Article

Pycnogonida developmental biology

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Abstract
The term anamorphic development is used to describe arthropods which add segments throughout their lives. Epimorphic development is used to describe arthropods which hatch with a set number of segments which does not increase with subsequent molts. Some arthropods add segments initially until a set number have been produced after which no further segments are produced with subsequent molts. The latter are said to have hemianamorphic development. In the Chelicerata the completion of embryonic development and hatching of the egg are not as intricately linked as in the other classes of the Arthropoda. Thus, making the distinction of which developmental pattern is occurring less obvious. The members of the Pycnogonida typically hatch as a “Protonymphon larva” having three pairs of appendages and a proboscis with a tripartite mouth. The subsequent growth of the animals displays certain developmental processes typically seen in embryos: (1) Apoptosis; (2) invagination of ectodermal tissues to initiate the formation of neurogenic niches. (3) organogenesis; and (4) limb development progressing in an anterior-posterior developmental gradient. If the “Protonymphon larva” and early nymphs are interpreted as embryonic stages, then the Pycnogonida may be considered to have epimorphic development.

Keywords apoptosis; developmental gradient; embryology; invagination; organogenesis; Protonymphon larva; Pycnogonida.

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1 Introduction

Those arthropods whose development is characterized by the addition of segments throughout their lives are termed as having anamorphic development. Those which complete embryonic development and hatch with the total number of segments and do not add more segments are said to have epimorphic development. Animals with hemianamorphic development complete embryonic development and after hatchingadd segments with successive molts followed by molts without any further segments being added. Hemianamorphicdevelopment is considered to be a plesiomorphic, primitive, developmental trait in the Pycnogonida by Brenneis et al. (2017). This last developmental pattern has been attributed to the Pycnogonida, sea spiders, and Acariformes, mites (Brenneis and Arango, 2019; Fuso and Minelli, 2021).

Hemianamorphic and epimorphic developmental patterns are sometime difficult to distinguish because in some arthropods, embryo-like hatchlings are known (Minelli et al., 2006; Fuso and Minelli, 2021). Epimorphic development in the Pycnogonidae: Nymphonidae was described in *Nymphon floridanum* and *N. micronesicum* in which the egg hatched as post Protonymphon stage nymphs with three pairs of underived walking legs but lacking the ovigerous appendages. In these species the hatchling had copious quantities of yolk (Arango and Brenneis, 2024).

2 Previous Work

The understanding of early development in the Pycnogonida depends on when the completion of embryonic developmentis achieved. In this study we endeavor to look at the evidence for considering the Pycnogonid protonymphon larva and Nymphon larval stages as displaying the characteristic of embryos.

The Pycnogonida are either chelicerates or they are the sister group to the Euchelicerata (Dunlop and Arango, 2004; Bamber, 2007). The Pycnogonida have a long fossil record extending into the early Paleozoic.

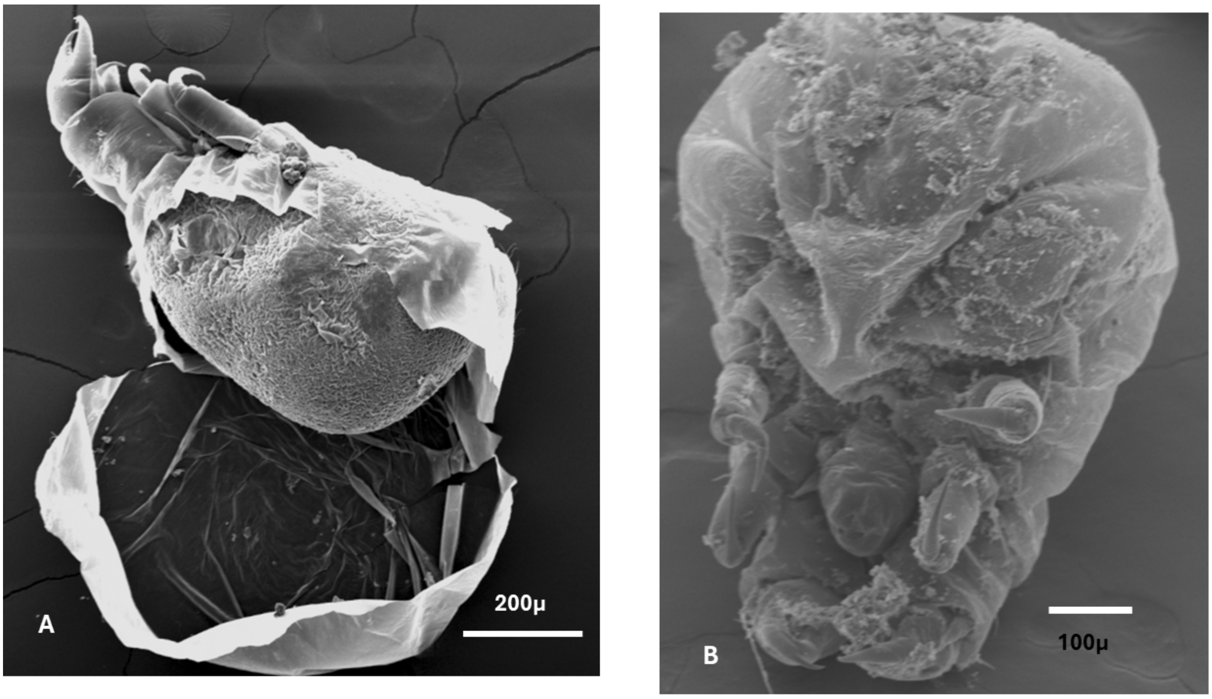

Fig. 1 (A) Lateral view of *Ammothea clausi* - Typical Protonyphon – the egg case can be seen below the Protonyphon. (B) Ventral viewof *Ammothea clausi* (Fornshell, 2019).

