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Abstract: *Onychites* aff. *barbatus* is excessively rare in the Polish Jura. This paper describes a recent find from the basal middle Oxfordian. The specimen is preserved in a manner typical for other finds of this kind in platy limestones, i.e., as compressed and flattened imprints with remnants of carbonized organic matter. Excellent preservation of the surfaces enables a precise reconstruction of the original structure. Accordingly, I hypothesize on the attachment to soft parts and the function of the belemnite onychites. The high diversity of known onychites, especially from Europe (NW Tethys), indicates that they served a variety of purposes.

Keywords: onychites; mega-hooks; Belemnitida; functional morphology; Oxfordian; paleogeography

1. Introduction

Onychites were first reported by Fraas [1], who described a single species that he named *Onychoteuthis barbata*. Quenstedt [2] described and illustrated further several species, including *O. barbata*. Following subsequent minor revisions, the most complete of which is that of Engeser [3], at present, 10 forms represented by numerous specimens are known from the German Jura, ranging from the Pliensbachian to the lower Tithonian. Further specimens were described from the Arctic (most recently [4]), from New Zealand [5], and, recently, from Poland [6].

Out of 27 specimens of belemnites with preserved arms including arm-hooks known from Europe (mostly Germany), only two bear onychites [5]. Hence, it is supposed that onychites were a sexual feature, found probably in mature males who may have used it for competition among one another or for mating, analogous to various arm modifications in the present-day cephalopods. Presumably, on the basis of the shape and size relative to the remainder of the body, most workers hypothesize that onychites may have served for holding the female during copulation (see discussion in [5]).

The find of a relatively well-preserved onychite in a fine-grained platy limestone, albeit separated from the remainder of the body, may shed new light on the mechanics of their work and, hence, probable function in the living organism, and as a sexual feature on mating habits.

2. Material and Methods

2.1. Geological Setting

The specimen examined here is part of a fossil suite collected during the deconstruction of two ruined houses in Częstochowa. The material used for construction was composed of platy limestones, splitting well along bedding planes. The recovered fossils included ammonites, e.g., *Cardioceras densiplicatum*, which constrains the age of the material to the *plicatilis* (or *densiplicatum*) zone of the middle Oxfordian.

Both houses were erected at the same time at the beginning of the 20th century, in the village Bór, immediately south of Częstochowa (today within the confines of the city). By the time of construction, this flat area of extensive clay outcrops would have been generally damp. Construction stone must have been transported from the nearest and most easily accessible site.



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In Częstochowa and its immediate surrounding, Jurassic limestones are found in a few inselbergs. According to the descriptions in Różycki [7], which presumably hold also for the preceding several decades, early middle Oxfordian platy limestones were quarried at two quarries: at Jasna Góra and Sobota's quarry in Błeszno (Figure 1). The construction stone must have originated from either of these. Unfortunately, neither of these quarries were described subsequent to Różycki [7]. As both quarries no longer exist, nothing more can be added to the site descriptions found in Różycki [7].



Figure 1. (**A**) Distribution of Jurassic deposits in Poland, with location of Częstochowa. (**B**) Study site (marked by contour of onychite) and nearest outcrops of Oxfordian (blue) with quarries worked at the beginning of the 20th century (red). A map from 1913 is used as a background. Geologic data mainly from Różycki, 1953; map from Mapster (http://igrek.amzp.pl/, accessed on 10 October 2021).

2.2. State of Preservation

The specimen is preserved in the form of nearly complete imprints (Figure 2). One side of the mold is missing the tip, although the terminal 0.5–1 mm appears to have been broken before burial. The other side is missing a minor section in the middle. The void features a small cluster of sparitic calcite at the shaft attachment to the base. Consistent with previous reports [1,5], remnants of black substance were found along the whole length of the void. These most likely represented carbonized organic matter, but were lost while splitting the rock and producing casts.

