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# Cephalic limbs in postembryonic development of sea spiders (Pycnogonida): a review

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ABSTRACT: Sea spiders (Pycnogonida) are an ancient group of marine arthropods, which has retained an oligomeric larva and hemianamorphic development. Postembryonic development varies across different pycnogonid taxa, producing terminological ambiguities, such as what instars can be reffered as "larva", what periods one should distinguish during postembryonic development of pycnogonids, and whether the unified scheme of such periodization can be elaborated. In this work, we review postembryonic development of sea spiders with focus on the metamorphosis of the anterior three pairs of limbs (cephalic limbs), which we believe to be the most clear indicator of life mode changes. Morphology of larval appendages and their metamorphosis are reviewed by families and types of development. Taxonomic as well as life mode related trends in the morphology and metamorphosis of the cephalic limbs are traced. Application of different criteria of the term "larva" is tested on pycnogonids with different types of development. Based on the cephalic limbs metamorphosis and criteria of "larva" delimitation of "larval", "postlarval" and "juvenile" periods in sea spiders development is suggested.
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KEY WORDS: Pycnogonida, sea spiders, postembryonic development, metamorphosis, larva, larval limbs, provisional structures, larval adaptations.

# Конечности цефалосомы в постэмбриональном развитии морских пауков (Pycnogonida): обзор

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РЕЗЮМЕ: Морские пауки (Pycnogonida) — древняя группа морских членистоногих, сохранивших олигомерную личинку и гемианаморфное развитие. Постэмбриональное развитие различается у разных таксонов пикногонид, что приводит к терминологической неопределенности, например, какие стадии можно называть «личинками», какие периоды следует выделять в постэмбриональном развитии пикногонид и можно ли разработать единую схему такой периодизации. В данной работе мы рассматриваем постэмбриональное развитие морских пауков, уделяя особое внимание этапам метаморфоза передних трех пар конечностей (головных конечностей), которые, по

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Devoted to memory of Claus Nielsen.

нашему мнению, являются наиболее четкими индикаторами смены образа жизни молоди. Морфология личиночных конечностей и их метаморфоз рассматриваются по семействам и типам развития. Прослеживаются тенденции в морфологии и метаморфозе головных конечностей, связанные как с таксономическим положением, так и с образом жизни. Обсуждается применение различных критериев термина «личинка» для пикногонид с разнличными типами развития. На основе метаморфоза головных конечностей и критериев термина «личинка» предложено разграничение «личиночного», «постличиночного» и «ювенильного» периодов в развитии морских пауков.

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КЛЮЧЕВЫЕ СЛОВА: Pycnogonida, морские пауки, постэмбриональное развитие, метаморфоз, личинка, личиночные конечности, провизорные органы, личиночные приспособления.

## Introduction

Pycnogonida or sea spiders are an ancient group of odd-looking marine arthropods, sister to Euchelicerata (Giribet, Edgecombe, 2019; Legg *et al*., 2013). They retain many traits considered to be plesiomorphic for arthropods, among them a hemianamorphic manner of development and an oligomeric larva, protonymphon. A typical protonymphon has four segments (Alexeeva *et al*., 2017, 2019; Brenneis *et al*., 2017), which become the cephalosoma of the adult animal, and that resembles the "head larva" of trilobites and is supposed to be the ancestral state for arthropod larvae (Minelli, Fusco, 2013). Yet, the term "larva" is extremely ambiguous when applied to arthropods. All arthropod "larvae" have several segments and at least three pairs of appendages, but otherwise their morphology and ecology are extremely variable (Minelli, Fusco, 2013). Which postembryonic stages the term "larva" can be applied to depend largely on the criteria used (Haug, 2020).

Over the past decades, information on the larvae of various genera and families of sea spiders has accumulated and a classification of the types of postembryonic development has been proposed (Brenneis *et al*., 2017). Difficulties have arisen in attempts to create a unified scheme for the periodization of postembryonic ontogenesis, since the number of instars varies across the different types of development. Up to what instar can a sea spider be called a "larva", and why should the demarcation line be drawn here or there? Is the term "post larva" appropriate, and up to what instar? What periods can be distinguished in the remaining "post larval" ontogenesis, and by what criteria? How comparable are these periods in different types of development? To answer these questions, we focused on the process of metamorphosis of the cephalic limbs (the anterior three pairs), which is especially dramatic in pycnogonids and correlates with the change in the life mode of animals as they grow and mature. We have reason to believe that the periods of metamorphosis of the head limbs can provide convenient marker points for the periodization of postembryonic ontogenesis. In this review, we provide the most complete and detailed comparison possible of the structure and development of the head limbs in pycnogonids with different types of development and propose criteria and an original scheme for the periodization of the ontogenesis of sea spiders.

## A brief glance at Pycnogonida

### Adult morphology and taxonomy

The body of an adult sea spider is divided into three regions: the cephalosoma, the trunk, and the abdomen (Fig. 1). The cephalosoma is composed of four fused segments and bears a proboscis with terminal mouth and four pairs of limbs: cheliphores, palps, ovigers, and the first pair of walking legs. Cheliphores are limbs of deutecerebral segment and are homologous to chelicerae and to crustacean antennules (Jager *et al*., 2006; Brenneis *et al*., 2008). They are located near the proboscis, chelate, and, if well-developed, are involved in prey handling. Palps are sensory limbs. Ovigers are regularly used by males to

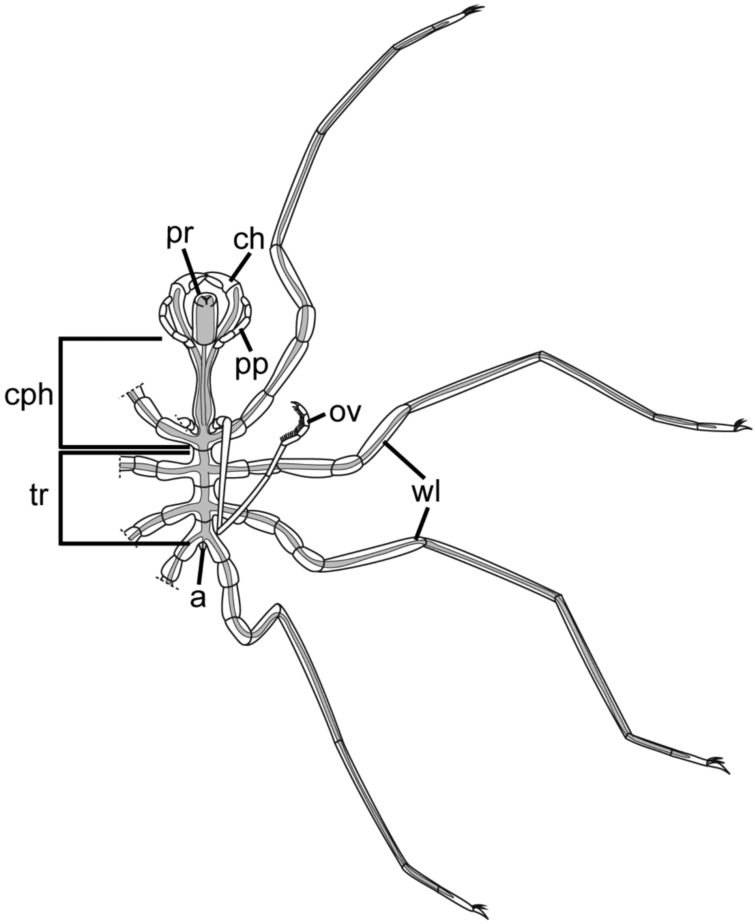


Fig. 1. Adult pycnogonid morphology exampled by *Nymphon* sp., ventral view.
Abbreviations: a — abdomen; ch — cheliphore; cph — cephalosoma; ov — oviger (ovigeous leg); pr — proboscis; pp — palps; tr — trunk; wl — walking legs (one side only). Digestive system is highlighted in gray.

carry the brood, by females to collect newly laid eggs and form egg batches (Petrova, personal observation), and as an extra function in both sexes of some species, for grooming the surface of their body. Palps and ovigers are innervated by the first and the second neuromeres of the ventral nerve cord, fused together into the suboesophageal ganglion (Arnaud, Bamber, 1988; Frankowski *et al.*, 2022). In this work, we refer to the anteriormost three specialized limb pairs (cheliphores, palps and ovigers) as *cephalic limbs*. This is done to distinguish them from walking legs of which the first pair also belongs to the cephalosoma, and the rest to the trunk segments. The trunk is usually composed of three segments bearing walking legs, but several species with four or five trunk segments exist. The abdomen is reduced and lacks any limbs (Arnaud, Bamber, 1988).

Each cephalic limb pair varies among families and genera in their comparative size, functionality and the number of segments (Fig. 1, compare images of adult stages). Any cephalic limb pair(-s) can be variably reduced in adult animals of certain taxa. The chelae or the whole cheliphores may undergo reduction from non-functioning forms to the complete disappearance. Moreover, ovigers and, less commonly, palps are characterized by sexual dimorphism and in extreme cases present in males only; number of segments and armor of palps and ovigers varies in a wide range (Nakamura, 1981; Arnaud, Bamber, 1988; Ballesteros *et al.*, 2021; Frankowski *et al.*, 2022). The state of the cephalic limbs gives clue to pycnogonid taxonomy based on morphological features. In the earlier works (Hedgpeth, 1947; Stock, 1994; León, 1999), the trend to the reduction of the cephalic limbs was assumed the main direction of the pycnogonids evolution. Families possessing well-developed cephalosomic limbs were considered to nest closer to the base of the tree consisting of one or two branches. It was believed that gradual reduction of cephalosomic limbs occurred during the evolution of the sea spiders, with the families lacking all three pairs considered to be the most derived sub-taxa (Hedgpeth, 1947; Stock, 1994; León, 1999). Cladistic studies with morphological and molecular data proved the hypothesis wrong. Nowadays, it is accepted that the reduction of cephalosomic limbs happened independently in several pycnogonid lineages, and, puzzlingly, Nymphonidae which retained the complete set are the most derived (Arango, 2002, 2003; Arango, Wheeler, 2007; Bamber, 2007; Nakamura *et al.*, 2008; Arabi *et al.*, 2010; Ballesteros *et al.*, 2021).

## Postembryonic development

### Protonymphon anatomy. Larval limbs

The taxon-specific larva of pycnogonids is the protonymphon. The protonymphon larva has three pairs of limbs corresponding to the cephalic limbs of an adult animal: cheliphores, palps and ovigers (Fig. 2) (Brenneis *et al.*, 2017).

The larval cheliphores differ from the definitive ones in proportions and position, and additionally, have provisory structures: spinning apparatus and chelar glands. The spinning apparatus includes a silk (attachment) gland and a spinning spine, on which tip the gland duct opens (Fig. 2). Spinning glands produce a silk thread, providing attachment of the larvae to the father's ovigers or the prey organisms such as cnidarians or mollusks (Brenneis *et al.*, 2017). Chelar glands are packed in larval chelae and open on the finger's tips (Fig. 2). They are believed to take part in dealing with prey, however, their exact function is enigmatic (Brenneis *et al.*, 2017; Alexeeva *et al.*, 2018). It was thought that the chelar glands are characteristic for all or most pycnogonid larvae, but thorough observations reveal that they absent in some species (Brenneis, Arango, 2019; Alexeeva, Tamberg, 2020, 2022).

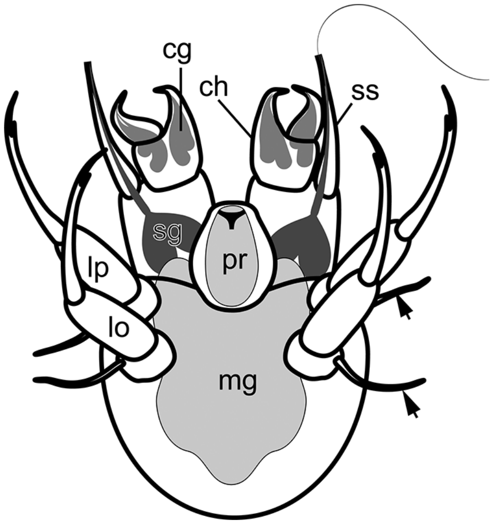


Fig. 2. Morphology of a "typical" protonymphon, ventral view.
Abbreviations: ch — cheliphores; cg — chelar glands; lo — larval ovigeral leg; lp — larval palpal leg; mg — midgut; pr — proboscis; sg — silk gland; ss — spinning spine. Arrows point at spines at the base of larval palps and ovigers. Digestive system is highlighted in light-gray, specific larval glandular apparatus is shown in darker shades.

The second and third pairs of larval limbs correspond to the definitive palps and ovigers and are innervated by the same neuromeres, but their structure is completely different (Dogiel, 1913; Brenneis *et al.*, 2008). In the present review, we term them *palpal* and *ovigeral larval legs*. Functionally, these are the provisory locomotor and grasping legs. Using palpal and ovigeral larval legs, the larvae crawl over their prey or attach themselves to the father's ovigers. Both larval leg pairs have the same structure (Fig. 2). Each comprises the three podomeres: the proximal one is short; the middle is considerably longer, and the distal is thin and often claw-like (Brenneis *et al.*, 2017). The proximal podomere usually bears a long spine with a terminal pore (Fig. 2). Meisenheimer (1902) and Dogiel (1912, 1913) described a gland opening on the tip of this spine and, consequently, considered the complex of the gland and the spine to be a serially homologous to the spinning apparatus. In later works, these glands were not mentioned, so the homology of the spines on larval legs is unclear (Brenneis *et al.*, 2017 and references therein).