The fossil record of the Pycnogonida indicates that in the Paleozoic era adult sea spiders had a more diverse morphology than extant forms, with some having anunsegmented abdomen reduced in size as in the case of *Paleopantopoda* Broili 1930,and others having a segmented abdomen, *Palaeoisopus problemanticua* Broili 1932 (Hedgepeth, 1956). *Palaeomarachne granulata* a fossil pycnogonid from the Ordovicianera described by Rudkin, et al. (2013) had a four segmented head. In Mesozoic fossils the abdomen, if present is reduced and unsegmentedas is the case with extant forms (Semper, 1874; Hedgepeth, 1953; Siveter, et al., 2004; Poschmann and Dunlop 2006; Bamber, 2007; Dunlop, 2010; 2011; Sabrouxa, et al., 2019; Ballesteros, et al., 2020).

The patterns of growth and development observed in the Pycnogonida is similar to other members of the Euchelicerata. The chelicerates frequentlydisplay a condition in which the completion of embryonic development and the hatching of the eggare not concurrent events (Fusco and Minelli, 2021). Scorpions, for example, typically hatch as late embryos and must undergo further development before undergoing a first molt into the form of a juvenile scorpion (Farley, 2005). Alternatelyin the case of the Horseshoe Crab, *Limulus polyphemus* (Linnaeus, 1758), the animal completes embryonic development and molts four (4) times before the egg hatches (Packard, 1880; Botton, et al., 2010). In true spiders, Order Araneae, an alternate developmental patternfrom the two patterns just mentioned is observed, embryonic development iscomplete when the embryo has chelicera, palps, four pair of walking legs, four gills and caudal segmentswhen the spider eggs hatch (Kumé and Dan, 1968). Spiders hatch as spiderlings and shed their embryonic cuticle. The spiderlings are, however, immobile and lack sensory sensilla at this stage. Only after further development do they molt and become mobile individuals (Wolf and Hilbrant, 2011). Tick embryos, OrderIxodida, undergo an embryonic development similar to spiders with the development of the primordium labium, chelicera, palps and initially four pairs of walking legs. The fourth pair of walking legs undergoes apoptosis before the egg hatches. Upon hatching the animal has only three pair of walking legs (Santos, et al., 2013).

