A proposal for standardization of the terms used to describe the early development of spiders, based on a study of *Theridion rufipes* Lucas (Araneae: Theridiidae)

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Summary

A review of the literature is summarized in a single schematic presentation of the development of spiders from hatching to the rejection of the first true integument moult. A simplified terminology (embryo, postembryo, first instar) is proposed and defined, to standardize the plethora of terms used to describe the early stages of araneid development. A diagrammatic comparison is made between the proposed terminology and that of four previous authors. The development of *Theridion rufipes* Lucas is detailed and included in the summary schema along with that of two other theridiid spiders, *Achaearanea decorata* (L. Koch) and *Latrodectus hasselti* Thorell, whose development was observed to follow the same pattern as *T. rufipes*.

Introduction

The major features of late embryonic and early post-embryonic development in spiders are reversion (inversion), hatching (eclosion) and the first true moult (ecdysis). Reversion is an embryonic event unique to arachnids and is a reversal of the orientation of the embryo with respect to the vitelline mass (Dawydoff, 1949; Savory, 1977; Foelix, 1982). It will not be considered further here.

There are three unresolved problems that bedevil the description of events subsequent to reversion. Firstly, there is no agreement on the point at which the embryonic period ends. Secondly, there is no consistent convention in numbering the instars, or rather in defining the features of the first instar. Lastly, a number of inappropriate and misleading terms have been coined to label the various stages of development. As a result of these difficulties, it is often hard in any given report to determine whether the 'postembryo' is enclosed in a 'membrane', the embryonic cuticle or the integument. This makes interpretation of recorded events often difficult and sometimes irreconcilable. An attempt is made here to rationalize these problems. Because the discussion necessarily details the findings of previous authors who have studied this phase of spider development, the same ground will not be covered here other than to acknowledge two important previous considerations of this problem, namely those of Peck & Whitcomb (1970) and Whitcomb (1978). No firm recommendations for reform were made in the former paper but in the latter Whitcomb strongly advocated studies of the postembryo and argued for the establishment of an international terminology for spider life-history stages. If the present study contributes towards the standardization of terminology in future reports it will be a belated result of these earlier authors' efforts.

Theridion rufipes Lucas, widely distributed in tropical, subtropical and temperate zones, was one of four theridiid spiders investigated in the present study. By far the most observations were made on *T. rufipes*, and its development forms the basis for the results of this paper. However, *Latrodectus hasselti* Thorell, *Achaearanea decorata* (L. Koch) and *A. tepidariorum* (C. L. Koch) were found to follow the same developmental pattern; the latter has been the subject of a similar previous report (Valerio, 1974).

Materials and Methods

Egg sacs produced in the laboratory by *T. rufipes* females were teased open and placed in glass cavity blocks or cavity slides, the glass covers of which were separated from the rims of the blocks (or slides) by a layer of non-absorbent cotton wool, with a little vaseline as adherent. These were incubated at constant temperatures of 25°C (48 sacs) and 30°C (15 sacs), ±1°C. In each case the photoperiod was LD 14:10. Observations were made daily with a zoom stereomicroscope, and photographs were obtained using a Wild M400 zoom photomacroscope. A related but separate study of *T. rufipes*, involving the examination of the contents of 763 full-term (post-emergence) egg sacs, gave data on the causes of early mortality. Death before hatching was recorded only for eggs that showed some development, i.e. were known to be fertile.

Results

The eggs of *T. rufipes* are normally pale off-white or cream (on a few occasions a rich yellow) and are robust enough to resist minor shocks. They will usually develop normally even if dropped through distances of 50 mm on to hard surfaces. They roll freely and do not normally stick to each other or to supporting surfaces. Occasionally, however, egg sacs contained a few to many eggs congealed together in an obviously inviable mass; in some cases all the eggs were thus congealed (this phenomenon has been noted by Bonnet (1935) who ascribed the incidence of such 'conglomerated masses' to the lack of the viscous substance that normally coats the eggs. The 'clumped' eggs of *Latrodectus geometricus* C. L. Koch described by Bouillon (1957) were probably showing the same deficiency). The mean diameter of the eggs was 0.71 mm, s.e. 0.006 ($n = 74$).