### Postembryonic development

For most of sea spiders, the paternal care for brood is characteristic. The males carry egg batches on their ovigerous legs at least until the larvae hatch. Many examples are found when the care extends over some larval or even juvenile instars (Arnaud, Bamber, 1988; Brenneis *et al.*, 2017). An exception that has only recently become known is *Colossendeis*, which attach fertilized eggs to the bottom surface (Moran *et al.*, 2024).

The postembryonic development of pycnogonids is of the hemianamorphic type, i.e., includes two phases: the anamorphic and the epimorphic. During the anamorphic phase, the post larval segments are added until the definitive number is attained. Walking legs appear as small unarticulated buds, and it takes three extra molts to develop the walking leg with the definitive number of leg segments. Larval cheliphores gradually transform into the definitive ones. Palpal and ovigeral larval legs gradually degenerate to small buds; the definitive palps and ovigers develop from these rudiments. Then, after the final number of segments is reached, several epimorphic molts occur. In addition to this basic pattern, in part of pycnogonid species the early "larval" instars are embryonized, so that the protonymphon larva is omitted, and/or development of two or more pairs of walking legs is synchronized (Arnaud, Bamber, 1988; Brenneis *et al.*, 2017; Alexeeva *et al.*, 2018).

Many attempts to classify the variations in the postembryonic development of sea spiders were done (Dogiel, 1913; Bain, 2003a; Bogomolova, Malakhov, 2006; Bogomolova, 2007, 2010; Brenneis *et al.*, 2017; Alexeeva, Tamberg, 2020). Here, we use the one suggested by Brenneis *et al.* (2017). They distinguish five types of development, differing in the morphology of the hatching stage, the lifestyle of the larvae, and the order of segments development.

**The first type.** A protonymphon with complete number of larval limbs hatches. The amount of yolk in egg is low, so the offspring leave their father soon after the hatching and feed exotrophically. The anamorphic phase proceeds in a typical manner, i.e., segments and legs are formed in a strictly sequential order. This anamorphic character of postembryonic development starting from a protonymphon is believed to be plesiomorphic for Pycnogonida, so below the other larvae will be compared to the protonymphon of the first type of development, which will be referred to as "the typical protonymphon".

**The second type.** A larva hatches possessing the set of limbs (externally visible) characteristic of a protonymphon, but its body is very large, and gut is loaded with yolk. Segments develop sequentially, but during early instars young remain attached to the adult male's ovigerous legs and feed lecithotrophically.

**The third type.** A protonymphon hatches. The larvae continue their development living as parasites on mollusks or tubeworms. The third type of development is clearly distinguished by the mesoparasitic life mode of the larvae and the synchronous, rather than sequential, development of all the walking leg-bearing segments with their limbs.

**The fourth type.** Protonymphon larvae scatter immediately after hatching, infect hydrozoans and live as endoparasites in their gastral cavity for several further instars. Anterior three pairs of walking legs develop synchronously, and the posteriormost pair later. A juvenile with three pairs of articulated walking legs emerges from the polyp.

**The fifth type.** In the fifth type the development is embryonized to some extent. Not a protonymphon, but an advanced "post larva" with the buds of two, three or four walking leg pairs hatches, and further on these legs develop synchronously. The first or several instars are lecithotrophic and remain attached to their father's ovigers. Instars with two or three articulated walking leg pairs disperse and pass to the exotrophic feeding.

## Instars numbering

Due to embryonization and, accordingly, the reduction of the postembryonic instars number, there is no clear way to match corresponding instars across all the developmental types. Also, for many species only incomplete postembryonic series were described, so it is impossible to know for sure the exact number of molts and the appearance of the hatching instar. Here we attempt to reconstruct the number of stages in postembryonic development of different species and genera comparing descriptions by different authors and for related species. For most families, at least one complete sequence of undoubtedly demarcated (by molts observed) instars for each type of development was published. Based on such work we can suppose the appearance of the hatching instar and the number of molts characteristic for related species with similar pattern of development.

Below, instars are numbered from the hatching instar (1st) to the last instar described in a series. This approach was impossible to apply to the third type of development, due to extremely scarceness of descriptions: molts were never observed, so it is not clear whether the stages described are instars or just different morphological states (for example, recently molted specimen and those at the verge of the next molt). In this case, in our text and schemes the stages were numbered as in the original descriptions.

### Questions to consider

Despite clear ecological and morphological trends characteristic of each type of development, it was demonstrated that larvae of two species with the same type of development can differ significantly (Alexeeva *et al*., 2019). For many species data on the development is limited by incomplete series of instars from museum collections, mostly found on the adult males' ovigers. Even if found alive in nature, observations on the biology of larvae are scant or absent. Is there any possibility to deduce the mode of life and the type of development from the larval morphology, or is it rather strictly taxon-specific?

The second question is the terminological uncertainty what to call larva in the case of the pycnogonids. A decision was proposed by Brenneis and coauthors (2017). According to them, only the protonymphon and sometimes the next instar closely resembling it should be called larvae, while all the later instars until the end of anamorphic phase should be called postlarvae. All immature epimorphic stages are named juveniles. However, in this terminology the delimitation of larval, postlarval and juvenile periods often appears not related to lifestyle change.

Larval limbs and their transformation into the definitive cephalic appendages are proposed here as obvious indicators of lifestyle change and metamorphosis because of drastic change of their function and morphology. To test this assumption, we aim to review the functional anatomy and development of cephalic limbs in sea spiders with a focus on their transformation during the metamorphosis. The main questions of the article are the following:

– Does the structure of the larval cephalic limbs correlate more with the taxonomic position or the mode of life in early instars?

– Is it possible to identify the lifestyle characteristics of pycnogonid young based on the structure of their larval limbs, and how reliably?

– To what extent does the timing of cephalic limb changes during metamorphosis correlate with changes in life mode?

– How can postembryonic development of pycnogonids be periodized based on cephalic appendages morphology, as the most easily discernible marker of the lifestyle change?

## Review of postembryonic development of cephalic limbs in Pycnogonida

### Gradual metamorphosis of cephalic limbs in the first type of postembryonic development

The first type of postembryonic development is characteristic of Pycnogonidae, Ascorhynchidae, Endeidae, part of Nymphonidae, part of Ammotheidae, and some Pallenopsidae (Brenneis *et al.*, 2017). Also, in some species of Pallenopsidae and Ascorhynchidae only protonymphon larvae (1st instar) were described (Carpenter, 1907; Burris, 2011; Hübner *et al*., 2017).

Sea spiders with this type of development are characterized by a certain trait in the protonymphon limbs morphology. The length of the spinning spine is comparable to those of the chela, the spinning gland consists of two secretory cells. In many species, chelar glands opening on the tips of the fingers was described (Brenneis *et al*., 2017). In larval legs the distal claw-like podomere is longer than the middle.

The development of the cephalic limbs is reviewed below for the species from different pycnogonid families. For the species with a comparatively complete series of instars known, a graphical summary of the development of the cephalic limbs is given (Figs 3–5).

**Nymphonidae**

The only nymphonid species with the first type of development for which the complete series of postembryonic instars was properly described is *Nymphon brevirostre*, Hodge 1863. The number of molts was documented by Alexeeva *et al*. (2018) and confirmed by our own observations.

The morphology of *N. brevirostre* protonymphon is typical of the first type of development.

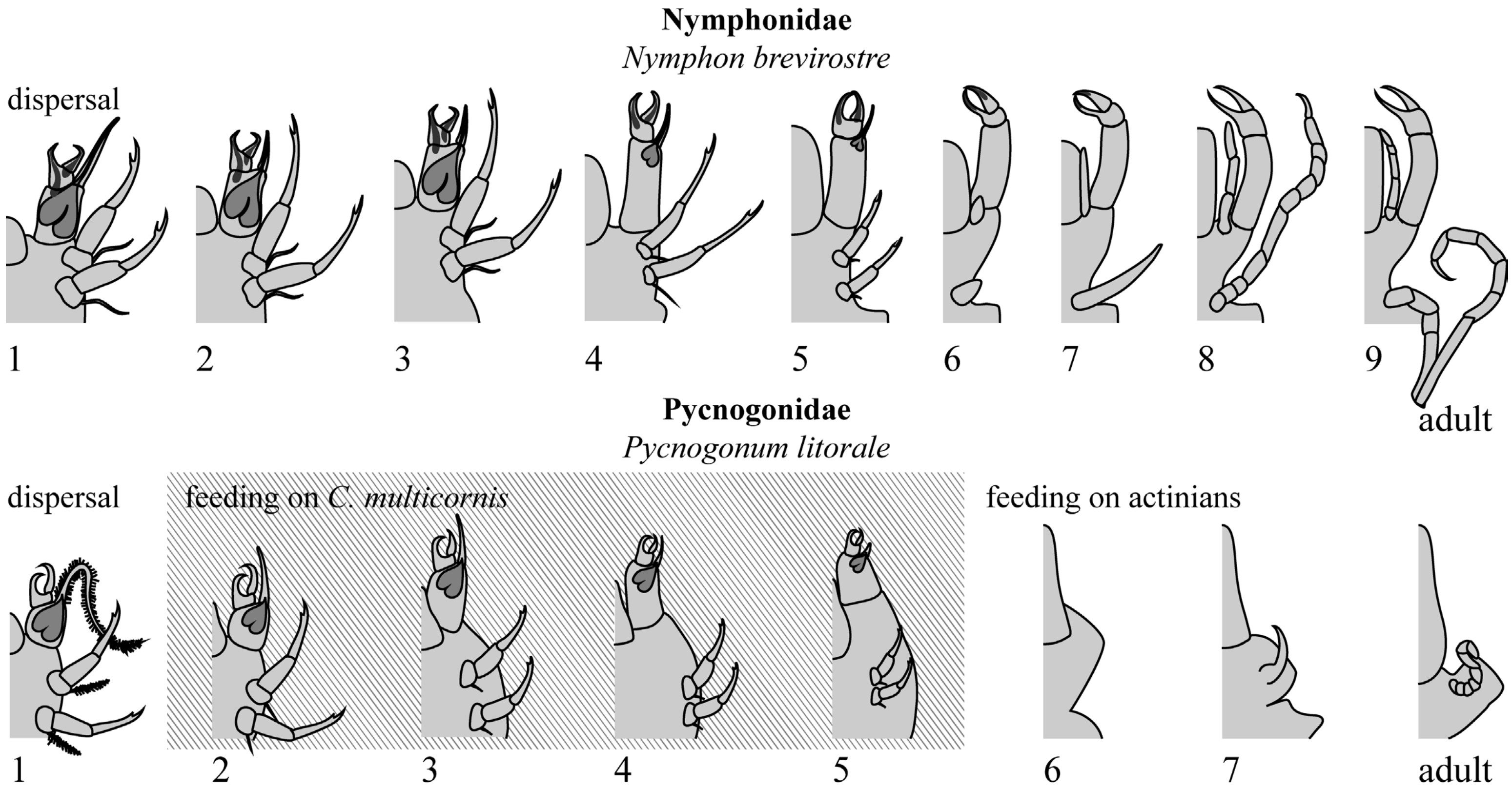


Fig. 3. Development of cephalic limbs in pycnogonids with the first type of development: Nymphonidae and Pycnogonidae (after Dogiel, 1913; Behrens, 1984; Vilpoux, Waloszek, 2003; Alexeeva *et. al*, 2018, Alexeeva, Tamberg, 2020). Instars are numbered below the diagrams and are all represented in ventral view. Chelar glands are dark gray, spinning glands are lighter gray.

The complete larval glandular apparatus present, including chelar glands opening on the tips of both fingers (Bogomolova, 2007; Alexeeva *et al.*, 2017, 2018).

Until the 5th instar, all the cephalic limbs do not change in their appearance and podomeres proportions, and only their relative size decreases, due to the growth of the rest of the body (Fig. 3).

Cheliphores transformation starts from the 4th instar. In the 4th and 5th instars the scape (basal podomere) of the cheliphore elongates, and the spinning spine diminishes. In the 6th instar, the spinning apparatus disappears, the chela, previously oriented forward and coaxially to the scape, now rotates to bend toward the mouth. During further instars, cheliphores gradually achieve their definitive proportions. In the 8th instar, chelar glands disappear (Fig. 3).

Palpal and ovigeral larval legs start to reduce from the 5th instar: their distal segments and basal spine diminish significantly compared to the 4th instar (Fig. 3). To the end of the 5th instar, muscles of larval legs resorb. In the 6th instar, in place of the palpal and ovigeral limbs, only remnants remain in the form of small, unsegmented buds. In the 7th instar, the buds elongate which marks the beginning of growth of the definitive limbs. In the 8th instar, ovigerous legs attain the definitive segmentation, and palps comprise three podomeres (Fig. 3). In the 9th instar, all the cephalic appendages have a definitive structure (Alexeeva *et al.*, 2018). Throughout all its post-embryonic development, *N. brevirostre* feeds exotrophically on *Obelia* hydrozoans. There is no radical change in the food source, although adult individuals, in the absence of preferred food, can switch to feeding on other cnidarians (Bogomolova, Petrova, personal observations).

