

## Hatching and early post-embryonic development in the Salticidae (Araneae)

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### Summary

The hatching and early post-embryonic development of four species of the subfamily Spartaeinae (including *Portia* spp.) and five non-spartaeine salticids are described. All of these showed the same sequence of morphological changes during this period of development, each passing through three stages: prelarva 1, prelarva 2, and larva. However, spartaeines differed from non-spartaeines in two ways. Firstly, the timing of hatching events and the duration of the post-embryonic stages varied less among spartaeines than it did among non-spartaeines. Secondly, and perhaps more significantly, the larval stage of spartaeines is distinguished by the appearance of several traits, both morphological and behavioural, that are characteristic of the next stage of spider development: the active instar. The implications of the "precocial" appearance in larval spartaeines of tarsal and metatarsal scopulate hairs, well developed fangs, pectinate tarsal claws, functional spinnerets, cannibalism on eggs and nest-mates, and the laying down of draglines and attachment discs are considered.

### Introduction

Salticids are unique among spiders because they have the most complex eyes and highest visual acuity (Land, 1985). They use their well-developed vision to detect mobile insects, which they typically capture by cursorial pursuit and a final pounce (Forster, 1977). As cursorial spiders, salticids use silk primarily for laying draglines and for the construction of tubular retreats ("nests") usually only marginally larger than themselves (Hallas & Jackson, 1986a).

Recently the subfamily Spartaeinae was erected (Wanless, 1984), consisting of genera with several unusual and purportedly primitive morphological traits. Behavioural studies on *c.* 10 species of this subfamily have revealed some anomalous behaviour patterns: web-building; predatory versatility; araneophagy; aggressive mimicry; oophagy; kleptoparasitism; and specialised "cryptic stalking" (Jackson, 1982; Jackson & Blest, 1982; Murphy & Murphy, 1983; Forster & Murphy, 1986; Jackson & Hallas, 1986a, b). Spartaeine hatching ("eclosion") and early post-embryonic development have never been studied. The aim of this paper is to investigate whether spartaeines differ from other salticids not only morphologically and behaviourally, but also in their hatching and early development (and if so, how). To this end, the events surrounding hatching and the changes occurring during early post-embryonic development were observed in four spartaeine species known to be atypical salticids behaviourally and morphologically.

For comparative purposes, early post-embryonic development was also observed in five non-spartaeine salticid species. In addition, because clues to the phylogeny of a group of species may be revealed in the ontogeny of some of its members (McNamara, 1982), hatching and post-embryonic development of the spartaeines is considered in the light of the potential phylogenetic significance of the subfamily.

### Methods

Eggs were obtained from four spartaeine species (*Cyrba algerina* (Lucas), *Portia fimbriata* (Doleschall), *P. labiata* (Thorell), *P. schultzei* Karsch) and five non-spartaeine species (*Euophrys parvula* Bryant, *Holoplatys* sp., *Lyssomanes viridis* (Walckenaer), *Plexippus paykulli* (Audouin), *Trite auricoma* (Urquhart)). Upon oviposition, each egg sac was removed from its substrate in the female's cage (see Jackson & Hallas, 1986a for feeding procedures and cage design). Subsequent dissection of the egg sac exposed the eggs; and the entire egg-sac complex, including eggs, was transferred to an incubator. The incubator consisted of a small glass dish which sat open in a film of water in the bottom of a covered petri dish (*c.* 90 mm in diameter). For some species, instead of a small glass dish, plastic dishes with small wells (2 mm across) in the bottoms contained the eggs within the incubator. The incubator design ensured a constant high humidity. Temperature and light regimes for all species were 25°C ( $\pm$  5°C) and 12 h light (beginning at 0800).

Manipulation of eggs and egg sacs was minimised, since Assi (1982) found that frequently disturbed eggs did not follow normal development. If condensation and fungus growth were detected, the petri dish cover was left ajar to increase ventilation. If mites were detected among the eggs, they were removed since they feed on both eggs and dead post-embryos, and possibly living tissue (Grim & Cross, 1980).