Embryonic development was not investigated, but frequent casual observations of developing eggs showed that early differentiation is marked by minor denting and collapse of the egg sphere. A general fine mottling of the chorion (or mottling of underlying structures seen through the chorion) was also observed before the appearance of any recognizable anatomical features, and the localization or polarization of germ tissue at one locus of the sphere was characteristic. These vague features preceded reversion. Between reversion and eclosion the dorsal surface of the embryonic cephalothorax rises above the general surface level of the sphere, and the developing limbs

appear, hugging the vitelline mass, their tarsi inter-locking at the tips (Fig. 1).

Lines of stress within the chorion, lying at right angles to the future shell rupture line, become apparent before hatching (Fig. 2). The first breach of the chorion occurs across the point of the embryonic chelicerae and rapidly traces a split along both sides at about the level of the coxae (Fig. 3). The ruptured chorion is now unevenly divided into a large posteroventral 'bowl' and a smaller, flatter, dorsal 'lid', hinged at a point above the position of the pedicel.

The chelicerae and pedipalps emerge first (Fig. 1), and the legs are gradually drawn free as both portions of the chorion slide back, finally to gather as a wedge of tissue which remains attached to the posterior tip of the abdomen (Fig. 4) until it is mechanically dislodged by
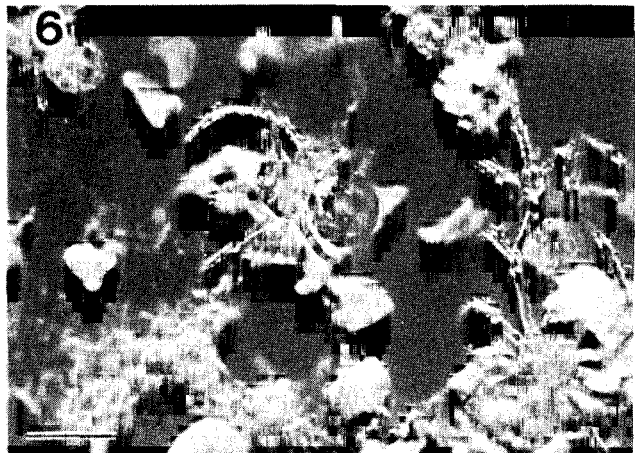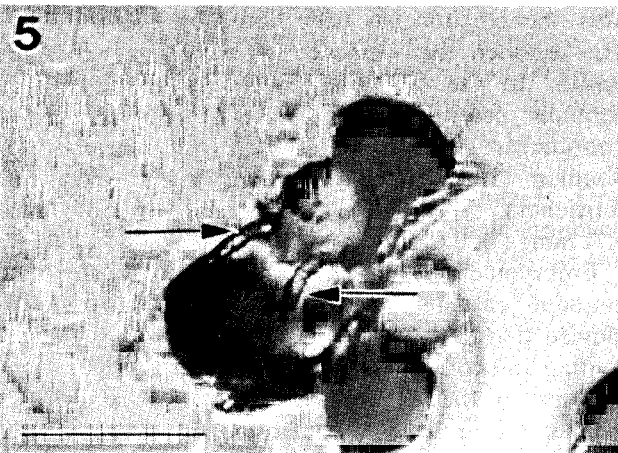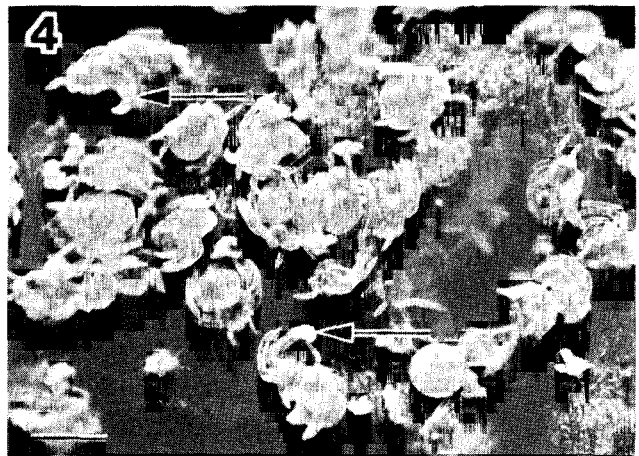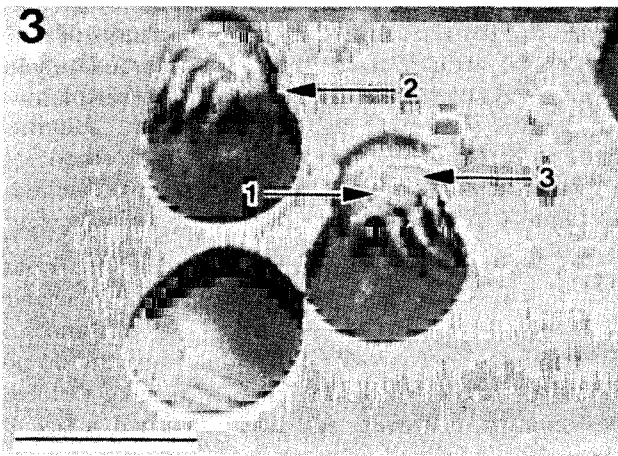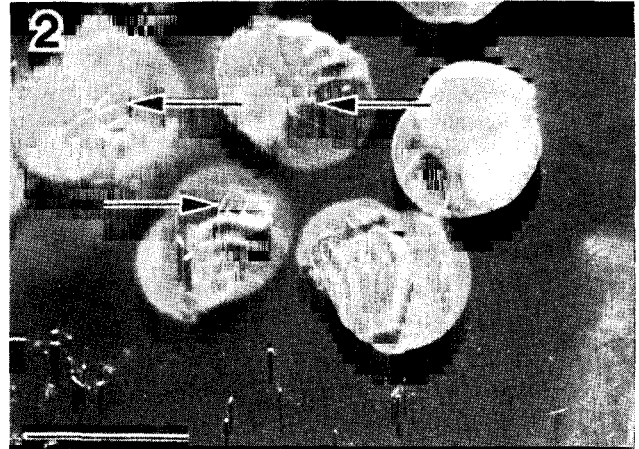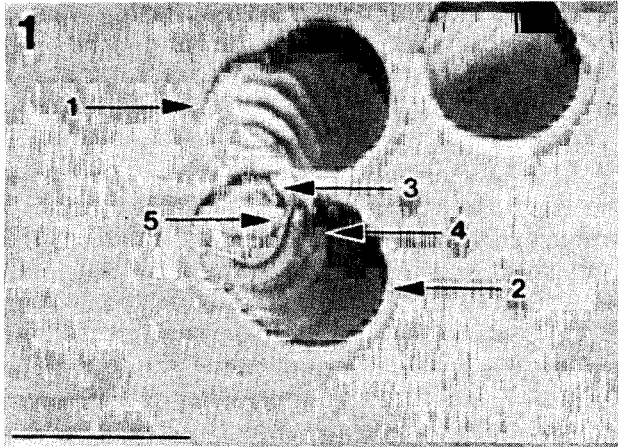
Figs. 1-6: *Theridion rufipes.* 1 Embryo about to hatch (1 = cephalothorax, 2 = vitelline mass, 3 = pedipalp, 4 = legs with interlocking tarsi beneath chorion, 5 = posterior rupture line of chorion); note that chorion is unruptured in individual at upper right; 2 At hatching; arrows indicate chorionic stress lines; 3 At hatching (1 = breach of chorion, 2 = hinge point of ruptured chorion, at position of pedicel, 3 = coxa of leg I); chorion as yet unruptured in individual at lower left; 4 Postembryos; arrows indicate undiscarded chorions still attached to posterior tips of abdomens; infertile egg at lower right; 5 Postembryo; arrows indicate constriction of pedipalps at future segmental junctions; note uneven development of pigment in eyes (AME mostly pigmented); 6 First instar spiderlings; note erect hairs, most easily seen on legs but also visible on abdomen. Scale lines = 1 mm.

