Contributions in Science, 526:189–311 21 December 2018

Armed to the Teeth: A New Paradigm for the Buccal Skeleton of Brittle Stars (Echinodermata: Ophiuroidea)[1]

Gordon Hendler[2]

CONTENTS

---

[1] URL: www.nhm.org/scholarlypublications

[2] Echinoderms Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA. E-mail: hendler@nhm.org

ISSN 0459-8113 (Print); 2165-1868 (Online)

ABSTRACT. The mouth of an ophiuroid is armed with ossicles that traditionally, and indiscriminately, were all designated as "oral papillae." This study offers a novel interpretation of ophiuroid buccal armature, which comprises oral papillae *sensu lato* (OPas *s.l.*) and a previously overlooked skeletal system within the buccal cavity, which is designated herein the peribuccal skeleton (PeSk). These structures are described in the present study. In addition, a nomenclature is provided to designate the different types of ossicles, and their homology is provisionally inferred on the basis of their ontogenesis, anatomical position, and morphology. Their biological functions are assessed in light of information on the morphology, feeding behavior, and diet of species in various families. The types of ossicles discerned include (1) teeth and tooth papillae, which develop on the dental plate; (2) buccal scales, infradental papillae, secondary infradental papillae, crest papillae, lateral oral papillae, accessory oral papillae, and spines, which develop on the oral plate; (3) homologues of arm spines, which develop on and adjacent to the adoral shield; (4) homologues of tentacle scales, which develop on the first ventral arm plate; and (5) components of the PeSk, which enclose the oral tentacles, link the arms and oral frame, and protect the nervous, water vascular, and muscle structures housed within perradial gaps between adjacent jaws. Differences in the morphology and configuration of OPas *s.l.* and PeSk elements are revealed in scanning electron microscopy micrographs of the articulated skeletons of 18 exemplar species from 16 representative ophiuroid families. Substantial new information is provided on ontogenesis of the buccal armature of Ophiopsilidae, Ophionereididae, Hemieuryalidae, Ophiolepididae, Ophiomyxidae, Ophiodermatidae, Ophiocomidae, and Ophiuridae. The major ophiuroid clades designated by O'Hara et al. (2017, 2018) are proposed to have characteristic, contrasting types and arrangements of buccal elements. A specialized suite of morphological features is postulated to have repeatedly evolved in a major guild of unrelated microphagous ophiuroid species that all exhibit a conical gap centered among the jaws, which is designated herein the "buccal funnel." It is composed of a graduated series of ossicles that may consist of small, modified ventral teeth; infradental papillae; tooth papillae; crest papillae; and a column of progressively longer dorsal teeth. Opposing teeth of ophiuroids are shown to have a staggered arrangement and to intermesh when jaws are closed. Newly discovered skeletal elements include a protuberant, anvil-shaped ossicle on the oral plate in Ophiocomidae and crest papillae on the oral plate of Ophiopsilidae. Several misconceptions regarding ophiuroid anatomy and ontogenesis are rectified. The first direct evidence for the fission of an ophiuroid ossicle is documented in the development of a multi-element dental plate. The putative distalmost "oral papilla" of some ophiuroids is shown to be a PeSk element (Lyman's ossicle), which develops in the buccal cavity. Discovery of a peristomial plate with a peduncle and an internal conduit indicates this structure can be more complex than was formerly assumed. So-called ontogenetic "migration" of the adoral shield spine, first ventral arm plate, and second oral tentacle pore is not, as previously thought, produced by independent movement of these structures. Rather, their position is modified by allometric growth of the oral plate and adoral shield on which they are borne. The morphology of Ophiuridae, which has been characterized as a paedomorphic family, is not necessarily shaped by the retention of juvenile characters. The distinctive appearance of their jaws is imparted by allometric growth of the oral plate, ventral arm plate, and ventral tentacle compartment plate; by a truncated ventral tentacle compartment; and by the location of OPas *s.l.* on the oral plate ridge. Remarkably, the water ring, which was presumed to overlie the buccal apparatus in all echinoderms, is shown to penetrate the oral plates of species from both superorders and all six orders of Ophiuroidea.

INTRODUCTION

Interpretations of the phylogeny, evolution, and ecology of members of the Mammalia are based, to a large extent, upon features of their teeth and jaws, and it has been asserted that "Nothing about mammals makes sense except in the light of their teeth" (Sperber, 2013:1, attributed to Kemp, 2005). As mammals evolved, the morphology of their oral structures diversified according to types of food consumed, as a result of selective pressure (Ungar, 2010). Consequently, a mammal's diet can be inferred from its dentition, and mammalian species can be identified "by the nature of the cusps of a single molar tooth" (Carroll, 1988:407; Christensen, 2014; Sansom et al., 2017).

Similarly, the oral skeleton found among members of Echinodermata registers the influence of adaptive evolution. Buccal armature of Echinoidea, particularly components of Aristotle's lantern, has "proved most useful in unraveling the phylogeny of echinoids" (Smith, 1984:64; Kroh and Smith, 2010). Buccal armature of Ophiuroidea (brittle stars), the most diverse class of echinoderms, might likewise illuminate their evolution, systematics, ecology, and behavior, and it merits scrutiny on this account. Nonetheless, their buccal armature has attracted negligible attention. Even founders of ophiuroid biology admonished "not to give…too great value…[to] those minute papillae which form the armature of the mouth," mistakenly assuming that all are "parts really homologous" (Lütken 1858:8; Lyman, 1874:258, 264). The notion persisted that "mouth papillae…borne on the flanks of the jaws" are not distinguishable from one another (MacBride, 1906:493). However, Verrill (1899a:24) upended this idea and advocated that species of the prolific genus *Amphiura* "are best characterized by the structure, number and arrangement of the mouth parts, as in most other ophiuran families." He radically revised amphiurid taxonomy in accordance with the configurations of species' "mouth papillae," and his methods were adopted, modified (e.g., by Matsumoto, 1915; A.M. Clark, 1970), and widely applied to taxonomic studies of other ophiuroids, albeit with scant consideration of the homologies of these ossicles. Acknowledging this oversight, a recent review of ophiuroid systematics concluded that "…the mouth papillae show a remarkable variation between species, but also stability that has lead [sic] to them being used in many identification keys, on species, genus and family level…" yet "…mouth papillae have not been subjected to a comparative analysis. Their function and evolution are unknown…" (Stöhr, 2012:155).

This is not to say investigations of ophiuroid systematics and evolution have wholly discounted the function, ontogenesis, morphology, and homology of buccal armature. Ludwig's (1878, 1882, 1899, 1901) pioneering analyses of asterozoan morphology inferred homologies of adult skeletal structures based in part on their development. Other investigators proved that a prominent skeletal element in the juvenile, which Ludwig misidentified as the precursor of a peristomial plate, was resorbed or else formed a so-called oral "tentacle scale" in various species (zur Strassen, 1901; H.L. Clark, 1914; A.M. Clark, 1970:4; Hendler, 1978). Subsequently, this papilla was designated the "buccal scale," and its homology with a tentacle scale was refuted on the basis of its ontogenesis (Hendler, 1978). Additionally, an ostensible "oral papilla" beside the second oral tentacle pore of *Amphioplus abditus* (Verrill, 1871) was shown to develop from a spine on a modified arm plate (adoral shield), and it consequently was designated the "papilla on the adoral shield" or "adoral shield spine" (A.M. Clark, 1970:5; Hendler, 1978:91). Remarkably, the position of the adoral shield spine was discovered to change during ontogenesis from the adoral shield to the oral plate of *A. abditus*, and putative homologues of the buccal scale, adoral shield spine, and infradental papilla were identified in juvenile stages of other ophiuroid genera and families (e.g., Hendler, 1978, 1988, 1998). These findings contradicted prevailing notions that each oral papilla *sensu lato* has a fixed position throughout development, and is homologous with tentacle scales on the arms, and that the adoral shield "does not bear a spine…at any stage of its development" (e.g., Matsumoto, 1915:69; H.L. Clark, 1914:110, 121).

Although information on mammalian dental homologies is routinely employed in systematic and evolutionary studies (e.g., Luckett, 1993), the significance of ophiuroid skeletal homologies was often overlooked. It was postulated that "oral papillae are merely 'groove spines' carried by the mouth-angle plate" and "the ancestral state of the oral papillae . . . implies their homogeneity and similarity in size and shape from the distal to the proximal jaw area" (Spencer, 1925:276; Martynov, 2010b:23). Furthermore, it was proposed that some characters traditionally used to define families, including oral papillae *sensu lato*, are "evidently homoplasic" (O'Hara et al., 2014; Hugall et al., 2015:290; Hunter et al., 2016; O'Hara et al., 2017). On this account, conventional taxonomic descriptions of adult ophiuroids routinely specify the number of oral papillae on a jaw without regard to the homologies of these ossicles (e.g., Hyman, 1955; Paterson, 1985; Smith et al., 1995; O'Hara and Stöhr, 2006; Stöhr, 2011; O'Hara and Harding, 2015; O'Hara et al., 2017; Okanishi and Fujita, 2018). Most studies of ophiuroid systematics characterize oral papillae solely according to their shape and proximity to the second oral tentacle (Smith et al., 1995:238; Stöhr and Martynov, 2016:8; Thuy and Stöhr, 2016:16). Likewise, investigations of ophiuroid ontogenesis conflate different types of "mouth papillae" aside from the buccal scale and adoral shield spine (e.g., Schoener, 1967, 1969; Webb and Tyler, 1985; Turner and Miller, 1988; Sumida et al., 1998, Stöhr, 2005:573; Borges et al., 2015).

It was recently proposed that ". . .a unified model of brittle-star postlarval development . . .would be useful as a practical tool for understanding the ophiuroid phylogeny and resolving complicated taxonomic problems" (Martynov et al., 2015:9). Likewise, a recent phylogenetic study of Ophiuroidea based on an analysis of dissociated ossicles contended that "studies of juvenile characters have shown promising results that may be highly valuable for phylogenetic inferences. . .. A future study built on species for which juvenile and adult stages are available may provide additional insights into the evolution of Ophiuroidea" (Thuy and Stöhr, 2016:23). It also was claimed that "Nothing is known about the function of the mouth papillae in ophiuroids. The great diversity in their shape, size, and number suggests that they are not just for closing the mouth gap, but somehow assist in feeding" (Stöhr and Segonzac, 2006:30). Moreover, "characteristics of the internal skeleton are unknown for the majority of . . . described species" (O'Hara et al., 2018:3). Unfortunately, only a few synoptic studies consider morphology of the ophiuroid skeleton (e.g., Lyman, 1882:pls. 37–43; Matsumoto, 1917:figs. 1–7; Murakami, 1963:text-fig. 1, pls. 1–7), and most examinations of ophiuroid ontogenesis have focused on the taxonomic identification of postlarvae (e.g., Schoener, 1967, 1969; Webb and Tyler, 1985; Turner and Miller, 1988; Sumida et al., 1998, Stöhr, 2005:573; Borges et al., 2015).

Consequently, a prime goal of the present study was to develop a conceptual model of the ophiuroid buccal skeletal system by characterizing the anatomy and morphology of the buccal armature, and by distinguishing between ossicles with different patterns of ontogenesis. Another goal was to relate information on buccal structure to the feeding behavior and systematic relationships of ophiuroids. To that end, exemplars of a phylogenetically broad range of families were examined. Adult and juvenile specimens were dissected and external and internal components of their articulated buccal skeletons were examined using scanning electron microscopy (SEM). A nomenclature was devised to identify the different types of ossicles that were revealed and to facilitate future studies of ophiuroid morphology. Although a phylogenetic evaluation of homology was beyond the scope of this study, presumptive homologies of buccal ossicles were inferred according to "similarities in structure, in anatomical position, and in developmental origin" (Roth, 1984:16). Morphologically similar ossicles arising in succession, in close association, and in a linear, unidirectional sequence were hypothesized to be serially homologous.

