est pas une enveloppe continue. Lors de la perte de ces dents et de leur support, il n'y a donc pas de renouvellement complet du tégument et l'on ne devrait ni parler de mue, ni distinguer de stade." But this is a misinterpretation of the facts, because Galiano (1969b) clearly established the existence of the embryonic cuticle as an integument that covered completely the body and independently the appendages of the postembryo. In fig. 2 (*op. cit.*) Galiano illustrated an egg two hours before hatching, showing the embryonic cuticle, already separated from the integument of the following instar. In *Grammostola pulchripes* and *G. vachoni* the presence of the



Figs. 11-18: **11,12** Fourth instar chelicerae, marginal tooth (a), lamella of fang (b). **11** *Thiodina punctulata*; **12** *Dendryphantus patagonicus*. **13** *Lyssomanes pauper*, third instar, tarsal tubercles (arrowed); **14** *L. pauper*, fourth instar, tarsal claw; **15** *Phiale roburifoliata*, third instar, tarsal tubercle (a), subapical spinule (b); **16** *P. roburifoliata*, fourth instar, tarsal claw. **17, 18** Fourth instar cephalothoracic integument (exuviae), frontal side, AME site (a), clypeal border (b). **17** *Tullgrenella serrana*; **18** *Phiale roburifoliata*. Scale lines = 0.05mm (11-16), 0.1mm (17,18).

embryonic cuticle with egg teeth is real, and after its shedding a different instar appears. Occasionally the embryonic cuticle is torn during hatching in some specimens, probably because the emerging postembryo spreads out its legs. The remains of the cuticle stay over the palps or legs, as shown in *Atypus affinis* (Canard, 1984: pl. IV, figs. 1, 2) and *Grammostola pulchripes* (Galiano, 1969b; fig. 4). See Galiano (1987) for more discussion about development in Mygalomorphae.

The described cases of deciduous teeth merit more research, as do the teeth of Argiopiformia, especially considering that some authors mentioned difficulties in SEM techniques due to the extraordinary thinness of the integuments. Canard (1984: 63) wrote: "son tégument est assez fin, et résiste mal aux traitements indispensables pour des observations au microscope électronique". Bonaric (1980: 13, 48) said: "les décollements accidentels qui apparaissent fréquemment au niveau des téguments prosomatiques ou abdominaux par exemple sont plus rares sur des portions cylindriques de fémur".

The mygalomorphs studied by Galiano (1969b, 1972, 1973a, 1973b), the araneomorphs *Loxosceles*, *Diguetia* and *Polybetes* (Galiano 1967, 1969a, 1971) and the Salticidae described here have the embryonic cuticle as a complete cover with attached egg teeth.

Some short reference must be made to Downes' definitions (1987: 190). He said, quoting V. Davies, that "a true moult is one that has limbs" and on p. 191: "First true integument moult (E): the shedding, but not necessarily the discarding, of the first integument that has legs". It is evident that for Downes the embryonic cuticle is a kind of spherical cover, similar to the egg membranes. Because of this mistake the following moults and instars are ill-defined and chronologically displaced.

#### Early development of Salticidae

Development in Salticidae was studied by Wagner (1888) and Holm (1940). For discussion of this literature see Canard (1984).

Crane (1948) studied the young of three species of *Corythalia*, and gave detailed descriptions of the shape and dentition of the tarsal claws and their changes during development. She found that the "first instar" had eyes "scarcely or not at all functional" and simple tarsal claws. The "second instar" had pectinate tarsal claws and well-developed eyes. These stages correspond to the fourth and fifth instars according to the present paper.

*Phidippus audax* was studied by Taylor & Peck (1975) who wrote: "the egg teeth on the vitelline membrane . . ." "After this membrane is shed . . . the spiderling is still enclosed in a third membrane . . . after . . . the shedding of this membrane . . . the spiderling's abdomen assumed the same plane as the carapace". "The first true molt . . . occurs inside the egg sac about ten days after the eclosion". Since Holm's and Legendre's (1958) papers it is known that the egg teeth are attached to the embryonic cuticle and not to the vitelline membrane.

Hill (1977) described in *Phidippus rimator* (Walck.) the pretarsus of the "first instar (larval)" with simple claws and of the "second instar" with whorled setae, tenent hairs and pectinate claws. They correspond to the fourth and fifth stages according to the present paper.

Richman & Whitcomb (1981) described nests and first instars of *Lyssomanes viridis* (Walck.). What they called first postembryos in their fig. 4 are here considered third instars.