the motion of the hatchling's closely-packed broodmates or until it is cast free along with the integument of the first moult. At no stage was a vitelline membrane observed; if it exists, as it probably does, it must be closely bound to the chorion.

Hatching constitutes the first notably hazardous event in the life cycle of *T. rufipes* (Table 1, death as postembryos), although it is less risky than the first moult judging by the relative numbers of first instar spiderlings that were found dead, defective or malformed inside abandoned full-term egg sacs. This relatively high mortality during the first moult may be due largely to jostling of late-moulting spiderlings by earlier-moulting individuals within the close confines of the egg sac before emergence. This would be substantiated if it could be shown that most first-moult failures occur among late-developing individuals. The value for death before hatching in Table 1 may be due largely to unsuccessful reversion, but this cannot be proved.

The postembryo spiderling (Fig. 4) that emerges from the chorion at eclosion is, apart from its denser, mottled abdomen, pigmented only in the anterior median eyes (in some individuals some pigment occurs in other eyes) and along two small posterolateral cephalothoracic streaks. The cephalothorax and appendages have a translucent, jelly-like appearance. The chelicerae are without fangs and are not free to move. The pedipalps, if not truly segmented, are at least constricted at future segmental junctions (Fig. 5), as are the legs. The labrum is defined. Small hairs, often difficult to see on early hatchlings, are visible but they arise from the cuticle of the first instar stage and therefore lie flat, depressed and covered by the semi-transparent integument of the postembryo which itself bears no such hairs.