Fractures visible on the specimen indicate that the hook was hollow and that it was compressed before sediment lithification. The fractures are often incomplete, and plastic deformation is observed, which points to some degree of resilience of the original structural material. The flattening of several specimens of *Cardioceras densiplicatum* (including a whorl fragment in the vertical position) indicates flattening most likely by a factor of three following aragonite dissolution (no signs of fractures are observed). Regardless of the non-plastic crushing preceding rock lithification, the hook underwent plastic compaction together with the rock. It is, however, impossible to estimate to what degree this happened; if the remaining part of the void was filled with sparitic calcite, and the degrading chitin was not entirely liable, the resultant degree of compaction should be lower than the estimated factor of three. If the granules representing the hook ornamentation were originally isometric, comparing their shape on surfaces parallel and oblique to bedding compaction reduced the hook dimension by a factor of <2. Unlike belemnite rostra, composed of solid calcite, however, the hook did not resist compaction altogether (Figure 3). The counterpart void is ~0.6 mm high (perpendicularly to the bedding plane) in the middle segment.



The height of the void of the base, including the incomplete posterior process, originally pointing nearly perpendicular into the sediment, is ~3 mm (measured on silicone casts).

Figure 2. (**A**,**B**) Fossil imprints MGUS/Sz.1942b and 1942a respectively; (**C**,**D**) Silicone molds of imprints; (**E**,**F**) Composite silicone cast of base. (**A**,**C**,**E**) Views from abprocessal side; (**B**,**D**) views from adprocessal side; (**F**) bottom side. (**C**–**F**) Whitened by MgO. Scale bars, 1 cm: upper for (**A**,**B**); lower for (**C**–**F**).

2.3. Methods

Upon splitting the rock, the content of the counterpart void (discussed above) mostly crumbled away. Latex casts were made and examined using scanning electron microscopy (SEM). Silicone casts were photographed following MgO coating. Measurements were made on both silicone casts and photographs.

Parataxonomic terms are used in the literature for describing onychites. This is justified by several arguments. First, onychites are almost exclusively found separated from rostra that serve as the basis for belemnite systematics. Second, belemnites bearing rostra classified as a single species may have had different onychites [3]. Lastly, specimens bearing onychites (mega-hooks) also had arm-hooks (micro-hooks), which are described separately [8,9]. Furthermore, some of these belemnites may have had more than one form of arm-hooks in one individual, as observed in other cephalopods (see discussion on parataxonomy in the case of onychites in [5]).



Figure 3. Comparison of taphonomies of ammonite (with photos of two specimens in orientations perpendicular and parallel to the bedding plane, scale bar 1 cm), belemnite rostrum, and examined onychites.

Morphological terminology mostly follows Hammer et al. [4] and Fuchs and Hoffmann [10].

The 3D reconstruction was made by hand on the basis of the observation of the surface morphology and cracks.

The only specimen is the entire material. This is sufficient to imagine the mechanical properties of this anatomical element. The comparison with other specimens, known from the illustrations (including complete belemnites with onychites), also allows drawing some conclusions about its action in a living organism and about the differences in the action of other parataxa of onychites, but it is more speculative.

3. Results and Discussion

3.1. Systematic Description

Uncinifera Engeser, 1990 (parataxon (form taxon) of ordinal level) form-genus *Onychites* Quenstedt, 1857

Type species: Onychites ornatus Quenstedt, 1857, SD Quenstedt, 1866. form-species *O.* aff. *barbatus* (Fraas, 1855)

pars 1855 Onychoteuthis barbata; Fraas 1855, 89

pars 1855 Onychites barbatus; Quenstedt 1857, 804, pl. 99 Figure 14 (non Figure 15)

1987 Onychites barbatus Quenstedt 1857; Engeser 1987, 12, pl. 2 Figure 3

pars 1999 *Onychites barbatus* (Fraas 1855); Schweigert 1999, 11, pl. 5 Figure 1, 3; pl. 6 Figure 5 2010 Onychites barbatus; Stevens 2010, 400, Figure 4h

2013 Onychites barbatus (Fraas 1855); Hammer et al., 2013, 833

The specimen is 31 mm long and 10 mm high (i.e., largest total dimension perpendicular to length).