Canard (1984) described the development of four species of Salticidae and agreed with Holm about the hatching, number of instars and characteristics of the stages, but differed in considering the intrachorionate postembryo which is covered by the embryonic cuticle as the first postembryonic instar. Canard found that the egg teeth in Salticidae were deciduous (a fact not observed by Holm) and he said that the spicules that appeared when the teeth "tombent" are elements for fixing them in place and prevent their displacement.

In the species of salticids studied here, deciduous teeth were never observed. It is believed that the spicules shown by Canard (1984: pl. 17, figs. 2, 3) belong to the integument of the third instar, already formed under the integument of the first and second instars.

Hallas (1988) described the development of nine species of Salticidae, four Spartaeinae and five non-spartaeines. She adopted the nomenclature of Vachon (1957) and said: "only two membranes, the chorion . . . and the vitelline membrane, were shed simultaneously during hatching . . . 24 h later, the cuticle of this first prelarva split dorsally and was totally rejected, revealing a second prelarva". The interval between hatching and first moult was 1-3 days (*op. cit.*, table 1) depending on the species. The descriptions and illustrations of the second prelarva reveal that Hallas is actually talking about the third postembryo (F3 of Canard) and what she called "larva" is the fourth instar (Ji 1 of Canard).

Holm (1940) and the experiments described here have demonstrated that the embryonic cuticle splits at eclosion. This fact was apparently missed by Hallas and in consequence the numeration of the instars is altered. She described eyes, tarsal claws and setae developing under the integument of her second prelarva, which is really the third instar.

Canard (1984) said that in the second postembryo "le tégument s'ouvre près de la base de l'abdomen, la fente gagne l'avant du céphalothorax, puis l'exuvie glisse sur le céphalothorax et l'abdomen". Hallas also said that the integument of her "first prelarva" split dorsally. In the present study, 40 marked specimens at the second stage were observed moulting, and in all of them the integument of the second moult broke at the anterior border of the cephalothorax, and its cover, which remained attached to the abdomen by the pedicel, slid backwards. If the exuviae broke dorsally, in order to be rejected they would have to slide forwards, in which case they must be attached to the chelicerae, and that was never observed in natural conditions.



Canard (1984) described the fourth instar (Ji 1) as lacking serrulae and with incompletely formed spinning-tubes. Hallas (1988: table 2) described the "larva" with "well differentiated eyes which completed development during this stage", tarsal claws simple in non-spartaeines and pectinate in spartaeines, spinnerets unisegmented, spigots absent in non-spartaeines and present and functional in spartaeines. *Portia* and *Cyrba* "spun draglines and attachment discs". These larvae "move about inside the egg sac and feed upon undeveloped eggs and on dead and developing nest-mates".

The species studied in the present work have pectinate claws (with the exception of *Phiale pantherina*), and spinning-tubes that in *Lyssomanes* and *Thiodina* spin silk. *L. pauper* and *Sarinda* have well-developed maxillary serrulae. None of the species have well-developed corneae, nor do *Corythalia* (Crane, 1948) or *Metaphidippus harfordi* (Land, 1969).

Blest & Carter (1987) studied *Plexippus validus* Urquhart and found that "Final reorganization of microvilli and of their dispositions in receptive segments to yield the mature pattern occurs after the post-embryos moult to the second instar between day 13 and day 15". Blest (1988) wrote about the same species that at days 4 and 5 from eclosion "The eye possesses a rudimentary corneal lens that cannot, because of its shape, be optically effective". The second instar of Blest & Carter corresponds to the fifth instar according to the present paper.

There is an interesting difference between the fourth instars of *Lyssomanes pauper* and *L. viridis*, whose adults are morphologically very similar. According to Hallas, *L. viridis* has simple tarsal claws, well-developed eyes and lacks spigots. *L. pauper* at the same stage has incompletely developed eyes, has functional spigots and the tarsal claws are not only pectinate but have the same particular form as have the claws of the adults of both species. *L. viridis* developed primordial retinae at the "prehatching stage" (Hallas, 1988) while *L. pauper* shows retinal pigmentation at the second instar.

Hallas wrote that *Cyrba* and *Portia* "are further distinguished from the studied non-spartaeine salticids by the precocial appearance in the larval stage of traits characteristic of active instars". They are: (1) tarsal and metatarsal scopulate hairs; (2) well-developed fangs; (3) pectinate tarsal claws; (4) cannibalism; (5) functional spigots (only in *Portia*); (6) variation in development timing and the rate of morphological changes.

Regarding the timing of events a comparison between Hallas' observations and Table 1 of this paper shows that the length of time from oviposition to hatching was from four to ten days in the neotropical salticids while the shortest time observed in spartaeines was six days in *Cyrba* and eight days in *Portia labiata* (Thorell). The duration of the stages following hatching must be compared bearing in mind that what Hallas called prelarva 1, prelarva 2 and larva, are here considered as second, third and fourth instars, respectively. Most of the neotropical species had

shorter second stages than the spartaeine species; third and fourth stages are also shorter or similar.