These postembryo spiderlings cannot stand. Their ability to move is restricted largely to a feeble flexing of the legs. This very limited power of movement does not change appreciably until the first moult. Peaslee & Peck (1983) reported the same thing for *Octonoba octonarius* (Muma).

Although the postembryo stage is short, normally lasting a day or two, some developmental advances occur during this time. The position of the lung books becomes more obvious and the coxae take on a better-defined appearance although they are not sharply delineated from the sternum. The non-functional spinnerets may become slightly better defined from their earlier appearance as four elevated bumps, and a posterior median protuberance is presumably the colulus. Above all, the first instar body hairs, which still lie flat beneath the postembryo's integument, become larger and thicker, making the 'pharate' nature of the postembryo stage very obvious, as was the case with Valerio's (1974) observations on *Achaearanea tepidariorum*. In addition to such external development, very important organogenesis occurs during the postembryonic period (Vachon, 1957).

During the first ecdysis the abdomen, held at right angles to the cephalothorax, undergoes considerable

elongation, but regains its normally more rounded form after the integument is shed along with the chorion and vitelline membrane which all this time have remained attached to the posterior tip of the abdomen. The first instar spiderling undertakes a good deal of leg movement to clear the final parts of the cast integument from its tarsi, rather like a wiping of sticky fingers and probably for the same reason. First instar spiderlings were not uncommonly found stuck by a tarsus to a cast integument and thus trapped inside an egg sac after the exodus of their more fortunate siblings.

The body hairs now stand erect on the first instar spiderlings (Fig. 6) which are fully motile and spin silk freely. The sternum is clearly marked off from the line of the coxal bases. Claws (including palpal claws) are present, as are fangs on the now freely-moving chelicerae. The anterior lateral eyes, and in some cases the posterior eyes, show more pigment. The cephalothorax and legs are still translucent but within a day or two they take on a golden-brown hue that matches the bronze-coloured abdomen.

Latrodectus hasselti, Achaearanea decorata and *A. tepidariorum* were observed to follow the same developmental pattern as *T. rufipes*, and the first two of these are included in Category II of Fig. 7 as results of this study (*A. tepidariorum* already appears under the authorship of Valerio (1974)).

Discussion

In common parlance 'hatching' is emergence from an enclosing eggshell; but eggshells consist of more than one embryonic membrane. A problem arises when attempts are made to define hatching in organisms that do not shed all embryonic membranes simultaneously, and the more membranes involved the more scope there is for confusion. Vachon (1957) may be right in his view that hatching as such is of secondary importance and that no significance should be attached to the point of development at which it occurs; but it is necessary to have a recognized framework of the event sequence so that descriptions of the transitional process from embryo to 'complete' spiderling are comparable and therefore throw light, not confusion, on the systematic, evolutionary and adaptive relationships among the species studied. Certainly it is a most important fact that all spiders do not hatch at the same ontogenetic stage (Holm, 1940).

The process of membrane rejection, at least, is similar in most spider species: a membrane ruptures across the base of the chelicerae, perhaps initiated by

	Mean	s.e.	n
Death before hatching	0.003	0.001	763
Death as postembryos	0.007	0.001	763
Death in first instar	0.037	0.004	763
Defects and malformations in first instar	0.016	0.002	763

Table 1: Mortality rate and development failure of *T. rufipes* before emergence. Mean values are (dead (or defective, as appropriate) individuals in a sac/sac fecundity) for *n* sacs. Most deaths as postembryos occurred at hatching; most deaths (and all defects and malformations) in first instar occurred during the first true moult.

the secretion of hatching enzymes from pedipalpal glands (Yoshikura, 1955), but usually assisted by the egg-teeth (cuticular denticles) which extrude as points from the embryonic cuticle and are shed along with the latter. The membrane then splits along the ventrolateral line of the cephalothorax at about the level of the coxae and recedes posteriorly to the tip of the abdomen. More often than not it remains attached at this position and is cast either with the shedding of a subsequent membrane or with the integument of the first true moult. A useful definition of a true moult is one that has limbs (V. Davies, pers. comm.).