The base is 8.5 mm long, measured parallel to total length. The inner (anterior) process is ~3 mm long and has a subtriangular outline. The outer (posterior) process tapers slightly and is broken at the tip. The posterior process projects slightly (>1 mm) toward the posterior and conspicuously (1 mm) downward (i.e., toward the axis of the animal body), which gives the base a concave profile. The base is positioned at a considerable angle

relative to the curvature plane of the shaft and uncinus (in vivo—ventrally or dorsally; in rock—probably downward), protruding ~1.3 mm toward this latter direction. Considering sediment compaction, the preserved part of the process originally protruded ~2–4 mm from the base, which is also strongly flattened. Thus, together with the process, the breadth of the base could have exceeded its length. The inner process also pointed in the same direction, albeit to a lesser extent. The position of the processes serves to differentiate onychite sides, i.e., the processes-bearing side and the side lacking processes (one of these was ventral, the other dorsal). Reconstructions of the onychite appearance before crushing and compaction are shown in Figure 4.



Figure 4. Reconstruction of the probable original appearance of the examined onychite. Basal (**A**) and lateral adprocessal (**B**) views. Scale bar, 1 cm.

On the processes-bearing side, at the base of the inner process, there is an inwarddirected (i.e., toward the body axis) slit that most likely is a collapsed opening or a depression. Despite relatively good preservation, the orbicular scar could not be located. On the opposite side, however, despite considerable crushing, there seems to be a fringed ridge along its edge on the inner process. This ridge could possibly represent the orbicular scar.

Along its entire length, the shaft is 3.5 mm wide (originally, before flattening, it was probably ~3 mm wide). The original cross-section was probably oval, slightly flattened laterally. The shaft is strongly bent near the base. The curvature is gradually reduced, and the shaft continues as a 5 mm straight section, approximately parallel to the basal line. Following this straight section, there is a uniform arch that passes into the uncinus. Over the terminal ~10 mm, the uncinus tapers. The specimen has a blunt termination, but the tip (1–2 mm the length) was probably broken off. The tip protruded beyond the basal line.

The ornamentation is the most pronounced at the tip. Ornaments are in the form of roundish knobs, usually linked in groups of few, in the form of irregular wrinkles. On the processes-bearing side, some 3 mm from the preserved tip of a knob, in the middle section of the side, the knobs become separated, less pronounced, slightly elongated, and finally disappear altogether some 8 mm from the tip. The remainder of the side is smooth. On the other side, the ornamentation disappears closer to the tip, and the smooth belt is broader. On the external side, the ornament disappears at the end of the uncinus arch. On the internal side, the ornament reaches almost to the end of the straight section of the shaft. At the uncinus deflection, the dominant direction of the wrinkles is skewed, approximately perpendicular to the longest dimension. Along the internal edge of the uncinus there appears to be a kind of a smooth edge, visible on both imprints. It is impossible to say whether this was indeed a smooth edge; it could possibly be a fracture within the plane of maximum width, along which both sides aligned.

The entire onychite was hollow inside, and the walls were ~0.1–0.15 mm thick.