It seems that the timing of development in salticids is more varied than was believed before and possibly depends on factors as yet poorly understood, e.g., it was observed that the last batches of eggs laid by a female took longer to develop than the first ones.

The study of the ten species of salticids described here shows that at least two of the characteristics of Spartaeinae (pectinate tarsal claws and functional spigots) are present in some non-spartaeine species. Only two traits distinguish the fourth instar of Spartaeinae from that of non-spartaeines: the tarsal and metatarsal scopulate hairs and the well-developed fangs. Similar structures (bulbous hairs in *Thiodina*, black palpal hairs in *Sarinda*) appear in other salticid species in the fifth instar (first "complete" instar of Holm).

## Conclusions

In Salticidae, hatching and shedding of the embryonic cuticle are simultaneous.

There are four postembryonic stages which correspond to the four "incomplete" stages of Holm (1940).

The first postembryonic instar is intrachorionate and is covered by the embryonic cuticle equipped with egg teeth. The embryonic cuticle is a chitinous layer that covers the body and the appendages independently.

The egg teeth are attached to the embryonic cuticle. In the species studied here they are not deciduous.

The embryonic cuticle breaks and is rejected in a similar process as all the other moults of the animal. It is considered a true moult and called the first.

The second postembryonic instar is partially covered by the egg membranes and the embryonic cuticle. The second moult is rejected together with the egg membranes and the embryonic cuticle, freeing the third instar.

In the first three instars the body is bent and the legs are close to the body.

The fourth instar has the cephalothorax and abdomen in the same plane and the legs spread laterally. Locomotion is feeble at the beginning but increases during the stage. The fourth instar has pectinate tarsal claws (with a few exceptions), tarsal and lyriform organs, spicules, spinules, serrula-like structures, filamentous and whorled setae and trichobothria. The chelicerae have at least one marginal tooth and the fang has a lamella. There are no poison gland openings or well-developed corneae. Spinning-tubes are present and they are functional in some species. Oophagy is suspected in some species.

The fifth is the first "complete" instar (Holm, 1940). The spiderlings disperse and feed actively.

## Acknowledgements

I thank A. Canard and M. F. Downes for their comments on the manuscript, and P. Merrett who made helpful criticisms and corrected the English.