Surprisingly, in the present investigation a previously overlooked system of ossicles designated herein the peribuccal skeleton (PeSk) was detected within the buccal cavity of every species examined. PeSk elements, and the integument in which they are embedded, shield the nerve ring and water ring, oral tentacles, and structures in perradial gaps between the jaws, including adradial muscles of the oral plates and radial branches of the nerve and water rings. The functional significance of these and of some other novel structures revealed in this study is evaluated, particularly with regard to ophiuroid feeding behavior. Previous interpretations of ophiuroid skeletal ontogenesis are reassessed, and the skeletal ontogenesis of several families is described for the first time. Additionally, elements of buccal armature are assessed, in light of ophiuroid phylogeny, for possible evidence of plesiomorphies, apomorphies, and rampant homoplasy. The phylogenetic tree and taxonomic classification of Ophiuroidea employed herein are based on systematic revisions by O'Hara et al. (2017, 2018).

MATERIALS AND METHODS

Specimens were prepared for SEM by dissecting a pair of arm bases and the attached jaw from each individual examined. Extraneous skeleton and soft tissue, including oral tentacles, were removed with fine forceps and scissors. Residual integument was dissolved by repeatedly applying a dilute (3–50%) aqueous solution of commercial bleach (sodium hypochlorite), using a Pasteur pipette with a filler bulb. After each exposure to bleach, the specimen was rinsed with 85% ethanol and examined microscopically to ascertain whether ossicles were adequately exposed. Cleaned specimens were dehydrated in 95% ethanol, air dried, and attached to an aluminum stub with colloidal silver paste. The mount was sputter coated with 80% Au, 20% Pd and examined with a Hitachi S-3000N variable-pressure scanning electron microscope.

In the present study, dorsal, ventral, and proximal aspects of representative jaws were documented with SEM micrographs, and morphology of the adult buccal armature of each species was described in a standardized sequence to facilitate comparisons among species. Although these descriptions of skeletal morphology are based on a limited number of SEM preparations and a restricted number of species and so do not expose the full extent of interspecific or intraspecific morphological variation, they reveal an unexpectedly elaborate ophiuroid bauplan. Herein, these findings are integrated with a novel interpretation of ophiuroid skeletogenesis and up-to-date information on feeding biology and phylogeny of the group, in order to provide a new paradigm for the buccal skeleton of Ophiuroidea. Body size of ophiuroids, expressed in terms of disk diameter (dd), was measured with vernier calipers or a calibrated ocular micrometer. Counts of the maximum number of segments in an arm (ASs) were recorded for some juvenile individuals.

The juvenile specimens examined were free-living individuals collected in the field or brooded young dissected from the bursae of preserved adults. Ontogenesis of their external buccal armature was analyzed by comparing series of different-sized specimens of each species. Development of their internal skeletal ossicles was examined by dissecting juvenile specimens in the same manner as the adults, except that these preparations were mounted for SEM study on double-sided carbon conductive tabs attached to aluminum stubs.

TERMINOLOGY AND ABBREVIATIONS

TERMINOLOGY

In the present study, morphological structures are denoted using terminology from Hendler (1978) and Hendler et al. (1995), but some terms are re-defined herein to reflect new interpretations of skeletal homologies. Novel terms were coined for the previously undescribed components of the peribuccal skeleton. Terminology that "implies assumed function" or "obscures homology with ambulacrals" (*sensu*

Stöhr, 2012:258) was not eschewed, because such terms as "jaw" and "vertebra" are evocative and ubiquitous in literature on ophiuroids, and because the homologies of ambulacral ossicles composing asterozoan jaws and arms have not been resolved (e.g., Mooi and David, 2000; Hotchkiss, 2012). Species are denoted using currently accepted scientific names, and synonymous names cited in historical literature are preceded by an equal sign and enclosed in brackets (e.g., *Ophiura ophiura* (Linnaeus, 1758) [=*Ophiura texturata*]).

Ophiuroid jaws are modified, evolutionarily repurposed arm structures. The jaw of an ophiuroid incorporates two oral plates (OPs), each of which is a compound skeletal element derived in part from a modified ambulacral ossicle. In addition to the OPs, a jaw comprises a dental plate (DP) and ossicles that are broadly termed oral papillae *sensu lato* (OPas *s.l.*) and PeSk (*contra* Stöhr et al., 2012a:5). A jaw is connected to the first vertebra (V-1) of both arms flanking the jaw. Consequently an ophiuroid has equal numbers of arms and of jaws that hold the arms together. A modified first lateral arm plate (i.e., LAP-1), which is referred to as an adoral shield (AdSh), is borne on each OP. The AdShs on adjacent jaws flank a modified ventral arm plate, the first ventral arm plate (VAP-1). Thus, each VAP-1, together with two adjoining AdShs and the distal elements of two OPs, compose a modified arm segment. Accordingly, the VAP and LAP ossicles that compose the first segment of the arm are referred to as VAP-2 and LAP-2. The jaws, AdShs, VAPs-1, and associated ossicles constitute an "oral frame" surrounding the "mouth" and "buccal cavity" (*sensu* Schechter and Lucero, 1968:452). The buccal cavity is connected to the stomach by the esophagus and a circumoral esophageal ligament (Deschuyteneer and Jangoux, 1978). The gaps between open adjacent jaws, referred to as oral slits (OSls), are stellate extensions of the mouth. When the jaws are closed, part of the OSl may be occluded by the edges of OPs, OPas *s.l.*, and PeSk elements. In some species, the mouth is sealed by intermeshing teeth when jaws are fully closed. Other species have foreshortened ventral teeth and OPas *s.l.* on the apex of the jaw, and their fully closed jaws circumscribe an open conical space, a buccal funnel**,** which is constricted by a graduated series of successively larger dorsal teeth.

Two specialized tube feet termed oral tentacles (OTs) arise from branches of the water canal penetrating each OP, and each OT protrudes from a perforated depression (tentacle basin) in the plate (Olsen, 1942; Pentreath, 1970). Tentacle basins of the dorsal oral tentacle (OT-1) and ventral oral tentacle (OT-2) are separated by a horizontal prominence on the adradial face of the OP, the oral plate ridge (OPR), previously termed a "ridge of the jaw" or "adradial ridge" of the OP (Lyman, 1874:263–264, pl.1, fig.3; Kutscher and Jagt, 2000:100, fig. 16). One or more oral plate ridge spines (OPRSps) and compartment plates (CtPs**)** may be borne on the OPR. OT-2 extends from its tentacle basin through an orifice, the second oral tentacle pore (OTPo-2), which is near the juncture between the AdSh and VAP-1 and is equivalent to a tentacle pore between the LAP and VAP of an arm segment. The AdSh may bear an adoral shield spine (AdShSp) and serially homologous secondary adoral shield spines (2°AdShSps), and the associated VAP-1 may bear tentacle scales (TScs). However, OT-1 is not associated with homologues of LAPs or VAPS. Therefore it lacks a tentacle pore, and it lacks homologues of tentacle scales and arm spines. Items of food are relayed by tube feet to OT-2 and thence to OT-1, which propel food into the stomach.

"Oral papilla" and synonymous terms have been applied to various types of skeletal armature borne on the oral frame (e.g., Lütken, 1858:8; Lyman, 1874:261; Verrill, 1899b:307; Matsumoto, 1917:243). In the present study, the general term oral papilla *s.l.* (OPa *s.l.*) is applied to several types of ossicles that are not necessarily homologues. Moveable OPas *s.l.* and their supporting ossicles are bound together by muscle and/or connective tissue that links the articular surfaces (ArtSs) of both elements.

Five different groups of OPas *s.l.* can be distinguished based on their ontogenesis and position in the adult. A given species may have some, but not all, of these different types of OPas *s.l.* Group I comprises ossicles associated with the AdSh (a lateral arm plate homologue) including the adoral shield spine (AdShSp) that develops on the adoral shield, an initial secondary adoral shield papilla (2°AdShSp) that arises on the OP beside the AdShSp, and additional, serially homologous 2°AdShSps that develop on the OP in a unidirectional sequence, with each new ossicle arising proximal to its predecessor. Group II comprises a tentacle scale (TSc) that may develop on VAP-1, and serially homologous VAP-1 TScs that develop in a unidirectional sequence, each new ossicle arising proximal to its predecessor. These VAP-1 TScs may compose a row of small ossicles extending from VAP-1 onto the ventral compartment plate (vCtP). Group III comprises ossicles that develop on the dental plate, including uniserial or irregular columns of teeth, and smaller tooth papillae (TPas) that are usually arrayed in symmetrical groups. Group IV comprises elements that develop on the oral plate, including buccal scales, infradental papillae, secondary infradental papillae, lateral oral papillae, and accessory oral papillae. The buccal scale (BSc) develops as an elongated ossicle within the OSl and beside the OPR. The infradental papilla (IPa) develops near the DP/OP juncture, and it protrudes from the OP toward the DP. Secondary infradental papillae (2°IPas) arise near the DP/OP juncture, and they develop in a unidirectional sequence, each new ossicle forming proximal to its predecessor on the OP. Lateral oral papillae (LOPas) develop distal to the IPa, and they may accrue in unidirectional distal sequence on the OP. Accessory oral papillae (AOPas) may develop between the principal OPas *s.l.* on the OP. Group V comprises elements of the peribuccal skeleton (PeSk) associated the vTCt, such as Lyman's ossicle (LyOs) and the ventral compartment plate (vCtP).

Components of the peribuccal skeleton (PeSk) encircle and shield the oral tentacles, and they buttress the oral frame and connect it to the arms. Additionally, the PeSk protects nervous, water vascular, and muscle structures that occur in the perradial gaps (PGs) between the jaws and in the neural and water vascular grooves above the jaws. Because this skeletal system is newly described in the present study, novel terms have been coined for its components. Tentacle compartments (TCts), which are composed of PeSk elements that surround the tentacle basins, are thought to shield the shaft of oral tentacles from abrasive items of food. The OPR forms a scaffold for the dorsal tentacle compartment (dTCt) enclosing OT-1 and for the ventral tentacle compartment (vTCt) enclosing OT-2. These compartments may be composed of relatively large compartment plates (CtPs) attached to the OPR and OP, smaller compartment ossicles (CtOss), and minute imbricated or tessellated squamous collar ossicles (CoOs) that form a tubular sheath enclosing the base of an OT. Lyman's ossicle (LyOs) is a component of the vTCt, which develops on the vCtP inside the OSl. It protrudes from the OSl between the vCtP, AdShSp, and the VAP-1, which it abuts. A falcate plate (FP), which is typically crescentic, arches over the OT-1 and dTCt, extending between the OPR or dCtP and the dorsal edge of the OP. Ludwig's ossicles (LuOss) are embedded in an integumental sheath that extends from VAP-1 to the FP and covers the PG. These ossicles and integument create a partition that shields structures within the gap, including the adradial muscle of the OP and radial extensions of the nerve ring, water ring, hemal, and perihemal ring that extend between the arms and oral frame (the configuration of these radial and annular structures is depicted in Cuénot, 1948:fig. 290; Ezhova et al., 2015:fig. 3, 2016:fig. 3). Furthermore the FPs, peristomial plates (PPs), and the integument binding them, shield the neural and water vascular grooves on the dorsal surface of the OPs and protect the structures therein. Single or multiple oral plate ridge spines (OPRSps) and OPas *s.l.* such as the BSc may project from the proximal edge of the OPR into the buccal cavity, and the flank of the OP may bear irregularly arranged AOPas. PPs are PeSk ossicles that overlap the dorsal surface of the oral plates, reinforcing the oral frame and shielding the nerve ring which traverses a circumoral groove between the proximal and distal skeletal elements of the OPs.

