

Hatching and early postembryonic development in three spiders, at four temperatures

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Summary

A description of hatching and the transition from postembryo to first instar is given for the theridiid *Achaearanea tepidariorum* (C. L. Koch), the araneid *Argiope aetherea* (Walckenaer) and the amaurobioid *Badumna longinqua* (L. Koch). These differ in the way they shed the chorion. Data on the development times of the embryos and postembryos of the three species at temperatures between 17°C and 30°C are provided; it is tentatively suggested that these data might reflect the spiders' centres of origin and history of dispersal.

Introduction

Information on the way spiders develop, and what similarities and differences exist between species in this regard, increases our understanding of the phylogenetic relationships between them, and indeed between them and other taxa at various levels. Information on the temperature relations of spiders throws light on their adaptations to the environment and improves our knowledge of their ecophysiology. In both cases, such information is in short supply and will need to be greatly increased before any broad understanding can emerge. This paper deals with the early development and temperature relations of three spiders, the theridiid *Achaearanea tepidariorum* (C. L. Koch), the araneid *Argiope aetherea* (Walckenaer) and the amaurobioid *Badumna longinqua* (L. Koch).

A recent paper (Downes, 1987b) described the early postembryonic development of the theridiid *Theridion rufipes* Lucas, and gave an extensive list (which will not be repeated here) of references to relevant previous studies. Photographs of the development of *T. rufipes* also appeared in the above paper, and since these showed features that are almost identical to those of *A. tepidariorum*, illustrations of the latter have been omitted from this paper. Very few studies have been made on the effects of temperature on the development of spiders; species that have been the subjects of such investigations include *Tegenaria atrica* C. L. Koch (Browning, 1941), *Cheiracanthium inclusum* (Hentz) (Peck & Whitcomb, 1970), *Thanatus striatus* C. L. Koch and *Allomengea scopigera* (Grube) (Schaefer, 1977), and *Latrodectus hasselti* Thorell (Downes, 1987a).

In this paper, hatching is taken to be the shedding (but not necessarily the discarding) of the chorion, and marks the close of the embryonic period; the postembryo stage is that between hatching and the discarding of the integument of the first true moult, which marks the appearance of the first instar (Downes, 1987b).

Some of the taxonomic problems concerning the

genus *Badumna* were resolved by Gray (1982).

Materials and methods

Field-mated female spiders were brought to the laboratory where they produced the egg sacs used in the study. The egg sacs were teased open and placed in glass cavity blocks, the glass covers of which were separated from the rims of the blocks by a layer of non-absorbent cotton wool, with a little vaseline as adherent. Incubation was carried out at 17, 20, 25 and 30°C ± 1°C. Unless otherwise stated, descriptions of development refer to the 25°C cultures. Sample sizes of eggs and egg sacs are given in Table 1. Photoperiod in all cases was LD 14:10. Observations were made daily. Photographs were obtained using a Wild M400 zoom photomicroscope.

Results

Descriptions of development

In *A. tepidariorum* the chorion is breached by the egg teeth across the base of the pedipalps, splits along the lines of the coxal bases and recedes to the tip of the abdomen. The resulting postembryo is hairless, without fangs or claws, and is normally immotile (at 30°C the postembryos were active, though not well coordinated). It is colourless apart from some faint red pigment in the AME, though the other eyes become pigmented to some extent before the first moult.

During the postembryo stage the first instar body hairs become visible beneath the postembryo's integument. When cast at the first moult, the latter carries with it the chorion which, unless dislodged mechanically, has remained attached to the posterior tip of the postembryo's abdomen.

At the low temperature (17°C), about 20 of the individuals that did not complete the hatch (the chorion still enshrouding about half the abdomen and the tips of all pairs of legs) nevertheless continued the development of hairs and pigment described above; some of these individuals even completed a successful first moult.