### Pycnogonidae

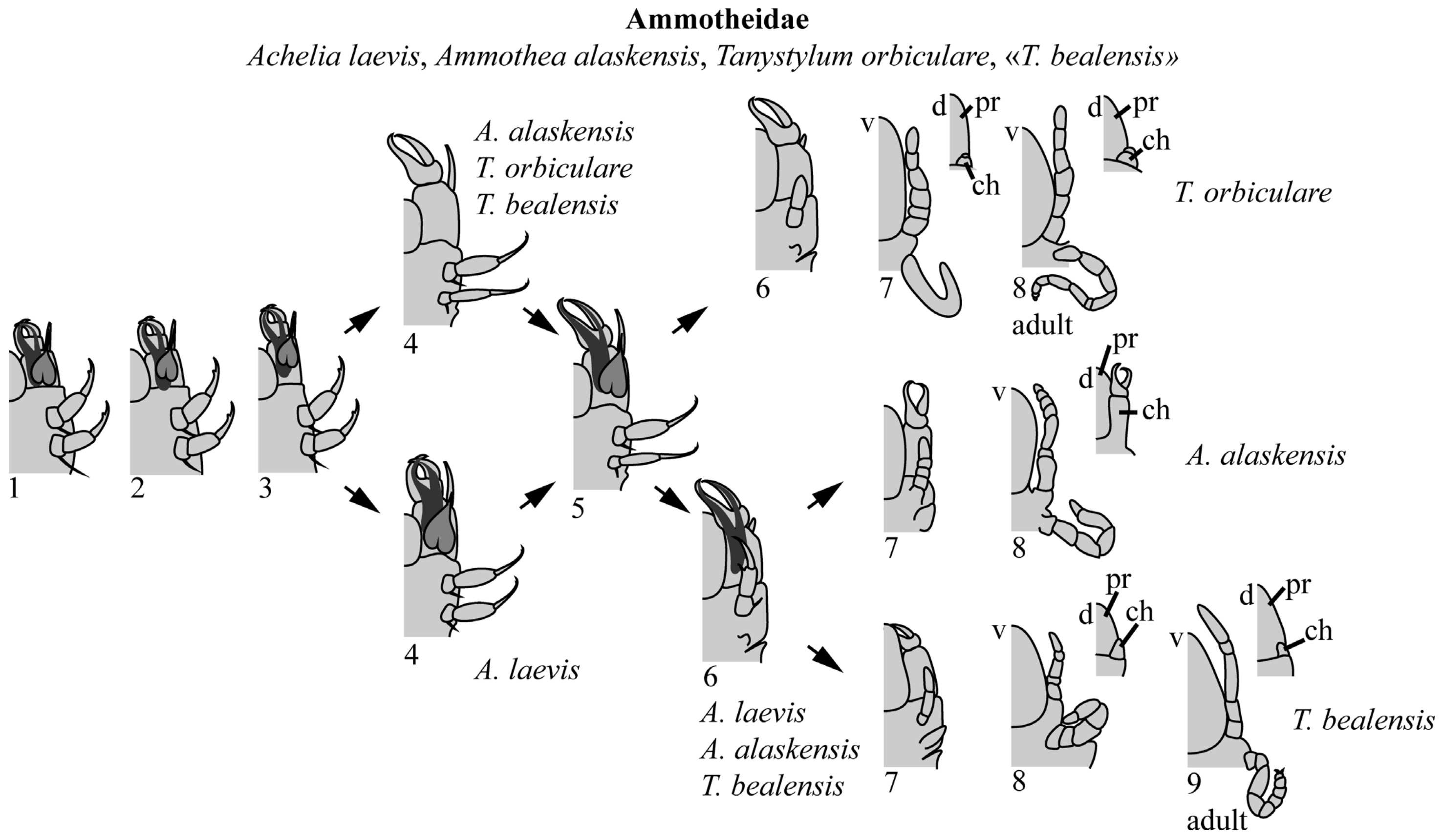
Of this family, several descriptions of complete development of *Pycnogonum litorale* (Strøm, 1762) by different authors are available. Also, protonymphons of *P. ricketsi* Schmitt, 1934 and *P. stearnsi* Ives, 1883 are known. Protonymphon larvae of *P. stearnsi* have quite typical morphology (Burris, 2011), but in *P. litorale* and *P. ricketsi* they have extremely elongated spinning spines and basal spines of ovigeral and palpal limbs, covered with cuticular hairs. Protonymphon larvae and all further instars of *P. litorale* lack chelar glands (Alexeeva *et al.*, 2019; Alexeeva, Tamberg, 2020), for two other species chelar glands were not mentioned. The description below is based on *P. litorale* development. Data on molts are published by several authors (Dogiel, 1913; Behrens, 1984; Tomaschko *et al.*, 1997; Vilpoux, Waloszek, 2003; Alexeeva, Tamberg, 2020) and consistent with each other.

Protonymphon larvae leave their father's ovigers and start feeding on a hydrozoan *Clava multicornis* (Forsskål, 1775). As a result of the first molt the spinning spine and basal spines of the larval palps and larval ovigers shorten and lose their pubescence. It can be speculated that the elongated appendages may aid in dispersal. Further on, the comparative size of the chela, the spinning spine, and the ovigeral and papal larval legs diminish until the 5th instar during which soft tissue in cheliphores and larval legs resorbs. The 5th instar is the last of those found on *C. multicornis*. After the molt to the 6th instar cheliphores and larval legs disappear and young *P. litorale* begin to feed on its definitive prey species, *Metridium senile* (Linnaeus, 1761) or other sea anemones. Buds of definitive ovigers appear at the 7th instar in males only and do not change during undetermined number of juvenile instars. After the last molt, definitive ovigers of eight podomeres release (Dogiel, 1913; Behrens, 1984; Tomaschko *et al.*, 1997; Vilpoux, Waloszek, 2003; Alexeeva, Tamberg, 2020).

### Ammotheidae

The metamorphosis of ovigeral and palpal larval legs was described for five species: *Achelia laevis* Hodge, 1864, *Achelia* (*Ammothea*) *alaskensis* (Cole, 1904), *Tanystylum orbiculare* Wilson, 1878, *Ammothella biunguiculata* (Dohrn, 1881), and *"T. bealensis*" (*nomen nudum*, no description published). Complete series of instars and exact number of molts are known for three species — "*T. bealensis*", *A. biunguiculata, A. laevis* (Morgan, 1891; Dogiel, 1913; Okuda, 1940; Gillespie, Bain, 2006).

In *A. laevis*, *A. alaskensis*, *T. orbiculare*, "*T. bealensis*" larvae and adults feed on the same kind of prey. Cheliphores do not change until the 6th instar, when the spinning spine shortens, and in the 7th instar, it disappears completely (Fig. 4) (Morgan, 1891; Dogiel, 1913; Okuda, 1940; Gillespie, Bain, 2006). Data on glands are available only for *A. laevis*: the silk gland


**Ammotheidae**

*Achelia laevis*, *Ammothea alaskensis*, *Tanystylum orbiculare*, «*T. bealensis*»

Fig. 4. Development of cephalic limbs in pycnogonids with the first type of development: Ammotheidae other than *Ammothella* (after Morgan, 1891; Dogiel, 1913; Okuda, 1940; Gillespie, Bain, 2006). Instars are numbered below the diagrams. In case the morphology of the same instars differs among species, the corresponding instars are represented above each other, and species noted next to the separate instar or the row of subsequent instars. In most diagrams, the ventral view is represented. Dorsal view (d) of the same instar is shown next to the ventral view (v).
Abbreviations: ch — cheliphore; pr — proboscis. Chelar glands are dark gray, spinning glands are lighter gray.

resorbs in the 6th instar, while chelar glands are not mentioned in the text, but depicted in the same size as in the previous instar; data on the further development of *A. laevis* are absent (Dogiel, 1913). In the 7th instar in *T. orbiculare* and the 8th instar in "*T. bealensis*" (the last pre-adult instar), cheliphores lose chela (Morgan, 1891; Gillespie, Bain, 2006). In *A. alaskensis*, the process of reduction of cheliphores has not been documented.

The palpal larval legs of Ammotheidae do not reduce to small, unsegmented buds, unlike in the Nymphonidae young. Until the 5th instar in *T. orbiculare* and the 6th in *A. laevis*, *A. alaskensis*, and "*T. bealensis*" they do not change. Then, in the next instar, juvenile palps with an incomplete number of segments appear, and after one more molt palps get definitive number of podomeres (Fig. 4).

The ovigeral larval legs become thinner in the 4th instar in *A. alaskensis*, *T. orbiculare*, *"T. bealensis*", and in the 5th instar in *A. laevis*. In the 6th instar, on the place of ovigeral larval legs, only small buds remain. In the 8th instar, they begin to elongate to become the definitive ovigers later on. In *T. orbiculare*, in the 9th instar, definitive ovigers are formed; in *A. alaskensis* and *T. bealensis* incompletely articulated limbs appear. In *T. bealensis* the 10th instar has definitive ovigers (Fig. 4).

*Ammothella biunguiculata* (Dohrn, 1881) development is of a special kind: while protonymphon anatomy and the order of walking legs formation remain typical of the first developmental type, the life mode of larvae is unique among other ammotheid larvae known. Protonymphons of *A. biunguiculata* infect sea anemones, molt inside, and over the further development live as endoparasites. The spinning spine disappears already in the 2nd instar. In the 3rd instar, distal segments and basal spines of larval legs reduce (Fig. 5). Excepting the early reduction of spinning spine and larval legs, the metamorphosis of *A. biunguiculata* in morphologigal aspect is very similar to those described for other ammotheids (Mochizuki, Miyazaki, 2017).

### Endeidae

*Endeis spinosa* (Montagu, 1808) is the only species of this family for which the postembryonic development including molts was documented (Dogiel, 1913).

Cheliphores do not change until the 4th instar. During the period from the 4th instar till the 6th instars, the spinning spine shortens, and the cheliphore scape elongates. In the 7th instar, the spinning spine disappears. Later during the same instar soft tissue in the cheliphores resorbs, and after the next molt, cheliphores disappear (Fig. 5). Until the 7th instar the spinning gland and chelar glands are present in cheliphores (Dogiel, 1913).

The reduction of palpal and ovigeral larval legs is synchronous and starts in the 5th instar with basal spines loss. In the 6th instar, only small buds remain, which smoothen in further development (Fig. 5). Palps are absent in adult Endeidae. The formation of definitive ovigers in males was not described (Dogiel, 1913).

## Accelerated metamorphosis in the second type of postembryonic development

The development of this type was reported for some nymphonids and ammotheids (Figs 6, 7) (Brenneis *et al.*, 2017). Graphical summary of known stages for the species with this type of development is shown in Fig. 6.

### Nymphonidae

This type of development has been revealed in *Nymphon hirtipes* Bell, 1855, *N. grossipes* (Fabricius, 1780), *N. macronyx* Sars, 1877, *N. unguiculatum* Hodgson, 1915, and *N. charcoti* Bouvier, 1911. All instars described were found on ovigers of males (Dogiel, 1913; Bogomolova, Malakhov, 2003; Bogomolova, 2007, 2010; Cano-Sánchez, López-González, 2010; Fornshell, 2017; Alexeeva, Tamberg, 2022).

In lecithotrophic protonymphon larvae of this developmental type, the posterior portion of the body is enlarged, resulting in their cephalic appendages being small in comparison to the rest of the body. Cheliphores are robust, with stout fingers. The spinning spine is shorter than the chela; the silk gland consists of more than ten secretory cells. Chelar glands are not found but there are pores on the fingertips, possibly sensory. Ovigeral and palpal larval legs have the same structure as in the larvae with first type of development but are more robust. Unlike in typical protonymphon, distal claw-like podomere is almost equal in length to middle podomere (Dogiel, 1913; Bogomolova, Malakhov, 2003;

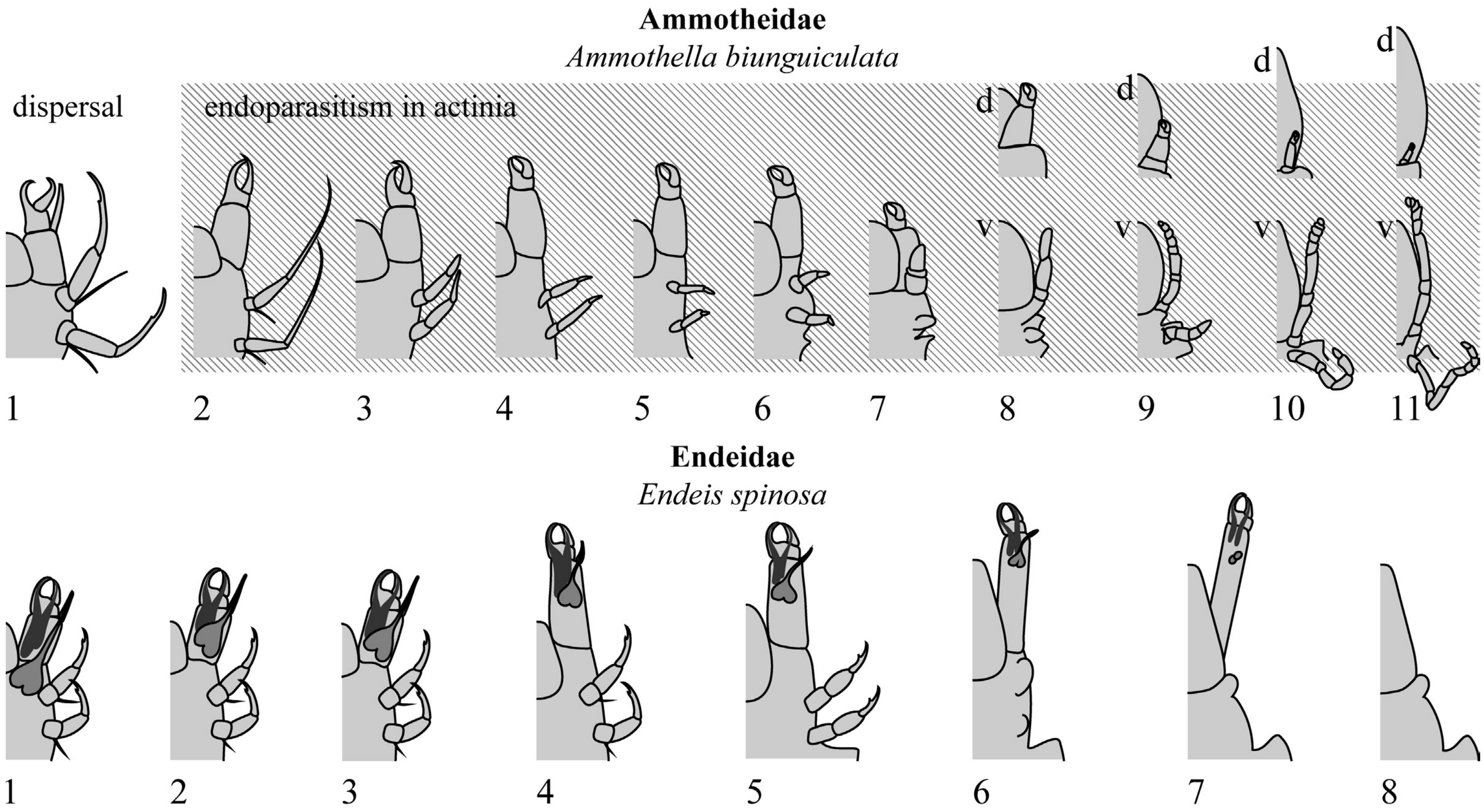


Fig. 5. Development of cephalic limbs in pycnogonids with the first type of development: *Ammothella biunguiculata* (Ammotheidae) and Endeidae (after Dogiel, 1913; after Mochizuki, Miyazaki, 2017). The instars are numbered below the diagrams. In most diagrams, the ventral view is represented. Dorsal view (d) of the same instar is shown above the ventral view (v). Chelar glands are dark gray, spinning glands are lighter gray.

