Research Article

Walking Behavior Observed in *Phoxichilidium femoratum* (Rathke, 1799) and *Nymphon brevirostre* Hodge 1863 Collected from Kandalaksha Bay of the White Sea, Russia

John A. Fornshell[1,2]

[1] *National Museum of Natural History, Department of Invertebrate Zoology, Smithsonian Institution, Washington, DC, USA*
[2] *Nikolai Pertsov White Sea biological Station, Lomonosov Moscow State University, Russia*

Correspondence should be addressed to John A. Fornshell; johnfornshell@hotmail.com

In this study, the walking behavior of *Phoxichilidium femoratum* and *Nymphon brevirostre* was investigated using video recordings. The walking behavior of *P. femoratum* while walking over the colonial hydroids that they normally feed on and on relatively smooth glass surfaces was observed. In the case of *N. brevirostre*, only walking on smooth glass was observed. The movement of the legs while waking does not display a metachronal pattern like that observed in the true spiders. As the animals move, the walking legs on the leading side of the animal are used to pull the animal forward while those on the trailing side make little or no contribution to the motion of the animal. The promoter/remoter motions of the coxa 1-coxa 2 joint of the walking legs are involved in azimuthal changes in the body's orientation, but not in paraxial locomotion. The extension of the tarsus and propodus segments appears to occur as a result of hydrodynamic drag when the legs are being flexed and/or pressed against a solid substrate.

1. Introduction

A study of the walking behavior of *Phoxichilidium femoratum* (Rathke, 1799): family Phoxichilidae and *Nymphon brevirostre* Hodge: family Nymphonidae was begun at the Nikolai Pertsov White Sea Biological Station (WSBS) operated by Lomonosov Moscow State University during the summer of 2013. The work on locomotion in the Pycnogonida prior to the 1970s was concisely summarized in P. E. King's book on the group [1]. More recently, the mechanics of walking in three species of two families of Antarctic pycnogonid, Family Colossendeidae, species *Colossendeis australis* and *Dodecolopoda mawsoni* and *family Pallenopsidae*: *Pallenopsis patagonica,* were described in some detail [2]. In the octopodous species, *C. australis, P. patagonica,* stepping motions were more variable than in the dodecapodous species, *D. mawsoni*. The promoter/remoter motions of the joint between coxa 1 and coxa 2 were of minor significance in moving the animals [2, 3]. The twisting motion in a single leg's movement was observed to be important in supplementing the promotion/remotion actions of the legs. The octopodous species rely on the flexing of the legs on the leading side of the animal to pull the animal in the chosen direction of movement.

In addition to walking motions, *C. australis, P. patagonica,* and *D. mawsoni* are observed to hold all of their legs in a vertical position, "The Basket Position," which will result in an animal descending very rapidly through the water column, plunging motion [2]. This behavior was also described as the plummeting maneuver [1].