Figure 7 brings together in a comparative schema various authors' descriptions of the embryo-first instar

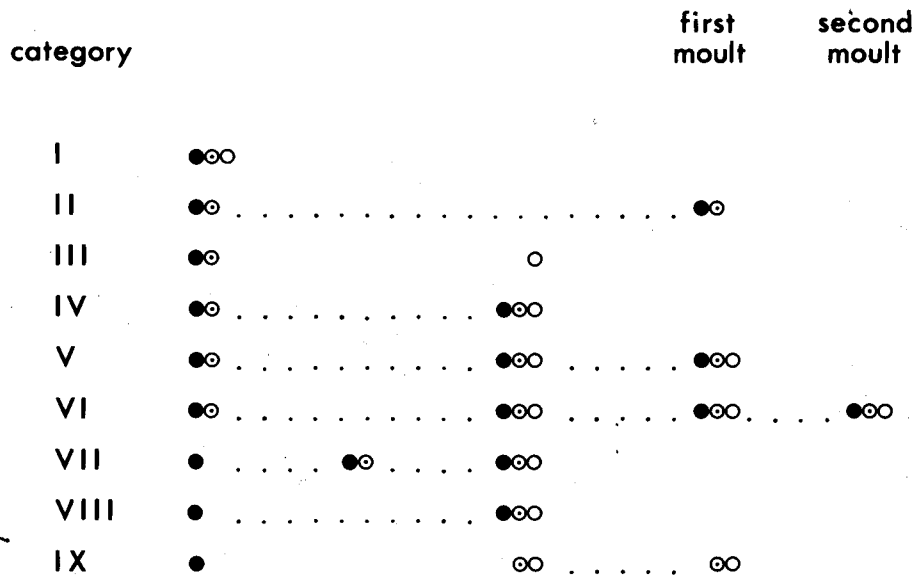| category		first moult	second moult
I	●⊙○		
II	●⊙ . . . . ●⊙		
III	●⊙	○	
IV	●⊙ . . . . ●⊙○		
V	●⊙ . . . . ●⊙○ . . . . . ●⊙○		
VI	●⊙ . . . . ●⊙○ . . . . . ●⊙○. . . . . ●⊙○		
VII	● . . . . ●⊙ . . . . ●⊙○		
VIII	● . . . . ●⊙○		
IX	●	⊙○ . . . . . ⊙○	

Fig. 7: The process of transition from embryo to first instar in spiders: a schematic presentation of the findings of fourteen investigators. First instar defined as the developmental stage resulting from the discarding (total rejection) of the integument of the first true moult, so all Categories except Category VI become first instars at the first moult. Dark circle = chorion; dotted circle = vitelline membrane; empty circle = embryonic cuticle. Dashed lines = shedding without total rejection.

Category I: *Grammostola pulchripes* (Simon), Theraphosidae (Galiano, 1969b); *Grammostola vachoni* Schiapelli & Gerschman, Theraphosidae (Galiano, 1973a); *Acanthoscurria sternalis* Pocock, Theraphosidae (Galiano, 1973a); *Avicularia avicularia* (Linnaeus), Theraphosidae (Galiano, 1973b); *Atypus karschi* Doenitz, Atypidae (Yoshikura, 1958); *Heptathela kimurai* Kishida, Liphistiidae (Yoshikura, 1955). All three membranes shed and totally rejected together at hatching. Subsequent first moult produces first instar from postembryo.

Category II: Argiopiformia (Holm, 1954); *Achaearanea tepidariorum* (C. L. Koch), Theridiidae (Valerio, 1974); *Theridion rufipes* Lucas, Theridiidae (present study); *Achaearanea decorata* (L. Koch), Theridiidae (present study); *Latrodectus hasselti* Thorell, Theridiidae (present study). Chorion and vitelline membrane shed together at hatching but not rejected; both membranes later cast along with integument of first moult, producing first instar from postembryo. Embryonic cuticle not present (suppressed in the Argiopiformia (Holm, 1954)).

Category III: *Segestria* Latreille, Segestriidae (Holm, 1954). Chorion and vitelline membrane shed and totally rejected together at hatching. Embryonic cuticle later shed and totally rejected. Subsequent first moult produces first instar from postembryo.

Category IV: *Ischnothele siemensi* Cambridge, Dipluridae (Galiano, 1972); *Ischnothele karschi* Bös. & Lenz, Dipluridae (Holm, 1954); Pisauridae and Lycosidae (Holm, 1954); *Loxosceles laeta* (Nicolet), Scytodidae (Galiano, 1967). Chorion and vitelline membrane shed together at hatching but not rejected. Both membranes later cast along with embryonic cuticle. Subsequent first moult produces first instar from postembryo.