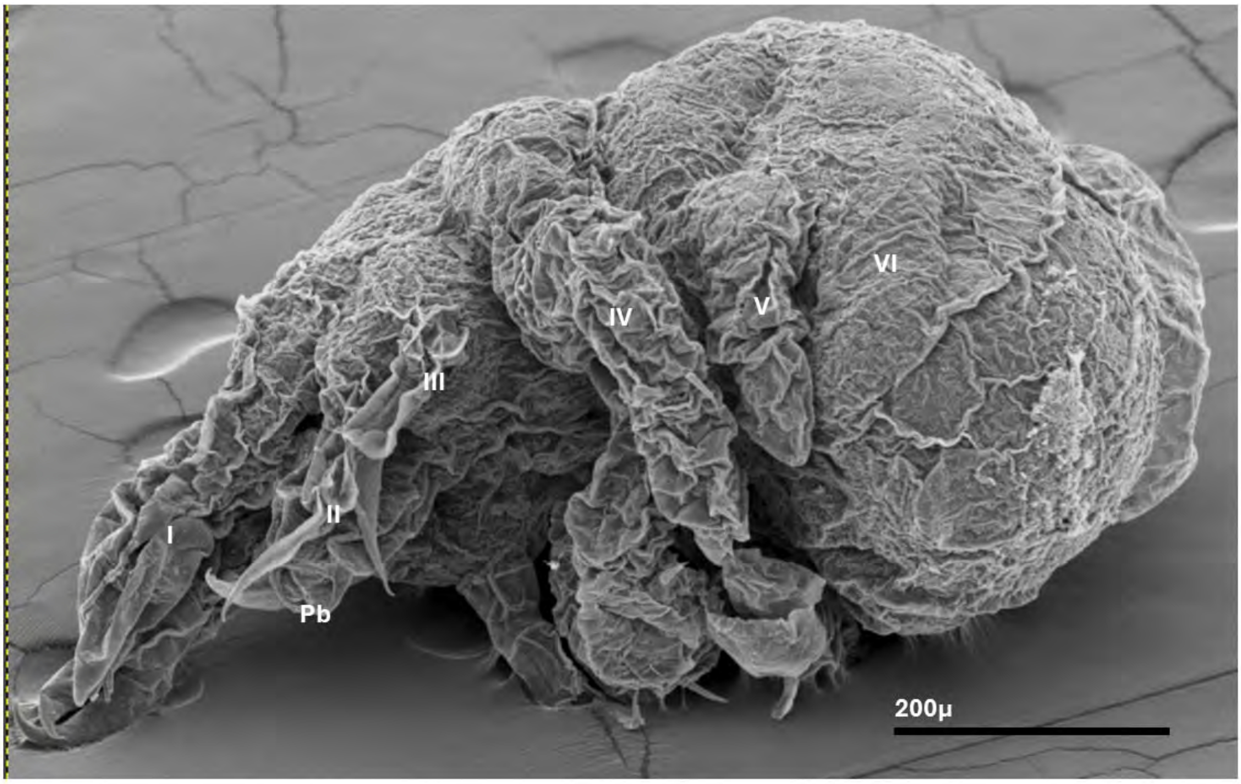

Fig. 2 *Nymphon tenellum,* Elvie's Larva First post hatching stage. Pb = proboscis with tripartite mouth. The Roman Numerals are I = Cheliphores; II = Larval palps; III= Larval Ovigerous Appendages; IV = First walking leg underived bud; V= Second walking leg underived bud; VI = Third walking leg underived bud (Fornshell, 2015).

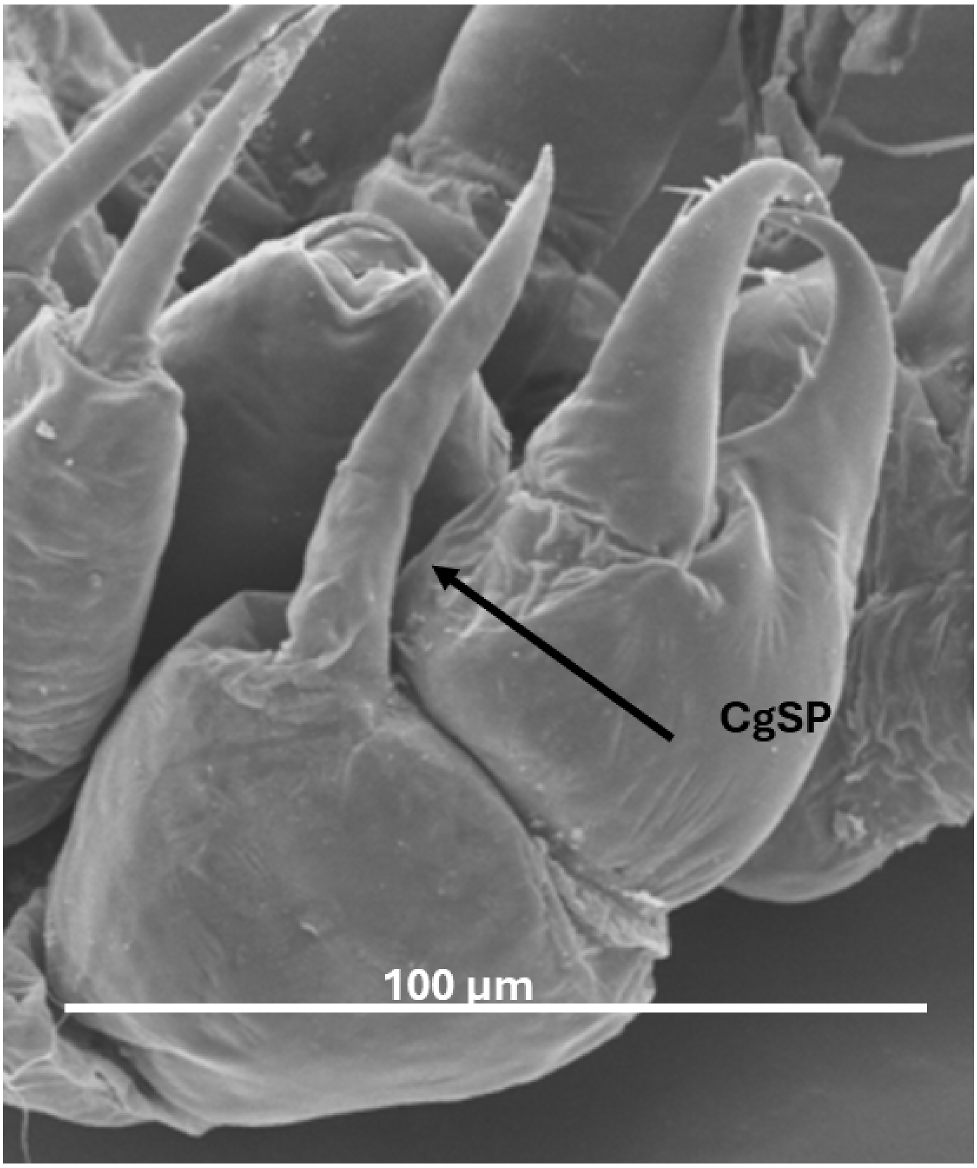

Fig. 3 *Ammothea clausi* protonymphon larva cheliphore showing the spine associated with the (CgSp) attachment gland (Fornshell, 2019).

The early development of the Pycnogonida with few exceptions is fairly similar to the Euchelicerata up to the formation of a cephalon with three pairs of appendages corresponding to the chelicera, palps and ovigerous appendages plus the proboscis (Brusca, 1975). The term Protonymphon larva was first used by Hoek (1881c). Hoek had described sea spider larva from both the Arctic and Antarctic oceans in earlier work (Hoek 1881a, 1881b). Encysted larvae were described by Morgan (1891) and Meinert (1899). The Atypical Pycnogonid larva was described by Oshima (1935, 1937). Nakamura (1981) first described the Attaching larva. At this time there are six identified developmental patterns (Semper, 1874; Hoek, 1881c; Morgan, 1891; Meinert, 1899; Oshima, 1935; 1937; Bain, 2003; Bogomolova, and Malakhov, 2006; Fornshell, 2015).

