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Tooth morphology and food processing in *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789) and *Ophiura albida* Forbes, 1839 (Echinodermata: Ophiuroidea)

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Abstract

Based on the main feeding modes of two common European brittlestars, *Ophiothrix fragilis* and *Ophiura albida*, the present study relates the species' tooth morphology to their function in processing food items of different structural quality. Clusters of grinding dental papillae in the suspension feeding *O. fragilis* seem most appropriate for loosening compound food items, *i.e.,* food boli, or potentially for grazing. Large triangular teeth are considered to be used as crushing and cutting instruments, most likely for processing loosened or broken up food masses into smaller digestible portions. In the mostly predating and scavenging *O. albida*, sharp and pointy or broad scale-like oral papillae may serve in gripping and fixing live benthic prey organisms or carrion, while the larger spine-like teeth may be applied as carnassial instruments thrusting into the flesh of a prey organism and tearing off pieces. Designating the two species either as grinders and cutters processing compound and hard structured food or as grippers and tearers handling softer textures, still awaits confirmation through feeding experiments and observational documentation.

Key words: Ophiuridae, Ophiothrichidae, feeding, teeth, functional morphology

Introduction

Ophiuroids are known to perform a large variety of different feeding modes such as surface and subsurface deposit feeding, suspension and filter feeding, browsing, scavenging and predating (Warner 1982 and references therein; Feder 1981). Most ophiuroids are capable of performing more than one feeding mode along with their designated main feeding mode, which in most cases may be directly linked to a specific life style. For example, epibenthic mobile species (*e.g.*, *Ophiura* spp.) typically feed as predators or scavengers, actively hunting their prey (Feder 1981; Warner 1982), whereas infaunal or rheophilic/cryptic species, such as *Amphiura* spp. or *Ophiothrix* spp. typically perform some mode of suspension feeding with their arms extending from their burrows (Warner & Woodley 1975; Loo *et al.* 1996).

Detailed descriptions have been given on behavioural, chemical and mechanical aspects of how food is sensed, trapped and collected in ophiuroids and how different structures (*e.g.*, tube feet and spines) may jointly interact (Austin 1966; Pentreath 1970; Reimer & Reimer 1975; Warner & Woodley 1975; Dearborn 1977; Dearborn *et al.* 1996). Yet, only little information is available on

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the mechanical functioning of the teeth when processing food of different structural quality. Hyman (1955: 597) gives the following description of teeth in ophiuroids: “The clusters of tooth papillae […] are continued inward by larger and heavier projections, the teeth, mostly in one row, more or less visible if the jaws are widely open. When tooth papillae are absent, the vertical row of teeth extends to meet the oral papillae”. A prominent reason for the scarcity in studies on the functioning of the teeth when feeding is due to the difficulties in observing them operating inside a living animal. Pentreath (1970), however, observed how the suspension feeding *Ophionereis fasciata* Hutton, 1872 and *Ophiopteris antipodum* E.A. Smith, 1877 pass a food bolus consisting of collected particles along the arm by means of their tube feet. When reaching the mouth and being gustatorily accepted by the oral tube feet, the boli are handled by the latter which “scrape it [the bolus] against the teeth and oral papillae” in *O. fasciata* or “scrape it on to the tooth papillae” in *O. antipodum*. Pentreath (1970) further describes how the carnivorous *Ophiomyxa brevirima* H.L. Clark, 1915 handles larger food particles which are “grasped by the teeth, which are serrated, as are the oral papillae, and then passed into the mouth by the buccal podia”. Similarly, Austin (1966) describes, how the suspension feeding *Ophiothrix spiculata* Le Conte, 1851 accumulates large masses of food boli at the level of the jaws, which “then close on the mass 30–40 times before the food is pushed into the mouth by the inner and outer buccal tube feet”.

Morphological descriptions, digital images and drawings of teeth and/or papillae have been provided for different ophiuroids on species and higher taxonomic levels (Hyman 1955; Stöhr 2005). Unfortunately, detailed descriptions of teeth in common European ophiuroid species are still very scarce (Madsen 1970; Hendler *et al.* 1995). Understanding the mechanical application of teeth with regard to their morphology when processing food and particularly when handling structurally different types of food would allow a deeper insight into the feeding ecology of extant ophiuroids and their role in trophic cascades. In addition, it would also allow implications on the feeding behaviour of ophiuroids from the fossil record.