3.2. Taxonomic Discussion

The specimens of O. barbatus illustrated in the literature, including the specimen of Fraas [1] that was chosen as a paratype by Schweigert [11] (pl. 5, Figure 1,3), the next two specimens illustrated by the latter author (pl. 6, Figure 5), and the specimens of Quenstedt [2] (pl. 99, Figure 14) and Engeser [3] (pl. 2, Figure 3), do not display significant differences among themselves. They are, respectively, 24, 18, 29, and 21 mm long and have basically the same shape and proportions (see comparison in Figure 5). Note, however, that Engeser [3] and Stevens [5] reported different lengths for the Quenstedt specimen. The specimen presented here has almost precisely the same outline and ornamentation as the above specimens, but it is slightly larger (31 mm) and considerably broader (0.11 of total length, against 0.08 for the remaining specimens). My specimen also has a shorter (0.1 vs. 0.11–0.17) and broader inner process. The larger breadth could have resulted from crushing, but the well-illustrated specimen of Engeser shows identical fracturing and, thus, likely a similar degree of broadening. Furthermore, the illustrated specimens of previous workers are less curved; their tips do not project beyond the basal line. The ornament visible in Engeser's illustration terminates more proximally on the shaft, but the smooth surface in the middle of the side is shorter. The previous authors also did not mention the lateral position of the outer process, although it should be visible on the specimens preserved to some degree three-dimensionally, since the ornament is visible. Even though the specimen presented here falls outside the range of variation of the material from Germany, the differences may not be sufficient to establish a separate form, especially given the variation known from a larger number of specimens such as O. macnaughti Marwick, 1956 [5] and O. quenstedti Engeser, 1987 [4].



Figure 5. Shapes of published *O. barbatus* (**A**–**D**) and described specimen (**E**). Pair of onychites from original Fraas slab of kalk (SMNS/24210—[11], Taf. 5 Figure 1,3, left—lectotype) (**A**); smaller specimen from the same slab (**B**); SMNS/63852 ([11], Taf. 6 Figure 5) (**C**); Quenstedt specimen ([3], Taf. 2, Figure 3) (**D**). Because of poor visibility in the illustrations and possible deformations due to the thickness of the bases, the orientations of the baseline are uncertain; thus, for better comparison, all specimens are oriented with the straight middle section vertically. Scale bar, 1 cm.

To date, the only specimens of rostra preserved together with onychites belong to *Passaloteuthis paxillosa* (Schlotheim, 1820). Recognized in association with these are *O. amalthei* Quenstedt, 1856 and *O. uncus* Quenstedt, 1856 [3]. Thus, it can only be stated with certainty that representatives of the family Belemnitidae had onychites. In the Oxfordian of the Polish Jura, however, they are extremely rare. I am familiar with two specimens only, from the lower Oxfordian of Wrzosowa (apical part only, MGUS/Sz.1943) and from Zalas (not numbered). In any case, the rare occurrence of both Belemnitidae and onychites (besides, in not exactly age-equivalent strata) is no evidence for their association.

The type material of *O. barbatus* comes from Nusplingen in Germany. Apart from numerous onychites (including *O. fraasi* Quenstedt, 1857 and *O. quenstedti*), the site yielded representatives of only one belemnite species, *Hibolites semisulcatus* (Münster, 1830) [11], which makes a strong case for the association between these onychite forms with that

particular belemnite species. Moreover, a rich assemblage of *O. macnaughti* from New Zealand co-occurs with representatives of the Belemnopseidae [5]. The only belemnite species that I found in the material from which the onychite reported here originates and in age-equivalent platy limestones of the Polish Jura are *Hibolites hastatus* Montfort, 1808 and *H. girardoti* (Loriol, 1902). It is, therefore, likely that the onychite comes from one of these species.

The morphological variation among onychites associated with *Passaloteuthis paxillosa* and *H. semisulcatus* may be interpreted as evidence for their higher specificity [3] or intraspecific variability [11]. The first option seems considerably more likely. Contrary to rostra (which are part of the internal skeleton and invisible to females), as a manifestation of sexual dimorphism, onychites were subject to sexual selection, which is known to be a strong driver of speciation and species diversification. It seems to be different for *O. macnaughti*, which co-occurs with several species of the Belemnopseidae. *O. macnaughti*, however, is so variable (as evidenced by illustrations in [5]) that, with a larger number of complete specimens, it would likely be possible to distinguish further species. It also seems unlikely that onychites have been found of all species of belemnites, identified on the base of rostra, which are many times more numerous. Thus, I suspect that belemnite species described using rostra include numerous cryptospecies. Unfortunately, this cannot be rectified on the basis of onychites, as they are too rare and almost invariably disarticulated from rostra.