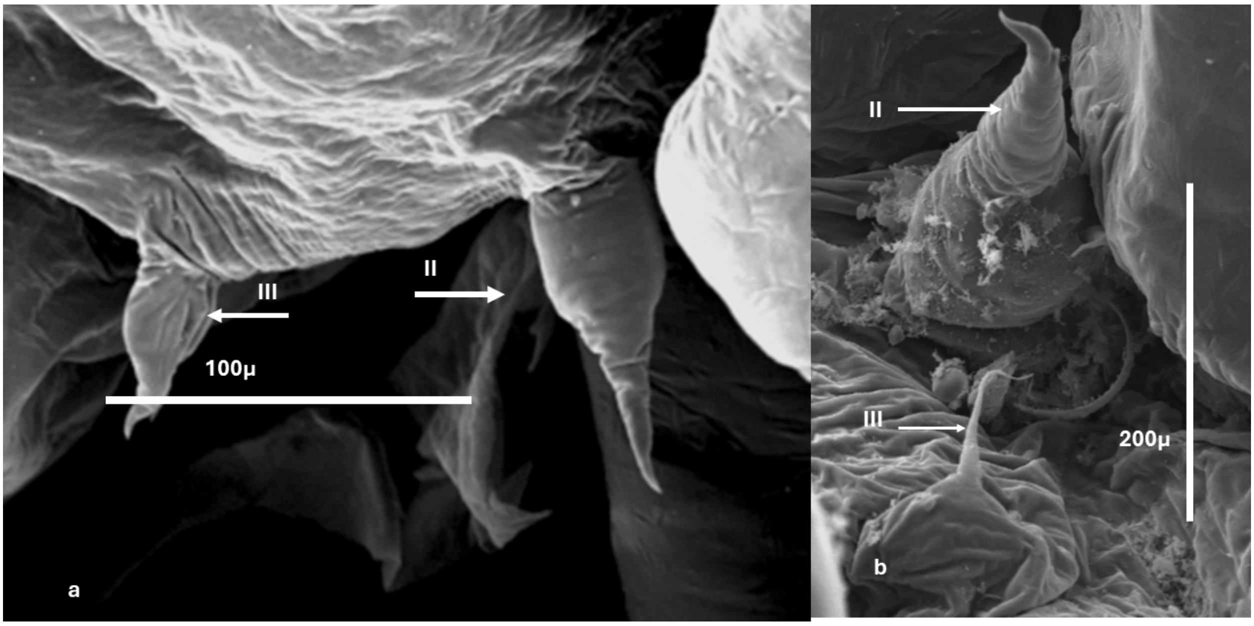

Fig. 4 Second and third larval appendages of *Ammothea striata* displaying apoptosis. (a) second Instar and (b) third instar (Fornshell, 2014).