Category V: Agelenidae (Holm, 1954); Dionychae (Holm, 1954). Chorion and vitelline membrane shed together at hatching but not rejected. Embryonic cuticle shed separately later, but neither it nor the previous membranes rejected. All three membranes later cast along with integument of first moult, producing first instar from postembryo.

Category VI: *Polybetes pythagoricus* (Holmberg), Sparassidae (Galiano, 1972); *Polybetes rapidus* (Keyserling), Sparassidae (Galiano, 1972); *Polybetes punctulatus* Mello-Leitão, Sparassidae (Galiano, 1972); *Polybetes pallidus* Mello-Leitão, Sparassidae (Galiano, 1972). Chorion and vitelline membrane shed together at hatching but not rejected. Embryonic cuticle shed separately later, but neither it nor previous membranes rejected. Subsequent first moult also remains unrejected, remaining attached together with all three embryonic membranes. Integument of first moult and three membranes later cast along with integument of second moult, producing first instar from postembryo.

Category VII: *Phidippus audax* (Hentz), Salticidae (Taylor & Peck, 1975); *Misumenops quercinus* Schick, Thomisidae (Schick, 1972); *Misumenops gabrielensis* Schick, Thomisidae (Schick, 1972); *Misumenops rothi* Schick, Thomisidae (Schick, 1972); *Misumenops schlingeri* Schick, Thomisidae (Schick, 1972); *Misumenops lowriei* Schick, Thomisidae (Schick, 1972); *Misumenops deserti* Schick, Thomisidae (Schick, 1972); *Cupiennius salei* (Keyserling), Ctenidae (Melchers, 1963). Chorion shed at hatching but not rejected. Vitelline membrane shed separately later but neither it nor chorion rejected. Both membranes later cast along with embryonic cuticle. Subsequent first moult produces first instar from postembryo.

Category VIII: *Loxosceles reclusa* Gertsch & Mulaik, Scytodidae (Hite *et al.*, 1966); *Octonoba octonarius* (Muma), Uloboridae (Peaslee & Peck, 1983); *Cheiracanthium inclusum* (Hentz), Clubionidae (Peck & Whitcomb, 1970). Chorion shed at hatching but not rejected. Chorion later cast along with vitelline membrane and embryonic cuticle which are shed and totally rejected together. Subsequent first moult produces first instar from postembryo.

Category IX: *Diguetia catamarquensis* (Mello-Leitão), Diguetidae (Galiano, 1969a). Chorion shed and totally rejected at hatching. Vitelline membrane and embryonic cuticle later shed together but neither rejected. Both the latter membranes cast later along with integument of first moult, producing first instar from postembryo.

transition for 34 species or higher taxa of spiders. It gives an overview of the period beginning with the rupture of the chorion and ending with the discarding (total rejection) of the integument of the first true moult. In one case (Category VI) the latter is not discarded until the second moult. It is unlikely that the schema is without error (of observation by original authors and/or of interpretation by the present one); if there were no irreconcilable confusion between the reports there would be no need for a comparative revision. Indeed, it is hoped that the present communication will elicit responses from the relevant workers and lead to a consensus for standardization.

In particular, there is considerable doubt about the status of the 'embryonic cuticle'. It is treated here as a third embryonic membrane (Peaslee & Peck, 1983). In those cases, if any, where it can be shown to be identical with the first true moult, the latter term should be retained and the embryonic cuticle considered absent. Its absence in Category II of Fig. 7 is based on observations made on *T. rufipes* and other theridiids in this study and on Holm's (1954) claim that the embryonic cuticle is suppressed in the Argiopiformia. The latter includes the Theridiidae but is not a useful higher taxon today; nor is the Dionychae (the two-clawed spiders).