3.3. Remarks on Functional Morphology

As only a minor fraction of the few complete belemnite finds include onychites, most authors since Engeser [3] have assumed they played a part in mating. On the basis of the shape of a particular paraspecies, Hammer et al. [4] performed a functional analysis, suggesting that the studied form followed a logarithmic spiral, typical of vertebrate claws. Hammer et al. [4] found that the spiral center in *O. quenstedti* occurred near the base, unlike in vertebrates, where it occurs adjacent to the top. On the basis of this difference, Hammer et al. [4] concluded that the function of the onychite must have been associated with pushing rather than pulling. Lastly, Hammer et al. [4] cited the opinions of other workers, who suggested that onychites served for holding the female during copulation [3], and that onychites may have served for fights among males [12,13], regarding the function of special arm hooks in present-day coleoid males.

The logarithmic spiral is a remarkable shape. Vertebrate claws (and mollusk shells) attain this shape naturally, owing to constant growth of the claw at one end, in a simultaneously growing individual. In this way, the claws have the same properties along the whole section, on a gradually larger scale. Mechanical properties of the logarithmic spiral are a benefit to vertebrates, but they are an added value to the laws of growth. Chitinous hooks of the cephalopods are not used before fully formed, and their logarithmic spiral shape (or whatever other shape) must have been attained by natural selection or accidentally. Not all paraspecies, including the studied one, have such shape. Thus, the logarithmic spiral shape was not always optimum, shape imperfections (giving a constant and uniform strain distribution during specific work) were equally well compensated for by structural variation (structure, wall thickness, cross-section shape), or the properties of the logarithmic spiral were of no significant importance.

All onychites are more or less bent into an arch and tapered at their tips, although some (*O. amalthei*, *O. ornatus*, and *O. contractus*, based on illustrations in Engeser [3]) have broad tips. These three relatively blunt forms would be unsuitable for stabbing. The remaining onychites must have served this function, as the necessity of holding a female by embracing her does not justify the presence of sharp tips that could have hurt her, unless holding the female required anchoring the male by driving the hooks into the female body. Efficient holding, regardless of the exact mode, would have required an appropriate hook curvature.

The shapes of sharp-tipped anatomical elements (serving for stabbing or piercing) depend on the work mechanics. In the simplest cases, in pushed elements, the tip is directed against the attachment point (as is typical of spines). In pulled elements such as hooks, the tip is directed toward the attachment point, and, in elements that rotate around an axis extending across the line linking the tip and the attachment (such as claws), the tip is directed perpendicularly relative to that axis, within the plane of rotation. The actual morphological diversity of sharp elements is due to more complex function, using two different forces. Thus, teeth of carnivores are often bent toward the rear. This serves to pierce by closing the jaw, which moves along an arch, and to both prevent the prey from setting itself free and facilitate moving the prey toward the esophagus (i.e., pushing and rotating). Harpoons have a spine directed toward the front and a second one (or more) directed toward the rear, in order to prevent the escape of the pierced prey (pushing and pulling). Claws are often bent further than perpendicular relative to the anchor point in order to effortlessly hold the captured prey (rotating and pulling). I cannot conceive any naturally occurring sharp object that would use a combination of all three of these forces or use the fourth possible force, i.e., revolving around an axis extending between the tip and the attachment point, such as a corkscrew or a screw. The work mechanism of these elements is schematically represented in Figure 6.



Figure 6. Shape of pointed elements in relation to their work. Two notes are important: (1) the point of force insertion can be placed outside of the element outline; (2) this point can change place during work (depending, e.g., on working muscles, especially in the case of elements anchored in a soft body).