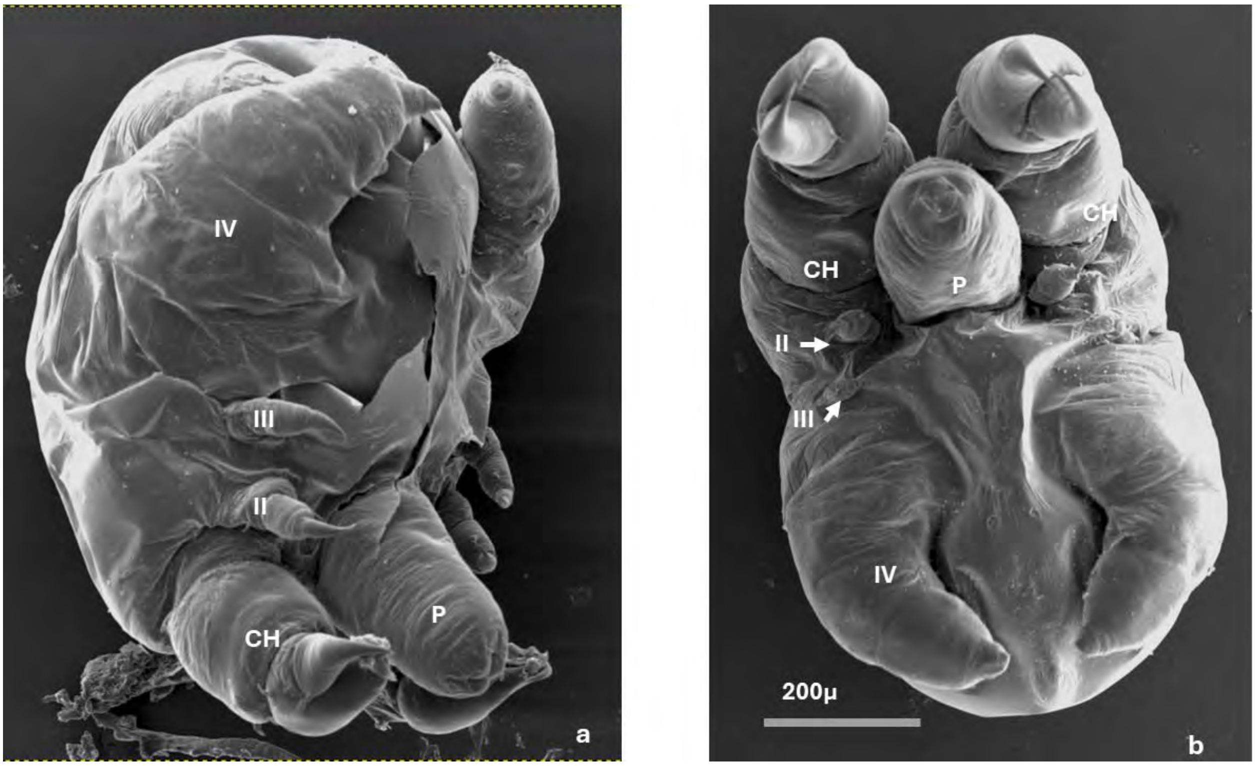

Fig. 5 (a) *Ammothea striata* First post hatching stage with the first walking legs present as underived appendages; IV= underived first walking legs. (b) *Ammothea gigantea* ventral view First post hatching stage with the first walking legs present as underived buds. Note the absence of a Proctodeum (Fornshell, 2014).

Bain (2003) summarized the sea spider larval types know up to the beginning of the twenty first century, identifying four developmental patterns: (I) Typical Protonymphon, a Protonymphon larva with only three appendages and a proboscis (Fig. 1) which is the most common hatching stage, found in three Families Ammotheidae, Nymphonidae and onPycnogonidae; (II) Encysted Larva,found in two Families, Ammotheidae and Phoxichilidae also hatch as a Protonymphon, but leave the male and burrow into the body of a coelenterate where they continue to develop; (III) Atypical Protonymphon, this developmental type has a form at hatching very similar to the typical Protonymphon, but leaves the male and becomes attached to the surface of a nudibranch or polychaete where it completes its development, acquiring all four walking legs in a single molt, found in one Family Ammotheidae and; (IV) The Attaching Larva found in two the Families, Callipallenidae and the Nymphonidae,hatches with the first walking leg present as an underived bud and remains attached to the male living on yolk while developing the remaining three walking legs in successive molts before leaving the male as a juvenile. To this we may now add the fifth (V) developmental type, the Lecithotrophic Larva, *N. grossipes,* a larva with copious amounts of yolk, which hatches as an Protonymphon-like oval larva with the first walking legs represented as a small protuberance and develops into a juvenilewhile still living on the male, consuming the stored yolk (Bogomolova and Malakhov, 2006; Alexeeva and Martynova, 2024.). The sixth (VI) developmental form, Elvie's Larva, *N. Tenellum* (Sars, 1888), characterized by a first hatching stage with (See Fig. 2) all three of the larval appendages and three underived walking legs and an incomplete digestive system indicated by the absence of aproctodeum, foundin the Nymphonidae (Fornshell, 2015). It should be noted that Elvie's Larva was figured by Hoek (1881a) from the HMS Challenger Expedition and by G. O. Sars (1891) from the Norwegian North-Atlantic Expedition, in both cases without any reference to the larva in the text of their work. Bogomolova and Malakhov (2014) described a similar larva in an abstract for the 8th International Crustacean Congress 2014. As statedearlier,Brenneis and Arango (2019) describe epimorphic development in *Pallenopsis villosa, P. hodgsoni and P. vanhoffeni* from the Antarctic. These two species have lecithotrophic larva which hatch at a much latter stage of development with three functional walking legs, when compared to the hatching stages of members of the Pallenopsidae which have Arango's Typical Larval Type. The larva of *N. Tenellum* (Fornshell, 2014) differ in that the latter hatch with the larval chelicera, palps and ovigerous appendages in addition to the first three walking legs as underived buds.

A seventh fossil larval form, a Cambrian fossil,*Cambropycnogon klausmuelleri*is referred to as a pycnogonid larva by Waloszek and Dunlop (2002). This fossil has definite Chelicerate characteristics, three larval appendages including chelicera. The fossil, however, lacks a proboscis, a trait found in all extant pycnogonid larva and has antennule-like structures at the anterior end of the body, also, there are two posterior annulated appendages much larger than the other appendages,these threetraits not seen on any pycnogonid developmental stage. Because these last three traits differ from all pycnogonid larva, both extant and fossils, it seems unlikely, to this author, that it is a pycnogonid larva.