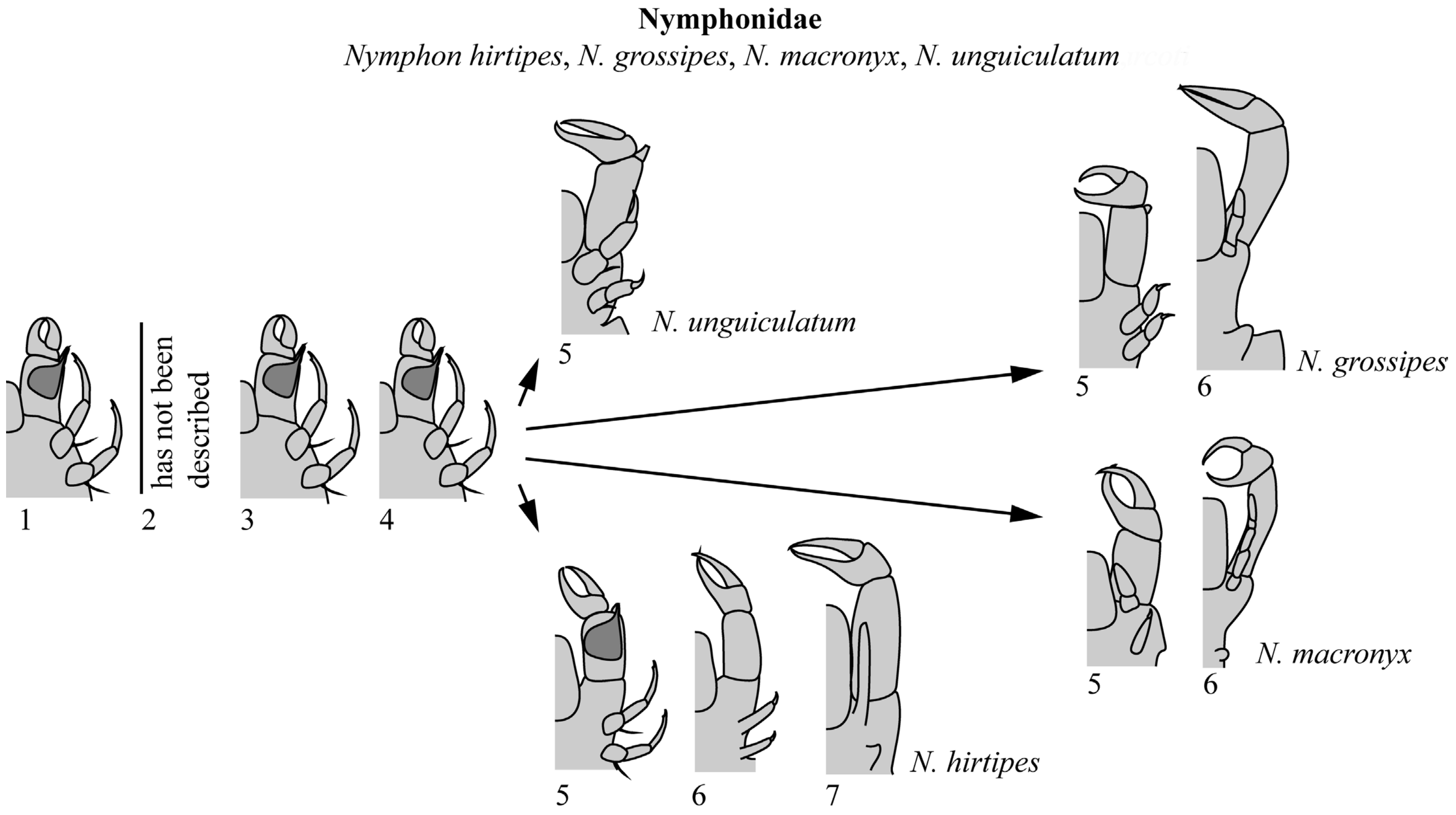


Fig. 6. Development of cephalic limbs in pycnogonids with the second type of development: Nymphonidae (after Dogiel, 1913; Bogomolova, 2007, 2010; Bogomolova, Malakhov, 2003; Cano-Sánchez, López-González, 2010; Fornshell, 2017). Instars are numbered below the diagrams. Instars 1–4 do not differ between species, for instars 5–7 species noted next to the diagrams. All pictures represent ventral view. Spinning glands are dark gray.

Bogomolova, 2007, 2010; Cano-Sánchez, López-González, 2010; Fornshell, 2017; Alexeeva, Tamberg, 2022).

During the first four instars, cephalic appendages do not change. In the 5th instar, the spinning spine shortens; the shape of the chela begins to change and during the next several instars it approaches the final form (Fig. 6). The spinning apparatus disappears in the 6th instar (Dogiel, 1913; Bogomolova, Malakhov, 2003; Bogomolova, 2007, 2010; Cano-Sánchez, López-González, 2010; Fornshell, 2017; Alexeeva, Tamberg, 2022).

The reduction of palpal and ovigeral larval legs starts in the 5th instar in all species except *N. hirtipes*. The process of reduction varies in detail among species, as well as its timing, but this may be explained by the incompleteness of the developmental series available for study and the molts not accurately documented. In *N. unguiculatum*, the distal claws of both pairs of larval legs shorten, the ovigeral larval legs diminished (Cano-Sánchez, López-González, 2010). In *N. grossipes*, both larval leg pairs reduce in the same way: their distal podomeres diminish, basal spines disappear. In the 6th instar, three-articled palps and short unarticulated buds of ovigers appear (Bogomolova, Malakhov, 2003; Bogomolova, 2007). In *N. macronyx*, palpal larval legs were never seen reduced to small buds, and in the 5th instar, two-articled palps already appear. Ovigeral larval legs lose segmentation and their distal podomere shortens in the 5th instar. In the 6th instar, palps attain the definitive number of podomeres; ovigeral larval legs further reduce to small unarticulated buds (Bogomolova, 2010). The further development was not described. In *N. hirtipes*, the reduction of larval legs starts in the 6th instar. Both legs become unarticulated, their distal podomeres shorten. Ovigeral larval legs become slightly smaller than palpal. In the 7th instar long unarticulated buds of palps and small unarticulated buds of ovigers appear (Dogiel, 1913). The further metamorphosis was not described for the *Nymphon* species listed above.

### Ammotheidae

In this family, the second type of development is ascribed to *Ammothea glacialis* (Hodgson, 1907), *A. carolinensis* Leach, 1814, *A. longispina* Gordon, 1932, *A. bicorniculata* Stiboy-Risch, 1992 (Cano, López-González, 2009; Cano Sánchez, López-González, 2013; Fornshell, Ferrari, 2012), and *A. gigantea* Gordon, 1932 (Fornshell, 2014). For *A. glacialis*, *A. carolinensis*, *A. longispina*, *A. bicorniculata*, first four instars are known, found on ovigers of males, and for *A. gigantea* only two instars (presumably the 3rd and the 4th). All the descriptions are based on preserved material from museum storage, so data on molts are absent, but Cano-Sánchez and López-González inferred the number of instars based on the morphology of all the instars of the different species found (Cano, López-González, 2009; Cano Sánchez, López-González, 2013). Here, we number instars following their assumption (Fig. 7).

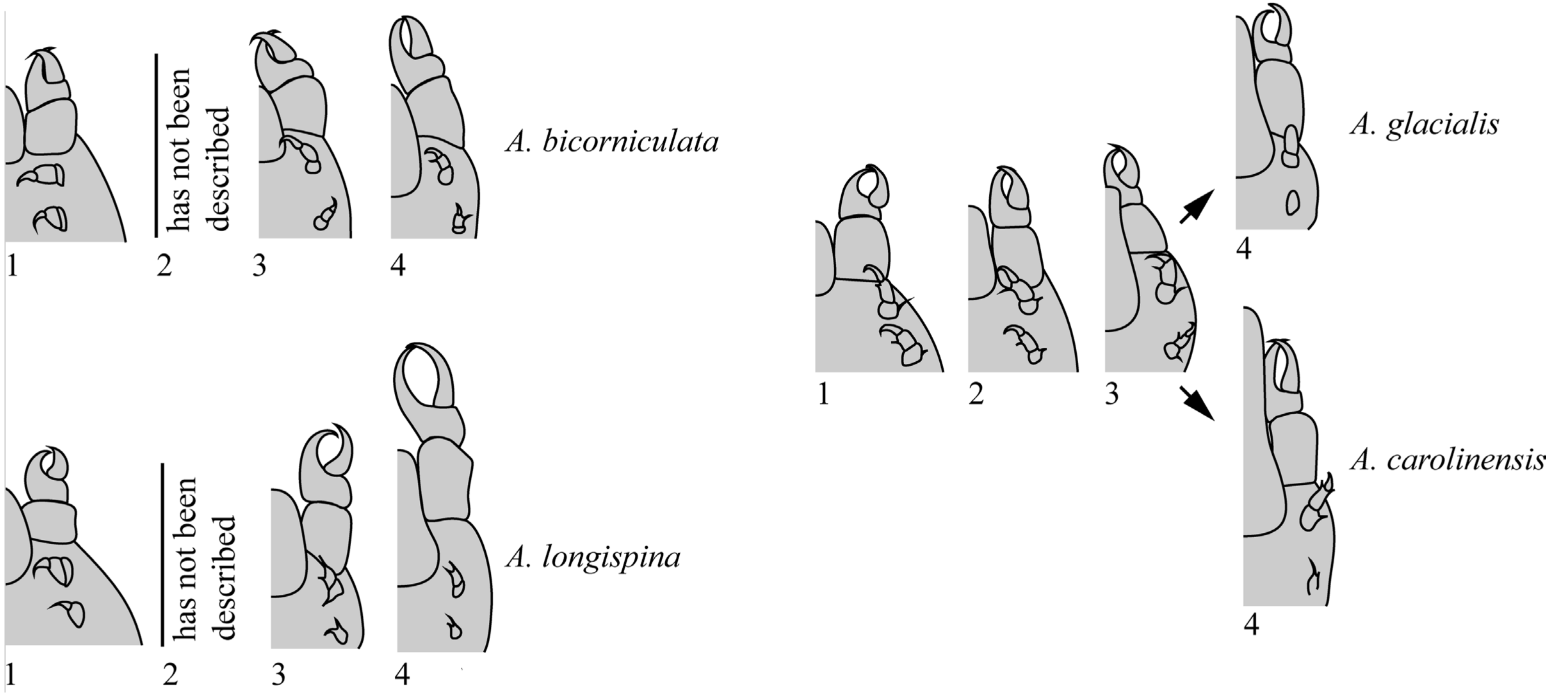
Protonymphon larvae have extremely small cephalic limbs compared to the body. On cheliphores, the spinning spine is absent, and possibly the silk glands as well. Chelar glands were not mentioned. Palpal and ovigeral larval legs are of different morphology across species. In *A. glacialis*, *A. carolinensis*, and *A. bicorniculata* limbs of both pairs consist of three podomeres with a claw-like distal one. In *A. bicorniculata,* ovigeral larval legs are smaller than palpal, basal spine is absent in both pairs. In *A. longispina,* palpal larval legs have the same structure as in *A. bicorniculata,* but in ovigeral legs only two podomeres revealed: the proximal and the claw-like distal.

The shape of the chela changes in the 3rd instar in *A. bicorniculata* and *A. longispina*, and in the 4th instar in *A. glacialis* and *A. carolinensis*. It becomes bigger if compared to the scape of the cheliphore, fingers become thinner and longer.

The reduction of palpal and ovigeral larval legs begins in the 3rd instar, that is one molt earlier than in species of the same family with the first type of development. Ovigeral larval legs reduce faster than palpal. In *A. glacialis* in the 4th instar, two-segmented palps and unarticulated buds of ovigers appear. In other described cases in this instar the reduction of larval legs still continues (Cano, López-González, 2009; Fornshell, Ferrari, 2012; Cano Sánchez, López-González, 2013). The further metamorphosis is not described.