## References

- ANDRÉ, H. M. & JOCQUÉ, R. 1986: Definition of stases in spiders and other arachnids. *Mém.Soc.r.ent.Belg.* **33**: 1-14.
- BALBIANI, E. G. 1873: Mémoire sur le développement des aranéides. *Annls Sci.nat. (Zool.)* (5) **18**:1-91.
- BLEST, A. D. 1988: Post-embryonic development of the principal retina of a jumping spider. I. The establishment of receptor tiering by conformational changes. *Phil.Trans.R.Soc. (B)* **320**: 489-504.
- BLEST, A. D. & CARTER, M. 1987: Morphogenesis of a tiered principal retina and the evolution of jumping spiders. *Nature, Lond.* **328** (6126): 152-155.
- BONARIC, J. C. 1980: *Contribution a l'étude de la biologie du développement chez l'araignée Pisaura mirabilis (Clerck, 1758); approche physiologique des phénomènes de mue et de la diapause hivernale.* 1-281. Thesis Etat Montpellier.
- CANARD, A. 1984: *Contribution a la connaissance du développement, de l'écologie et de l'écophysiologie des aranéides des Landes Armoricales.* 1-389. Thesis Univ. Rennes I.
- CANARD, A. 1987: Analyse nouvelle du développement postembryonnaire des araignées. *Revue arachnol.* **7** (3):91-128.
- CRANE, J. 1948: Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part I. Systematics and life histories in *Corythalia*. *Zoologica, N.Y.* **33**(1-3):1-38.
- DOWNES, M. F. 1987: A proposal for standardization of terms used to describe the early development of spiders, based on a study of *Theridion rufipes* Lucas (Araneae: Theridiidae). *Bull.Br.arachnol.Soc.* **7**(6):187-193.
- GALIANO, M. E. 1963: Las variaciones individuales en *Evophrys sutrix* Holmberg, 1874 (Araneae, Salticidae). *Revta Soc.ent.argent.* **24**(1-4):23-28.
- GALIANO, M. E. 1967: Ciclo biológico y desarrollo de *Loxosceles laeta* (Nicolet, 1849) (Araneae, Scytodidae). *Acta zool. lilloana* **23**:431-464.
- GALIANO, M. E. 1969a: El desarrollo postembrionario larval de *Diguetia catamarquensis* (Mello-Leitão, 1941) (Araneae, Diguetidae). *Physis, B. Aires* **28**(77):395-405.
- GALIANO, M. E. 1969b: El desarrollo postembrionario larval de *Grammostola pulchripes* (Simon, 1891) (Araneae, Theraphosidae). *Physis, B. Aires* **29**(78): 73-90.
- GALIANO, M. E. 1971: El desarrollo postembrionario larval en especies del género *Polybetes* Simon, 1897 (Araneae, Sparassidae). *Acta zool. lilloana* **28**:211-226.
- GALIANO, M. E. 1972: El desarrollo postembrionario larval de *Ischnothele siemensii* Cambridge, 1896 (Araneae, Dipluridae). *Physis, B. Aires* **31** (82): 169-177.
- GALIANO, M. E. 1973a: El desarrollo postembrionario larval en Theraphosidae (Araneae). *Physis, B. Aires (Sec. C)* **32** (84):37-46.
- GALIANO, M. E. 1973b: El desarrollo postembrionario larval de *Avicularia avicularia* (Linnaeus, 1758) (Araneae, Theraphosidae). *Physis, B. Aires (Sec. C)* **32** (85): 315-327.
- GALIANO, M. E. 1987: Remarques sur la nomenclature et les caractères des stades postembryonnaires incomplets des araignées. *Revue arachnol.* **7** (2): 65-69.
- GRANDJEAN, F. 1954: Les deux sortes de temps et l'évolution. *Bull.biol.Fr.Belg.* **88** (4): 413-434.
- GRANDJEAN, F. 1957: L'évolution selon l'âge. *Archs Sci. Genève* **10** (4): 477-526.
- HALLAS, S. E. A. 1988: Hatching and early post-embryonic development in the Salticidae (Araneae). *Bull.Br.arachnol.Soc.* **7** (8): 231-236.
- HILL, D. E. 1977: The pretarsus of salticid spiders. *Zool.J.Linn. Soc.* **60** (4): 319-338.
- HITE, J. M., GLADNEY, W. J., LANCASTER Jr., J. L. & WHITCOMB, W. H. 1966: Biology of the brown recluse spider. *Bull.Ark.agric.Exp.Stn* **711**: 1-26.
- HOLM, A. 1940: Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. *Zool.Bidr.Upps.* **19**: 1-214.
- HOLM, A. 1954: Notes on the development of an orthognath spider, *Ischnothele karschi* Bös. & Lenz. *Zool.Bidr.Upps.* **30**: 199-221.
- LAND, M. F. 1969: Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J.exp.Biol.* **51**: 471-493.
- LEGENDRE, R. 1958: Contribution a l'étude du développement embryonnaire des araignées. *Bull.Soc.zool.Fr.* **83** (1): 60-75.
- PEASLEE, J. E. & PECK, W. B. 1983: The biology of *Octonoba octonarius* (Muma) (Araneae, Uloboridae). *J.Arachnol.* **11** (1): 51-67.
- PECK, W. B. & WHITCOMB, W. H. 1970: Studies on the biology of a spider, *Chiracanthium inclusum* (Hentz). *Bull.Ark.agric.Exp.Stn* **753**: 1-76.
- RICHMAN, D. B. & WHITCOMB, W. H. 1981: The ontogeny of *Lyssomanes viridis* (Walckenaer) (Araneae: Salticidae) on *Magnolia grandiflora* L. *Psyche, Camb.* **88** (1-2): 127-133.
- SCHICK, R. X. 1972: The early instars, larval feeding and the significance of larval feeding in the crab spider genus *Misumenops* (Araneida: Thomisidae). *Notes Arachnol. SW.* **3**: 12-19.
- SIMON, E. 1901-1903: *Histoire naturelle des araignées* **2** (3-4): 381-1080.
- TAYLOR, B. B. & PECK, W. B. 1975: A comparison of northern and southern forms of *Phidippus audax* (Hentz) (Araneida, Salticidae). *J.Arachnol.* **2** (2): 89-99.
- VACHON, M. 1957: Contribution a l'étude du développement post-embryonnaire des araignées. Première note. Généralités et nomenclature des stades. *Bull.Soc.zool.Fr.* **82** (5-6): 337-354.
- VACHON, M. 1958: Contribution a l'étude du développement post-embryonnaire des araignées. Deuxième note. Orthognathes. *Bull.Soc.zool.Fr.* **83** (5-6): 429-461.
- WAGNER, W. 1888: La mue des araignées. *Annls Sci. nat. (Zool.)* (7) **6** (3): 281-393.