Spiders are referred to by their generic names only, except in cases where confusion may arise. The day on which oviposition occurred was designated as day 0. Each egg sac was examined 1-4 times daily, using a binocular microscope. A Cambridge Mach 2 Stereoscan SEM was used to examine *Portia labiata* at various stages of post-embryonic development. Two non-spartaeines (*Plexippus*, *Trite*) were similarly examined. Specimens were killed in 70% alcohol, then dehydrated to 100% ethanol. They were then transferred to amyl acetate in an amyl acetate-ethanol series and dried in a liquid CO<sub>2</sub> critical-point dryer. Photographic copper or silver emulsions were used to mount specimens onto SEM stubs, then specimens were coated with 7 nm of gold.

### Terminology

Following the embryonic period within the egg, the two egg membranes (the inner vitelline membrane and outer chorion) rupture, freeing a 'post-embryo'. Although some authors have used nomenclatural systems which do not distinguish post-embryonic

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developing under the cuticle within a few days after hatching. To the naked eye, the spiderlings appeared smooth and shiny, but the cuticle was actually finely granulate (*Plexippus*, *Portia*, *Trite*) or papillate (*Euophrys*).

#### Post-hatching development

One to seven days after hatching and the first moult, a second moult occurred exposing a mobile larva (Fig. 4), with completely segmented legs spread laterally. The larvae possessed several characteristics of the active, free-living instars (Table 2).

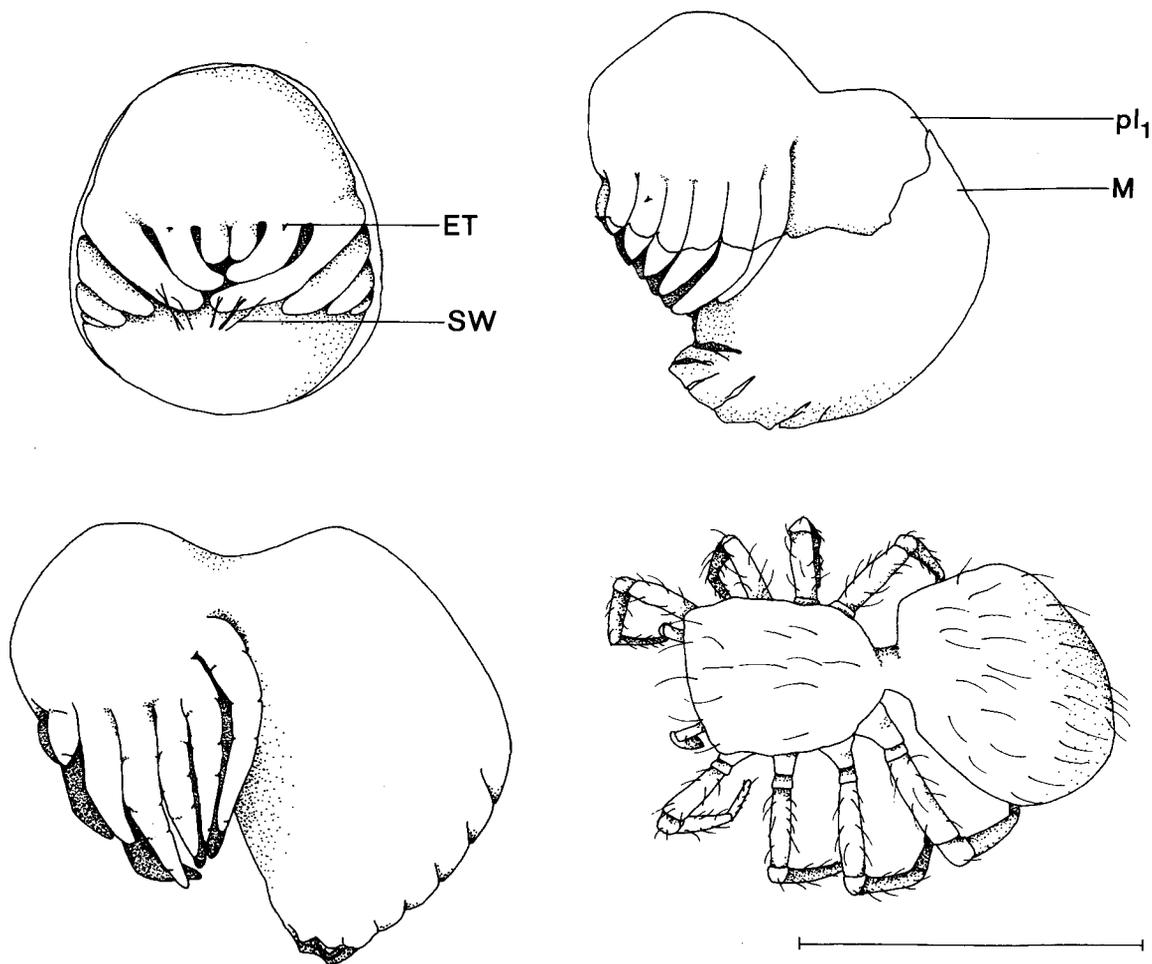
Chemo- and mechanosensory setae were distributed over the body of each larva. Larval *Cyrba* and *Portia*, but no other salticid larvae, were equipped with rows of scopulate hairs on the ventral sides of the tarsi and metatarsi. These scopulate hairs, which are unique among salticids to the spartaeines, are adhesive and may have a role in prey capture (Foelix, Jackson, *et al.*, 1984). They are morphologically similar to claw tufts (Hill, 1977), which are adhesive hairs found between the tarsal claws of the active instars of all salticids (sometimes called scopulae). However no larval salticids possessed claw tufts.