## Specialization for attachment to the host in the third type of postembryonic development

This is the rarest type of development based on available data. Postembryonic developmental



**Ammotheidae**

*Ammothea glacialis*, *A. carolinensis*, *A. longispina*, *A. bicorniculata*

Fig. 7. Development of cephalic limbs in pycnogonids with the second type of development: Ammotheidae (after Cano, López-González, 2009; Cano-Sánchez, López-González, 2013). Instars are numbered below the diagrams. In *Ammothea glacialis* and *A. carolinensis* instars 1–3 do not differ between species. All pictures represent ventral view.

series have been reported for two species only: *Ammothella spinifera* Cole, 1904 (Ammotheidae) and *Nymphonella tapetis* Ohshima, 1927 (Ascorhynchidae) (Brenneis *et al*., 2017), but no reliable observation of molts was made for these species. Here we keep stages demarcation according to original descriptions. The development of cephalic limbs is redrawn in Fig. 8.

Protonymphon was found in a single species with proved further development of the third type, *N. tapetis.* The spinning spine is absent, chelar glands were not mentioned. Ovigeral and palpal larval legs are typical, i.e., with three podomeres, the distal of which is the longest, basal spine present (Ohshima, 1935).

***Nymphonella tapetis***

After the larva invades the mantle cavity of the host, a bivalve *Ruditapes philippinarum* (Adams et Reeve, 1850), it molts. It is not clear whether parasitic stages identified by Ohshima are separated by molts. Cheliphores do not change their morphology throughout the endoparasitic period; young use them to fasten on the host. During the first two parasitic stages the larval legs retain their distal claws, but the joints smoothen. In the last stage described (stage 4, walking legs are long unarticulated buds), definitive palps and ovigers start to develop: the limbs segment into five and four podomeres, correspondingly (Fig. 8). According to Ohshima, these two pairs of limbs do not participate in the attachment of the larva to the host (Ohshima, 1927, 1933, 1935, 1937). The further development is unknown. As the adults in this genus have reduced cheliphores (Ohshima, 1927) their reduction must happen after the parasitic period.

***Ammothella spinifera***

Larvae develop inside the tubes of sessile polychaetes *Bispira melanostigma* (Schmarda, 1861). The earliest stage described is, probably, the first parasitic instar: it has very small anlagen of trunk segments. As in *N. tapetis,* cheliphores of *A. spinifera* do not change during the parasitic period. In the earliest of instars described, larval legs are already reduced, their distal claw absent and joints smoothened (Fig. 8). According to drawings in the original description, after the next molt they articulate again into three podomeres with hook-like distal one and participate in the attachment of the larva. Ovigeral and palpal larval legs grow with the rest body, so their comparative size does not change. In the latest parasitic instar described, palpal legs become five-articled and ovigeral limbs four-articled, but their distal-most podomeres remain hook-like (Fig. 8). It is supposed to be the beginning of the formation of the definitive limbs (Salazar-Vallejo, Stock, 1985). In adult animals palps and ovigers have nine segments (Hedgpeth, 1948), so at least one more molt is necessary to form definitive limbs. Adult specimens of *A. spinifera* also have reduced cheliphores (Hedgpeth, 1948), so their reduction must happen after the parasitic period.

## Early loss of palpal and ovigeral legs in the fourth type of postembryonic development

The fourth type of development is found almost exclusively in Phoxichilidiidae (Bettim, Haddad, 2013; Brenneis *et al*., 2017) and modified protonymphon morphology is characteristic for the family. Among ammotheids, the fourth type of development was proved for *Ammothea hilgendorfi* (Böhm, 1879) only (Russel, Hedgpeth, 1990). In this species, protonymphon has the typical appearance; the morphology of further instars was not described (Brenneis *et al*., 2017). The development of cephalic limbs in this type of development is summarized in Fig. 9.

**Phoxichilidiidae**

In Phoxichilidiidae, protonymphon is miniaturized; it lacks a spinning apparatus, but has huge chelar glands that occupy the entire volume of the cheliphores (Fig. 9). The chelar glands open on both fingertips. Ovigeral and palpal legs in these larvae have very long thread-like distal podomeres (Dogiel, 1913; Bogomolova, Malakhov, 2003). Observations of molts were made by Dogiel (1913).

Further development of *Phoxichilidium* and *Anoplodactylus* was described many times by different authors. Observation of larvae living inside polyps is difficult, so different authors divide the development into stages by various ways: some trying to detect molts, other following alternative criteria (Adlerz, 1888; Loman, 1907; Dogiel, 1913; Hilton, 1916; Lebour, 1916; Lovely, 2005; Maxmen, 2013). The most detailed descriptions were made for *Phoxichilidium* by Lovely and Dogiel (Do-

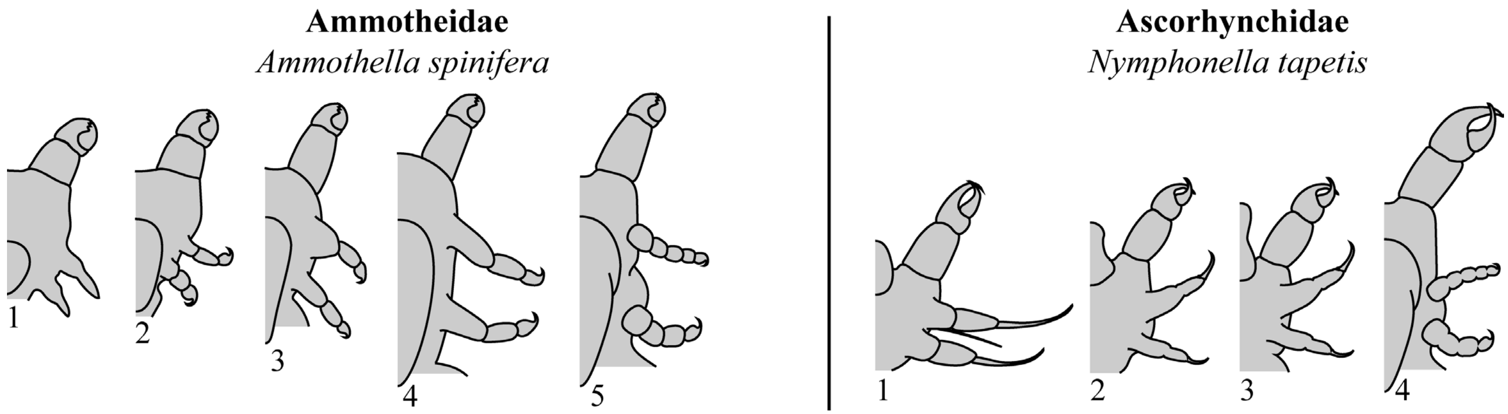


Fig. 8. Development of cephalic limbs in pycnogonids with the third type of development (after Oshima, 1927, 1935, 1937; Salazar-Vallejo, Stock, 1985). Instars are numbered below the diagrams. All pictures represent ventral view.

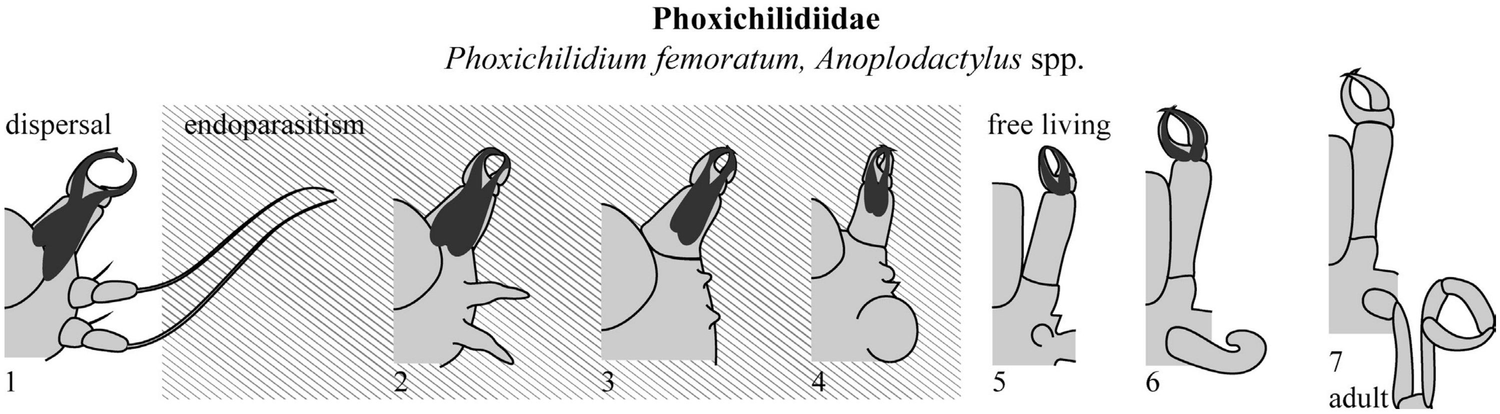


Fig. 9. Development of cephalic limbs in pycnogonids with the fourth type of development. Instars are numbered below the diagrams (after Dogiel, 1913; Hilton, 1916; Lebour, 1916; Lovely, 2005; Maxmen, 2013). All pictures represent ventral view. Chelar glands are dark gray.

giel, 1913; Lovely, 2005). Dogiel worked on *Phoxichilidium femoratum* (Rathke, 1799), and Lovely on "*Phoxichilidium tubulariae"*. The second of the two species was later accepted as a synonym of the first (Bamber *et al*., 2025), but the descriptions of their development slightly differ. Dogiel also claims that the development of *Anoplodactylus* spp. follows the same pattern as that of *Phoxichichilidium* (Dogiel, 1913). Here we adopt stages distinguished by Lovely (2005) and Dogiel (1913), who suppose that they are separated by molts.

According to Dogiel's and Lovely's observations, position and proportions of cheliphores change insignificantly, they grow proportionally to the rest body until the 5th instar, when the juvenile emerges from the polyps (Fig. 9). After that cheliphores attain shape and proportions close to definitive ones without any intermediate condition. SEM micrographs in Lovely's paper show that in the endoparasitic stages the chela fingers are more robust than in the protonymphon. The relative size of the chelar glands gradually diminishes, but even late juvenile instars have well-developed chelar glands.

Palpal and ovigeral larval legs start to reduce in the 2nd instar, their distal filaments disappear, joints between the rest two podomeres smoothen (Fig. 9), and the limbs almost lose movability. In the 3rd instar, the limbs reduce to small buds and remain in this state until the 5th instar, when the young emerge from the polyps. In this stage in females, the cephalic limbs disappear completely, while in males the ovigerous legs start to grow. The development of ovigers takes three instars: in the 5th, they are small buds; in the 6th, elongate and are hook-shaped, and in the 7th, they become segmented and attain the definitive structure (Fig. 9) (Dogiel, 1913; Lovely, 2005).

## Reduction of palpal and ovigeral legs in the fifth type of postembryonic development

The fifth type of development was described in Callipallenidae, several Nymphonidae, and several Pallenopsidae species (Brenneis *et al*., 2017). A graphical summary is given in the Fig. 10.

### Nymphonidae

The fifth type of development was observed in five nymphonid species: *Nymphon australe* Hodgson, 1902, *N. brevicaudatum* Miers, 1875, *N. floridanum* Hedgpeth, 1948, *N. micronesicum* Child, 1982 and *Boreonymphon abyssorum* (Norman, 1873) (Hoek, 1881; Meinert, 1899; Cano-Sánchez *et al*., 2020; Arango, Brenneis, 2024). No reliable data on molts are available, so here we number instars after Cano-Sánchez *et al*. (2020), who made the fullest description of this type of development in Nymphonidae.

Young hatch bearing cheliphores, three or four pairs of walking leg buds, and, depending on the species, different sets of larval legs (Fig. 10). According to the drawings provided in the descriptions, the chelae are elongated, the chela:scape and the fingers:chela length ratios (Hoek, 1881; Meinert, 1899; Cano-Sánchez *et al*., 2020) are higher, and so, closer to the definitive state, than in the larvae of the same family but with different (first or second) types of development. Hoek and Meinert did not describe the glandular apparatus of the larvae (Hoek, 1881; Meinert, 1899). In *N. australe, N. micronesicum* and *N. floridanum* the spinning spine is extremely short, number of cells in spinning glands is not known, chelar glands were not mentioned (Cano-Sánchez *et al*., 2020; Arango, Brenneis, 2024).

According to Meinert's drawings, *B. abyssorum* possess both palpal and ovigeral larval legs of the same appearance as in nymphonid larvae of the second type of development, but the ovigeral leg is slightly smaller than the palpal (Meinert, 1899). Larvae of *N. brevicaudatum* and *N. australe*, *N. micronesicum* and *N. floridanum* have one pair of unarticulated larval legs with small distal claws (Fig. 10) (Hoek, 1881; Cano-Sánchez *et al*., 2020; Arango, Brenneis, 2024). In *N. australe*, *N. micronesicum* and *N. floridanum* the subsequent development of these limbs reveals them as palpal (Cano-Sánchez *et al*., 2020; Arango, Brenneis, 2024).