ABBREVIATIONS

Morphological Structures

1°T	first-formed tooth
2°AdShSp	secondary adoral shield spine
2°IPa	secondary infradental papilla
AdSh	adoral shield (=LAP-1)
AdShSp	adoral shield spine
AOPa	accessory oral papilla
ArtS	articular surface
AS	arm segment
ASp	arm spine
BSc	buccal scale
CoOs	collar ossicle
CPa	crest papilla
CtP	compartment plate
CtOs	compartment ossicle
DAP	dorsal arm plate
dCoOs	dorsal collar ossicle
dCtOs	dorsal compartment ossicle
dCtP	dorsal compartment plate
dd	disk diameter
DP	dental plate
DP/OP juncture	ventral crevice between DP and OP
dTCt	dorsal tentacle compartment
FP	falcate plate
IPa	infradental papilla
LAP	lateral arm plate
LAP-2	lateral arm plate of the first arm segment
LOPa	lateral oral papilla
LuOs	Ludwig's ossicle
LyOs	Lyman's ossicle
Mad	madreporite
OPa	oral papilla
OPas *s.l.*	oral papillae *sensu lato* (i.e., IPa, CPa, 2°IPa, LOPa, BS, AdShSp, 2°AdShSp, LyOs, tooth, TPa, VAP-1 TSc)
OP	oral plate
OPR	oral plate ridge
OPRSp	oral plate ridge spine
OSh	oral shield
OSl	oral slit
OT	oral tentacle
OT-1	dorsal oral tentacle
OT-2	ventral oral tentacle
OTPo-2	oral tentacle pore of the ventral oral tentacle
PeSk	peribuccal skeleton
PG	perradial gap
PP	peristomial plate
TCt	tentacle compartment
T	tooth/teeth
TPa	tooth papilla (=dental papilla)
TP	terminal plate
TSc	tentacle scale
V	vertebra
VAP	ventral arm plate
VAP-1	first ventral arm plate
vCoOs	ventral collar ossicle
vCtOs	ventral compartment ossicle
vCtP	ventral compartment plate
vT	ventralmost tooth/teeth
vTCt	ventral tentacle compartment

Abbreviations are pluralized by adding "s" to the root, for example, the plural of VAP-1 is VAPs-1; the plural of LuOs is LuOss.

Museum Collections

LACM	Natural History Museum of Los Angeles County
USNM	National Museum of Natural History, Washington, D.C.
F	Museums Victoria, Melbourne, Australia

Museum catalog numbers are enclosed by [brackets].

SPECIES ACCOUNTS

Asteronyx longifissus Döderlein, 1927

Fig. 1

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and on their skeletal ontogenesis in *Asteronyx loveni* Müller and Troschel, 1842 (described below). Teeth, TPas, and OPas *s.l.* are composed of labyrinthic stereom (Fig. 1A, C, D). Several spiniform TPas are beneath a column of lanceolate, dorsoventrally compressed teeth and occupy the apex of the DP. Spiniform OPas *s.l.* , and ossicles provisionally identified as AOPas, each are set on a small protuberance on the adradial face of the OP (Fig. 2C, F). VAPs on each AS consist of a primary plate with small stereomic pores, and a secondary plate composed of retiform stereom (Mortensen, 1912) (Fig. 1E). VAP-1 overlaps the edge of the OSl near the AdSh and OT-2, but it does not abut the AdSh or OPR. It is small and is composed of denser stereom than distal VAPs (Fig. 1B, E). Retiform ossicles are embedded in the integument surrounding the tentacle basins and covering the PG (Fig. 1C–E). Elements of the oral frame are unified by a sheath of connective tissue that connects the large AdShs, small OShs, stout LAPs-2, delicate primary and secondary VAPs-1, and the massive, conjoined OPs (Fig. 1B).

PROXIMAL ASPECT. Teeth are aligned in a column on the DP and are separated from one another by narrow gaps (Fig. 1C). Each TPa and tooth is borne on a rounded protuberance with a central fossa (Fig. 1C). OPas *s.l.* are aligned on the OPR, rather than on the ventrolateral edge of the OP of this species and *A. loveni* (Fig. 1A, B, C, F; Murakami, 1963:fig. 1C). Each OPa *s.l.* is borne on a protuberance lacking a central fossa; the base of the papilla is concave and composed of sparsely perforate, dense stereom (Fig. 1A, C, D, F). Supernumerary OPas *s.l.*, which are attached to the adradial surface of the OP, at a distance from the OPR, are provisionally designated AOPas (Fig. 1C, F). Integument sheathes the jaw and the TCts, forming a collar that encircles the base of each OT (Fig. 1C). The DP and proximal edge of the OP extend considerably above the dTCt and well below the vTCt. Dorsal and ventral surfaces of the OP are narrow and slope toward the protuberant OPR. When the jaws close, the down-curved ventral apices of the jaws assemble in a conical cluster that protrudes below the center of the mouth (Fig. 1B). TPas and teeth on the closed, opposing jaws intermesh and the OPas *s.l.* and AOPas on adjacent jaws may touch, cross, or interdigitate (Fig. 1B). OT-2 is elevated on the lateral flank of the OP and lies in the spacious distal OSl. However, when the jaws are closed, the interdigitating OPas *s.l.* on the OPR exclude OT-2 from the proximal OSl. CtPs, CtOss, and FPs are lacking. *Asteronyx loveni* has similar, steep-sided, protuberant jaws, and OPas *s.l.* that can isolate the OT-2 from the mouth [LACM E.1976-524.1]. It could not be discerned whether the DP is a single ossicle or is composed of multiple ossicles similarly to *A. loveni* (Fig. 1C; Murakami, 1963:text-fig. 1A).

DORSAL AND VENTRAL TENTACLE COMPARTMENTS. TCts are composed of the flank of the OP and the OPR and an integumentary sheath surrounding the tentacle basin (Fig. 1A–C, E). Small, spiniform or lenticular ossicles may articulate with the OP, beside the OT-2 on some jaws (Fig. 1B; [LACM E.1976-524.1; LACM 75-226.1]). The water ring canal traverses dual water ring foramina in each OP of *A. loveni*. One foramen is above the adradial muscle fossa of the OP, beside the groove for the radial water canal, and the other foramen is above the abradial muscle fossa (see Murakami, 1963:fig. 1B, C; see "Foramina of the Water Ring and of Podial Nerves in the Oral Plate," in the Discussion).

PERRADIAL ARMATURE. The PG is covered by integument containing two roughly parallel columns of LuOs composed of retiform stereom and VAP-1 is embedded in the contiguous integumentary sheath (Fig. 1B, C, E). There is an ovoid PP centered on the jaw, which may overlap interradially positioned PPs on either side. However, the latter plates are not clearly delineated in the specimen examined (Fig. 1F).

Skeletal Ontogenesis and Homologies of Oral Armature

Postlarval specimens of *Asteronyx longifissus* were not accessible for study, but juvenile stages of *Asteronyx loveni* have been described, some of which were initially identified as *Ophiuraster patersoni* Litvinova, 1998, or *Ophiomyxa serpentaria* Lyman, 1883 (Mortensen, 1912; Litvinova, 1998; Stöhr 2004, 2005). A juvenile 1.8–2.0 mm dd had a tooth on the ventral apex of the DP and an OPa *s.l.* near the proximal edge of the OP but at a distance from the DP (Mortensen, 1912:pl. 15, fig.1; Stöhr 2004:fig. 3B). A pair of presumptive TPas formed on the DP of individuals 2.1–2.5 mm dd (Mortensen, 1912:pl. 15, fig. 2; Stöhr, 2005:fig. 3F). These ossicles are regarded as TPas because they develop concurrently on the DP. However, the TPas are arranged irregularly in the adult, unlike TPas of typical Ophiurida and Ophintegrida. When the juvenile was 3.5 mm dd, a second OPa *s.l.* had developed on the OP, distal to its predecessor (Mortensen, 1912:figs. 4, 6). The first OPa *s.l.* that developed on the OP did not appear to be an IPa or BSc, judging from its shape and from its initial position on the OP of the juvenile, and its position in the adult. The shape and position of the second OPa *s.l.* was not characteristic of an IPa, 2°IPa, BSc, LOPa, AdShSp, 2°AdShSp, or LyOs. Although the two OPas *s.l.* arose in a proximal-to-distal sequence, they did not develop distal to an IPa. Therefore identifying these ossicles as LOPas is problematic. Moreover, OPas *s.l.* are arranged irregularly in adult *A. loveni*, and some appear to have developed between larger OPas *s.l.*, like AOPas [LACM E.1976-524.1]. There also are varying numbers, shapes, sizes, and positions of the OPas *s.l.* on the OP of adult *A. longifissus* [LACM 77-204.1].

The OPas *s.l.* of juvenile *Asteronyx loveni*, which developed near the OPR, became long, slender, and spiniform ossicles in adult individuals. However, additional spiniform or tubercular OPas *s.l.* may develop dorsal or ventral to the OPR in larger individuals. The apex of the jaw was considerably more protuberant in the adult than in the juvenile stage, as a result of positive allometric growth of the proximal edge of the OP and DP (compare: juvenile OPs of *A. loveni* in Mortensen, 1912:pl. 15, figs. 1, 6, and the adult OPs in Murakami, 1963:text-fig. 1C; Martynov, 2010b:fig. 15D).

An AdShSp and a spine on LAP-2 were lacking in the youngest *A. loveni* examined (1.8 mm dd, 2 ASs) (Stöhr, 2004:fig. 3B) and in adult *A. loveni* and *A. longifissus* (Fig. 1C; Matsumoto 1917:fig. 6b). Inexplicably, Mortensen (1912:271, pl. 15, figs. 2, 3, 5) described a small, vertical plate in juvenile *A. loveni* as the true first ventral arm plate ("Sie repräsentiert unzweifelhaft die innere, eigentlich *erste Ventralplatte*"), although he expressly stated it was above the proximal end of the first ventral arm plate ("dem proximalen Ende der *ersten Ventralplatte*") [italics mine]. Presumably the vertical plate referred to was a PeSk ossicle such as a LuOs or the rudiment of a peristomial plate.

Diet, Feeding, and Operation of the Jaws

Asteronyx loveni is the only asteronychid whose feeding has been investigated. Small individuals are thought to be epibenthic, and individuals larger than 9–15 mm dd are epizoic on pennatulaceans and alcyonaceans (Mortensen, 1912; Fujita and Ohta 1988; Fujita, 2001). Gislén (1924:256–257) found "unrecognizable detritus, organic matter containing abundant fat globules" in stomach contents of *A. loveni*, and reported that individuals injure the host by eating "whole tentacle crowns" that they purportedly removed using hook-shaped arm spines. However, Mortensen (1912) discovered that host tissue was lacking in stomach contents of epizoic *A. loveni*. Furthermore, he found that adult individuals consumed copepods almost exclusively, whereas young epibenthic individuals ingested benthic detritus. Although Gislén's and Mortensen's interpretations both were accepted in the literature (Hyman, 1955; Warner, 1982), it was eventually established that *A. loveni* does not damage or prey upon a chrysogorgiid host species, *Radicipes pleurocristatus* Stearns, 1883. Rather, it feeds on suspended material and its stomach contains "flocculent material, sediment particles, fragments of small crustaceans and setae of polychaetes" (Fujita and Ohta 1988:2039; Fujita, 2001).