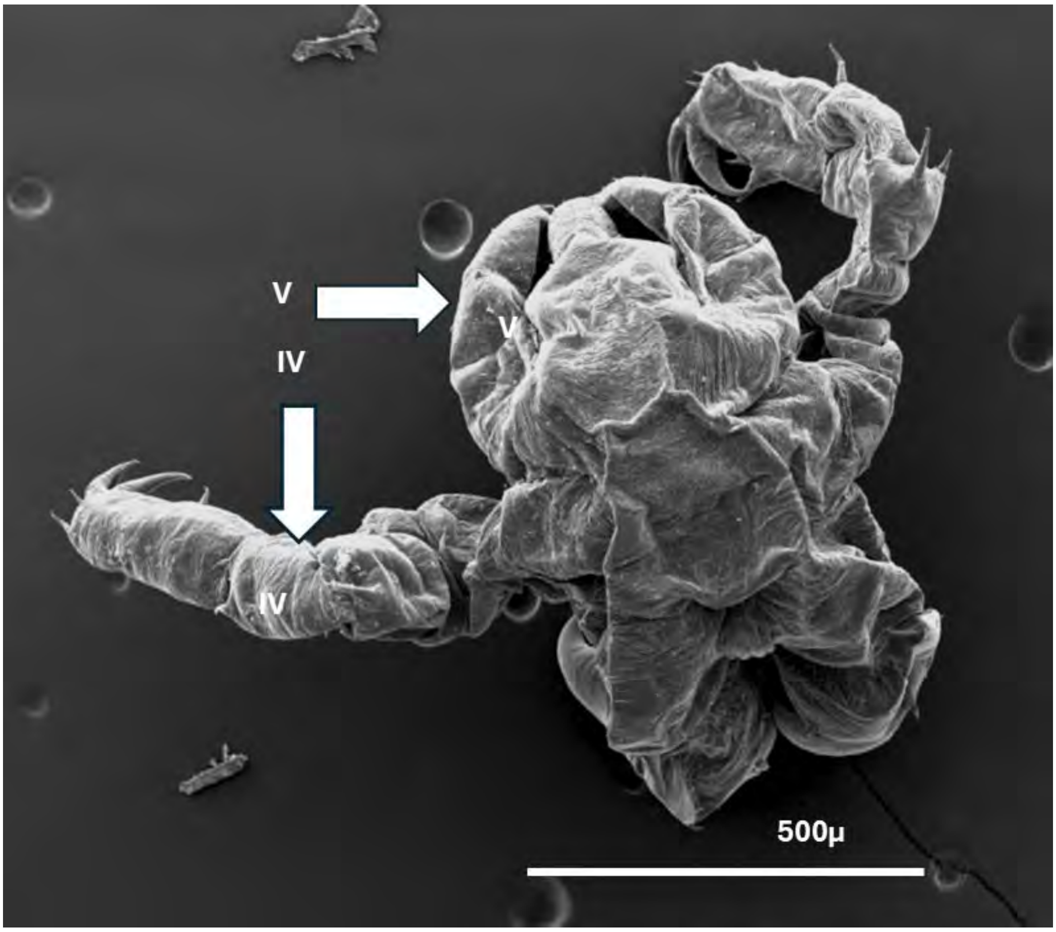

Fig. 6 *Ammothea striata*second post hatching stage showing seven segmented fourth walking legs (IV) and three segmented fifth walking legs (V)(Fornshell and Ferrari, 2012).

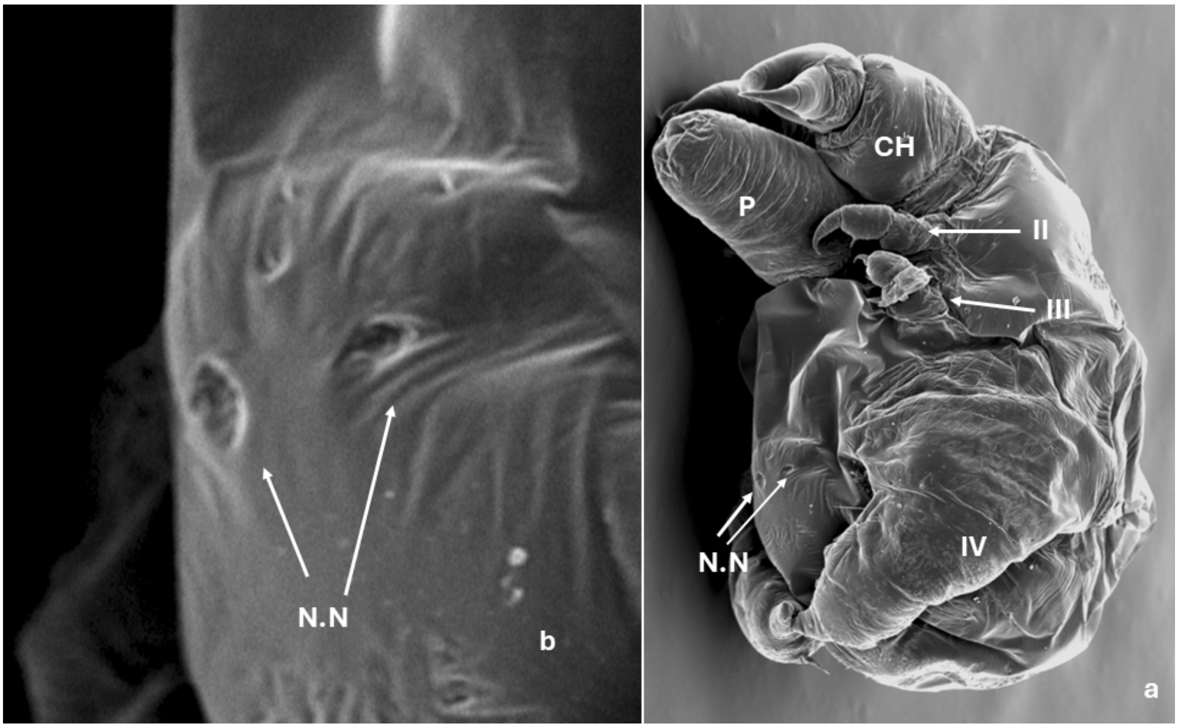

Fig. 7 *Ammothea gracilis* neurological niches (N.N) invaginations of the forming ventral nerve chord ganglia as indicated by the arrows. P = proboscis with tripartite mouth; CH = Cheliphores; II = larval palps; III = Larval ovigerous appendages; IV = underived first walking legs (Fornshell, et al., 2011).