The further development was described for *N. australe* only; all five instars described were found on males' ovigers and, consequently, are lecithotrophic. The shape and proportions of cheliphores gradually change toward definitive ones during all the development described. The spinning spine disappears in the 3rd instar. In the same instar, two anterior pairs of walking legs become segmented. The basal podomere of palpal larval leg elongates in the 2nd instar, while the distal claw diminishes (Fig. 10). In the 3rd instar, palps with definitive articulation appear. Ovigers appear for the first time in the 3rd

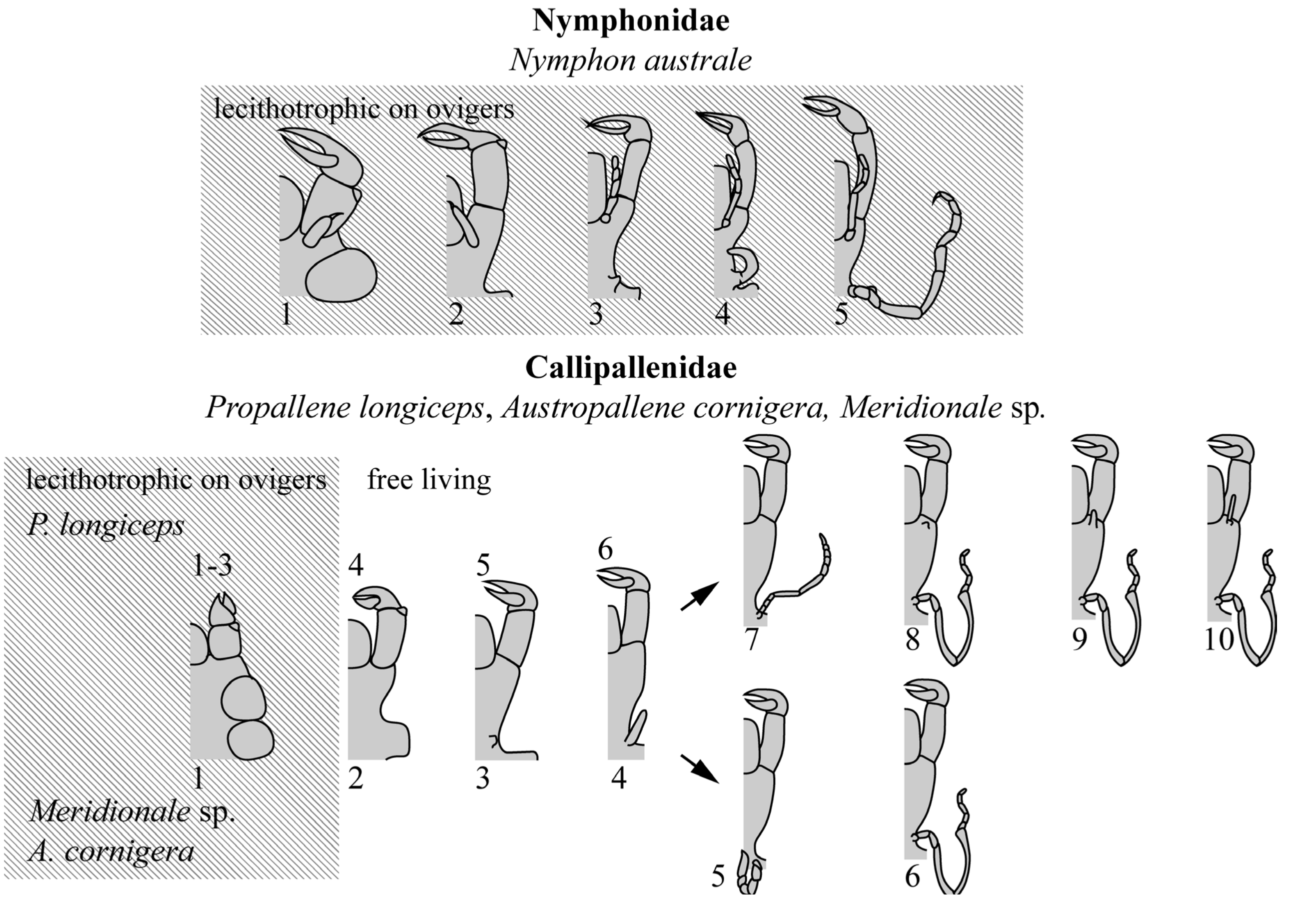


Fig. 10. Development of cephalic limbs in pycnogonids with the fifth type of development (after Nakamura, 1981; Bain, 2003b; Brenneis *et al.*, 2011; Cano, López-González, 2009; Cano-Sánchez, López-González, 2013, 2020). Instars are numbered above the pictures for *P. longiceps*, and below the pictures for *Meridionale* sp. and *A. cornigera*. From the instar 7/5 the above row represents development of *P. longiceps*; the below those of *Meridionale* sp. and *A. cornigera.* All pictures represent ventral view.

instar as small buds. In the next, 4th, instar they become elongated, curved but unsegmented, and in the 5th instar attain the definitive number of segments (Cano-Sánchez *et al.*, 2020).

### Callipallenidae

Hatching instars of Callipalenidae bear buds of two pairs of walking legs, and therefore are at more advanced stage than the protonymphon. They have cheliphores with a conical spinning spine much shorter than the chela (Nakamura, 1981; Bain, 2003b; Bogomolova, Malakhov, 2003; Brenneis *et al.*, 2011). Chelae are robust (Fig. 10). In *Austropallene cornigera* (Möbius, 1902), *Meridionale* sp. and *Pseudopallene spinipes* (Fabricius, 1780) the tip of the immovable finger looks bidentate since it bears a shallow groove where the tip of the movable finger fits when the chela is closed (Bain, 2003b; Brenneis *et al.*, 2011). In *Meridionale* sp., chelar glands were described in the movable finger. All described hatclings of Callipallenidae lack larval legs (Nakamura, 1981; Bain, 2003b; Bogomolova, Malakhov, 2003; Brenneis *et al.*, 2011), but in some specimens of *P. spinipes*, small rudiments just behind the proboscis base were found. These possibly correspond to one of the larval leg pairs (Bogomolova, Malakhov, 2003). Molts were documented by Brenneis *et al.* (2011) and Nakamura (1981).

More or less complete series of instars were described for *Propallene longiceps* (Bohm, 1879), *A. cornigera*, and *Meridionale* sp., data on the life mode of young are available on *P. longiceps* and *Meridionale* sp. (Nakamura, 1981; Bain, 2003b; Brenneis *et al.*, 2011). In *Meridionale* sp. and *A. cornigera*, the development proceeds almost identically (Fig. 10). The 1st instar bears two pairs of long unarticulated buds of walking legs. In the 2nd instar, two pairs of articulated legs appear (Bain, 2003b; Brenneis *et al.*, 2011). Two instars, described for *P. spinipes* are almost identical to the 1st and 2nd instars of previous species (Bogomolova, Malakhov, 2003). In *P. longiceps*, earliest three instars bear unarticulated walking legs, gradually elongating, and only the 4th one attains two pairs of articulated walking legs (Nakamura, 1981). So, the 2nd instar of *Meridionale* sp., *P. spinipes* and *A. cornigera* is comparable to the 4th instar of *P. longiceps* by the set of limbs.

Cheliphores do not change until two pairs of segmented walking legs are released. Then, cheliphores proportions change: the basal segment elongates compared to the chela, shape of the fingers become closer to the definitive one, the chela tilts and bends toward the mouth; the spinning spines still present (Fig. 10) (Nakamura, 1981; Bain, 2003b; Bogomolova, Malakhov, 2003; Brenneis *et al.*, 2011). In the same instar, in *Meridionale* sp. and *P. longiceps* in the same instar, larvae abandon the adult male and start feeding on their definitive prey. In 5th instar, in *P. longiceps* chelae are quite similar to adult ones (Nakamura, 1981), while in *Meridionale* sp. differ from both larval and adult with an elongated curved tip of the movable finger (Brenneis *et al.*, 2011). In *A. cornigera*, the larvae stay on father's ovigers until the molt to the 6th instar. In this instar, the shape of the chelae differs from both larval and definitive ones (Bain, 2003b). In the instar with three pairs of segmented walking legs (5th in *P. longiceps,* 3rd in *Meridionale* sp. and *A. cornigera*), the spinning spine disappears (Nakamura, 1981; Bain, 2003b; Brenneis *et al.*, 2011). In *P. longiseps,* a change of feeding mode is described in the 6th instar (all walking legs segmented), but without any morphological changes in cheliphores; while, in the morphologically analogous (3rd) instar in *A. cornigera,* cheliphores become adult-like. In the 3rd instar of *Meridionale* sp., the chelae are of juvenile shape, different from both larval and definitive, and attain the definitive one in the next instar only.

Ovigers start to develop in the instar with three pairs of segmented walking legs, i.e., the 5th in *P. longiceps* and the 3rd in *Meridionale* sp. and *A. cornigera* (Fig. 10). They appear as small buds (Nakamura, 1981; Bain, 2003b; Brenneis *et al.*, 2011). Further development was described only for *P. longiseps* and *Meridionale* sp. In the next instar (three segmented walking legs, the 4th in *Meridionale* sp., the 6th in *P. longiceps*), ovigers buds become elongated but still unsegmented. After the molt, they attain definitive number of podomeres in *P. longiseps* (Nakamura, 1981), and six podomeres in *Meridionale* sp. In *Meridionale* sp., ovigers attain definitive segmentation in the 6th instar, the earliest of those with four pairs of segmented walking legs (Brenneis *et al.*, 2011).

In *P. longiseps*, males possess small palps. The palps first appear in the 8th instar as unarticulated buds, then elongate, and in the 10th instar (adult), attain the definitive two podomeres (Fig. 10) (Nakamura, 1981).

**Pallenopsidae**

In Pallenopsidae the fifth type of development was described for three species: *Pallenopsis hodgsoni* Gordon, 1938, *P. villosa* Hodgson, 1907, and *P. vanhoeffeni* Hodgson, 1915. Only two early instars for each species are found (Brenneis, Arango, 2019).

In all described species the earliest known instars (“postlarvae”) have cheliphores, palpal and ovigeral larval legs and variously developed walking legs. They have spinning apparatus with very short spines. In *P. villosa* in place of the regular spinning spine, there are 2–4 “attachment gland processes” present. The shape of the chela does not change during the documented period of development. In earliest instar, palpal and ovigeral larval legs both consist of typical three podomeres, but ovigeral legs are thinner and smaller than palpal. In the next instar the divergence between these pairs of limbs increases, and by the end of the intermolt soft tissue in both pairs resorbs (Brenneis, Arango, 2019). The further development was not described.

## Patterns and trends in postembryonic development of cephalic limbs in pycnogonids

### Cheliphore morphology and metamorphosis

In all described early larvae of sea spiders regardless of the type of development cheliphores are positioned laterodorsally and have similar proportions: the chela is almost equal in length to the scape. Major differences occur in the chela shape and the spinning apparatus. Data on chelar glads are too sparse to find any clear patterns. The metamorphosis of cheliphores is expressed in that their proportions and position, the shape of the chela fingers and the glandular apparatus encased in cheliphores are transformed into more or less those that characteristic of adult individuals.

**The chela shape**

Most researchers do not pay special attention to chela morphology in different postembryonic stages, and conclusions could be done mostly based on photos and drawings provided in the descriptions, which, however, are of unequal quality and therefore difficult to compare. Details of chela shape vary considerably among species, but generally, chela fingers are noticeably curved and cross each other when the chela is closed (Meisenheimer, 1902; Dogiel, 1913; Behrens, 1984; Bogomolova, Malakhov, 2002, 2003, 2004; Vilpoux, Waloszek, 2003; Lovely, 2005; Gillespie, Bain, 2006; Bogomolova, 2007; Cano, López-González, 2009; Bogomolova, 2010; Cano-Sánchez, López-González, 2010; Burris, 2011; Lehmann *et al.*, 2011; Cano Sánchez, López-González, 2013; Fornshell, 2014; Mochizuki, Miyazaki, 2017; Hübner *et al.*, 2017; Alexeeva *et al.*, 2018; Alexeeva *et al.*, 2019; Cano-Sánchez *et al.*, 2020).

Both taxon-specific and life mode-related patterns in the chela shape can be revealed. For example, chelae of all the three callipallenid species described with SEM have double-tipped fixed fingers which grip the tip of the movable finger when chela is closed, likely such chela structure is taxon-specific for Callipallenidae (Bain, 2003b; Brenneis *et al.*, 2011). If young spend most of their time fixed on single spot (being lecithotrophic or parasitic), their chelae are generally more robust with tougher fingers than in actively moving free-living larvae. Thus, in *Phoxichilidium*, endoparasitic instars demonstrate wider finger bases than protonymphon larva of the same species as can be seen in SEM micrographs (Fig. 9) (Lovely, 2005). In families and genera comprising both free-living and lecithotrophic larvae (situation found among Nymphonidae, Ammotheidae, Pallenopsidae), the first have markedly more gracile fingers than the second (Bogomolova, Malakhov, 2006; Gillespie, Bain, 2006; Bogomolova, 2007; Cano, López-González, 2009; Bogomolova, 2010; Cano-Sánchez, López-González, 2010; Brenneis *et al.*, 2011; Burris, 2011; Cano Sánchez, López-González, 2013; Fornshell, 2014; Alexeeva *et al.*, 2017; Mochizuki, Miyazaki, 2017; Hübner *et al.*, 2017). Possibly, it is related to the fact that palpal and ovigeral larval legs are often reduced in lecithotrophic or endoparasitic instars, so that cheliphores take the main role in the attachment of the larva to the substrate/host.

In species possessing functional adult cheliphores, the chelae change their shape simultaneously with the change of life mode which usually occurs (in case it takes place at all) when two or three pairs of segmented walking legs are acquired. Chela shape and glandular apparatus transform quickly. During one or two instars the chela may have transitive shape. Dramatic change of chela morphology which takes a single molt is found mostly in the fourth and fifth types of development, which imply a quick change of the life mode (Figs 9, 10); and in *P. litorale*, simultaneously with the switch between prey species (Fig. 3). In sea spiders which live on the same type of prey throughout their entire life cycle, the change in the shape of the chelae occurs gradually and requires several molts. Cheliphore proportions change gradually through all the rest development to adult (Figs 3–5) (Bogomolova, Malakhov, 2003; Lovely, 2005; Bogomolova, 2007, 2010; Cano-Sánchez, López-González, 2010; Brenneis *et al*., 2011; Alexeeva *et al*., 2018; Cano-Sánchez *et al*., 2020).