All larvae possessed well-differentiated eyes which completed development during this stage. Near the end of the larva stage, the retinae of the anterior median (AM) eyes were observed to track on moving objects (i.e., shift to keep the image on the fovea, see Land, 1969). Uniquely, larval *Portia* possessed large posterior median (PM) eyes (typical of adult *Portia*), PM eyes being small in the other studied salticids at this and every other stage of development.

The degree of cheliceral development of larvae varied between species from a broad conical fang like that of the second prelarva to longer, more pointed forms.

Larvae of all species possessed the number of tarsal claws typical of the active instars of salticids (i.e., two on each leg). In several species, the claws were pectinate, like the claws of active instars.

Larvae of each species possessed movable spinnerets. Active instars of salticids have four lateral spinnerets, each of two segments. All larvae, however, possessed spinnerets that were unisegmented. Also, the larvae of most species lacked spigots on their spinnerets. The exception was *Portia*: the larvae of *Portia* spun draglines and attachment discs.



Figs. 1-4: Salticid development. **1** Embryo with air spaces surrounding appendages, showing egg teeth (ET) on pedipalps and stress wrinkles (SW) on egg membrane; **2** Chorion and vitelline membranes (M) partially shed during first phase of eclosion, exposing a first prelarva ( $pl_1$ ); **3** Second prelarva of post-embryonic development resulting from combined eclosion and first ecdysis ("shiny stage"); **4** Larval stage of post-embryonic development resulting from second ecdysis ("setose stage"). Scale line = 1 mm.

Some of the larval *Cyrba* and *Portia*, the studied spartaeines, were observed to move about inside the egg sac and feed upon undeveloped eggs, and on dead and developing nest-mates. This "larval cannibalism", however, was not observed in any other species.

Most species spent 1-2 weeks as larvae before moulting to fully developed spiderlings, the first active instars (i.e., miniature, asexual, adults). Generally, the spiderlings dispersed from the egg sac 7-10 days after this moult to begin their independent existence.

#### Developmental timing

The timing of hatching events and the duration of each post-embryonic stage (Table 1), and the rate at which various structures developed (Table 2) varied both within and between species. However, the variation in the timing of development was less among the group of spartaeine species than it was among the non-spartaeine group (e.g., range of 27-31 and 23-47 days, respectively, for the time from day 0 to becoming first instars).

The total length of time taken from oviposition to the first instar varied from 23 days (*Euophrys*) to 47 days (*Plexippus*). The median length of the embryonic period ranged from 11 days (*Euophrys*) to 22 days (*Plexippus*), but for most species evidence of the imminent eclosion was apparent c. 13 days after oviposition. Once hatching began, all species spent 1-3 days as a prelarva 1 (membranes only partially shed).

The median times spent as a prelarva 2 varied between 1-5 days, and the times spent as a larva varied between 7-18 days.