Epizoic *A. loveni* has dimorphic arms. The short, slender arms bear hooked spines, and the long, thick arms have flesh-covered, clavate spines in addition to hooked spines. According to Fujita and Ohta (1988:2013) "both types of arms either were wound around the trunks [of the host] or outstretched into the water, suggesting that the functional differentiation between the two arm types is not distinct." The arms were extended in a series of sinusoidal curves, tightly coiled around the host, or loosely looped around the host with most of the appendage outstretched in the water. Since long arms with clavate spines usually encircled the host, it was inferred that "the clavate spines…are probably not employed in feeding" and "are probably important for grasping the [host] colony" (Fujita, 2001:271–272). The slender, outermost portion of the arms occasionally contracted in a tight coil, indicating that the distal, sharply hooked spines "may be used to secure prey" (Fujita, 2001:270). Tube feet of *A. loveni* are smooth, tapering, and protrude from a fleshy sheath that lacks supporting ossicles (Sars, 1861; Fujita, 2001). Thus, they lack the erect glandular papillae like those on the tube feet of microphagous suspension feeders. Prey capture, transport of food items, and the process of ingestion have not been documented in *Asteronyx* species, although it was suggested that its occupancy on stalked cnidarians may enable *A. loveni* to optimize its access to particles of food in the benthic boundary layer (Fujita and Ohta, 1988). It is also possible that *A. loveni* is a facultative commensal or kleptoparasite, consuming food captured by the host or particles adhering to the host or material secreted or released by the host, similarly to epizoic species such as *Astrobrachion constrictum* (Farquhar, 1900) and *Ophiothrix lineata* Lyman, 1860 (Hendler, 1984; Stewart, 1998).

Buccal Morphology

Paradoxically, the PPs of *A. loveni* have been described as a "large, transverse oval, and in a single piece," as a pair of unfused interradial ossicles, and as "simple" (Lyman, 1881:285; Mortensen, 1912:268; Matsumoto, 1917:385, pl. 1, fig. 14). X-ray micro-computed tomography (μCT) imaging of this species revealed irregularly shaped, oblong , interradial PPs on the jaws and "Smaller additional plates. . .between the larger peristomial plates, variable in shape and one-third to one-fourth of the peristomial plates in length" (Okanishi et al., 2017:6, fig. 1F). The rudiments of these "additional plates" may have been misinterpreted as the inner, true first ventral arm plate ("innere, eigentlich erste Ventralplatte") by Mortensen (1912:271). *Asteronyx longifissus* appears to have a small, elliptical PP centered on each jaw, overlapping larger perradial PPs on either side. However, these plates were not clearly delineated in the present study (Fig. 1F). The occurrence of rings of PPs in other Euryalida is discussed below in the treatment of *Asteroporpa annulata* Örsted and Lütken, and it is suggested that interconnected perradial and interradial PPs may be a synapomorphy of Asteronychidae, Euryalidae, and Gorgonocephalidae.

It appears that Okanishi et al. (2017:fig. 2B, D) labeled the tentacle basin of OT-2 of *A. loveni* as the first tentacle pore, and identified the tentacle pore of the proximalmost AS as the "2nd tentacle pore." The tentacle basin of OT-1 was not labelled in their figures, but in a lateral view of the jaw it was apparent above the OPR (compare: Okanishi et al., 2017:fig. 2D, with Murakami, 1963:text-fig. 1C; *A. longifissus* Fig. 1A, C, E, herein). As noted above, the water ring penetrates the jaws of *A. loveni* and extends through foramina on opposite sides of each OP. This channel, which is below the PPs, is visible in a horizontal μCT section through the jaws of *A. loveni* (Okanishi et al., 2017:fig. 3B). Occurrence of similar foramina in other Euryalida is described in the treatment of *Asteroporpa annulata* (see "Foramina of the Water Ring and of Podial Nerves in the Oral Plate" in the Discussion).

Döderlein (1927:66) described OPas *s.l.* on the OP of *A. longifissus* as very irregular ("sehr unregelmässig") since there may be 4–5 in a row, and additional papillae above this primary series. In the present study, the latter ossicles were provisionally referred to as AOPas, to distinguish them from the primary OPas *s.l.* on the OP. However, their position, shape, and ontogenesis differ from AOPas of Ophiurida, and the relationship between the OPas *s.l.* of Euryalida and other ophiuroids is debatable.

Asteroporpa annulata Örsted and Lütken in Lütken, 1856
Fig. 2

VENTRAL ASPECT. Lanceolate teeth, spiniform TPas, and abruptly tapering OPas *s.l.* are composed of labyrinthic stereom with surficial, spinose microsculpture (Fig. 2B, F). There are approximately four blunt OPas *s.l.* on the ventrolateral edge of the OP, although the number and positions vary (Fig. 2A, B). Information on the ontogenesis of buccal armature in gorgonocephalids (reviewed below) does not establish that these OPas *s.l.* on the OP are homologous with OPas *s.l.* of Ophiurida and Ophintegrida, which they may resemble. The largest, distalmost OPa *s.l.* is on the OP below the orifice of the vTCt and a considerable distance from the AdSh, indicating that it is not an AdShSp homologue (Fig. 2A–C). Buccal armature is embedded in dense, refractory integument that envelops the oral frame and disk (Fig. 2A, B). VAP-1 is separated from the AdShs and LAP-2, but bridges the flanking OPs and protrudes into the OSl (Fig. 2C). VAP-2 appears to comprise of several small ossicles, and the size of LAP-2 is greatly reduced in comparison to distal LAPs. Notably, the V-1 is also reduced in size compared to other basal vertebrae (Fig. 2D). Several minute, slender ossicles, possibly LuOss, link the proximal tip of VAP-1 to the adjacent OPRs (Fig. 2D). Stout AdShs of adjacent arms abut one another and are connected by integument to the conjoined OPs, LAP-2, and LAP-3 (Fig. 2A, C), and the oral frame is unified by connections of these plates to one another. Additionally, the jaws are interconnected by a ring of large interradial PPs and small, perradial PPs (Fig. 2D, H).

PROXIMAL ASPECT. Teeth on the dorsal portion of the DP are aligned in an irregular column (Fig. 2F). Loosely clustered spines on the ventral portion of the plate are provisionally identified as TPas, although they are neither uniformly nor symmetrically arrayed. Each tooth and TPa has a narrow base that articulates with a low, round protuberance surrounding a central fossa (Fig. 2F). However, OPas *s.l.* attached to the adradial flank of the OP, which are provisionally regarded as AOPas, are borne on rounded protuberances that lack a central fossa or foramina (Fig. 2I). There may be several small, tapering ossicles directly above (and sometimes between) the OPas *s.l.* on the ventrolateral edge of the jaw, and small, blunt spines may be present on the adradial face of the OP near the OPR (Fig. 2F, G, J). It was not determined whether the DP is single, or composed of several ossicles like that of *Asteroporpa hadracantha* H.L. Clark, 1911 [=*Astroporpa hadracantha*] (Murakami, 1963:pl. 1, fig.7). When the jaws are fully closed, teeth and TPas on opposing jaws interdigitate to a limited extent, and OPas *s.l.* may touch, cross, or interdigitate.

DORSAL AND VENTRAL TENTACLE COMPARTMENTS. TCts are composed of the flank of the OP and the OPR, and of a cylindrical collar surrounding the base of the OT, which is composed of abutting CtOss and smaller, imbricating CoOss. CtOss of the dTCt are smaller and more crowded than those of the vTCt. FPs appear to be lacking. The dorsal surface of the oral frame is encircled by a continuous ring of PPs (Fig. 2D, H). The water ring traverses dual foramina in each OP, and a connection between these pairs of foramina was demonstrated by passing an eyelash through both foramina and the OP (Fig. 2H, J, K). The water ring runs above the abradial muscles of each jaw, and enters a foramen beside the abradial muscle fossa of each OP, penetrates the OP, and sends out bifurcating branches to the OTs. The water ring emerges from the OP through a foramen above the adradial muscle fossa, where it joins the radial water canal. Similar foramina are evident in *Asteroporpa hadracantha* [=*Astroporpa hadracantha*] (Murakami, 1963:pl. 3, figs. 31, 32). The nerve ring is sheathed in a dense layer of integument and covered by the PPs. The radial nerve cord occupies a groove that is proximal to the adradial muscle fossa on the OP, and a branch of the nerve may pass through a notch above the tentacle basin to innervate OT-2 (Fig. 2K).

PERRADIAL ARMATURE. The proximal portion of VAP-1, which extends into the OSl and partway to the OPR, is linked to the OPR by several small ossicles embedded in a short band of connective tissue (Fig. 2D). The VAP-1 and these interconnected ossicles partially cover the ventral portion of the PG. Squamous LuOss of different sizes are embedded in integument sheathing the entire PG and irregularly dispersed between VAP-1 and the OT collars (Fig. 2F). Small scales are embedded in the circumoral esophageal ligament and around the PPs.

Skeletal Ontogenesis and Homologies of Oral Armature

Juvenile *A. annulata* were not available for study, in lieu of which a growth series of *Gorgonocephalus arcticus* Leach, 1819, and several small specimens of *Gorgonocephalus eucnemis* (Müller and Troschel, 1842) were examined with a stereomicroscope. The smallest juveniles of *G. arcticus* (1.6–2.2 mm dd) had teeth, and larger individuals (3.3–4.8 mm dd) had several TPas that were smaller than the teeth. A 5.2-mm dd juvenile had 1–2 minute, rudimentary OPas *s.l.* on the ventrolateral edge of the OP, below the OPR, which were distal to the DP/OP juncture, and 0–1 spiniform ossicles on the adradial surface of the OP [LACM 1993-197.1]. A similar configuration of OPas *s.l.* occurred in small specimens of *G. eucnemis* (5.2–19.9 mm dd), which had teeth and TPas on the DP; 1–3 prominent, spiniform OPas *s.l.* on the ventrolateral edge of the OP; and spiniform ossicles on the adradial surface of the OP. Some proximal OPas *s.l.* were longer than the distal ossicles, but their size and number varied, and based on their size it was not possible to infer the sequence in which they had formed [LACM 1962-246.1, LACM 1971-683.1]. Adult *G. arcticus* had more numerous teeth and TPas than juveniles, and they had numerous, spiniform AOPas on and above the ventrolateral edge of the OP. These AOPas intergraded with the series of larger OPas *s.l.*, and were similar in appearance to the larger, first-formed OPas *s.l.* and with the other spiniform ossicles on the adradial surface of the OP ([LACM 1972-376.1]; see Martynov, 2010b:fig. 15A)].

On the basis of the specimens examined, there was no indication that a BSc developed or that a spine developed on the AdSh or on LAP-2. A pair of OPas *s.l.* occurred near the apex of the jaw, but these were clearly distal to the DP/OP juncture, and thus they did not appear to be IPas. OPa *s.l.* on the ventrolateral edge of the OP were not aligned regularly, like LOPas, and ossicles provisionally identified as AOPas were not clearly distinguishable from other spiniform ossicles on the adradial surface of the jaw. Although some pairs of TPas and OPa *s.l.* were positioned on opposite sides of the jaw, the number, arrangement, and size of these ossicles was not consistent in the growth series examined, confounding an interpretation of their sequence of development and homologies. Although pairs of ossicles that develop ventral to the teeth are referred to as TPas, it is debatable whether they are equivalent to TPas of other ophiuroids, because the presumptive TPas of Euryalida are irregularly arranged, intergrade with teeth, and are borne on a protuberance with a central fossa like the teeth.