In the present study, morphological descriptions of oral and dental papillae and teeth in two common European ophiuroids, the rheophilic suspension feeder *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789) and the predatory and scavenging epibenthic *Ophiura albida* Forbes, 1839, are provided. The aim was to relate the tooth morphology of these two species to their functional use as applied tools in processing differently structured and textured food items. As no experimental feeding studies were conducted, implications remain speculative and are solely built on information published in the literature and discussed in comparison to other species.

Materials and Methods

During the summer of 2009, subtidal individuals of *O. fragilis* were collected with dredges in the vicinity of the island of Helgoland, German Bight (North Sea). Ten adult individuals (*i.e.*, disc diameter > 7.0 mm) were preserved in 70 % ethanol and then air-dried. Images of open mouths revealing the oral views of all five jaws and visible dental papillae were captured digitally. The mouthparts were dissected under a stereo microscope to profile and full views for descriptions of the dental papillae and teeth on the dental plates of individual jaws, and digitally documented. For length, width and depth measurements of the dental papillae and teeth in relation to the body size, three individuals of similar disc diameters were chosen and structures from the individual jaws were measured by using

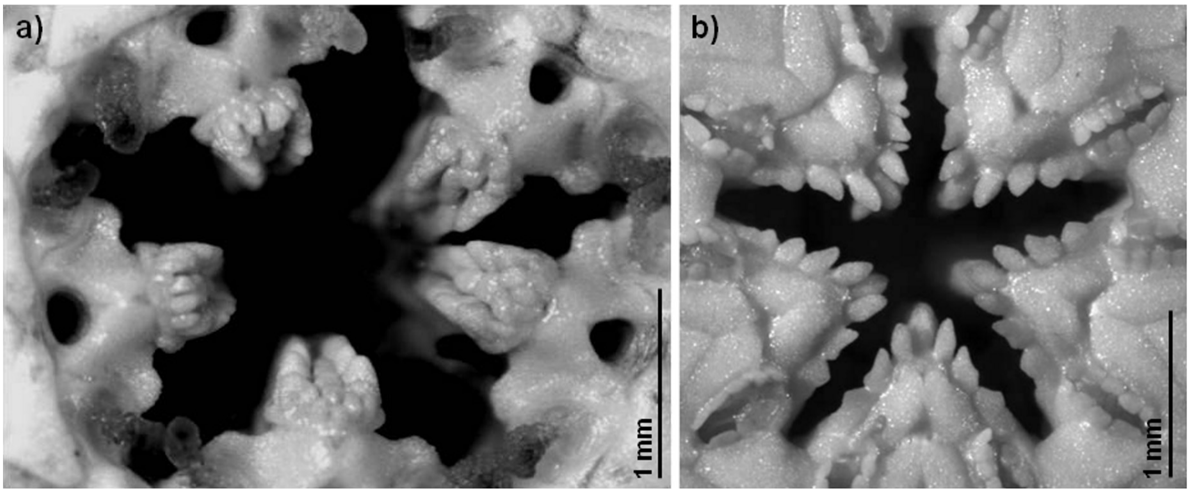

FIGURE 1. Oral views of the opened mouths of a) *Ophiothrix fragilis* revealing dense clusters of dental papillae located on the oral halves of the dental plates and of b) *Ophiura albida* revealing lateral oral papillae along the edges of the jaws and apical papillae on the oral sides of the dental plates. In both species, the teeth, located deeper inside the mouth along the aboral halves of the dental plates, are not visible clearly.

digital imaging and the PC-based digitizing software ImageJ, scaled relative to the scale bar on the images. Originating from an earlier work (Boos 2004), ten preserved (70% ethanol) and air-dried individuals of adult *O. albida* (*i.e.*, disc diameter >7.0 mm), previously collected with 0.1 m² van Veen grabs, were dissected for full and profile images for the descriptions and measurements of teeth and mouth parts as described above. Information on feeding modes and behaviour as well as food spectra and lifestyles were drawn from the literature. Because all observations and measurements remained descriptive, no statistical analyses were conducted.