#### Discussion

Judging from this and other studies (Holm, 1940; Taylor & Peck, 1975), the basic sequence of morphogenesis seems to be consistent in salticids. However, this study has shown that there is variation between species in the duration of the stages and the rate of the morphological changes of post-embryonic development, with four species of the Spartaeinae forming a separate, cohesive group. The variation in developmental timing of the studied non-spartaeines probably reflects intersubfamily variation, as the five non-spartaeines studied were from five different subfamilies. Results from studies of other families of spiders show that among closely related species the timing of post-embryonic development is similar. For example, the onset and duration of every post-embryonic stage were similar among the four congeneric thomisids studied by Schick (1972). In fact, for each of the 22 families studied by Holm (1940), these measurements fell within a five day range (two to twelve species studied per family).

The two studied genera of spartaeines, *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.

|                           | Setae | Scales | Tarsal scopulate hairs | Well-developed eyes | Fangs               | Tarsal claws | Spinnerets spigots | Spinnerets segmentation | Larval cannibalism |
|---------------------------|-------|--------|------------------------|---------------------|---------------------|--------------|--------------------|-------------------------|--------------------|
| <b>Spartaeines</b>        |       |        |                        |                     |                     |              |                    |                         |                    |
| <i>Cyrba algerina</i>     | +     | ○      | +                      | +                   | slightly pointed    | pectinate    | ○                  | ○                       | +                  |
| <i>Portia fimbriata</i>   | +     | ○      | +                      | +                   | like active instars | pectinate    | +                  | +                       | +                  |
| <i>Portia labiata</i>     | +     | ○      | +                      | +                   | like active instars | pectinate    | +                  | +                       | +                  |
| <i>Portia schultzi</i>    | +     | ○      | +                      | +                   | like active instars | pectinate    | +                  | +                       | +                  |
| <b>Non-spartaeines</b>    |       |        |                        |                     |                     |              |                    |                         |                    |
| <i>Euophrys parvula</i>   | +     | ○      | ○                      | +                   | pointed             | simple       | ○                  | ○                       | ○                  |
| <i>Holoplatys</i> sp.     | +     | ○      | ○                      | +                   | —                   | simple       | ○                  | ○                       | ○                  |
| <i>Lyssomanes viridis</i> | +     | ○      | ○                      | +                   | —                   | simple       | ○                  | ○                       | ○                  |
| <i>Plexippus paykulli</i> | +     | ○      | ○                      | +                   | pointed             | simple       | ○                  | ○                       | ○                  |
| <i>Trite auricoma</i>     | +     | ○      | ○                      | +                   | broad conical       | simple       | ○                  | ○                       | ○                  |

Table 2: Traits specific to post-embryonic larvae of 9 species of salticids. + indicates trait present. ○ indicates trait absent. — indicates observations not possible.

Spartaeine larvae possess tarsal and metatarsal scopulate hairs, well-developed fangs, and pectinate claws on the tarsi; and they capture and consume prey (eggs and nest-mates). Larval *Portia* are unique among the studied salticids in possessing functional spinnerets, laying down draglines, and spinning attachment discs.

The capture and consumption of prey by spiderlings in the egg sac, "larval cannibalism", has been documented for five other spider families: Clubionidae, Gnaphosidae, Uloboridae, Theridiidae and Thomisidae (Schick, 1972; Valerio, 1974; Canard, 1979; Peaslee & Peck, 1983; Downes, 1987). Interestingly, for all the species known to cannibalise as larvae, sibling individuals that do not cannibalise can nevertheless successfully reach the first active instar. This suggests that larval cannibalism may confer advantages that become evident only some time after the spiderlings leave the egg sac. Schick (1972) reported that spiderlings that were cannibalistic as larvae were larger than spiderlings that were not cannibalistic as larvae, and suggested that this size advantage may enable them to capture larger prey and, therefore, acquire nutrients and energy more rapidly when they begin their independent existence. In addition, cannibalism may increase the ability of dispersing spiderlings to survive food shortages when free living (Schick, 1972). The energy and nutrients acquired by cannibalistic spiderlings would give them a food store on which they could draw until they caught their first meal. The high incidence of death, apparently by starvation, in first instars of non-cannibalistic Pisauridae (Bonaric, 1974), Salticidae (Jackson, 1978) and Clubionidae (Austin, 1984) suggests that prey availability may be a problem for dispersing spiders.