The first instar spiderling is active, co-ordinated, has erect hairs, functional spinnerets, claws and fangs and well-pigmented eyes (AME still the more prominent). The colour of the abdomen darkens considerably if the first instar spiderling feeds on eggs; if not it remains little darker than the colour of the eggs (pearly white). The cephalothorax and legs take on a pale watery-bronze colour. The extent of such coloration also seems to relate to the occurrence of egg-feeding, being darker in those individuals that have fed, as almost all do if given the opportunity.

In *A. aetherea* the chorion, between reversion and hatching, is moulded to the shape of the cephalothorax, abdomen and appendages, as these become distinctly visible (Fig. 1). Lines of chorionic stress are evident. The embryo thus appears much the same as its theridiid counterparts (Downes, 1987b). However, the role of the egg-teeth (if present) is questionable in this species because the first breach of the chorion occurs not across the pedipalps as in the theridiids but between the distal

parts of the curled legs, commonly between the first and second leg pairs but sometimes between the fourth legs and the closely applied abdomen. All the legs are freed from the chorion before it recedes past about halfway along the abdomen.

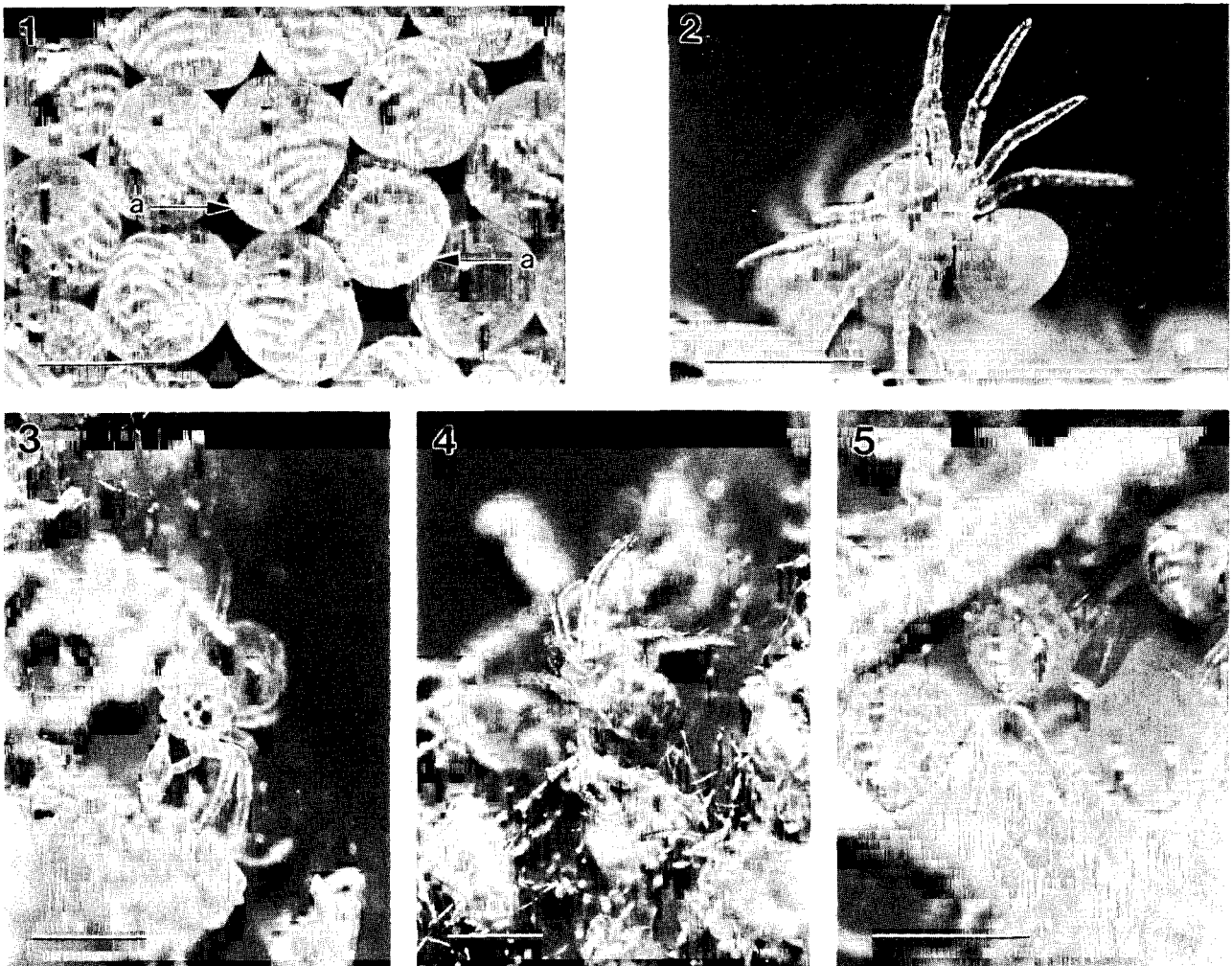
The postembryos stick to each other in small or large clumps, making the oncoming first moult look a hazardous, if not impossible, prospect. However, this effect lessens as the postembryo stage progresses and in fact, other than at 17°C (where about half did not develop successfully to first instar), all but two individuals moulted successfully and got clear of the tightly-packed mass of chorions and cast integuments. This was in opened egg sacs; the close confinement must be even greater in intact sacs.