Results

Ophiothrix fragilis. As previously described, the dissections of the mouthparts of *O. fragilis*, and in particular the profile and full views of the individual jaws confirmed dense clusters of up to 22 conical dental papillae with rounded tops and no infradental or oral papillae (Hendler *et al.* 1995; Southward & Campbell 2006). Typically, these papillae are arranged in two rows that frame a middle row of three to five comparatively smaller papillae located on the lower third of the dental plate (Tab. 1; Figs. 1a, 2a–c). The size of the dental papillae in the lowermost position (*i.e.*, closest to the mouth opening) increased gradually with position further up the dental plate (*i.e.*, closer to the aboral surface) to about twice the size (Tab. 1; Fig. 2a–b). Similarly, the lowermost dental papillae with rounded shapes slightly increased in width with position further up the dental plates, giving the uppermost positioned papillae a more oval appearance in cross-view. The largest were even of triangular shape and, thus, appeared pointed at their tips (Fig. 2b). The clusters of dental papillae are typically confined to the lower (oral) half of the dental plates. Along the upper (aboral) half of the dental plates towards the aboral surface, the papillae were followed by single rows of typically five large and projecting teeth, with their tips sharply edged to the shape of an arrowhead (Fig. 2a–c). This was most pronounced in the first three to four teeth. The uppermost tooth appeared nearly rounded in cross-view, bearing no edges at all (Fig. 2b–c). The teeth were about twice the length of the orally positioned dental papillae and generally all similar in length. Both, papillae and teeth appeared to have smooth surfaces.

Ophiura albida. In *O. albida*, neither infradental nor dental papillae are present (Mortensen 1927; Fell 1960; Southward & Campbell 2006). However, a series of three to four lateral papillae on either side of the jaw edges can be found (Fig. 1b). Typically, three apical papillae located at the proximal tips of the jaws, were the largest and were of prominent conical appearance with tapered pointed tips. Nearly equal in width and depth, the apical papillae revealed rounded shapes in cross-view (Tab. 1; Fig. 2d–e). In contrast, the lateral papillae were generally shorter, wider and thinner, revealing a broad and scale like appearance. Lacking dental papillae, the entire dental plates are equipped with teeth (Fig. 2d–e). Similar in shape, yet slightly larger than the apical papillae, the teeth may be arranged in single or double rows, or may start as a single row on the oral side of the dental plate and then deviate from this pattern while moving aborally (Fig. 2d–e). As in *O. fragilis*, both, papillae and teeth had smooth surfaces. Although the images may reveal a very finely granulated appearance, this is more likely due to the magnification in the images as well as to epidermal remnants fixed during preservation, as to actual structuring of the papillae and teeth.

Discussion

Since there are only few reports on brittle stars with strong tendencies to herbivory, *e.g.*, *Ophiolepis elegans* Lütken, 1859 or *Ophiactis resiliens* Lyman, 1879 (Pentreath 1970; Stancyk 1970), ophiuroids are generally considered carnivorous macro- or omnivorous microphages (Warner 1982 and references therein).

Regarded as omnivorous microphage, the rheophilic *O. fragilis* can be found in habitats of bedrock, boulder, gravel or sedimentary substrata in densities forming entire brittle star beds often exceeding 1,000 indiv./m² (Warner 1971; Hughes 1998). *Ophiothrix fragilis* feeds primarily as a podial suspension-feeder by trapping planktonic organisms and detritus with its tube feet while extending its arms into the water column (Warner & Woodley 1975; Hughes 1998). Particles are trapped on the sticky papillate surfaces of the tube feet equipped with extensive deposits of mucus and are subsequently agglutinated into a growing food bolus (Warner 1971). In consecutive waves of the tube feet, the periodically collected food boli are then passed along the arms to the mouth (Warner & Woodley 1975, Warner 1982).

TABLE 1. Morphological measurements (mean ± SD) of papillae and teeth in relation to the body size of each three individuals of *Ophiothrix fragilis* and *Ophiura albida*. Because in some jaws the teeth or papillae were broken off or damaged during dissection, the number of measured structures varied per jaw. Measurements of individual structures, however, were at minimum n = 5 for each species. dd = disc diameter.