Given all of the above, the function of arm hooklets is also easily explained. Individuals with diverse hooklets preserved make especially interesting cases. In the diplobelid *Chondroteuthis wunnenbergi* illustrated by Hoffmann et al. [14], hooklets characteristically differ according to their location along an arm ([14] Figure 9). The closer to the tips of the arms, the stronger the curvature of the hooklets, which suggests that they served to capture and transfer the prey toward the less curved, proximal hooklets, onto which the prey was threaded. The pronounced difference in the size of some hooklets may be explained by their use against considerably larger objects; belemnite prey was, on average, circa an order of magnitude smaller than belemnites themselves [15,16]. Fighting males, however, were similar in size. The cited workers [14] reached similar conclusions on the basis of more complex analyses.

In the studied specimen (as with most other onychite paraspecies), the tip is directed away from the base, inclined $\sim 45^{\circ}$ relative to the basal line. Morphologically, therefore, it falls precisely between a spine and a hook from Figure 6, which suggests it served for stabbing with rotation. Teeth of carnivorous vertebrates, arthropod chelicerae, or scorpion stings, which operate in precisely the same way, sometimes have similar shapes. Notably, in both arthropods and vertebrates, these elements are supported by the skeleton, which—being resistant to compression—enables pushing them toward the prey. Theoretically, in their heads and arms, belemnites could only use their hydraulic skeleton (like a wasp extending its sting), but the structure of the onychite base and the curvature of other onychites argue against this. Onychites were probably supported by an elastic cartilage and were moved by muscles that could direct them in the appropriate direction, but could not push them away from the body.

An element rotated by a muscle needs support from elsewhere than muscle attachment. The larger the distance between the point of support and the muscle attachment, the longer the lever, and the higher torque required from the muscles. No apparent muscle attachment is seen on the studied element. They were definitely absent beyond the base; circular structures on the shaft of the specimen illustrated by Hammer et al. [4] are, in my opinion, silicification nodes or similar structures described by Klug et al. [17] formed during diagenesis rather than muscle impressions. Both the shaft and the uncinus lack structures resembling an orbicular scar or longitudinal ridges, which indicates that the element was attached to the body only through the base, and it is the base diameter that determines the maximum lever length. Considering the cartilaginous (i.e., elastic) substratum and the diminutive diameter of the base relative to the total length of the onychite, torque levels must have been low. It is highly unlikely that a belemnite could efficiently hold anything with such structures, including a female, especially given that the onychite tips were directed away from the base. It is also entirely impossible that the onychites were positioned at the ends or in the middle of the arms' length, as reconstructed by Stevens [5]. The arms lacked a skeleton and, therefore, could not offer sufficient support for a lever the length of an onychite in order to operate it in any way.

Complete belemnite specimens [16,18] reveal that onychites were anchored at the head or at the base of a pair of arms, with tips directed toward the body axis. The stabbed object must have been located in front of the animal, and the purpose of the action must have been to bring the prey to the tips of the onychite by means of the arms or to direct these tips toward the aggressor, which charged on its own and drew the competitor toward itself. In the latter case, it could have been a form of defense against getting bitten on the head by the beak of the opponent.

The slight curvature of the hooks did not facilitate holding the stabbed object and, further, the dominant direction of the wrinkles likely did not favor a deep stab. Assuming that onychites served for male fights, they were likely a defensive weapon, used for rapid repulsion of an attack and deterrence. The curvature helped to dispose of the stabbed element by abduction of the onychites (following the mechanism described by Hammer et al. [4] for the logarithmic spiral). This would have been impossible with hypothetical straight onychites (which have never been found).