The postembryo of *A. aetherea* (Fig. 2) has virtually no eye pigment nor any colour in the cephalothorax and legs, though both become faint watery-pink over a few days, the eyes meanwhile developing substantial pigmentation (Fig. 3). During this stage the small claws also take on a red colour, but fangs are not apparent. The postembryos are more active than those of *L. hasselti* (Downes, 1987a) or *T. rufipes* (Downes, 1987b), though co-ordination is not very good.

The first instar spiderling (Fig. 4) has rather small fangs, functional spinnerets, well-developed claws and erect body hairs, the latter (as in the theridiids) developing during the postembryonic stage, at which time they lie flat beneath the integument that is to be cast at the first moult. The abdomen has six grey-green tergites, thick and irregular anteriorly but thinner and well-defined posteriorly, clearly demonstrating the segmental nature of the opisthosoma, a feature that was evident also in the postembryo stage (Fig. 5).

In *B. longinqua* the breach of the chorion is not uniform. Although the egg-teeth are prominent and without doubt contribute to the splitting of the stressed chorion, in most individuals it splits around the area of the pedicel and begins to slide away from that site before a breach is made across the pedipalps (Figs. 6, 7). Nonetheless, the chorion crumples uniformly towards the posteroventral aspect of the animal (Fig. 8) and finally gathers as a wedge of tissue attached to the tip of the abdomen, as in theridiids.

The newly-hatched postembryo is immotile and rarely has any pigment at all in the cephalothorax, legs, eyes, fangs or claws. Both the latter are visible. Spinnerets are present but poorly defined. The labium



Figs. 1-5: *Argiope aetherea*. **1** Post-reversion embryos prior to hatching; lines of stress can be seen radiating from the cephalothorax (a) of the individual to right of centre; **2** Early postembryo, dorsal view; abdomen is pointed ventrally (see Fig. 5) and therefore looks somewhat truncated here; **3** Late postembryo; **4** First instar; **5** Late postembryos; tergites are visible on the posterodorsal aspect of the abdomens. Scale lines = 1 mm.

moves actively.