2. Methods

Live specimens of *P. femoratum* were collected from Kandalaksha Bay of the White Sea along with a colony of hydroids, *Ectopleura larynx* (Ellis & Solander, 1786), on which they were living and feeding. Specimens of *N. brevirostre* were collected at the same time. The specimens were kept at a temperature of 5°C in a cold storage unit. For observations of the walking motions, the animals were placed in a Petri dish with the same water that they had been maintained in after
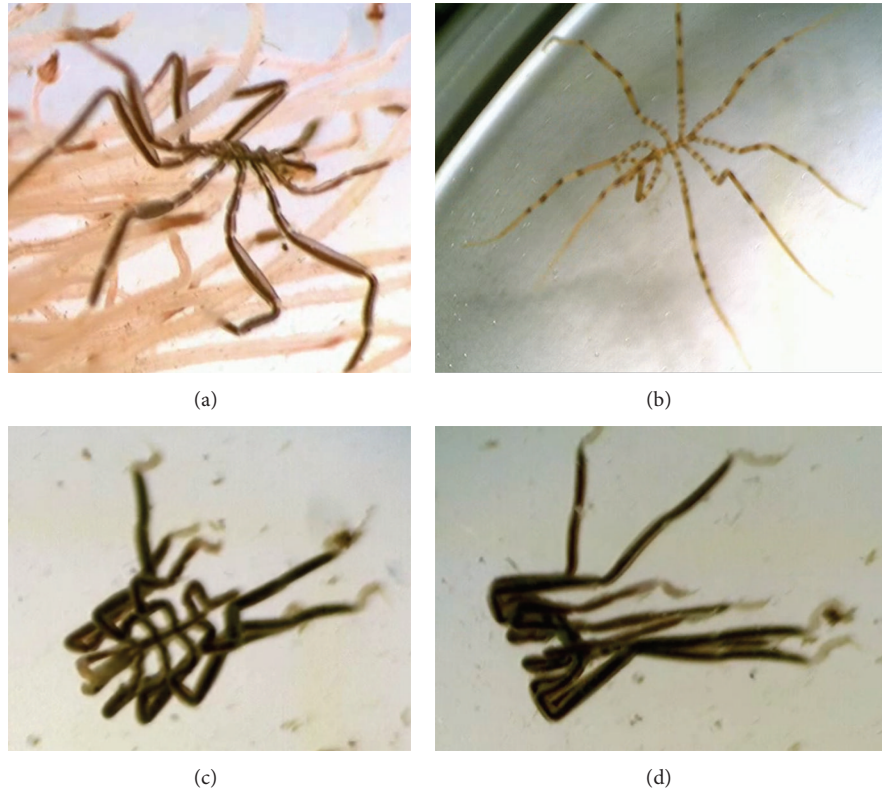
(a)

(b)

(c)

(d)

FIGURE 1: (a) *Phoxichilidium femoratum* walking with the anterior legs pulling the animal forward over a colony of hydroids, *Ectopleura larynx*. (b) *Nymphon brevirostre* walking with the left and right walking legs one pulling the animal forward over smooth glass. (c) *Phoxichilidium femoratum* in the basket position and beginning to rotate. (d) *Phoxichilidium femoratum* in the basket position rotated about 90°.

collection. Video recordings of the walking motions of these animals were made using a ScopePhoto MI-DC1300 digital camera Home Science Tools 665 Carbon Street, Billings MT 59102 USA. A total of 400 minutes of recordings were made in the course of the study. All video recordings were made using natural sunlight as the light source. Each recording was limited in duration by the need to study the animals while the water in which they were swimming remained near the 5°C water temperature that they were adapted to.

3. Results

Readers not familiar with Pycnogonid anatomy should refer to the well-illustrated and detailed works of King and Manton [1, 4]. The walking legs of sea spider *Phoxichilidium femoratum* (Rathke, 1799) have eight segments, coxa 1, coxa 2, coxa 3, femur, tibia 1, tibia 2, tarsus, and propodus. At the distal end of the propodus is an articulated spine with two auxiliary spines (Figures 1(a) and 1(b)).

Both *N. brevirostre* and *P. femoratum* use their legs to pull the body in a particular direction. In this process, the legs on the side of the animal which is the leading side reach out to pull the animal forward in that direction. The legs on the opposite side usually remain motionless and are stretched until almost straight before beginning to move with the animal. These trailing legs may in many cases be dragged when on a smooth surface (Figures 1(a) and 1(b)). In general,

if the animal changed its direction, it changed the legs which were being used to drag it forward and it did not rotate its axis. Sideways or posterior movement was as common as moving with the anterior end on the leading side. The promoter remoter movement of the coxa 1-coxa 2 joint is used to make azimuthal changes in the body's orientation, but not in paraxial locomotion of the animal.