My observations on *Gorgonocephalus arcticus* and *G. eucnemis* were consistent with previous accounts of juvenile gorgonocephalids, including *G. arcticus* (2 mm dd), which appeared to have only teeth, and "very young specimens" that had 2–3 spiniform OPas *s.l.* on the adradial edge of the OP (Lyman, 1882:pl. 36, figs. 1, 17). An "ophiocrenoid stage" of "?*Gorgonocephalus* or *Astrodendrum*" (2.5 mm dd) had teeth and paired ossicles on the DP or OP, and a juvenile *Astrotoma agassizii* Lyman, 1875 (1 mm dd) had only teeth (Matsumoto, 1917:69, fig. 18; Bartsch, 1985:fig. 7). Notably, all these juvenile stages of gorgonocephalids lacked an AdShSp and an arm spine on the first arm segment.

Ontogenesis and Skeletal Homologies of Gorgonocephalidae

Döderlein (1911:19) indicated that Gorgonocephalidae characteristically lack arm spines (so-called "tentakelpapillen") on the first AS. Elsewhere in the literature, species descriptions and illustrations of Euryalida indicate that most (and possibly all) species lack AdShSps as well as ASps on LAP-2. It was stated that *Astrophyton muricatum* (Lamarck, 1816a) has "arm spines on lateral arm plates of *all* segments and *subsequently* [my italics] loses them from basal segments with growth" (Turner and Boucher, 2010:23). However, the smallest juvenile *Gorgonocephalus arcticus* examined in the present study lacked spines on the AdSh and on LAP-2, as do juvenile *Astrotoma agassizii* and *Asteronyx loveni* (Mortensen, 1912; Bartsch, 1985). Thus, there is no concrete evidence that spines develop, or that they are resorbed, on the AdSh and LAP-2 of Euryalida. However, it is clear that arm spines, girdle hooklets, tentacle pores, and tube feet on proximal arm branches may be modified, reduced, or resorbed as gorgonocephalids grow (Wolfe, 1982; Turner and Boucher, 2010). Gislén (1924:258) proposed a "division of labor" between the "distal arm divisions with their girdle-hooks, adapted exclusively for catching food, while the thick and short. . .proximal arm-divisions have gained the rôle of anchoring organs." Ontogenetic modifications of the vertebrae enable the basal arm segments to rigidly support arborescent, distal arm divisions, even in swift currents, but absence of spines on the AdSh and first arm segment seems not to confer an apparent advantage (see "Adoral Shield Spine (AdShSp), 2°Adoral Shield Spine (2°AdShSp), and Tentacle Scale of VAP-1 (VAP-1 TSc)" in the Discussion).

Diet, Feeding, and Operation of the Jaws

Asteroporpa annulata and confamilials capture zooplankters in circlets of microscopic, girdle hooklets on their prehensile arms. Their small, smooth tube feet extend beyond the girdle hooklets and may manipulate or sense prey (Wolfe, 1982; Emson et al., 1991). Girdle hooklets of *Gorgonocephalus eucnemis* "were seen to be holding down appendages of captured *Calanus*, and when an insect pin was laid across a row of hooks, the hooks bent over and caught it," and these girdle hooklets reportedly were activated by muscles (Patent, 1970:156). Contrariwise, the hooklets and ASps of *Gorgonocephalus arcticus* were stated to lack muscles and have "collagenous tendons" instead (Fricke, 1968; Emson et al., 1991:453; Turner and Boucher, 2010). Arborescent and simple-armed gorgonocephalids suspension-feed by erecting arm branches in a parabolic array, directing the concave, doral side of the arms toward the current. Plankters such as active copepods are captured on slender, terminal tendrils of the arm, which roll into knots to secure prey. Periodically, an arm branch is coiled against the disk, and the knotted, food-laden branches are inserted in the open mouth. The spiniform buccal armature is believed to collect prey items as the tendrils are unfurled and withdrawn from the mouth (Fricke, 1968; Patent, 1970; Meyer and Lane, 1976; Hendler, 1982a; Hendler and Miller, 1984; Ferrari and Dearborn, 1989; Emson et al., 1991). Whether or not the spiniform oral armature of Gorgonocephalidae is "plesiomorphic" or "ancestral" (Martynov, 2010b:23) as has been suggested, it appears to be adaptive for a unique mode of feeding. Their buccal morphology is radically different from that of microphagous suspension feeders with a buccal funnels, and of other Euryalida.

Euryalidae have a column of compressed teeth on the DP, rather than a bristling cluster of spiniform teeth and TPas, which is characteristic of gorgonocephalids (Ljungman, 1867:334–335; Lyman, 1882:258, 265; Doderlein 1911:11, 14; Matsumoto, 1917:27, 59; Okanishi and Fujita, 2013). Feeding was studied in the epizoic euryalids *Asteroschema tenue* Lyman, 1875, and *Astrobrachion constrictum*, which gather microscopic items from the water column and from their host species with their tube feet and clavate arm spines. This material, which may be compacted into boluses, is transported to the mouth by the tube feet (Emson and Woodley, 1987; Grange, 1991; Stewart, 1998). It was conjectured the *Euryale purpurea* Mortensen, 1934, which has arborescent arms but lacks girdle hooks, is "probably. . .a macrophagous suspension feeder," although its feeding behavior and stomach contents have not been examined (Emson,1990:226).

Buccal Morphology

Several remarkable features of *Asteroporpa annulata* are the reduced size of the first vertebra and LAP-2, large AdShs that overgrow LAP-2 and abut LAP-3, and a multi-element VAP-2 (Fig. 2C, D). Although authors asserted that "in the ophiurids and euryalids. . .the second oral tentacle pore opens outside the mouth slit" (Thuy and Stöhr, 2016:16), the tentacle basin of OT-2 of *A. annulata* and other Gorgonocephalidae (e.g., *Gorgonocephalus arcticus* [LACM E1933-216.1]; *Astrocaneum spinosum* (Lyman, 1875) [LACM E.1940-39.7]) is entirely within the OSl. The vTCt of Euryalidae is shallower and more conspicuous, but is enclosed within the broad OSl (e.g., *Trichaster palmiferus* (Lamarck, 1816a) [LACM E.1948-96.2], *Astrobrachion constrictum* [LACM E.892]; *Asteroschema sublaeve* Lütken and Mortensen, 1899 [LACM E.1964-300.1]).

PPs of *A. annulata*, which comprise small perradial ossicles and large interradial ossicles, differ from single, paired, or triple PPs of

Ophintegrida, which are interradial (see Smith et al., 1995:239, fig. A9). The configuration of PPs in *A. annulata* resembles that of other Euryalida, including *Asteronyx loveni*, the "*Asterophyton*" of Müller, *Astrocrius sobrinus* (Matsumoto, 1912) [=*Astrotoma sobrina*], *Gorgonocephalus arcticus* Leach, 1819 [=*Gorgonocephalus agassizii*], *Ophiocreas japonicus* Koehler, 1907 [=*Asteroschema* (*Ophiocreas*) *japonicum*], and *Astrobrachion constrictum*, although the latter has three or more interradial PPs (Lyman, 1882:pl.36, fig. 18; Müller, 1854:pl. 7, fig. 5; Matsumoto, 1917:pl. 2, figs. 2, 9; Stewart, 2000:fig. 7c; Okanishi et al., 2017:fig.1F). Lyman (1882:354, pl. 36, fig.18) referred to the perradial PP in a juvenile *G. arcticus* as "the small angle piece sometimes considered the first under arm plate," and Matsumoto (1917:32, pl. 2, fig. 2) referred to it as "Ludwig's 'first ventral arm plate'...present at the dorsal outer corner of each oral slit" of *O. japonicus*. However, it is a PeSk element, rather than a VAP, and Ludwig's interpretation of the VAP-1 was incorrect (see "Ludwig's Ossicle (LuOs)" in the Discussion).

As indicated above, the water ring of *Asteroporpa annulata* passes through dual foramina in each OP. Similar foramina and an intraossicular water ring are described herein in other ophiuroids, including Ophiurida and Ophintegrida (see "Foramina of the Water Ring and of Podial Nerves in the Oral Plate" in the Discussion). Dual water ring foramina may be characteristic of many Euryalida, as they appear to be shown in 11 species illustrated by Murakami (1963:text-fig.1, pl.3, figs. 22–40), in the juvenile of *Astrotoma agassizii* (Bartsch, 1985:figs. 15–16), in *Asteronyx loveni*, and *A. annulata*. Furthermore, an adradial foramen was figured in *Astrophyton muricatum* [=*Astrophyton costosum*] and an abradial foramen was figured in *Asteroschema oligactes* (Pallas, 1788) (Lyman, 1882:pl. 35, fig. 23, pl. 47, fig. 1).

Ophiomusa lymani (Thomson, 1873)
Fig. 3

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *O. lymani* (described below). Teeth and OPas *s.l.* are composed of labyrinthic stereom (Fig. 3A, F, J). Adults typically have a continuous row of five OPas *s.l.* on the OP. In the individual illustrated, the proximalmost papilla is presumed to be the last OPa *s.l.* to develop and is interpreted to be a 2°IPa. It projects from the ventral apex of the OP and overlaps the ventral edge of the DP, and it is not seated in a fossa on the DP (Fig. 3A, C, H). Distal to the 2°IPas are an IPa, a BSc, a 2°AdShSp, and a wide AdShSp that overlaps VAP-1 and the vCtP (Fig. 3A, C, H). Ossicles tentatively interpreted as AOPas develop above other OPas *s.l.* and insert between them (Fig. 3A, C). Large individuals of *O. lymani* (>20 mm dd [LACM E.1962-283.2]) may have 6–7 OPas *s.l.* on the OP, and up to two TPas below the vT. TPas were also seen in large specimens of *Ophiosphalma familiare* (Koehler, 1897) (17.6 mm dd [LACM E.1934-334.1]; 19.5 mm dd [LACM E.1934-334.2]) and *Ophiosphalma glabrum* (Lütken and Mortensen, 1899) (25 mm dd [LACM E.197]). The OPas *s.l.* and teeth have irregularly shaped adradial edges, and OPas *s.l.* on adjacent jaws precisely dovetail with one another and interlock when the jaws are closed (Fig. 3B, D; Hendler, 1998:fig. 1N, O). VAP-1 abuts the beveled edges of the flanking vCtPs, AdShs, and LAPs-1, and the oral frame is unified by connections of these plates with each other and with the OShs and conjoined OPs (Fig. 3A).

PROXIMAL ASPECT. Teeth are aligned in a column and are separated from one another by gaps (Fig. 3C, F, H). They are dorsoventrally compressed, with notched edges. When the jaws close, opposing teeth intermesh and notches in teeth dovetail (Fig. 3F, J). The dorsalmost tooth tapers to a blunt point (Fig. 3F, H, M). DP is a single ossicle. The serried row of beveled OPas *s.l.* overlaps the ventrolateral edge of the OP (Fig. 3F, H, J, M). The bases of proximal OPas *s.l.* are associated with fossae in the OP (Fig. 3G). 2°IPas are connected to the OP and their edges may conform in shape to the vT (Fig. 3A, C). AOPas near the ventral edge of the OP may insert between larger OPas *s.l.* (Fig. 3A, C).