	Length (mm)	Width (mm)	Depth (mm)
***Ophiothrix fragilis* (dd: 7.9 ± 0.2 mm)**			
Outer dental papillae	0.15 ± 0.04	0.06 ± 0.04	0.05 ± 0.01
Inner dental papillae	0.09 ± 0.01	0.05 ± 0.02	0.03 ± 0.00
Teeth	0.22 ± 0.03	0.12 ± 0.03	0.07 ± 0.01
***Ophiura albida* (dd: 9.0 ± 0.8 mm)**			
Apical papillae—conical	0.28 ± 0.03	0.13 ± 0.02	0.11 ± 0.01
Lateral papillae—broad	0.17 ± 0.03	0.22 ± 0.04	0.05 ± 0.01
Teeth	0.31 ± 0.05	0.12 ± 0.03	0.09 ± 0.02

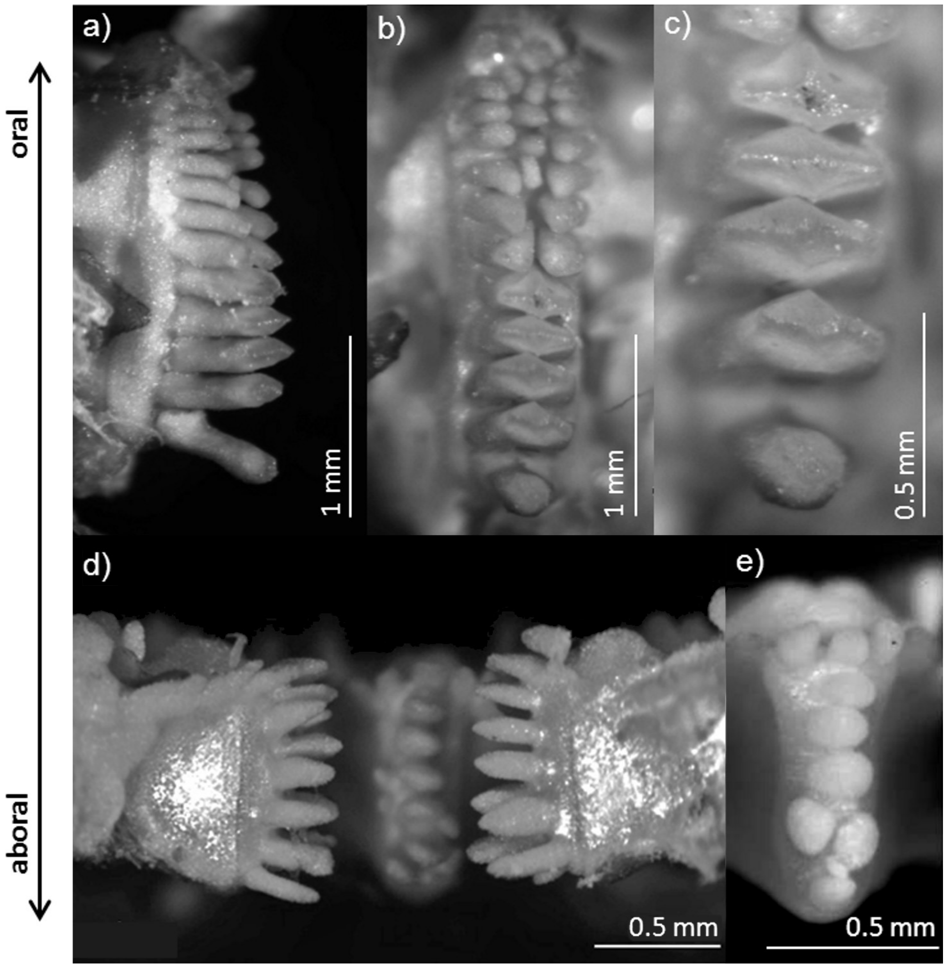

FIGURE 2. a–c) Single dental plates of *Ophiothrix fragilis* holding a) dental papillae and teeth in profile view, b) dental papillae and teeth in frontal view and c) enlarged frontal view on the teeth. d) Side view of jaws in *Ophiura albida* and e) teeth on the dental plate in frontal view. The arrow on the left indicates the orientation of the teeth and papillae.