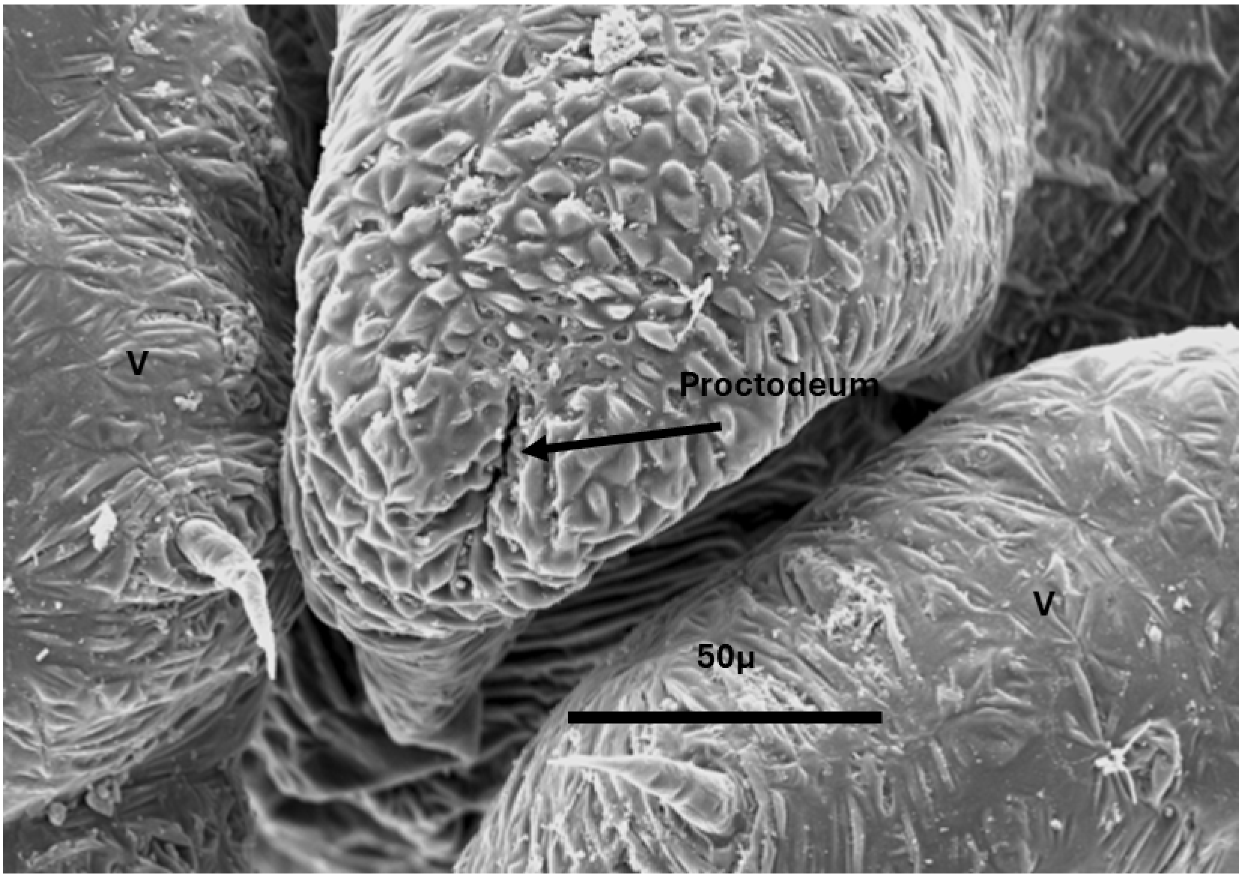

Fig. 8 *Ammothea striata* showing the appearance of the Proctodeum in the third post hatching stage (Fornshell and Ferrari, 2012).

3 Discussion

The Family Nymphonidae then has four (4) of the six developmental types, as does the Family Ammotheidae. The Families Callipallenidae, Phoxichilidae, and Pycnogonidae each contain one. Alternately the Typical Protonymphon Larva is found in three families. The Attaching Larva and Encysted Larva are both found in two different families. It is very atypical to find such diversity of developmental patterns in a single family as in the case of the Nymphonidae and Ammotheidae, or such similarities in different families as in the case of the typical Protonymphon Larva and Attaching Larva. This level of variability in development is striking when compared to that found in the Crustacea and other members of the Chelicerata (Bain, 2003; Cano and López-González, 2009, 2013; Fornshell and Ferrari, 2012; Fornshell, 2014; Bogomolova and Malakhov, 2014; Fornshell, 2015).