Vachon (1953, 1957) asserted that the true embryonal stage ends with reversion and that the stage between reversion and the rupture of the chorion is the first in a series of phases together constituting a 'larval' stage which separates the embryo from the first instar. He also pointed out that the 'larval' stage is essentially a continuation of the embryonal process. This is reasonable, since embryonic features such as lack of appendage segmentation, lack of hairs or pigment, poor motility and in some species traces of abdominal segmentation characterize this stage (Valerio, 1974). However, while eyes and book lungs may be incompletely formed and no silk or sex glands are normally present, the latter are formed before hatching in *Agelena* sp. (Purcell, 1895; Strand, 1906; Kautzch, 1910). Extension of the post-eclosion 'embryonal' stage, through several moults in the case of the theraphosids, seems to be a feature of those spiders with the most abundant yolk reserves (Galiano, 1969b), and the number and features of such stages have been used in classification at the subfamily level, dividing the Theraphosidae into Grammostolinae and Theraphosinae (Galiano, 1973a). These moults and stages are not shown in Category I of Fig. 7 because under the present proposal the rejection of the integument of the first of these moults produces the first instar. Any inactive developmental stages that followed the total rejection of the first true moult could usefully be called 'quiescent' instars. Hence instars one to three are probably quiescent in most theraphosids.

Several recent reports (Yoshikura, 1955, 1972; Galiano, 1967, 1969a, 1969b, 1971, 1972, 1973a, 1973b; Hydorn, 1977; Whitcomb, 1978) have followed Vachon in taking the embryonic period, strictly concluding at reversion, to have a postembryonic extension until the

first active instar appears. However, the term 'post-embryo' seems inappropriate for a life-history stage that is implied to be essentially embryonic. Other reports (Ewing, 1918; Holm, 1940; Gertsch, 1949; Juberthie, 1954; Eason & Whitcomb, 1965; Hite *et al.*, 1966; Peck & Whitcomb, 1970) have assumed that eclosion, despite its attendant imprecision, marks the close of the embryonic period.

It is often the fate of ill-defined, variable processes to become littered with terminology. The terms applied to developmental stages in spiders between the time the egg-tooth ruptures the chorion and the time the first true integument is moulted are (1) embryo, (2) postembryo or postembryonal stadium or 'free' postembryo (Holm, 1954), (3) deutovum (Gertsch, 1949), (4) exchorionate stage (Hydorn, 1977), (5) interchorional stage (Galiano, 1973a), (6) endovitelline and exovitelline stages (Whitcomb, 1978), (7) quiescent stage or quiescent nymph (Ewing, 1918), (8) protonymph (Jézéquel, 1960), (9) prenymph (Vachon, 1957), (10) nymph (Ewing, 1918), (11) nymphal instar (Vachon, 1953, 1957), (12) prelarva (Vachon, 1953, 1957), (13) pullus (Canard, 1984), (14) larva (Vachon, 1953, 1957), (15) postpullus (Canard, 1984), (16) incomplete stadia A, B, C, D (Holm, 1940, 1952, 1954), (17) prejuvenile (Canard, 1984), (18) spiderling, (19) first instar.

Not only is the plethora of terms a problem in itself, but among the most widely accepted terms are several with unfortunately inappropriate connotations. In particular, a larva is understood by entomologists to be an actively feeding form so different from the adult (imago — another term that Vachon (1957) has applied to adult spiders) that it is separated from the latter by a metamorphosis. The spider 'larval' stage, comprising 'prelarvae' and 'larvae', differs not in gross form but only in developmental detail from the later instars, and is normally to be found not actively feeding but lying on its back and feebly waving its unsegmented legs. Terminological confusion prevents a definite assessment of whether or not spider 'larvae' ever feed (on eggs). The first active instar would seem to be the first potentially feeding one; it may be necessary to repeat previous observations to resolve this problem — a most unfortunate outcome of the proliferation of descriptive terms. Nymphs in entomology are the immature forms of hemimetabolous insects, with reasonably well-defined and significant differences

Embryo (S): the developmental stage concluding at hatching.

Hatching (E): the shedding, but not necessarily the discarding, of the chorion.

Postembryo (S): the developmental stage between hatching and the discarding (total rejection) of the integument of the first true moult.

First true integument moult (E): the shedding, but not necessarily the discarding, of the first integument that has legs.

First instar (S): the developmental stage resulting from the discarding of the integument of the first true moult.

Table 2:   A proposed descriptive convention, with definitions, to standardize the terms used to describe the stages (S) and events (E) of the early development of spiders.

from the adults; spider 'nymphs' are simply young spiders. Bonnet (1981) has specifically urged that the term 'nymph' be abandoned. 'Deutovum' is a specialized term in acarology describing a particular immature form (the second egg stage) of mites. One may as well speak of spider 'tadpoles' when describing stages of spider development.