The qualitative food spectrum of *O. fragilis* is highly diverse. Inspected food boli included large amounts of diatoms and coccoliths, comparably fewer amounts of faecal pellets, foraminifera and remnants of crustaceans (Warner & Woodley 1975). Gut content analyses confirmed the above findings along with considerable amounts of silt and detritus (Brun 1969; Warner & Woodley 1975). The collection of particles implies to be unselective in *O. fragilis*. In the bolus collecting suspension feeder *O. spiculata* and in deposit feeding amphiurids, a final gustatory decision whether to accept or to reject a food bolus for ingestion depending on what it contains, is performed by the oral tube feet (Austin 1966; Pentreath 1970). This may hold true for *O. fragilis* as well, more so as unselective particle selection may include impalatable, inorganic or even anthropogenic substances (Austin 1966). Observations on the food bolus collecting species *O. fasciata*, *O. antipodum* and *O. spiculata* showed the oral tube feet to scrape the boli against the [oral and dental] papillae and teeth prior to ingestion (Pentreath 1970). Austin (1966) refers to *O. spiculata* closing its jaws repeatedly on the food masses before pushing them into the mouth. Considering the food bolus to be a fairly compound body when travelling along the arms and growing in size, the scraping behaviour may be regarded as a mechanism to loosen the firm structure and to mechanically help dissolve the mucus holding the food particles together. Closing movements of the jaws on the bolus after it is initially loosened may subsequently break it into little pieces and making the food mass more manageable for digestion. Transferring these implications to *O. fragilis*, the rough surface provided by the clusters of dental papillae may serve the purpose of loosening the firm structure of the bolus, while the teeth with their triangularly pointed tips may serve in crushing the bolus to pieces. The arrowhead-shaped edges in the teeth of *O. fragilis* may hereby serve as cutting surfaces, supporting not only the food bolus to ultimately fall apart by being repeatedly crushed, but to actually cut it into pieces and thereby serve as knives in processing food prior to digestion. Besides its main feeding mode, frequently and occasionally observed feeding modes in *O. fragilis* include deposit-feeding, browsing, grazing, scavenging and even predating upon small macroinvertebrates (Warner 1982 and references therein; Hughes 1998). Benthic diatoms being part of the food spectrum suggest deposit feeding, browsing or grazing as the applied feeding mechanisms. During deposit feeding, the animal would most likely dab its tube feet over the sediment surface, thereby collecting material (*e.g.*, benthic diatoms) which is most likely handled into a food bolus as described above. Browsing or grazing, however, may involve actively scraping and/or detaching fouling organisms such as algal mats and biofilms or sessile invertebrates (*e.g.*, bryozoans) with calcareous structures from surfaces. This requires the use of appropriate tools and a higher effort than just dabbing tube feet over the surface. Browsing with the jaws and oral tube feet has rarely been observed in ophiuroids (Warner 1982). Pentreath (1970), however, observed *O. antipodum* to remove algal and detrital films from glass plates with its dental papillae and the oral tube feet. In addition, Gordon (1972) showed that this species is also capable of breaking off and ingesting pieces of bryozoan colonies. Similarly, *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1789) was found to browse on epiphytic hydroids and bryozoans growing on kelp fronds (Wintzell 1918). Equally equipped with dental papillae as *O. antipodum* and *O. nigra*, browsing may hold true for *O. fragilis* as well, using the rough surface of the dental papillae, and maybe even the lowermost teeth, to scrape off fouling organisms from surfaces. In fact, Hughes (1998) reported areas of grazed bedrock and boulders which were found scattered around the entrances of two Scottish Sea Loch systems inhabited by dense populations of *O. fragilis* and *O. nigra*. Predatory activity in *O. fragilis* may be related to the species' ability to extend its tube feet in order to capture larger food particles (*i.e.*, planktonic prey organism) as opposed to unselectively collecting suspended matter (Warner 1971). This, however, seems to occur only on very rare occasions (Warner 1982). Mortensen (1927) and Fell (1966) listed polychaetes and crustaceans, small mussels, echinoderms and compound ascidians as food items for *O. fragilis*. According to these prey species' typically epi- or endobenthic lifestyles, a predatory feeding behaviour in *O. fragilis* seems likely. Yet, the above listed prey species could also have been acquired by means of scavenging, which was observed by Nagabhushanam & Colman (1959) in *O. fragilis* held in an aquarium feeding on dead fish, and has been listed as a probable additional feeding mode for *Ophiothrix* spp. by Warner (1982). According to its dental equipment, it seems very likely that *O. fragilis* is able to use its dental papillae to grab and fix small macroinvertebrates and to cut, crush or even tear pieces of flesh from carrion, thus making predation and scavenging indeed a likely additional feeding mode to occur.