VENTRAL TENTACLE COMPARTMENT. Composed, in part, of the flank of OP and the OPR, a large vCtP extending from OPR to AdShSp, and the AdShSp itself (Fig. 3F, H, K). There may also be a small vCtOs on the ventral edge of the OPR. The ventral edge of the vCtP is thick, and the distal edge of the plate inserts in a groove beside a proximal, medial ridge on VAP-1 (Fig. 3E, H, K). The slender, tapering proximal lobe of VAP-1 inserts behind the vCtPs and abuts the OPR (Fig. 3E, F, H, K). The AdShSp rests on the OP, vCtP, and VAP-1, and abuts the AdSh (Fig. 3A). A branch of the radial nerve cord to OT-2 enters the ventral tentacle basin via a notch between VAP-1 and the OPR (Fig. 3D).

DORSAL TENTACLE COMPARTMENT. Composed of a prominent dCtP that is surrounded by smaller, block-like CtOss. The latter buttress a cylindrical collar composed of imbricate CoOss that encircle the base of OT-1 and extend across the dorsal rim of the dTCt, overlapping a slender FP (Fig. 3F, I, K, M). Similar, small ossicles are associated with the circumoral esophageal ligament on the dorsal surface of the oral frame above the dTCts and the PPs (Fig. 3I). The radial water canals merge with the water ring in the PG between adjacent jaws. The water ring passes through dual foramina in each OP, and within the OP the ring gives rise to branches that terminate in OT-1 and OT-2 (Fig. 3I, L, N, O, P). One foramen is above the adradial muscle fossa of the OP, beside the groove holding the radial water canal, and the other foramen is above the abradial muscle fossae (Fig. 3L, O, P). An eyelash inserted in the foramina passed through the channel connecting them. PPs overlap the proximal edge of the water ring and cover part of the nerve ring, and the PPs and adjacent structures are overlain by the circumoral esophageal ligament and integument embedded with microscopic ossicles (Fig. 3I, L–P).

PERRADIAL ARMATURE. The tapering, proximal lobe of VAP-1 blocks the ventral portion of the PG, and the narrow dorsal portion of the gap is covered by integument (Fig. 3E, F, H, K).

Skeletal Ontogenesis and Homologies of Oral Armature

The smallest juvenile *O. lymani* examined, 0.8 mm dd, had an elongated BSc spanning the OSl between the DP and VAP-1, and an echinulate, spiniform AdShSp projecting ventrally from the distal end of the AdSh (Hendler, 1998:fig. 1A–N). A 1.8-mm dd juvenile had an IPa extending from the OP to the DP and abutting the BSc. By this stage the AdShSp formed a blunt, tab-shaped papilla covering the orifice of the vTCt, and some individuals had developed a 2°AdShSp proximal to the AdShSp. Disk, oral frame, and OSl were dramatically transformed by the 2.4-mm dd stage. The perimeter of the disk extended to AS-2, and the distal end of the AdSh extended beyond the OS and OTPo-2. Increased height and breadth of OPs, AdShs, VAP-1, and other components of the oral frame extended the length and expanded the depth of the OSl. Although IPa and BSc previously were separated from 2°AdShSp and AdShSp, both the latter elements were shifted onto the OP, and together with the IPa and BSc they formed a serried row of ossicles on the ventrolateral edge of the jaw. At this stage, VAP-1 was dramatically shorter than the AdShSp, and it inserted between the AdShs at the distal edge of the OSl. Larger individuals, such as a 4.65-mm-dd specimen, had an identical sequence of OPas *s.l.* as the 2.4-mm individual, consisting of an IPa, a BSc, a 2°AdShSp, and an AdShSp. However, a 6.64-mm-dd individual in the same lot [LACM 1969-73.1] had developed a 2°IPa at the tip of the OP, proximal to the IPa. Small TPas and AOPas only occurred in large, adult individuals.

Ontogenesis and Skeletal Homologies of Ophiomusaidae

Previously, it was presumed that distal tube feet of *Ophiomusa* species were lacking and that OTPos-2 were "withdrawn into the oral region" during ontogenesis, until they "are no longer visible, and only the two pairs of tentacle pores remain [on the arms]" (e.g., Schoener 1967:660). However, the orifice of the vTCt of *O. lymani* lies between the AdSh and VAP-1 throughout ontogenesis, and it is overtopped by the OP and concealed by the AdShSp in the adult (Hendler, 1998). Furthermore, tentacle pores and tube feet occur in every arm segment, although the very small, smooth tube feet protrude through a foramen in the LAP, rather than through a tentacle pore between the LAP and VAP (Hendler, 1998). It was presumed the oral papillae of *Ophiomusa* [=*Ophiomusium*] are "fused together to form a single piece" that "probably represents the stage previous to the division of a common rudiment into individual papillae" (Matsumoto, 1917:379; Stöhr et al., 2012a:5). However, OPas *s.l.* of *O. lymani* arise as discrete elements and remain separated throughout ontogenesis, although they may appear to be united in preserved specimens, if gaps between ossicles are concealed by opaque integument (Fig. 3A, B; Hendler, 1998).

Diet, Feeding, and Operation of the Jaws

Ophiomusa lymani was inferred to facultatively prey on small crustaceans and polychaetes on the basis of stable isotope analysis. However, its diverse stomach contents suggest it "takes whatever organic material it is able to ingest" including polychaetes; crustaceans; fragments of animals, algae, and mineral particles; and flocculent detritus (Pearson and Gage, 1984:254; Iken et al., 2001). Gut contents of Ophiomusina such as *Ophiosphalma armigerum* (Lyman, 1878b) [=*Ophiomusium planum*] and *Ophiosphalma glabrum* [=*Ophiomusium multispinum*] were similarly varied and included shells of incompletely digested pteropods (Litvinova, 1979). *Ophiosphalma glabrum* was attracted to submerged baited cameras and fed on small pieces of bait abandoned by scavenging fish (Leitner et al., 2017; A. Leitner, pers. comm.). Distal tube feet on the arm segments of *O. lymani* are minuscule, and they are likely used to detect food rather than to manipulate it (Hendler, 1988, unpubl. obs.). The dovetailed OPas *s.l.* and tightly interlocking jaws and OPas *s.l.* of *O. lymani* are capable of retaining minute particles of food and of shielding the retracted OTs (Fig. A, B). It is possible that Ophiomusina species use OTs and OPas *s.l.* to gather and transfer food to the buccal cavity, and may use hooked, dorsal ASps on their distal arm segments to snag food items, but these behaviors have not been directly observed.

Buccal Morphology

Water ring foramina above the adradial and abradial muscle fossae of the OP of *O. lymani* were previously figured, but escaped comment (Bartsch, 1983b:figs. 4–5). The present study showed that these dual foramina are interconnected and that the water ring traverses an intraossicular canal. The water ring enters the abradial foramen, penetrates the OP, passes through the adradial foramen, and merges with a radial water canal that descends through the PG before entering the arm. Within each OP, the water ring emits bifurcate branches that terminate in OT-1 and OT-2 (see "Foramina of the Water Ring and of Podial Nerves in the Oral Plate" in the Discussion).

Ophiura sarsii Lütken, 1855
Fig. 4

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their pattern of skeletal ontogenesis in *O. sarsii*, *Ophiura luetkenii* (Lyman, 1860), and other congeners (described below). Teeth, TPas, and OPas *s.l.* are composed of labyrinthic stereom (Fig. 4A, B). The vT and two pairs of TPas project from the ventral apex of the DP. A row of OPas *s.l.* ascending the adradial edge of the OPR consists of 1–3 2°IPas, an IPa, and a BSc. These elements are separated by a conspicuous diastema from the AdShSp and four 2°AdShSps beside the orifice of the vTCt, which are borne on the AdSh and OP. A row of three TScs extends from VAP-1 onto the vCtP; the distalmost TSc is the oldest and largest in this series. OPas *s.l.* on the AdSh, OP, and VAP-1 beside the orifice of the vTCt are set on ridge-shaped ArtSs composed of sparsely perforate stereom (Fig. 4A, B, I). These are similar to ArtSs occupied by TScs on the LAP (Fig. 4D, E). OPas *s.l.* on the OPR are connected to separate ArtSs (Fig. 4B, J). The orifice of the vTCt opens on the ventral surface of the oral frame, and the vTCt forms the distal portion of the OSl. The vTCt is confluent with the proximal OSl and the buccal cavity when the jaws are opened, and OT-2 can extend below the disk or into the buccal cavity (Fig. 4A, B, C, G, I). But when the jaws are closed, the vTCt and OT-2 are separated from the proximal OSl and the buccal cavity by OPas *s.l.* on the OPR. The protuberant, tapering, proximal edge of VAP-1 inserts between the vCtP and OPR, and distolateral margins of VAP-1, which are composed of sparsely perforate stereom, attach to beveled edges of LAP-2 and the AdSh (Fig. 4F, G, I, J). The oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs. Preserved specimens of *O. sarsii* that were examined had jaws that were not tightly closed, and although abutting dCtPs and OPas *s.l.* on the OPR obstructed the OSl, the teeth on opposing jaws barely touched or intermeshed. Teeth of *O. luetkenii* were reported to intermesh when the jaws tightly closed (Austin, 1966:118).

PROXIMAL ASPECT. Teeth and TPas are composed of stereom with small pores, which is not reinforced by supplementary deposits of calcite. Teeth are set close together in a staggered vertical series on the DP. They taper to a blunt point, and their irregular contours conform to adjacent teeth (Fig. 4B, F, G). Each tooth and TPa is borne on a round ArtS composed of sparsely perforate stereom that surrounds a central fossa (Fig. 4F, H; see also Martynov 2010:fig. 65P). There are not "multiple openings per tooth" on the DP (*contra* Stöhr et al., 2012a:6, fig. 5F). The DP is a single ossicle. The proximal aspect of the jaw is dominated by large orifices of dTCts that are separated by thick OPRs from smaller orifices of the vTCts (Fig. 4B, F, G). The divergent angles of inclination of dorsal and ventral TCts are evident when the jaw is tilted upward (compare: Fig. 4F, G; see also Martynov 2010:fig. 65Q).

VENTRAL TENTACLE COMPARTMENT. Forms a deep cavity on the ventral surface of the jaw, which is delimited by the flank of the OP and OPR, AdSh, VAP-1, and vCtP, and it is fringed by the AdShSp, 2°AdShSps, and VAP-1 TScs (Fig. 4F, G, I). The vTCt forms the distal portion of the OSl, and its elliptical orifice is apparent on the ventral surface of the jaw. The vTCt is confluent with the proximal OSl when the jaws are opened (Fig. 4A, G). The vCtP does not abut the AdSh or AdShSp. A foramen beside the tentacle basin of OT-2, which penetrates the OP, probably receives a branch of the radial nerve cord innervating the tentacle (Fig. 4I; see Murakami, 1963:pl. 6, figs. 39, 40). An equivalent foramen, not depicted herein, was revealed in a dissection of *Ophiura luetkenii.*

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP and OPR and the abutting dCtP and FP (Fig. 4B, G, H). The FP arches above the compartment, extending nearly to the dorsal edge of the OP (Fig. 4F, H, K). A panel of irregularly shaped, interlocking CtOs supports a collar of integument encircling the base of OT-1 and borders the proximal edges of the dCtP and FP (Fig. 4B, F).