In adult individuals of a number of sea spider taxa, the chelae are non-functional, and the cheliphores are small or even completely reduced. Among such species, the process of cheliphores reduction has been described for those with the first type of development only. Their chelae shape almost does not change until the reduction since it is not necessary to adopt it to a new mode of living. The exact time of the cheliphore loss or reduction is taxon-specific (Figs 3–5) (Dogiel, 1913; Okuda, 1940; Vilpoux, Waloszek, 2003; Mochizuki, Miyazaki, 2017; Alexeeva, Tamberg, 2020).

Based on the observations listed above we can conclude that the shape of the chela is essential for attachment or grasping and manipulating food in the process of feeding.

### The spinning apparatus

The larval spinneret, a provisory attachment structure which disappears completely during metamorphosis, seems to be an apomorphic feature of sea spiders. Within the group, “typical protonymphon larvae” of the first type of development exhibit the spinning apparatus with a silk gland comprising two secretory cells and a spinning spine comparable in length with the chela (Fig. 3). The number of glandular cells, the length and shape of the spine vary among taxa and developmental types. In some cases, the entire spinning apparatus complex is absent (Figs 3, 6, 8, 9).

The spinning apparatus was not revealed in the species with the third and fourth types of development (Figs 8, 9), which include parasitic instars (Dogiel, 1913; Ohshima, 1927, 1933, 1937; Salazar-Vallejo, Stock, 1985; Bogomolova, Malakhov, 2003). During the endoparasitic period, the young do not need such attachment structures. Notably, the spinning apparatus degrades in the endoparasitic instars of *A. biunguiculata*, too (Fig. 5), although judging by protonymphon morphology and the order of segments development this species might belong to the first type of development (Mochizuki, Miyazaki, 2017).

Lecitotrophic larvae usually have enlarged silk glands composed of more than two secretory cells. The spinning spine is more robust than in free-living larvae and shortened to different extent, in some cases to only a bulging cuticular ring around the opening of the gland (Fig. 6;7; 10) (Meinert, 1899; Dogiel, 1912, 1913; Nakamura, 1981; Bain, 2003b; Bogomolova, Malakhov, 2003; Bogomolova, 2007; Cano-Sánchez, López-González, 2010; Brenneis *et al*., 2011; Fornshell, 2017; Brenneis, Arango, 2019; Cano-Sánchez *et al*., 2020). An exception is the lecithotrophic larvae of ammotheids, which apparently lack a spinning apparatus at all (Fig. 7); however, this assumption, which has so far been based only on SEM results, needs to be confirmed by histological and TEM data (Cano, López-González, 2009; Cano Sánchez, López-González, 2013; Fornshell, 2014). Presumably, an enlarged number of silk-secretory cells provide a thicker thread for better fixation of a large larva. Shortened and robust spinning spine likely provides more firm attachment in a lecithotrophic young as opposed to a wider range of movement allowed by the long spine in free-living larvae (Fig. 3).

In species with the first, second, and fifth types of development the spinning apparatus present and functional in early postembryonic instars, and resorbs when two or three pairs of segmented walking legs are formed, although the ordinal numbers of such instars does not match exactly across developmental types (Meinert, 1899; Dogiel, 1913; Nakamura, 1981; Behrens, 1984; Vilpoux, Waloszek, 2003; Bain, 2003b; Bogomolova, Malakhov, 2003; Bogomolova, 2007, 2010; Cano-Sánchez, López-González, 2010; Brenneis *et al*., 2011; Fornshell, 2017; Alexeeva *et al*., 2018; Brenneis, Arango, 2019; Cano-Sánchez *et al*., 2020; Alexeeva, Tamberg, 2020). In lecithotrophic development, these instars are the oldest ones found on the ovigers of males, thus larvae simultaneously lose the spinning apparatus and disperse. In summary, it seems that two pairs of segmented walking legs are a minimal number necessary to perform adult mode of locomotion, and as soon as it is attained there is no more need in larval locomotory and attachment adaptations. This also applies to the larval legs (see next section).

## Metamorphosis of palps and ovigerous legs

### Morphology of second and third limb pairs at hatching

Despite the common general morphology, proportions of palpal and ovigeral larval legs differ in larvae with different types of development. The whole larval legs, as well as their distal claws and basal spines are shorter and more robust in lecithotrophic larvae than in those feeding exotrophically (Meisenheimer, 1902; Dogiel, 1913; Behrens, 1984; Bogomolova, Malakhov, 2002, 2003, 2004; Vilpoux, Waloszek, 2003; Lovely, 2005; Gillespie, Bain, 2006; Bogomolova, 2007, 2010; Cano, López-González, 2009; Cano-Sánchez, López-González, 2010; Cano Sánchez, López-González, 2013; Burris, 2011; Lehmann *et al.*, 2011; Fornshell, 2014; Mochizuki, Miyazaki, 2017; Hübner *et al.*, 2017; Alexeeva *et al.*, 2018, 2019; Cano-Sánchez *et al.*, 2020).

In lecithotrophic second developmental type, the larval legs often begin to reduce earlier compared to exotrophic larvae. Moreover, ovigeral larval legs are often reduced compared to the palpal (Fig. 7): smaller and more gracile, or even composed of only two podomeres instead of three, and usually bear fewer number of spines (Meinert, 1899; Cano, López-González, 2009; Cano Sánchez, López-González, 2013; Fornshell, 2014; Brenneis, Arango, 2019). There is a still more evident trend toward larval legs reduction in larvae with embryonized development (the fifth type of development, Fig. 10). At the beginning of the row Pallenopsidae stand, with the fifth type of development, in which the reduction is least expressed. In this family the larvae possess both pairs of larval legs, however ovigeral legs are thin and degradation of the larval legs starts as early as at the second postembryonic stage (Brenneis, Arango, 2019). Next, in *Nymphon australe* (the fifth type of development), only palpal larval legs are present, composed of two podomeres only, the distal (second) one is very short compared to those in other species of the family (Fig. 10) (Cano-Sánchez *et al.*, 2020). Callipallenids (all have the fifth type of development) do not have visible larval legs at all at hatching stages (Fig. 10) (Nakamura, 1981; Bogomolova, Malakhov, 2003; Bain, 2003b; Brenneis *et al.*, 2011). The described tendency is consistent with the idea that the second type of development (lecitotrophic protonymphon) is transitional between the first (exotrophic development with a morphologically “typical” protonymphon) and the fifth (lecitotrophic and partly embryonized). The best illustration is the family Nymphonidae in which three types of development are revealed, and among described embryonized larvae there are both species with two pairs of larval legs (*B. robustum* (Meinert, 1899)) and with palpal larval legs only (*N. brevicaudatum* and *N. australe* (Fig. 10)*, N. micronesicum* and *N. floridanum* (Hoek, 1881; Cano-Sánchez *et al.*, 2020; Arango, Brenneis, 2024). In the second type of development the hatching stage has more advanced condition of nervous system compared to the first type of development although both larvae possess the same set of limbs visible externally (Alexeeva, Tamberg, 2022). This fact is also in agreement with the hypothesized gradual embryionization.

### Development of second and third limb pairs

Ovigeral and palpal larval limbs are provisory legs used for locomotion or attachment, and their reduction begins as soon as these functions are no longer necessary. In the first and second types of development, this happens when two pairs of segmented walking legs are developed to functionally replace the larval legs. In the third type, there is a quick reduction, after which locomotory ovigeral and palpal legs change their function to the attachment (Ohshima, 1927, 1933, 1937; Salazar-Vallejo, Stock, 1985). In the fourth type, the larvae use ovigeral and palpal legs to come in contact with their host before infecting it, and afterwards does not need them while housing inside the host (Bogomolova, Petrova, personal observation on *Phoxichilidium femoratum*). Thus, regardless the type of development, the moment of ovigeral and palpal legs reduction corresponds to the change of the life mode of a young animal (Morgan, 1891; Meinert, 1899;

Dogiel, 1913; Ohshima, 1937, 1940; Behrens, 1984; Salazar-Vallejo, Stock, 1985; Wilhelm *et al.*, 1997; Bain, 2003b; Lovely, 2005; Gillespie, Bain, 2006; Bogomolova, 2007, 2010; Brenneis *et al.*, 2011; Maxmen, 2013; Fornshell, 2017; Mochizuki, Miyazaki, 2017; Alexeeva *et al.*, 2018; Alexeeva, Tamberg, 2020; Cano-Sánchez *et al.*, 2020). A notable example is *A. biungiculata* again (the first type), in which reduction of palpal and ovigeral larval legs begins in the 3rd instar, after invading the host (Fig. 5), earlier than two pairs of articulated walking legs appear (Mochizuki, Miyazaki, 2017).

There are two trends in development of larval legs in ammotheid and nymphonid lecithotrophic larvae: 1) accelerated transformation of palpal larval legs into definitive palps; 2) earlier larval legs reduction compared to exotrophic larvae. In both exotrophic and lecithotrophic ammotheid larvae, the palpal larval legs are immediately replaced by segmented rudiments of definitive palps, without a transitional stage of unsegmented buds (Figs 4, 7). In lecithotrophic larvae, the reduction of palpal and ovigeral legs starts one instar earlier (Morgan, 1891; Dogiel, 1913; Okuda, 1940; Gillespie, Bain, 2006; Cano, López-González, 2009; Cano Sánchez, López-González, 2013; Fornshell, 2014; Mochizuki, Miyazaki, 2017). Among Nymphonidae, palp metamorphosis accelerates in lecithotrophic larvae only, which is the most pronounced in *N. australe* (Fig. 10), *N. micronesicum* and *N. floridanum,* which does not demonstrate any transitional stage between palpal legs and definitive palps (Cano-Sánchez *et al.*, 2020; Arango, Brenneis, 2024). In other lecithotrophic larvae of the family, palpal larval legs reduce not to small buds but to long unsegmented anlagen, or even directly to palps with an incomplete number of podomeres (Fig. 6). In nymphonid lecithotrophic larvae, reduction of larval legs starts at the same (5th) instar as in exotrophic larvae, but proceeds more rapidly (Dogiel, 1913; Bogomolova, Malakhov, 2003; Bogomolova, 2007, 2010; Fornshell, 2017). In all Pycnogonida, definitive ovigers start to develop after all walking legs became segmented.

During the development of definitive palps and ovigers, taxon-specific traits prevail over trends characteristic of any type of development. Family-specific features are the shape of the rudiments; the number of molts required for the morphogenesis of the definitive limbs; number of articles in transitional incompletely segmented limbs; and the external armature of the limbs (Morgan, 1891; Meinert, 1899; Dogiel, 1913; Okuda, 1940; Nakamura, 1981; Behrens, 1984; Tomaschko *et al.*, 1997; Bogomolova, Malakhov, 2003; Bain, 2003b; Gillespie, Bain, 2006; Bogomolova, 2007, 2010; Brenneis *et al.*, 2011; Maxmen, 2013; Mochizuki, Miyazaki, 2017; Fornshell, 2017; Alexeeva *et al.*, 2018; Cano-Sánchez *et al.*, 2020; Alexeeva, Tamberg, 2020).

## Three periods in the metamorphosis of the cephalic limbs in pycnogonids

To sum up all of the above, the development of the cephalic limbs in sea spiders may be subdivided into larval, transitional, and juvenile periods. During the larval period, the cephalic limbs perform locomotion and/or attachment, there are common features in the cephalic limbs' appearance in larvae with a similar lifestyle, but some taxon-specific traits are also present. During the transitional period, cheliphores have intermediate traits between larval and juvenile; palpal and ovigeral larval legs undergo reduction. During the juvenile period, palps and ovigerous legs develop in place of the resorbed larval limbs and gradually attain their definitive structure and function. Now, taxon-specific features start to prevail over the trends characteristic of a certain developmental type.

In types of development with long anamorphic phase (the first and second) and in the fifth type all three cephalic limb pairs pass through these three periods in comparatively synchronous manner: the reduction of larval legs proceeds simultaneously to change of chela shape and loss of spinning apparatus (Figs 3–7). In parasitic types of development (the third and fourth) the timing of metamorphosis is asynchronous for the different cephalic limbs. The larval legs reduce earlier, soon after infecting hosts, while the change of chela shape and development of definitive palps and ovigers begin much later, after the emergence of a young free-living animal (Fig. 9). Thus, in parasitic young the transitive period is prolonged for the second and third limbs while shortened for the first (cheliphores).

The transformation of the cephalic limbs is the most striking component of the metamorphosis of pycnogonids. The periods distinguished in the development of cephalic appendages reflect not just morphological transformations, but also changes in the mode of life and feeding traits as animals progress through their ontogenesis.

## Periodization of pycnogonids' postembryonic development

### What postembryonic stages should be defined as larvae in sea spiders?

There is terminological uncertainty as to what is meant by "larva" in case of pycnogonids. A decision was proposed by Brenneis *et al*. (2017). The suggested criterion for the transition from "larva" to "postlarva" was the appearance of visible walking legs rudiments in postlarvae. Accordingly, only the protonymphon, and sometimes the next instar closely resembling it should be called larvae, while all later instars until the end of anamorphic phase should be called post larvae. All immature epimorphic stages were termed juveniles. As we study more and more examples of postembryonic development of pycnogonids, it becomes clear that such a criterion is too formal and artificial, since it does not fully reflect the morphological aspect of development and virtually does not consider the life mode changes throughout the postembryonic ontogenesis.

The term "larva" is broad and ambiguous; there are many criteria, used to name a certain postembryonic stage of an animal "larval". A reasonably clear and universal summary of criteria used to define larval stages is suggested by Haug (2020). According to Haug, three groups of criteria to define larvae are identified: semaphoront, sequence and evolutionary. Semaphoront criteria use a comparison of a single stage with the adult organism. Sequence criteria mean presence of metamorphosis, and, under such an approach, all stages before metamorphosis are called larval. Evolutionary criterion uses a comparison of a larva with relative species to conclude, whether the larva is apomorphic or plesiomorphic, and admits as larval the stages apomorphic for the clade.