In contrast, *O. albida*—as most representatives of the genus *Ophiura*—is considered an omnivorous macrophage, chiefly predating on epibenthic or infaunal organisms and scavenging on carrion. Hunted or encountered prey or pieces of carrion, respectively, are typically gripped in arm slings or dug out of the sediment (Möbius & Bütschli 1875; Feder 1981). In European waters, *O. albida* can be found in abundance on a variety of different soft bottoms, such as mud, gravel, sand and broken shell (Dahm 1993; Kühne & Rachor 1996; Niermann 1997), reflecting a variety of feeding grounds. Feder (1981) found the congeneric *Ophiura ophiura* (Linnaeus, 1758) to be a true predator of small benthic invertebrates and confirmed, among 41 different prey organisms, polychaetes, bivalves and crustaceans to comprise the main food source of *Ophiura* spp. (Warner 1982). Tyler (1977), conversely, found *O. albida* to rely on microalgae and detritus rather than on carnivorous food. In fact, stomach content analyses of *O. albida* revealed comparably high amounts of sediment in comparison to remains of small benthic organisms (Eichelbaum 1910; Warner 1982). This may be on account of surface and sub-surface deposit feeding recorded as additionally probable feeding modes (Feder 1981; Warner 1982; Sköld & Rosenberg 1996). Dabbing their tube-feet over the sediment surface looking for food may contribute to the active intake of sediment particles (MacGintie 1949). High amounts of deposit material in the gut, however, are also likely to have resulted from burrowing activity while searching for food and predating on infaunal organisms. Together with a preference for soft over coarse sediments, this, in fact, has been considered a main factor allowing for the broad overlap in habitat use and coexistence between *O. albida* and *O. ophiura* in the southern North Sea (Boos *et al.* 2010).

The present study revealed *O. albida* to be equipped with predaceous dental equipment. Not only the teeth, but also the apical papillae revealed to be prominent pointy structures possibly used in gripping or spearing captured prey before ingestion. This behaviour was observed in the predatory *Ophiosparte gigas* Koehler, 1922 (Dearborn *et al.* 1996) and *Ophioplinthus brevirima* (Mortensen, 1936) (Pentreath 1970). The authors described how both species, after handling larger food particles by means of arm coiling, grasped their food with their teeth and then passed it into their mouths with their oral tube feet. In *O. gigas*, dental papillae are lacking, oral papillae are described as "generally tapering and pointed" and the teeth arranged in many rows are described as "large, spine-like, somewhat spatulate and serrate" (Dearborn *et al.* 1996). Likewise, the teeth in *O. brevirima* are mentioned to be serrated, as are the oral papillae (Pentreath 1970). It seems plausible that serrated surfaces serve better in grasping and fixing a prey organism than do smooth surfaces in spine like structures, which is the case for the teeth in *O. albida.* Possibly, this function is served more effective by the entire arm when capturing prey organism in an arm-sling, whereas the teeth are more often used for thrusting into the flesh of captured prey or carrion and tearing off pieces of tissue. Similarly, Austin (1966) reported how *O. luetkeni* would grip "with the jaws while pushing away with the arms to tear pieces from a large food mass". If prey is not swallowed whole, which has been observed in *O. ophiura* (Feder 1981), grasping and tearing seems appropriate to be applied to prey organisms with tissues soft enough to be handled that way (*e.g.*, polychaetes) or to tissues structured in a manageable way to be gripped and torn (*e.g.*, segmented carapaces in peracarid crustaceans).

Conclusions

Clusters of dental papillae found in the suspension-feeding bolus forming *O. fragilis* seem most appropriately applied as grinding instruments in loosening the tight structure of a compound food item. Sharply edged teeth are likely to fulfil the job of crushing and cutting up the loosened food masses prior to digestion. Though considered chiefly a podial suspension feeder, *O. fragilis* may perform additional feeding modes: browsing, grazing, scavenging and even predating may be achieved through the grinding and thus gripping motion of the dental papillae. Crushing and cutting of individual larger food particles may then be served by the teeth in *O. fragilis*.

In contrast, cutting or crushing seems unlikely in the predominantly predatory and scavenging *O. albida*. Predation and scavenging requires a fast and good grip of a live prey organism or a piece of carrion. Pieces of flesh torn from the food source require adequate carnassial instruments, which seem to be served by the pointed and tapered spine-like teeth as well as the spine-like apical papillae found in *O. albida*.