PERRADIAL ARMATURE. The tapering proximal lobe of VAP-1 extends upwards to the vCtP and OPR, occluding the lower portion of the PG (Fig. 4G, I, J). A column of imbricate LuOss extends from VAP-1 to the circumoral esophageal ligament and bifurcates, and the divergent branches overlie the FP and associated CtOss (Fig. 4F, H, J). A single foramen on the dorsal surface of each OP is set within a groove that is occupied by the water ring (Fig. 4H, K, L). An offshoot of the water ring enters this foramen and bifurcates within the OP, and the branches terminate in OTs. This was confirmed by passing an eyelash from the dorsal foramen into the vTCt, which a connection between the water ring foramen and both OT basins (Fig. 4K, L).

Skeletal Ontogenesis and Homologies of Oral Armature of *Ophiura* Species

The smallest juvenile of *Ophiura sarsii* that was examined by Sumida et al. (1998:fig. 5B) was 0.37 mm dd, and it had one tooth on the DP and a spiniform AdShSp on the distal end of the AdSh. A 0.45-mm-dd individual had a BSc in the OSl, bridging the DP and VAP-1. A 1.0-mm-dd individual had a small IPa abutting the BSc and DP, and it had a tab-like 2°AdShSp on the AdSh, abutting the AdShSp (Sumida et al., 1998:fig. 5D, F). A 1.5-mm-dd juvenile had developed an additional ossicle proximal to the IPa, at the DP/OP juncture (Sumida et al., 1998:"MP3" in fig. 5H), which I interpret to be a serial homologue of the IPa and refer to as a 2°IPa. At this stage, the 2°AdShSp was larger than the AdShSp and both of these ossicles overlapped OTPo-2. Opposite these ossicles, and directly across the OTPo-2, a newly formed TSc projected from VAP-1. A 6.3-mm-dd specimen of *O. sarsii* had an elongated TPa on the DP, proximal to the 2°IPa, IPa, BSc, three 2°AdShSps, and AdShSp. In addition the specimen had three TScs on the VAP and vCtP [LACM E.1949-308.10]. Larger specimens presented additional 2°IPas, between which there sometimes were inset small, slender ossicles. These I tentatively regard as AOPas, rather than 2°IPas, because they did not arise at the DP/OP juncture.

The smallest juvenile *O. luetkenii* examined in the present study, which were 2.4 and 2.6 mm dd, had a 2°IPa, an IPa, and a BSc, on the OP, a 2°AdShSp and AdShSp on the AdSh, and two TScs on VAP-1. Their PeSk comprised a vCtP on the ventral edge of the OPR between the AdSh, BSc, and VAP-1, as well as a larger dCtP on the dorsal edge of the OPR, abutting an FP (Fig. 5A, C, D). A 4.3-mm-dd individual had a TPa, 2°IPa, IPa, BSc, and a 2°AdShSp on the OP, 1–2 2°AdShSps and an AdShSp on the AdSh and OP, and three TScs on the VAP-1 and vCtP (Fig. 5B, E). In all of these juveniles, VAP-1 abutted the OPR and the AdSh, a vCtP abutted the vTCt, and a blunt BSc projected from the edge of the OPR between the vCtP and the other OPas *s.l.* However, the proximal lobe of the VAP-1 was larger and more steeply inclined in the OSl in the larger juvenile (compare: Fig. 5A, B). OTPo-2 of the smallest individual might be said to "open outside the mouth," even though it is above the ventral plane of the oral frame, because its connection to the buccal cavity was partially obstructed by the vCtP and the row of OPas *s.l.* on the OPR (Fig. 5A). However, in the largest individual the row of OPas *s.l.* on the OPR inclined upward into the buccal cavity, and the orifice of the vTCt was confluent with the OSl when the jaws were open (Fig. 5B). These growth-related changes did not result from independent movements of the OPas *s.l.* and vCtP or "migration" of OTPo-2. Rather, they were produced by ontogenetic alterations in the size and shape of the OPs and associated ossicles, including the AdSh and VAP-1, which increased the dimensions of the OSl and vTCt, and lengthened the distance between the OPR and the orifice of the vTCt.

The sequence and position in which the elements of buccal armature develop in *O. sarsii* and *O. luetkenii* is comparable to that in other *Ophiura* species including *Ophiura albida* Forbes, 1839, *Ophiura carnea* Lütken, 1858, *Ophiura leptoctenia* H.L. Clark, 1911, *Ophiura ljungmani* (Lyman, 1878b), *Ophiura ophiura*, and *Ophiura robusta* (Ayres, 1852) (Webb and Tyler, 1985:figs.1–4; Sumida et al., 1998:figs. 5–8; Stöhr, 2005:figs. 8–10; Borges at al., 2015:figs. 21–23; Martynov et al., 2015:fig 20). A tooth and AdShSp were present in a 0.3-mm-dd *O. ophiura*, and a BSc and IPa had developed in 0.7- and 1.5-mm-dd juveniles, respectively (Webb and Tyler, 1985:fig. 2). Teeth, AdShSp, BSc, and IPa developed before 2°IPas on the OPs of *O. sarsii* and *O. carnea*. In the latter species, TPas formed after two 2°IPas had developed, and row of 2°AdShSps arose on the AdSh and the OP, which was opposite a row of TScs on the VAP-1 and the vCtP (Sumida et al., 1998:figs. 5, 6; present study). Ventral CtPs resembling those of *O. luetkenii* were figured in *O. leptoctenia* of 2.0 and 10.0 mm dd, but were not identified as such (Martynov et al., 2015:fig 20).

Thus, OPas *s.l.* of *Ophiura* species typically comprise TPas, 2°IPas, IPas, BScs,VAP-1 TScs, 2°AdShSps, and AdShSps, but the number, shape, size, and arrangement of OPas *s.l.* change during ontogenesis. Usually, rows of serially homologous ossicles arise in a unidirectional sequence, from distal to proximal (e.g., Murakami, 1941; Sumida et al., 1998; present study). Series of TScs develop proximally to the initial VAP-1 TSc, series of 2°AdShSps develop proximally to the initial AdShSp, and series of 2°IPas develop proximally to the initial IPa.

Ontogenesis and Skeletal Homologies of Ophiurina

The OPas *s.l.* in Ophiurida such as *Ophiocten affinis* (Lütken, 1858), *Ophiocten gracilis* (G.O. Sars, 1872), *Amphiophiura sculpta* (Duncan, 1879) [=*Stegophiura sculpta*], and *Stegophiura brachyactis* (H.L. Clark, 1911) develop similarly to homologues in *Ophiura* spp. (Sumida et al., 1998; Murakami, 1941; present study). *Ophiopleura borealis* Danielssen and Koren, 1877, is exceptional in that juveniles 0.6–1.0-mm dd appeared to lack an AdShSp; hence an AdShSp was presumed to be absent in the adult (Stöhr, 2005:574). However, a 1.8-mm-dd juvenile had a papilla on the AdSh (Stöhr, 2005:fig. 7H), which may be an AdShSp that is late-appearing as a result of heterochronic postdisplacement. A remarkable deep-sea ophiurid, *Ophioctenella acies* Tyler et al., 1995, had an identifiable AdShSp, 2°AdShSp, VAP-1 TSc, and an unusual, two-part "oral blade" extending over the vT, which may comprise an IPa (or TPa?) and a BSc (Tyler et al., 1995; Stöhr and Segonzac, 2005). An ophiopyrgid, *Spinophiura jolliveti* Stöhr and Segonzac, 2006, was described to lack a BSc, but to have "tentacle scales on the first tentacle pore inside the mouth slit [which have] not been described for any other species of ophiuroid" (Stöhr and Segonzac, 2006:20, figs. 2–4). Yet these so-called "tentacle scales" seem homologous with the 2°IPa, IPa, and BSc on the OPR of other Ophiurina. Moreover, a 1.3-mm-dd juvenile *S. jolliveti* appears to have a BSc that is similar to the BSc of a 0.57–1.0-mm-dd juvenile *A. sculpta*, a confamilial species (compare: Murakami, 1941:fig. 5, and Stöhr and Segonzac, 2006:fig. 3G). Some Ophiurina were reported to have BScs that divide during ontogenesis, or are "replaced" by multiple OPas *s.l.* (e.g., Stöhr, 2005:557; Stöhr and Segonzac, 2005:395), but this assertion is unconfirmed (see "Ossicle Fusion and Fragmentation" in the Discussion).

Diet, Feeding, and Operation of the Jaws

Ophiura species consume a variety of animals, plants, and detritus, and they have been characterized as deposit feeders, detritivores, and scavengers, and as predators on small, active animals (Turpaeva, 1953; Warner, 1982; Pearson and Gage, 1984). *Ophiura sarsii* consumes at least 31 taxa of macrobenthic epifauna and infauna including crustaceans, polychaetes, echinoderms, and foraminiferans, and amphipods may compose 50% of its stomach contents (Harris et al., 2009). Planktonic Euphausiacea, Copepoda, and detritus were reported in its stomach contents (Turpaeva, 1953; Litvinova, 1979; Kogure, 2010). Moreover, *O. sarsii* responds to seasonal falls of ice algae and phytoplankton, and groups of individuals, which have been observed to pursue, capture, and consume fishes, euphausiids, and squids, exhibit a capacity to subdue and dismantle large prey (Stancyk et al., 1998; North et al., 2014). Confamilial *Ophionotus victoriae* Bell, 1902, is a necrophagous, cannibalistic, and opportunistic carnivore that preys on a wide range of invertebrate prey. It is not a suspension feeder, but similarly to *O. sarsii* it predominantly consumes swimming eupausiids, mysids, and amphipods when these prey are abundant (Fratt and Dearborn, 1984).

The natural diet of *Ophiura luetkenii* is varied, and individuals monitored in the laboratory transported small items to the mouth "by co-operating pairs of arm podia." They also grasped extremely large items between the jaws, which were torn by the arms. It was observed that "material brought below the disk is subsequently pushed between the jaws by the oral podia, the jaws generally close rapidly once on it, then open and the material is pushed into the open mouth by the oral podia. Occasionally material may be pushed into the gut without prior jaw closure. Elongate objects may be swallowed in stages." It was also suggested that the teeth could "partially break up or crush material before it enters the gut" (Austin, 1966:61, 66). Although, "pointed and tapered spine-like teeth as well as the spine-like apical papillae" of *Ophiura albida* [=*Ophioglypha albida*] were characterized as "carnassial instruments" used to grip and tear prey, this interpretation is not substantiated by the species' diet of small invertebrates and benthic material (Eichelbaum, 1910; Boos et al., 2010:180; *contra* Boos, 2012:111). On the other hand, behavioral observations on *Ophiura* spp. indicate that the teeth and jaws clench items fleetingly before they are swallowed.

Ophiura ophiura [=*Ophiura texturata*] was observed to bound ahead "jump, and land with the food below its mouth," seconds before "...the mouth area dilated, and the tube feet moved the material into the gaping oral area. The oral teeth further manipulated the food, and moved it into the stomach" (Blegvad, 1914; Feder, 1981:224). The OTs of this species "serve to convey food to the mouth, but they also serve to eject the matter digested. They are continuously in motion, waving up and down; and every now and then when the stomach pouts up and ejects some digested matter, the lowermost or inner tentacula shovel it up, and the uppermost or outer clear it away" (Forbes, 1841:24).

Living individuals of *Ophiura luetkenii* that were restrained in an inverted position extended both sets of oral tentacles from the mouth (Fig. 4C). OT-1 appeared to be thicker than OT-2, but OT-2 extended farther. As they protracted, OTs displaced OPas *s.l.* from their resting position. The teeth, VAP-1 TScs, and 2°AdShSps beside the vTCt fell back to their resting position when the tentacles retracted. When a 2°AdShSp on the OP was lightly prodded with fine forceps, all the adjacent papillae moved, indicating these OPas *s.l.* may be interconnected by integument.