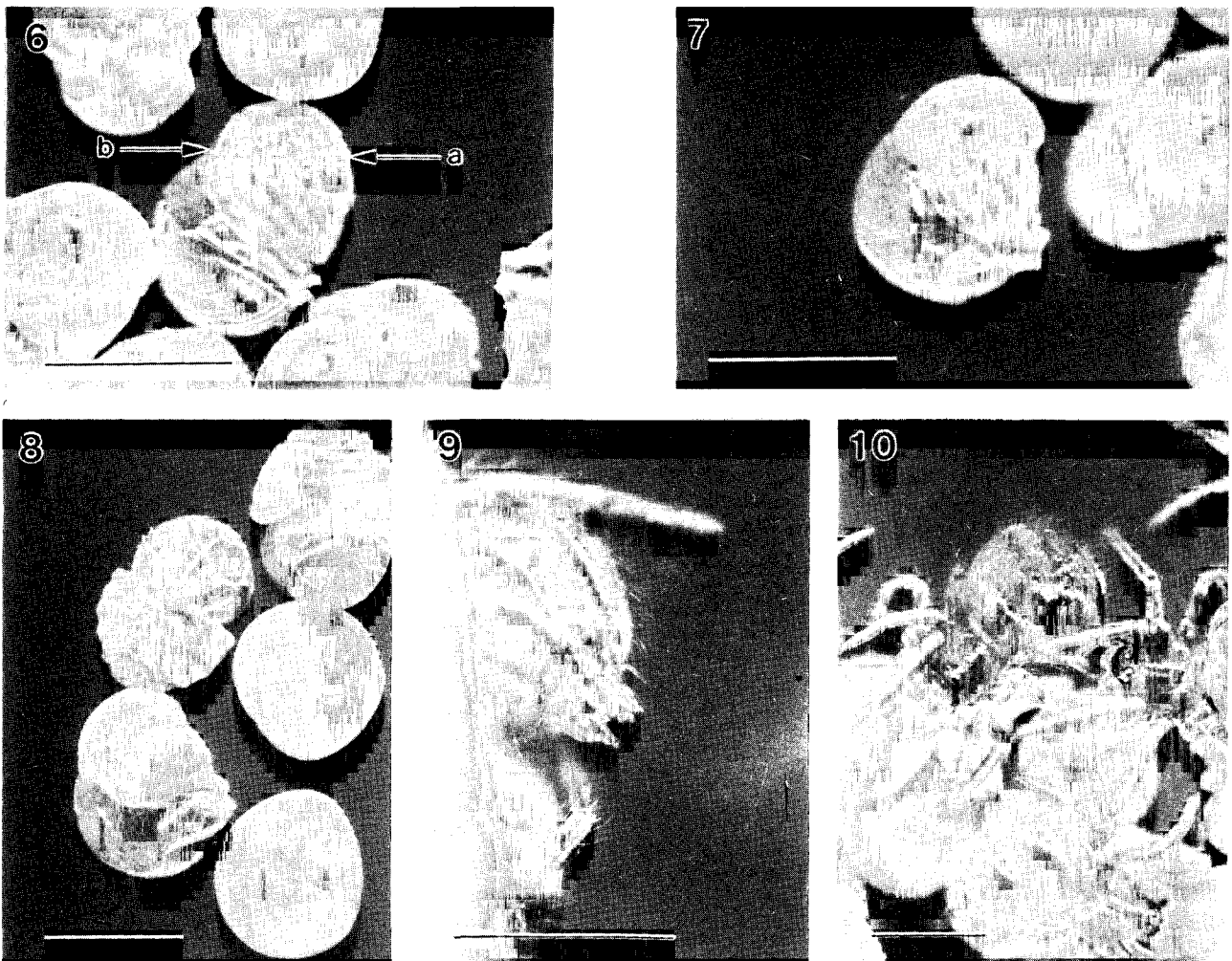
Moulting takes three minutes to get the integument to the leg tips, a vigorous pumping action within the cephalothorax being evident at intervals during this process. A further three minutes of more delicate manipulation frees the integument from the tarsi and claws. Up to ten minutes later the first instar spiderling is still performing leg flexion movements.

Directly after moulting, the posterior spinnerets are well-defined and quite active, but no silk is produced (Fig. 9). The calamistrum is undeveloped. Erect body hairs are present, all eyes except PME are pigmented, claws and fangs are coloured black. On suitable (rough) surfaces the spiderling is fully motile, if a little clumsy, and after a time spins small amounts of silk. The cephalothorax is pale pink (this darkens over a few days, Fig. 10) but the legs still have little or no colour. Any undeveloped eggs are rapidly consumed (Fig. 10). Within a few days, the first instar spiderlings have constructed a flat horizontal sheet of silk; they cluster tightly under this during the day, and become active at night.