Covering wide ranges of edible material in the diets of both species under study, the present work showed the functional morphology of the teeth generally to apply to grinding and cutting instruments in *O. fragilis*, processing hard-structured and compound food items, and to gripping and tearing instruments in *O. albida*, handling pieces of soft tissued flesh. As these present implications are solely built on a theoretical background, empirical evidence is urgently required.

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References

Austin, W.C. (1966) *Feeding mechanisms, digestive tracts and circulatory systems in the ophiuroids Ophiothrix spiculata Le Conte, 1851 and Ophiura luetkeni (Lyman, 1860).* Stanford University Press, Stanford, xi + 278 pp.

Boos, K. (2004) *Ökologische Untersuchungen an Ophiuren der Deutschen Bucht*. Unpublished Diploma thesis. Freie Universität Berlin, Berlin, 85 pp.

Boos, K., Gutow, L., Mundry, R. & Franke, H.-D. (2010) Sediment preference and burrowing behaviour in the sympatric brittlestars *Ophiura albida* Forbes, 1839 and *Ophiura ophiura* (Linnaeus, 1758) (Ophiuroidea, Echinodermata). *Journal of Experimental Marine Biology and Ecology*, 393, 176–181.

Brun, E. (1969) Aggregation of *Ophiothrix fragilis* (Abildgaard) (Echinodermata: Ophiuroidea). *Nytt magasin for zoologi*, 17, 153–160.

Clark, H.L. (1915) Catalogue of Recent ophiurans. *Memoirs of the Museum of Comparative Zoology*, 25, 163–376.

Dahm, C. (1993) Growth, production and ecological significance of *Ophiura albida* and *O. ophiura* (Echinodermata: Ophiuroidea) in the German Bight. *Marine Biology*, 116, 431–437.

Dearborn, J.H. (1977) Foods and feeding characteristics of Antarctic asteroids and ophiuroids. *In*: Llano, G.A. (Ed.), *Adaptations within Antarctic Ecosystems.* Smithsonian Institute Publications, Washington, D.C., pp. 293–326.

Dearborn, J.H., Hendler, G. & Edwards, K.C. (1996) The diet of *Ophiosparte gigas* (Echinodermata: Ophiuroidea) along the Antarctic Peninsula, with comments on its taxonomic status. *Polar Biology*, 16, 309–320.

Eichelbaum, E. (1910) Über Nahrung und Ernährungsorgane von Echinodermen. *Wissenschaftliche Meeresuntersuchungen, Abteilung Kiel (N.F.)*, 11, 187–274.

Feder, H.M. (1981) Aspects of the feeding biology of the brittlestar *Ophiura texturata*. *Ophelia*, 20, 215–235.

Fell, H.B. (1960) Synoptic keys to the genera of Ophiuroidea. *Zoology Publications from Victoria University of Wellington*, 26, 1–44.

Fell, H.B. (1966) The ecology of ophiuroids. *In*: Boolootian, R.A. (Ed.), *Physiology of Echinodermata.* Interscience Publishers, New York, pp. 129–143.

Forbes, E. (1839) On the Asteriadae of the Irish Sea. *Memoirs of the Wernerian Society*, 8, 1–114.

Gordon, D.P. (1972) Biological relationships of an intertidal bryozoan population. *Journal of Natural History*, 6, 503–514.

Hendler, G., Miller, J.E., Pawson, D.L. & Kier, P.M. (1995) *Echinoderms of Florida and the Carribean – sea stars, sea urchins and allies*. Smithsonian Institution Press, Washington, 392 pp.

Hughes, D.J. (1998) Subtidal brittlestar beds. An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. *Scottish Association for Marine Science (UK Marine SACs Project), vol. IV*. Scottish Marine Institute, Oban, 78 pp.

Hutton, F.W. (1872) Catalogue of the echinodermata of New Zealand, with diagnoses of the species. *Colonial Museum and Geological Department*, i–iv + 1–18.

Hyman, L.H. (1955) *The Invertebrates. IV. Echinodermata*. McGraw-Hill, New York, 763 pp.