By preying upon infertile and fertile eggs, and other developing nest-mates, cannibalistic larvae reduce the number of spiderlings that would have dispersed from the egg sac, had larval cannibalism not occurred. Since larval cannibalism, therefore, effectively reduces batch size, either smaller batches should occur in species practising larval cannibalism or else females of species practising larval cannibalism have evolved oviposition patterns to counteract the effect of larval cannibalism on batch size. For example, species in which larval cannibalism has evolved might lay larger batches, perhaps of smaller eggs, than similar non-cannibalistic species. The effect of providing larvae with prey (i.e. "trophic", infertile eggs; fertile eggs; or other post-embryos) would be increased hardiness of the survivors that would otherwise be small in size. As yet, this issue has not yet been addressed in the literature for the Salticidae or other families of spiders.

The interspecific variation of salticid post-embryonic development found in this and other studies (Holm, 1940) shows that the timing, but not the sequence, of the changes of early development might be useful in elucidating salticid phylogeny. The most striking difference in timing found in this study is the earlier ("precocial") appearance of several behavioural and morphological traits uniquely in the studied spartaeines: larval spartaeines alone possessed traits characteristic of active instars. Therefore, the

spartaeines are not only morphologically and behaviourally unusual for salticids, but they also seem to have a distinctive pattern of post-embryonic development. Establishing how widespread this pattern is among spartaeines and whether it is limited to the Spartaeinae will require study of more spartaeine and non-spartaeine salticids.

It is significant that the Spartaeinae, the salticid group with an unusual pattern of post-embryonic development, has been considered to be a primitive subfamily of the Salticidae (Wanless, 1984). These findings suggest that the early appearance of traits characteristic of active instars could be primitive in the Salticidae. If this is true, then the cause of the delayed appearance of these traits in non-spartaeines is not known. However, the subfamily Lyssomaninae has also been considered primitive (Wanless, 1980; Hallas & Jackson, 1986b), but the post-embryonic development of *Lyssomanes*, like that of other non-spartaeine salticids, is not generally precocial. Furthermore, outgroup comparisons show that one trait of precocial post-embryonic development, larval cannibalism, is not confined to proposed sister-groups of the Salticidae, or to families that are considered primitive. Although larval cannibalism is present in the Thomisidae (Schick, 1972), the Clubionidae and Gnaphosidae (Canard, 1979), families which have been suggested as sister-families of the Salticidae (Lehtinen, 1967; Kraus, 1984), it is also present in the Uloboridae (Peaslee & Peck, 1983) and Theridiidae (Valerio, 1974), families of web-builders that are very unlikely to be closely related to the Salticidae.

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instars from free-living "active instars" (Galiano, 1971; Austin & Anderson, 1978), this study follows the convention of treating each morphologically discrete post-embryonic stage as unique and distinct from active instars.

Several systems of nomenclature have been employed for post-embryonic stages using the terms 'deutovum' (Eason & Whitcomb, 1965; Schick, 1972), 'quiescent nymph' (Valerio, 1974), 'pullus' (Neet, 1985), and 'A to D' stages (Holm, 1940; Schick, 1972; Canard, 1979). The system adopted in this paper is that of Vachon (1957): spider post-embryonic development is divided into 'prelarva 1', 'prelarva 2' and 'larva' stages. Membranes and exuviae are accurately accounted for, and the names of the stages clearly reflect the relative morphological complexity of each (see Peaslee & Peck, 1983).

## Results

For the most part, hatching events and the rate and changes of post-embryonic development were similar for spartaeine and non-spartaeine salticids (Tables 1, 2). Specific deviations will be indicated as the "basic" pattern is described.

### Eclosion

The first changes discernible in the eggs occurred 1-2 weeks after oviposition, when the spheroid egg became ovoid. Shortly afterwards, the shape of the embryo became imprinted on the egg (Fig. 1), with the narrow spaces between adjacent appendages taking on a powdery white appearance which Holm (1940) and Galiano (1971) attribute to the infiltration of air into the egg. A dark, pointed egg tooth was clearly visible on the base of each palp in most species. However, the egg teeth of *Euophrys*, *Holoplatys* and *Trite* were pale

yellow and difficult to see.