Temperature relations

Figure 11 shows mean development times for the embryo and postembryo stages of the three species. Sample sizes (with survivorship data) are in Table 1. For example, 241 embryos of *A. tepidariorum* developed at 17°C but only 149 of these survived to the first instar; the latter, then, is the sample size for *A. tepidariorum* postembryos. Of the three species, only *A. tepidariorum* showed evidence of being stressed at 30°C; 55 of the 165 specimens incubated at that temperature did not survive to first instar, whereas all individuals of *A. aetherea* and *B. longinqua* developed to first instar at 30°C. From this it might be expected that *A. tepidariorum* would have a relatively high development success rate at the lower temperatures, but although less than half of the *A. aetherea* individuals survived to first instar at 17°C, *A. tepidariorum* also did poorly, only 149 specimens surviving from a total of 241 (Table 1).

It is clear from Fig. 11 that a decrease in temperature from 30°C to 17°C has markedly different effects on the development rates of the three species. In all cases, as



Figs. 6-10: *Badumna longinqua*. **6** Hatching; the chorion has breached separately at the pedipalps (a) and the pedicel (b); **7** Hatching; the chorion has breached at the pedicel but not yet at the pedipalps; **8** Hatching; the chorion crumples ventrally; **9** Spinnerets of first instar; part of the egg sac obscures the left edge of the photograph; **10** First instars; note the darker abdomen of the upper specimen; two of the three specimens are feeding on undeveloped eggs. Scale lines = 1 mm.

the temperature drops the rate of development slows and the development time therefore increases, but the time increase is not linear and departs from linearity more markedly in *B. longinqua* than in *A. tepidariorum*, and most markedly of all in *A. aetherea*. Apart from a two-day overlap between *B. longinqua* postembryos and *A. aetherea* embryos, the mean development time-spans are completely separate at 17°C.

Not only is there lower survivorship at temperature extremes (Table 1); the standard error bars of Fig. 11 also show that development rate is more variable at nonoptimal temperatures.

Discussion

Descriptions of development

The breaching of the chorion at hatching may be a less uniform process than previous observations on three species of theridiid (Downes, 1987b) suggested. It still appears that a major breach runs more or less along the lines of the coxal bases in most spiders, and that the cuticular denticles are important as egg-bursters, but breaches at other stress points may be common. These observations, especially those on *A. aetherea*, support Yoshikura's (1955) views on the importance of enzymes secreted by pedipalpal glands in the initiation of hatching.

The chorion is not cast completely at the time it is shed, although it may be dislodged mechanically. In the case of *A. aetherea* there was such close packing of the postembryos and so much jostling that it was difficult to be sure whether the chorion would otherwise have remained attached to the posterior tip of the abdomen until being cast along with the integument of the first moult.

All three species in this study would be included in Category II of the hatch-first moult schema of Downes (1987b).

Species	Temp. (°C)	Eggs	First instars	Mort.	% Mort.
<i>Achaearanea tepidariorum</i>	17	241 (7) (4)	149	92	38
	20	142 (6) (4)	133	9	6
	25	98 (6) (4)	79	19	19
	30	165 (8) (5)	110	55	33
<i>Badumna longinqua</i>	17	34 (4) (4)	32	2	6
	20	64 (5) (5)	50	14	22
	25	51 (4) (4)	50	1	2
	30	39 (3) (3)	39	0	0
<i>Argiope aetherea</i>	17	95 (3) (3)	44	51	54
	20	30 (3) (3)	30	0	0
	25	120 (3) (3)	118	2	2
	30	100 (3) (3)	100	0	0

Table 1: Mortality rates of embryos and postembryos (combined) of *Achaearanea tepidariorum*, *Badumna longinqua* and *Argiope aetherea*. Number of eggs in each case is followed by (number of egg sacs these came from) and (number of females providing egg sacs).