Kühne, S. & Rachor, E. (1996) The macrofauna of a stony sand area in the German Bight (North Sea). *Helgoländer Meeresuntersuchungen*, 50, 433–452.
Koehler, R. (1922) Echinodermata: Ophiuroidea. *Australasian Antarctic Expedition 1911–1914. Scientific Report, Series C*, 8, 5–98.
Le Conte, J.L. (1851) Zoological Notes. *Proceedings of the Society of Natural History Philadelphia* 5, 317–320.
Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. Laurentius Salvius, Holmiae, ii+824 pp.
Loo, L.-O., Jonsson, P.R., Sköld, M. & Karlsson, Ö. (1996) Passive suspension feeding in *Amphiura filiformis* (Echinodermata: Ophiuroidea): feeding behaviour in flume flow and potential feeding rate of field populations. *Marine Ecology Progress Series*, 139, 143–155.
Lütken, C.F. (1859) Additamenta ad historiam Ophiuridarum. Anden Afdelning. *Det kongelige danske Videnskabernes Selskaps Skrifter. 5 Raekke, Naturvidenskabelig og mathematisk Afdelning*, 5, 177–271.
Lyman, T. (1879) Ophiuridae and Astrophytidae of the "Challenger" expedition. Part II. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 6, 17–83.
MacGintie, G.E. (1949) The feeding of ophiurans. *Journal of Entomology and Zoology*, 41, 27–29.
Madsen, F.J. (1970) West African Ophiuroids. *Atlantide Report: Scientific results of the Danish Expedition to the coasts of Tropical West Africa 1945–1946*, 11, 151–243.
Möbius, K. & Bütschli, O. (1875) Zoologische Ergebnisse der Nordseefahrt. IV. Echinodermata. *Jahresbericht der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere in Kiel*, 23[1872/1873], 143–152.
Mortensen, T. (1927) *Handbook of the Echinoderms of the British Isles*. Oxford University Press, Oxford, 471 pp.
Müller, O.F. (1789) *Zoologica Danica seu animalia Daniae et Norvegiae rariorum ac minus notorum descriptions et historia, Vol III*. Møller, Kopenhagen, 71 pp.
Nagabhushanam, A.K. & Colman, J.S. (1959) Carrion-eating by ophiuroids. *Nature*, 184(4682), p. 285.
Niermann, U. (1997) Macrobenthos of the south-eastern North Sea during 1983–1988. *Berichte der Biologischen Anstalt Helgoland*, 13, 1–144.
Pentreath, R.J. (1970) Feeding mechanisms and the functional morphology of podia and spines in some New Zealand ophiuroids (Echinodermata). *Journal of Zoology*, 161, 395–429.
Reimer, R.D. & Reimer, A.A. (1975) Chemical control of feeding in four species of tropical ophiuroids of the genus *Ophioderma*. *Comparative Biochemistry and Physiology (A: Molecular & integrative physiology)*, 51, 915–927.
Sköld, M. & Rosenberg, R. (1996) Arm regeneration frequency in eight species of ophiuroidea (Echinodermata) from European Sea areas. *Journal of Sea Research*, 35, 353–362.
Smith, E.A. (1877) Description of a new form of Ophiuridae from New Zealand. *Annals and Magazine of Natural History*, 15, 305–309.
Southward, E.C. & Campbell, A.C. (2006) Echinoderms: keys and notes for identification of the British species. *Synopsis of the British Fauna (New Series)*, 56, viii+272 pp.
Stancyk, S.E. (1970) *Studies on the biology and ecology of ophiuroids at Cedar Key, Florida.* Unpublished Master's thesis, University of Florida, Gainesville, FL, 92 pp.
Stöhr, S. (2005) Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society*, 143, 543–576.
Tyler, P.A. (1977) Seasonal variation and ecology of gametogenesis in the genus *Ophiura* (Ophiuroidea: Echinodermata) from the Bristol Channel. *Journal of Experimental Marine Biology and Ecology*, 30, 185–197.
Warner, G.F. (1971) On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom*, 51, 267–282.
Warner, G.F. & Woodley, J.D. (1975) Suspension-feeding in the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom*, 55, 199–210.
Warner, G.F. (1982) Food and feeding mechanisms: Ophiuroidea. *In*: Jangoux, M. & Lawrence, J.M. (Eds.), *Echinoderm nutrition.* A.A. Ballkema, Rotterdam, pp. 161–181.
Wintzell, J.F. (1918) *Bidrag till de skandinaviska ophiuridernas biologi och fysiologi.* Appelbergs, Uppsala, 147 pp.