As noted earlier, hatching does not always separate embryonic and post embryonic development in the chelicerates (Farley, 2005 ;Minelli et al., 2006; Botton, et al., 2010; Wolf & Hilbrant 2011; Fusco, & Minelli, 2021). Embryonic development, however, has certain developmental processes which are frequently associated with this portion of the lifecycle of an animal. The earliest process, which are common to all arthropods including chelicerates are fertilization of an egg cell (ovum) by a sperm cell, (spermatozoon) to form a zygote. The zygote undergoes mitotic divisions with no significant growth, cleavage divisions, followed by gastrulation, where cells are moved into different parts of the embryo and cellular associations are followed by differentiation. The process of gastrulation is necessary before organ formation by the invagination of endoderm tissue to form new organs as in the case of the digestive tract. Similarly, the ectoderm gives rise to ganglia of the central nervous system and sense organs like eyes beginning with the process of invagination. In the process of embryonic development, the process of organ formation usually begins with the invagination of groups of cells which then begin the process of differentiation to form an organ. In spider, tick, mite, Harvestman, and Horseshoe Crab embryos, appendages including chelicera, palps, and walking legs arise in sequence from anterior to posterior with underived buds followed by partial segmentation followed by the final adult number of segments (Packard, 1880; Kumé and Dan, 1968; Brusca, 1975; Farley, 2005; Wolff and Hilbrant, 2011;Scholtz and Wolff, 2011; Fusco and Minelli, 2021; Janssen, 2021; Gainett, et al., 2022).

The following four developmental processes normally associated with embryonic development are observed during the protonymphon and nymph stages of post hatching pycnogonids.

Apoptosis: The process of apoptosis, programmed cell death, also occurs in embryonic development as the developing animal attains its' juvenile form. This process of programmed cell death is one of the most distinct embryological processes (Cambell, et al. 2008). The larval appendages display this process. The cheliphores of many pycnogonid protonymphon larva have a spinning gland and associated spine. This spine is large compared to the first instar larva but disappears by the process of apoptosis after the larva leave the parent's ovigerous appendage usually by the fifth instar. The larval palps and ovigerous appendages in some pycnogonid larvae also display the process of apoptosis by degenerating in size to a simple spine or no visible structure at all (Fornshell, 2014)(See Figs 3 and 4).

Limb Development: In Chelicerates, limbs begin as underived buds which then produce a number of segments, typically less than the number present at the end of embryonic development (Packard, 1880; Mittmann and Wolff, 2012). In chelicerate embryos the appendages, chelicera, palps, (ovigerous appendages in pycnogonids) and walking legs develop in this pattern (Wolff and Hilbrant, 2011; Ferrari, et al., 2011; Mittmann and Wolff, 2012; Santos, et al., 2013; Scholtz and Wolff, 2013; Barnett and Thomas, 2018; Fusco and Minelli, 2021; Janssen, et al., 2021; Gainett, et al., 2022). This pattern of development of the walking legs is seen in several pycnogonid post protonymphon larva stages. The development of walking legs beginning as underived buds followed by segmented walking legs with a reduced number of articles compared to the adult stage (See Figs 5 and 6). In Chelicerate embryonic development there is an anterior to posterior gradient in the development of organs. This gradient is also present in the development of post hatching Pycnogonida. (Packard, 1880; Morgan, 1891; Kumé and Dan, 1968; Brusca, 1975; Farley, 2005; Wolff, 2011; Ferrari et al., 2011; Fornshell and Ferrari, 2012; Scholtz and Wolff, 2011; Santos, et al., 2013;F ornshell, 2014, 2015; Brenneis, et al., 2017; Brenneis and Arango, 2019; Fornshell and Harlow, 2019; Farley et al., 2021; Gainett, et al., 2022).

Invagination of Ectodermal Tissues: The post hatching instars of the Pycnogonida all display the embryonic development processes of invagination of tissue layers to form new organs.For example, Neurogenic niches are known to form on post hatching pycnogonids (Brenneis and Scholtz, 2014) (See Fig. 7).

Organogenesis: The development of organs and organ systems is a process seen in all embryos. In Protostomes the digestive system develops from the mouth posteriorly to the annus.The digestive tract of members of the Pycnogonida is incomplete at the time of hatching consisting of the tripartite mouth on the proboscis and only attains its' final form with the development of a proctodeum after one or more post-hatching molts(See Fig. 8)(Morgan, 1891; Kumé and Dan, 1968; Brusca, 1975; Farley, 2005; Wolff and Hilbrant, 2011; Mittmann and Wolff, 2012; Fornshell, 2014; 2015; Barnett, & Thomas, 2018; Fornshell and Harlow, 2019; Gainett, et al., 2022; Arango and Brenneis, 2024).

Brenneis and Arango (2019) describe epimorphic development in *Pallenopsis villosa, P. hodgsoni and P. vanhoffeni* from the Antarctic. These two species have lecithotrophic larva which hatch at a much latter stage of development with three functional walking legs, when compared to those members of the Pallenopsidae which have Arango's Typical Larval Type). The larva of *N. Tennellum* (Fornshell, 2014) differ in that the latter hatch with the larval chelicera, palps and ovigerous appendages in addition to the first three walking legs as underived buds.

It is proposed that the post hatching development of the Pycnogonida be considered as a continuation of embryonic development until the juvenile animal form with four pairs of walking legs and a functional and complete digestive tract are achieved. As such the Pycnogonida would then be said to display epimorphic development. This would mean that they, like the Euchelicerata, display epimorphic development, that is, all segments are formed during embryonic development. This interpretation assumes that these animals hatch before the completion of embryonic development. As pointed out earlier hatching of the egg does not always mark the dividing line between embryonic development and post embryonic development in chelicerate's (Farley, 2005; Botton, et al., 2010; Wolf and Hilbrant 2011; Fornshell and Ferrari, 2012; Minelli, 2021).

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