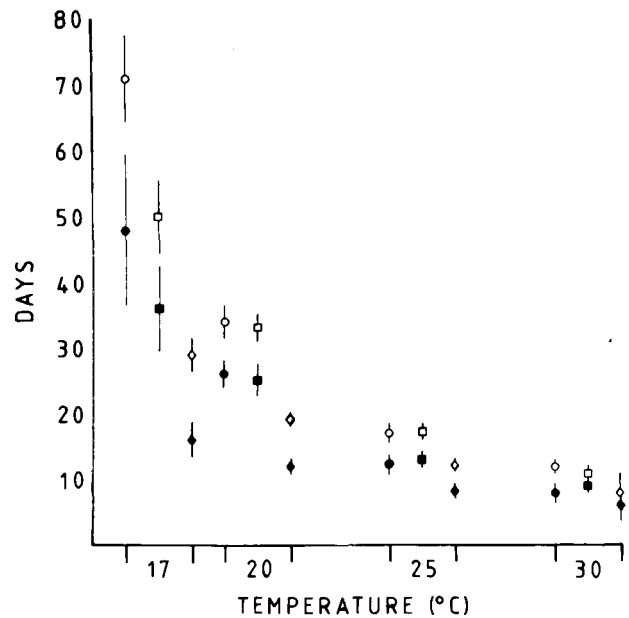


Fig. 11: Development times of the embryos (open symbols) and postembryos (closed symbols) of *Argiope aetherea* (circles), *Badumna longinqua* (squares) and *Achaearanea tepidariorum* (diamonds), with respect to temperature. Standard errors given as extensions to symbols. Sample sizes are in Table 1 (see text).

Temperature relations

The optimum level and the range of tolerance of temperature of a species, while not in isolation a direct index of adaptation to environment, are ecophysiological features suggestive of centre of origin, history of dispersal and natural or artificial introduction to areas outside its normal range. No claim is made here that the present data demonstrate any of these things, but it is interesting to consider the distribution of the three species for which data on temperature relations are provided in Fig. 11 and Table 1.

A. aetherea is a species of the (mostly tropical) north of Australia (Main, 1964; Davies, 1984). It develops normally at 30°C but at 17°C retardation of development is markedly greater than for *B. longinqua* or *A. tepidariorum* (Fig. 11). Mortality at 17°C is relatively high (Table 1).

The cosmopolitan species *A. tepidariorum* breeds all the year round in Australia (Main, 1976). It is accepted that it has been widely transported world-wide by man in historical times. If its centre of origin was temperate, tropical populations may show only moderate (but improving) tolerance of high temperatures, while their tolerance of low temperatures would not have been as strongly or as rapidly modified by natural selection, and development rate might therefore be less affected by a temperature drop of 8°C from 25°C than it is for a tropical species like *A. aetherea*. If development rate is in any way related to tolerance, as it probably is in most poikilotherms, the data of Fig. 11 are consistent with this interpretation. On the other hand, the low survival rate of *A. tepidariorum* at 17°C (Table 1) lends no support to such a hypothesis, and it must also be borne in mind that in Britain this species is normally restricted

to heated glasshouses and is only occasionally found out of doors (Locket & Millidge, 1953).

B. longinqua is clearly an intermediate case in terms of development rate and its linearity. It occurs along the east coast of Australia and is found in Tasmania and on both islands of New Zealand (Hickman, 1967); it has also been introduced into California (Main, 1971).

That individual variation in the development rate is greater at nonoptimal temperatures (Fig. 11) is another interesting demonstration of the broader principle that variability for a physiological trait within a population will normally be expressed more strongly if that trait becomes subject to stress. The same principle can be applied to behavioural or morphological traits (see, for example, Kettlewell, 1963). Continued presence of such stressful or unusual conditions in the population's environment would lead to a reduction of the variability through natural selection.

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