Phoxichilidium femoratum and *N. brevirostre* may attempt to turn over, placing the dorsal side of the animal down, especially when suddenly exposed to very bright sunlight. The animals turn over rolling along the longitudinal axis but never on the transverse axis. When the animal turns over, it uses two or three legs on the side opposite to which it is turning to push in the dorsal direction while extending two or three legs on the side towards which it is rolling in the ventral position under the animal. *Phoxichilidium femoratum* and *N. brevirostre* may also assume "The Basket Position" as described by King [1] and Schram and Hedgpeth [2] while on the bottom of the Petri dish. This places the center of mass above the trunk of the animal and results in the animal slowly rolling over, placing the dorsal side down. This behavior pattern was also observed when the animal was exposed to bright sunlight (Figures 1(c) and 1(d)).

When crawling on another organism such as algae or colonial hydroids, *P. femoratum* uses the last two segments of the walking legs, the tarsus and propodus, and the claw to hold onto the tubular body of the hydroid (Figure 1(a)).

The propodus and claw flex at the claw-propodus joint and tarsus-propodus joints to form a clamp to hold firmly to the algal or hydroid body.

4. Discussion

The walking pattern displayed by *P. femoratum* and *N. brevirostre* is well adapted to an animal which is remaining closely attached to its food supply. As they move from one place to another, the legs on the leading side reach out for a new attachment point while the legs on the trailing side maintain contact with the hydroids or algal filaments. This would serve to keep them from falling off of the colony when moving. The Tarsus-propodus-claw acts as a grasping mechanism for *P. femoratum* as it moves over the colonial hydroids. The animals may be observed to hang upside-down from these hydroids as they move about. The joints between tibia 2 and tarsus and tarsus and propodus have contraction muscles, but no extensor muscles. Thus, while these joints are articulated to permit extensor movement, there are no muscles bundles to produce this motion [1, 2, 4, 5]. Because they lack the musculature in the body to generate an increase in hydrostatic pressure, they cannot extend these joints in the same fashion as true spiders [6, 7]. It is proposed that the mechanism for extending the tarsus-propodus-claw joints is by mechanical force resulting from hydrodynamic drag when the legs are being flexed and/or pressed against a solid substrate.

Azimuthal changes in motion are produced by the flexing of the coxa 1-coxa 2 joint. This is the only joint articulated and for motion in the horizontal [3]. The joint between the tubular extension of the body and coxa 1 is articulated for movement in the vertical plane. The joint between coxa 1 and coxa 2 is articulated for motion in the horizontal plane as well as the vertical plane. The joints between the remaining segments distal to coxa 2 are all articulated for motion in the vertical plane. Joints body-coxa 1, coxa 2-coxa 3, coxa 3-femur, and femur-tibia 1 have muscles in opposing bundles facilitating extension and contraction of the leg segments plane [1, 2, 4, 5].

The two Antarctic octopodous species, *C. australis* and *P. patagonica,* also move by extending the legs on the leading side of the animal, but because they are typically found on a soft bottom habitat, the trailing legs are not grasping the substrate [2]. *Phoxichilidium femoratum* is typically found on the colonial hydroids which it feeds upon, whereas *C. australis* and *P. patagonica* are more commonly found walking on a soft bottom environment.

In contrast to the walking pattern of *P. femoratum* described in this work and the octopodous Pantopoda described by earlier researchers [1, 2], most arthropods move by means of metachronal waves of activity passing over the paired appendages [5]. A metachronal pattern in the swimming of the octopodous *Nymphon gracile* has been described [8]. A metachronal pattern in the walking of the dodecapodous species *D. mawsoni* has also been reported [2]. These authors attributed the difference in gate to anatomical factors resulting from the extra pairs of legs. *Nymphon brevirostre* was also observed to swim in the same fashion as *N. gracile* with the dorsal side forward.

All chelicerates other than the Pycnogonida have an Entosternite within the prosoma cavity to which the leg muscles are attached [9]. This difference in the anatomy of the walking legs and muscular attachment(s) may account for the absence of metachronal waves in the walking of octopodous Pycnogonida. The occurrence of similar walking patterns in four families, Colossendeidae, Pallenopsidae, Phoxichilidae, and Nymphonidae would indicate that this may be the normal walking pattern for octopodous pycnogonids.

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

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