To rectify these problems, or at least to do what is possible towards preventing their escalation in the future, the following is proposed as a descriptive convention (Table 2); it is hoped that the arachnological community will recognize it, or at least the need for something like it, and that editors will encourage future authors to present their findings in a consistent and comparable fashion. There are three guiding principles in this proposal: simplicity, the avoidance of terms with misleading connotations and the need to stick to terms already in use (to introduce any new terms would be the final irony).

First, Vachon's notion that reversion marks the close of the embryonic period is here discarded. The embryo incorporates reversion as one of its developmental events. Hatching is considered the close of the embryonic stage, and is defined as the shedding (but not necessarily the total rejection) of the chorion. Peck & Whitcomb (1970) and Peaslee & Peck (1983) have defined hatching in this way. The stage between hatching and the final rejection (discarding) of the integument of the first moult is the postembryo stage (Whitcomb (1978) adopts this usage).

That the postembryo stage should not be included in the instar sequence is a view supported by the observations of Peck & Whitcomb (1970). These authors described how the postembryo stage of *Cheiracanthium inclusum* (Hentz) grows actively, doubling its carapace width, and they suggest that this

emphasises the fact that the postembryo stage is fundamentally different from the stages following (but not in a way comparable to the difference between insect larvae and imagines). Since various species' postembryos differ in their degree of activity, the term 'quiescent' should be used purely descriptively whenever appropriate, and should be excluded from standard terminology; it may, however, be useful to apply the qualifier 'quiescent' to first and later instars that are inactive, as was suggested above for the theraphosids.

Under this convention, the young of most spiders will normally emerge from the cocoon as first instars, defined as the developmental stage following the total rejection of the first true integument moult. Figure 8 shows how the present proposal relates to some previous descriptive terminologies. Emergence from the cocoon is not a developmental event comparable to reversion, hatching and the first moult, but is included for consistency with previous descriptions. The proposals of Canard (1984) and Neet (1985), coining new terms and applying old terms in new ways, emphasise the pressing need to resolve this long-standing problem.
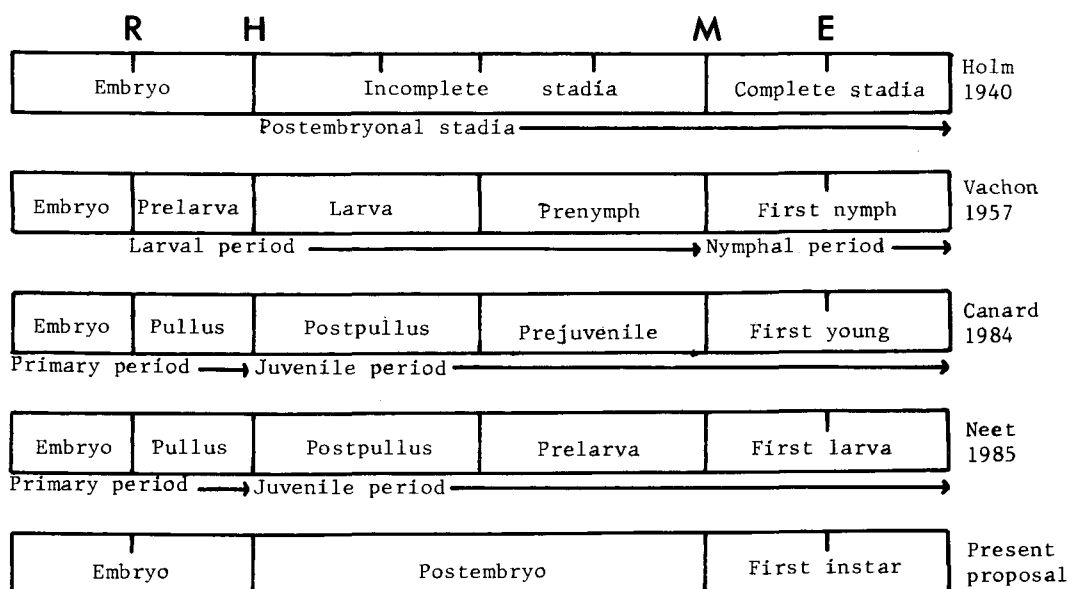
Fig. 8:   Five proposals for descriptive terminology of the early development of spiders. R = reversion; H = hatching as defined in Table 2 (i.e. shedding of chorion); M = first true integument moult (NB — total rejection of the integument of that moult, in the case of the present proposal); E = emergence from the cocoon (often, but not always, occurring at this point of development). The 'primary period' of Canard (1984) and Neet (1985) may refer to the 'pullus' stage only. The figure format is based on that of Valerio (1974).

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