Possible onychite mobility could be hypothesized on using the shapes of the base and muscle attachments. Unfortunately, no muscle attachments are seen, and the shape reconstruction is only tentative because the base is crushed (Figure 2). An interesting feature of the base, typical also for fossil arm hooks, is that the base was directed toward the body axis. Arm hooks, however, bear orbicular scars and longitudinal ridges, indicating that they were anchored or supported also on the internal side. Nothing similar is to be seen on the specimen examined here. This would suggest that the studied specimen was attached to the head rather than an arm. If it was attached to an arm, however, it would have been placed at the base of an arm and more likely offset to a side rather than attached

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on the internal side. The strong base asymmetry suggests a functional difference between the two onychite sides (i.e., processes-bearing side and the one lacking processes). Perhaps these hooks were not facing one another but placed at an angle on one side of the animal (ventral or dorsal), and they worked in partly intersecting planes. This could explain their parallel position in the specimen illustrated by Dick et al. [18].

A hypothetical muscle anchored in the onychite's interior could have passed through the opening in the base. If the posterior part of the base with the posterior process was the point of support, such a muscle could have served for rotating the onychite toward the body axis. Furthermore, it acted to increase the force of onychite anchoring in the body, and, if the muscle was set sufficiently deep in the onychite, it could have reduced bending moments within the onychite walls during some actions (similar to musculus intramandibularis in archosaurian mandibles), reducing the skeletal material required to form an onychite.

3.4. Geographic Variation of Published Onychite Morphologies and Functions

The above considerations cannot be accurate with regard to some other onychite paraspecies. Some had a relatively longer base (*O. fraasi*), which may have enabled higher torque. Some appear to have lacked a well-delineated base altogether (*O. uncus*, although the distinctly crushed distal part may suggest that it gradually transitioned into cartilage). *O. uncus* and (to a lesser extent) *O. ornatus* were more curved, and their tips were perpendicular to a line connecting them to the base. Thus, they were not suitable for stabbing toward the front, but instead could embrace and hold an object with little effort. Moreover, *O. ornatus* had broad and likely blunt tips which made it useless for stabbing. At present, little can be said on the functional mechanics of weakly curved, thick, and probably blunt *O. amalthei* and *O. contractus*. Their only purpose may have been for showing off.

The tuberculated surface not only made using the onychite for stabbing more difficult, but it could also have served as a sexual ornament, both visual and sensory; today's cephalopods are sensitive to the texture of the surfaces they touch.

In this context, it is notable that onychites display a geographic variation. Specimens from New Zealand (included in one species, *O. macnaughti* [5], despite a high diversity) differ from the remaining ones, known from the NW Tethys region. The former are more strongly sculpted than nearly all Tethyan specimens and usually less strongly curved (the tip is distant from the basal line and sometimes even points away from the basal line). The differences in onychite forms may be explained by differences in arbitrary preferences of females rather than differences in environmental conditions.

It is also intriguing (as also noted by Stevens [5]) that *O. macnaughti* is the most similar to *O. contractus* from the Pliensbachian of Germany. *O. macnaughti* co-occurs with belemnites from the suborder Belemnopseina, which first occurs in the Bajocian, and *O. contractus* has to be linked to the suborder Belemnitina, which means that the similarity between the two species is almost certainly due to convergence. It is impossible to determine, however, how this related to similarities in mating rituals.

4. Conclusions

The function of onychites remains unclear, but an analysis of the morphology of a well-preserved specimen sheds some light on the mechanics of its operation and its possible function. The good preservation enabled the first approximate three-dimensional reconstruction of an onychite. The processes, especially the posterior process, were found to occupy a lateral position. An opening was found within the base, and the specimen was found to be hollow. No muscle attachments were found outside the base. An analysis of the onychite shape and its position relative to the body indicates that the onychite served for passive stabbing of a charging object or an object that was pulled using arms. Active abduction of both onychites enabled the release of the pierced object. Neither the curvature nor the forces acting upon the onychite enabled holding a female during copulation. It was also impossible (this refers to all the remaining mega-onychite forms) for the onychite to be attached to arms away from their bases. The ornament hindered deep penetration and could have served as a sexual signal during mating.

The diversity of European onychites indicates variable mating rituals among belemnites in the seas of the western Tethean realm, considerably more so than in other regions. In addition to the mechanics of the onychite function, no other details of these behaviors can be determined.

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