For developing terminology for an isolated animal taxon, the first two criteria are more useful, while the last one is more relevant in comparative developmental biology. Haug's criteria (Haug, 2020) provide the basis for three approaches to defining a "larva". Here we try to apply them to Pycnogonida; examples in graphical form are given in Fig. 11.

***1. Morpho-larva***. This approach suggests "larva" as a stage morphologically different from the adult. In broader meaning the larva needs just to be different in any details, in a stricter it is implied to have some specific larval features of adaptive significance.

If applied this to sea spiders, young individuals before the formation of definitive palps and ovigers fulfill the broader criteria, and instars before the reduction of larval legs and the spinning apparatus fulfill the stricter one (Fig. 11). So, the morphological criterion of larval stage is applicable for most pycnogonids. However, with a broad criterion one gets a "larval period" that lasts until the appearance of immature but morphologically formed sub-adults (Fig. 11). The strict criterion, on the contrary, is more or less easily applicable, since at least some provisory structures of adaptive significance (spinning apparatus and/or larval legs) are present in all the cases studied.

***2. Eco-larva***. In broader meaning the ecological niche of eco-larva significantly differs from the one of the adults. In stricter meaning, larva is a dispersal stage, especially in sessile animals.

In case of pycnogonids, in the first type of development eco-larval stage is hardly distinguished, because such species feed on the same kind of prey (and the same parts of the prey organisms) during their entire lifespan. Eco-larvae *sensu lato* present in all types of development except the first, and in *Pycnogonum* (its development is conditionally classified as belonging to the first type, yet protonymphon morphology casts some doubts) (Fig. 3). In parasitic types (the third and fourth), "eco-larva" embraces parasitic instars, while in lecititrophic types (the second, fifth) it covers all lecitotrophic instars (Fig. 11). Developmental patterns including lecithotrophic or parasitic period are considered more specialized among sea spiders (Brenneis *et al*., 2017), and they exhibit a clear tendency to separation of ecological niches between larvae and adults. Such tendencies can be also traced among crustaceans and holometabolous insects.

Eco-larvae *sensu stricto* are not that common among pycnogonids, however, protonymphons of *Pycnogonum* (Fig. 3) and of species with parasitic types of development are the dispersal stage (Figs 8, 9).

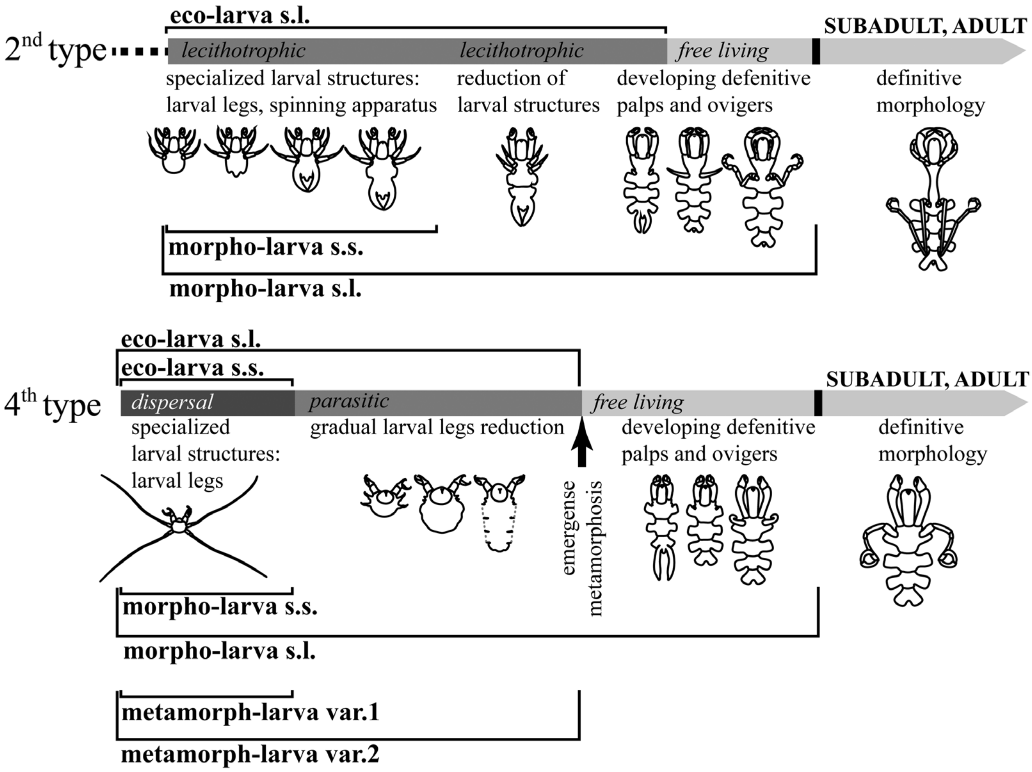


Fig. 11. Application of criteria of the term “larva” after Haug (2020) for Pycnogonida exampled by second and fourth developmental types (after Brenneis *et al*., 2017). Each criterion (see text) is indicated by a frame. “Metamorph-larva” can be unubiquitely applied to the fourth type, but not the second, because the absence of quick morphological transformations. “Eco-larva” and “morpho-larva” do not completely coincide under both the strict and soft approaches. The description of each period of the postembryonic development is provided in the text.

In summary, the ecological criterion of the larval stage is applicable to sea spiders, but the duration of the larval period determined by the ecological criterion varies significantly depending on the type of development (Fig. 11). We believe lecithotrophic or parasitic eco-larvae in pycnogonids are secondary evolved.

***3. Metamorph-larva.*** The difficulty with this criterion is the definition of metamorphosis which is even more ambiguous than “larva”. However, most definitions refer to drastic change of morphology and/or mode of life and decrease of provisory features being substituted by the definitive ones. With this meaning of metamorphosis, it turns out that “metamorph-larva” combines the two previous approaches.

In pycnogonids with long anamorphic period, changes in morphology and life mode are not drastic but rather extended over several instars: sequential development of walking legs, gradual reduction of provisory structures. If parasitic stages are absent, the most noticeable manifestations of metamorphosis are associated with switching from larval style of locomotion and feeding to adult mode with a corresponding reduction of larval legs and spinning apparatus. Thus, young individuals before the beginning of reduction of larval legs and spinning apparatus are metamorph-larvae. If there is a parasitic period, there are two transitional stages: when infecting the host and when leaving it (Fig. 11). It seems to us that the second boundary is better applicable to limit the “metamorph-larva” in pycnogonids with the third and fourth developmental types for comparison with non-parasitic ontogenetic patterns.

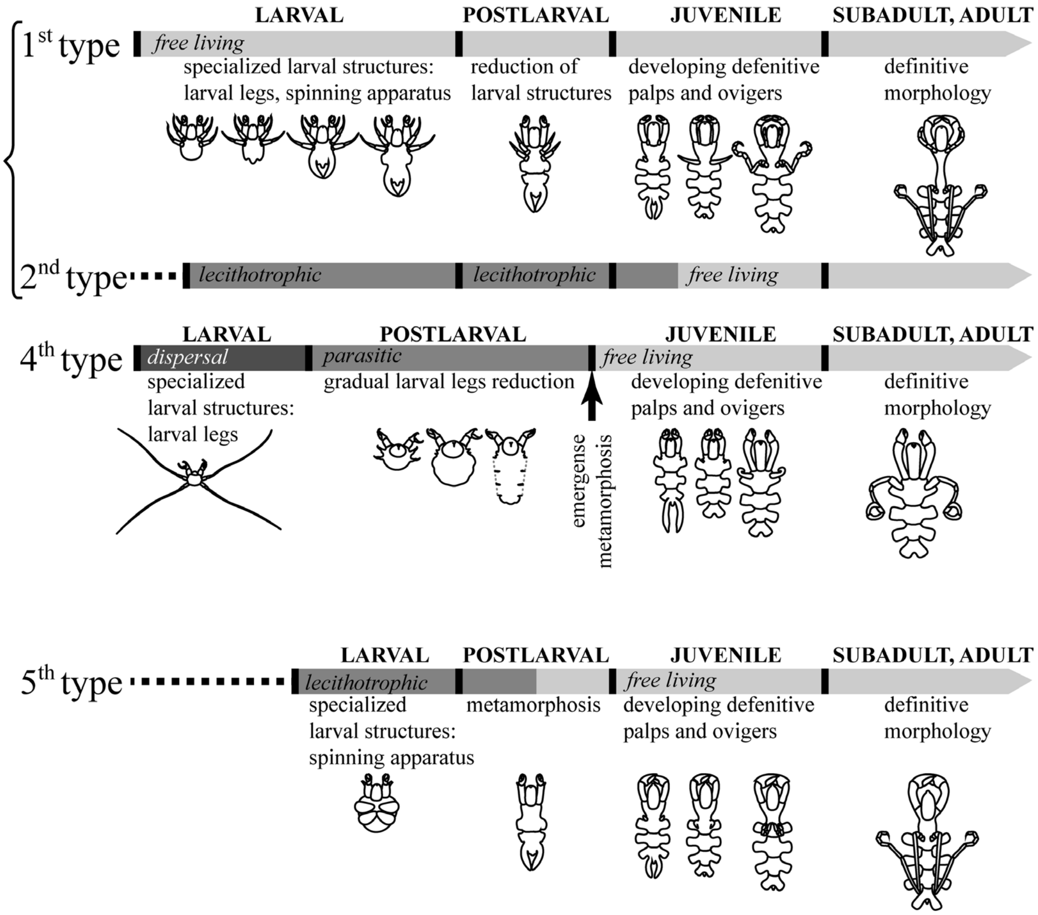


Fig. 12. Proposed periodization of postembryonic ontogenesis of Pycnogonida with different types of development. The leading criteria concern the metamorphosis of the cephalic limbs, since they integrate the "eco-larva" and "morpho-larva" approaches and are easily determined by external morphology. Dashed line refers to embryonized early development compared with "typical" pattern (the first type). The description of each period of the postembryonic development is provided in the text. The first and second types of development are illustrated by the same diagrams, since the development of the limbs proceeds almost identically, and the second type differs only in a larger body.

## What periods should be distinguished in sea spiders' postembryonic ontogenesis?

We here suggest the delimitation of larval, postlarval, juvenile, and sub-adult+adult periods by the periods in the cephalic limb development because these are reliable markers of life mode changes and are easily recognizable externally. The larval period is characterized by presence of larval cephalic limbs. During the postlarval period the cephalic appendages are reducing. In juveniles, the development of the definitive cephalic limbs proceeds. Finally, the sub-adults get the cephalic appendages of the definitive structure, but are not sexually mature.

The scheme is relatively easily applicable to sea spiders with different types of development (Fig. 12). The difficulties emerge with parasitic types of development and some hatching instars of the fifth type. In parasitic fourth type, the spinning apparatus absent and the larval legs reduce very early in development (Fig. 9). In this case, only the protonymphon fulfills the strict criteria of "larva" since it has specific larval structures, represented by larval legs (Figs

11, 12). Under the same criteria, in the third type only the protonymphon should be named larva, and parasitic instars are postlarval (Fig. 12). At the same time, parasitic instars in the third and fourth types remain eco-larvae *sensu lato*, and some kind of metamorph-larvae (Fig. 8), because out of the host a juvenile emerges with segmented walking legs and adult-like cheliphores, which is a drastic morphological change. In the fifth developmental type, larval legs of hatchlings are variously developed in different species, however in all cases the spinning apparatus present and chela shape differs from the definitive one (Fig. 10). So, under the criteria discussed above, they should be referred to as larvae even in case of absence of the larval legs (Fig. 12).

## Conclusions

1. Despite a limited amount of data, some important details in the cephalic limb morphology are revealed as correlates of the life mode of larvae:

– cheliphores: position, proportions, angle of chela to basement attachment, chela proportions, shape, and armature, chelar glands (presence/absence, openings on one/both fingers), spinning apparatus (presence/absence, spinning spine proportions and size, silk thread thickness, number of glandular cells);

– palpal and ovigeral larval legs: position, relative proportion of the legs to the body, proportions of the podomeres, basal spines (presence/absence, length), and the armature of other podomeres.

– sequence of the cephalic limb transformations during the transitional period (number of molts required, early or late time in postembryonic period, whether it goes through the unsegmented buds or not).

Features listed above can give a clue to the type of development in cases when it cannot be identified directly (e.g., material preserved in museum collections or lack of developmental series).

2. Since the larval cephalic limbs bear many provisional adaptations necessary before the definitive limbs are formed, trends in cephalic limbs morphology and metamorphosis determined by life mode (type of development) prevail during the early periods of postembryonic development over the taxon-specific traits.

3. It is advisable to name some pycnogonid instars “larvae” based on the combination of the criteria “morpho-larva” and “eco-larva”, since it gives the best result for different types of development. Periods in cephalic limbs development of pycnogonids correspond to life mode change during the postembryonic ontogenesis and are effective for demarcation of larval, postlarval, juvenile, and sub-adult + adult periods. With this approach, the periods are comparable between development types, despite each of them may include a different number of instars across species (Figs 11–12).

4. Reliable observations of the life mode of larvae of different species, coupled with detailed morphological studies, are needed. This is necessary to verify our proposed approaches to periodization of development and to clarify the exact functions of larval structures. For many species feeding on the same kind of prey during their entire lifecycle the mode of feeding of larvae and adults is neglected in the literature. Careful direct observation on live young and adults of such species could shed light on the meaning of changes in cephalic limb morphology through the postembryonic ontogenesis.

**Compliance with ethical standards**

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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