During this pre-hatching stage *Lyssomanes* developed primordial retinae (i.e., pigmented regions on the anterior end of the cephalothorax). These retinae were not seen in any other species.

In all the salticids, as hatching approached, the embryos lengthened, causing stress wrinkles in the egg membranes near the pedicel and the tips of the appendages.

Hatching began with the rupture of the egg membranes near an egg tooth. Initially, it was difficult to determine which membranes were being shed during hatching because the thin inner vitelline membrane often adhered to the chorion (as reported by Holm, 1940). However, SEM examination revealed that only two membranes, the chorion (discernible by surface spheres) and vitelline membrane, were shed simultaneously during hatching.

The egg membranes split along the base of the cephalothorax and then slid posteriorly, exposing the chelicerae, the bases of the palps and the egg teeth, the bases of the legs and the cephalothorax of a first prelarva (Fig. 2). About 24 h later, the cuticle of this first prelarva split dorsally and was totally rejected, revealing a second prelarva. The egg membranes were sloughed off during this first ecdysis, thus completing eclosion.

The immobile second prelarva was bent c. 90° at the pedicel. Its palps were long (almost as long as the legs), and its chelicerae had broad conical fangs at their distal ends. Vestiges of abdominal segmentation were visible in all species, as were the beginnings of leg segmentation. Eyes, tarsal claws, spinnerets, mechanosensory setae, chemosensory setae (curled setae with apical pores) and scales (non-filamentous setae responsible for colour) were lacking. However, all of these features except scales could be seen

| Species                     | N     | Appearance of air spaces | Onset of hatching | Duration of prelarva 1 | Eclosion and 1st ecdysis | Duration of prelarva 2 | 2nd ecdysis | Duration of larva | 3rd ecdysis |
|-----------------------------|-------|--------------------------|-------------------|------------------------|--------------------------|------------------------|-------------|-------------------|-------------|
| <i>Lyssomanes viridis</i>   | 5,55  | 15(12-18)                | 16(11-21)         | 2                      | 18(13-21)                | —                      | —           | —                 | —           |
| <i>Plexippus paykulli</i> * | 4,47  | 19(17-25)                | 22(19-28)         | 2                      | 24(22-32)                | 5                      | 29(24-37)   | 18                | 47(47-48)   |
| <i>Holoplatys</i> sp.       | 3,11  | 11(11-13)                | 14(13-16)         | 3                      | 17(16-18)                | 4                      | 21(19-23)   | 13                | 34(33-38)   |
| <i>Trite auricoma</i> *     | 9,12  | 14(8-20)                 | 15(9-17)          | 1                      | 16(8-19)                 | 4                      | 20(13-27)   | 7                 | 33(29-35)   |
| <i>Portia fimbriata</i> (S) | 8,41  | 14(11-15)                | 15(12-16)         | 1                      | 16(14-17)                | 1                      | 17(15-20)   | 14                | 31(29-32)   |
| <i>Portia schultzei</i> (S) | 6,31  | 11(10-14)                | 16(13-21)         | 1                      | 17(11-19)                | 1                      | 18(14-22)   | 11                | 29(24-35)   |
| <i>Cyrba algerina</i> (S)   | 4,6   | 10(6-17)                 | 14(6-19)          | 1                      | 15(6-21)                 | 3                      | 18(7-26)    | 9                 | 27          |
| <i>Portia labiata</i> * (S) | 29,60 | 13(7-15)                 | 14(8-16)          | 1                      | 15(8-17)                 | 1                      | 16(8-18)    | 11                | 27(21-36)   |
| <i>Euophrys parvula</i>     | 8,15  | 10(9-15)                 | 11(10-16)         | 1                      | 12(9-16)                 | 1                      | 13(11-22)   | 10                | 23(19-32)   |

Table 1: Medians and ranges (days) for type from oviposition (= day 0) to the various events of salticid post-embryonic development. Durations of prelarvae and larva are the differences between the preceding and following events. Species ranked in decreasing order of median time to first instar. N = number of egg sacs observed, and mean number of eggs per sac. \* = species examined under SEM; — = data not available; (S) = spartaeine.