Buccal Morphology

It was verified in *Ophiura sarsii* that a branch of the water ring enters a single water ring foramen on the dorsal surface of each OP, bifurcates within the plate, and terminates in the OTs. Similar single water ring foramina have been figured in other Ophiuridae including *Ophiura* (*Ophiuroglypha*) *lymani* (Ljungman, 1871) and *Ophiocten sericeum* (Forbes, 1852), and in Ophiopyrgidae such as *Amphiophiura bullata* (Thomson, 1877), *Ophioplinthus carinata* (Studer, 1876) [=*Ophioglypha deshayesi*], *Ophiomastus secundus* Lyman, 1878a, and *Stegophiura sladeni* (Duncan, 1879) (Lyman, 1882:pl. 38, fig. 10, 14, 18, 22; pl. 39, fig. 14; Matsumoto, 1917:pl. 15, fig. 6). However, the OP of *Uriopha ios* Paterson, 1980, an Ophiurida *incertae sedis*, appears to have dual water ring foramina (Paterson, 1980:fig. 1d, e).

In the present study, *Ophiura sarsii* and *Ophiura luetkenii* were found to have a foramen that pierces the tentacle basin of OT-2, and which may admit a branch of the radial nerve cord innervating the tentacle. Similar presumptive neural foramina associated with the OTs, which occur in other species of ophiuroids, are described below (see "Foramina of the Water Ring and of Podial Nerves in the Oral Plate" in the Discussion).

Although buccal morphologies of *O. sarsii* and *Ophiomusa lymani* are dissimilar in some respects, both species have a VAP-1 with a thick, truncate proximal edge that projects upward in the OSl (compare: Figs. 3E, 4I). The vTCt of *O. sarsii* is shallow, exposed to view, and framed by the small AdShSp, 2°AdShSps, and VAP-1 TScs, but a broad, operculate AdShSp conceals the vTCt of *O. lymani*. OPas *s.l.* of *O. sarsii* are separated by gaps and borne on the OPR, in contrast to the serried papillae of *O. lymani*, which adjoin the ventrolateral edge of the OP. TScs on basal arm segments of *O. lymani* are solitary and articulate on the LAP, but *Ophiosphalma glabrum* (Lütken and Mortensen, 1899) [LACM E.197] has paired TScs on the LAP and VAP of basal arm segments, like *O. sarsii*.

Ophiocten sericeum (Forbes, 1852)
Fig. 6

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their pattern of skeletal ontogenesis in *Ophiocten* species (described below). Teeth, TPas, and OPas *s.l.* are composed of labyrinthic stereom (Fig. 6A, B, D). The vT and a pair of TPas project from the ventral apex of the DP. The ventral apex of the jaw protrudes ventrally, and the ventral adradial edges of the OPs incline dorsally. Consequently, the rows of OPas *s.l.* distal to the TPa, which are borne on the OPR, slant upward in the mouth. These consist of a 2°IPa, an IPa, and an elongated BSc abutting VAP-1, which are separated by a diastema from a squamous AdShSp on the AdSh and several, squamous VAP-1 TScs (Fig. 6A). The 2°IPa and IPa are borne on separate ArtSs that are composed of sparsely perforate stereom and may be adjacent to minute fossae in the OP (Fig. 6E). The obliquely angled orifice of the vTCt is isolated from the OSl by a BSc, VAP-1, and the OP (Fig. 6A, C). VAP-1 inclines upward toward the mouth, and stout, proximal protuberances on the plate abut the OPR (Fig. 6E). Distal, beveled edges of VAP-1 abut the adjacent LAPs-1 and AdShs (Fig. 6A, E). The oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs. OT-2 can extend between vTCt and the OSl when the jaws are open, but when the jaws are closed the teeth on opposing jaws intermesh and the OPas *s.l.* on adjacent jaws abut, sealing the OSl [LACM 1972-244.2].

PROXIMAL ASPECT. Teeth are dorsoventrally compressed, irregularly triangular, or trapeziform in cross section. They are arranged in staggered vertical series, such that teeth on opposite sides of the DP are wedged between one another, similarly to the teeth of *Ophiura sarsii* (Figs. 6B, C, D, 4F). DP is a single ossicle. The proximal aspect of the jaw is dominated by the large orifices of the dTCts, separated by thick OPRs from the vTCts. VAP-1 inclines into the OSl at a shallow angle. When the jaw is tilted, it can be seen that the dorsal and ventral surfaces of the jaw converge at the OPR, and that the orifice of the vTCt is directed ventrally, and proximally towards the mouth, whereas the orifice of the dTCt is directed dorsally (compare: Fig. 6B, C).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP and OPR, VAP-1, AdSh, and bordered by an AdShSp and VAP-1 TScs (Fig. 6A, B, E). A vCtP is lacking. The vTCt forms a deep cavity on the ventral side of the jaw. The vTCt is nearly separated from the proximal OSl by the ventral surfaces of the VAP-1, OPR, and BSc (Fig. 6A, C, D). A foramen penetrates the OP beside the tentacle basin of OT-2, which may receive a branch of the radial nerve cord innervating the tentacle (Fig. 6E).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, a dCtP, and a wide FP that arches between the OPR and the dorsal edge of the OP (Fig. 6B, D).

PERRADIAL ARMATURE. The PG is occluded by VAP-1 and FPs of the adjacent jaws and the integument in which they are embedded (Fig. 6B, C). LuOss were not detected.

Skeletal Ontogenesis and Homologies of Oral Armature

The ontogenesis of oral armature was similar in *Ophiocten affinis* and *Ophiocten gracilis* that were studied by Sumida et al. (1998:figs. 9, 10), and in *O. sericeum*, *Ophiura* spp., and *Stegophiura* spp. that were examined in the present study. In juvenile *Ophiocten*, the OPR isolates the orifice of the vTCt from the OSl, and a diastema separating the BSc from VAP-1 TScs and a spiniform AdShSp. 2°AdShSps can develop proximally to the AdShSp in large individuals of *O. sericeum*, *O. gracilis*, and *Ophiocten hastatum* Lyman, 1878b (Paterson et al., 1982:figs. 2a, 4a, 5d).

The smallest specimens of *O. gracilis* (0.48 mm dd) and *O. sericeum* (0.34 mm dd) that were examined had a tooth on the DP, a BSc on the OP, and an AdShSp on the distal edge of the AdSh. In somewhat larger individuals of *O. gracilis* (0.9 mm dd) and *O. sericeum* (0.8 mm dd), length of the OPs had increased, an IPa had developed at the DP/OP juncture proximally to the BSc, the AdShSp had become papilliform, and there were two TScs on VAP-1. At a later stage, a 2°IPas formed proximally to the IPa at the DP/OP juncture, and a TPa developed on the DP (*O. gracilis*, 1.6 mm dd; *O. sericeum*, 1.2 mm dd). Adult specimens of *O. affinis* typically have a TPa, IPa, BSc, and VAP-1 TSc and lack a 2°IPa (Mortensen, 1927; Sumida et al., 1998). It appears that in *Ophiura* and *Ophiocten* spp. "mouth papillae are added in a unidirectional sequence from distal to proximal along the jaw" beginning with the BSc (Sumida, 1998:297); however, these ossicles vary in their rate of growth, making it difficult to infer the order in which they developed. I examined >50 specimens of alcohol-preserved, juvenile *O. sericeum* at 50× magnification, and the sequence in which 2°IPas and TPa had developed was indeterminable in many individuals [LACM 1975-712.1, LACM 1976-707.5, LACM 1977-309.9, LACM 1977-317.3].

Diet, Feeding, and Operation of the Jaws

Ophiocten species feed on epibenthic phytodetritus, amorphous aggregates (marine snow), and microorganisms associated with these substrates, and their tightly sealing buccal armature may enable individuals to ingest particulate matter and small prey and retain fine material in the buccal cavity. The seeming absence of *Ophiocten gracilis* in benthic photographs of areas where this species is abundant suggests individuals are "shallow burrowers" that nestle beneath a thin layer of sediment. However, upraised disks and arms of *O. gracilis* were recorded on the current-swept continental slope off Scotland (Gage et al., 1983:297; Pearson and Gage, 1984; Lamont and Gage, 1998). Seasonal fluctuations in the quantity of mineral particles, flocculent organic material and foraminiferans ingested by *O. gracilis* indicated that the population in the Rockall Trough harvested fast-sinking, freshly deposited particles (Pearson and Gage, 1984; Gage, 2003). *Ophiocten hastatum* also "seems to be very efficient in tracing fresh phytodetritus even in times of low deposition rates," and it may significantly deplete and "substantially modify the composition of the organic matter available to other components of the benthos". In addition to flocculent organic material, stomach contents of *O. gracilis* and *Ophiocten sericeum* contained small invertebrates such as copepods, bivalves, juvenile mollusks, foraminiferans, and polychaetes (Turpaeva, 1953; Schoener, 1971; Paterson et al., 1982; Pearson and Gage, 1984). *Ophiocten* species may feed preferentially, or most efficiently, on small items. An unidentified *Ophiocten* sp. was weakly responsive to a natural fish food-fall, but the density of individuals was no different on and around the carcass than upslope or downslope (Smith, 1985:429; Soltwedel et al., 2003).

Stegophiura nodosa (Lütken, 1855)
Fig. 7

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in confamilial *Amphiophiura sculpta* (described below). Teeth, TPas, and OPas *s.l.* are composed of uniform, labyrinthic stereom (Fig. 7B, C). There are two pairs of TPas beside the vT, and the pair closest to the tooth presumably develops before the smaller, ventral pair nearer the growing edge of the DP (Fig. 7B). There is a continuous row of OPas *s.l.* on the adradial edge of the jaw, from the OPR to the ventral apex of the DP. This series comprises a BSc near VAP-1, an IPa near the DP/OP juncture, and an additional 2°IPa on some jaws. Above these ossicles there are 1–2 AOPas on the flank of the OPR (Fig. 7A, C, E). The preceding ossicles on the OPR are separated by a diastema from two serried rows of ossicles beside the orifice of the vTCt, which consist of an AdShSp on the AdSh and 4-6 2°AdShSps on the OP, and a row of TScs on the adradial edge of VAP-1 (Fig. 7A). OPas *s.l.* on the AdSh and VAP-1 are borne on ridge-shaped ArtSs composed of sparsely perforate stereom, which are similar to those of TScs on LAP-2 (Fig. 7F, G, I). However, rudimentary ArtSs that support the IPa and 2°IPa are associated with irregular fossae on the OP (Fig. 7I). The truncate apex of the OP and the ventral surface of the OS protrude somewhat, and the adradial edge of the OPR slopes dorsally (Fig. 7C–E, I). The thick, up-curved proximal lobe of VAP-1 abuts the OPR and rudimentary vCtPs. Its lateral edges border the orifice of the vTCt, and its disto-lateral edges abut LAP-2 and the broad, beveled edge of VAP-2 (Fig. 7D, F, G).

VAP-1 does not contact the AdSh, but it is attached to adjacent vCtPs and LAPs-2, and the latter adjoin the AdShs. The oral frame is reinforced by the connections of these plates to one another and by their connections to the OShs and conjoined OPs (Fig. 7A, F, G). A rudimentary vCtP inserts between the proximal tip of VAP-1 and the OP, forming a sill that obstructs, but does not entirely close, the channel between vTCt and OSl (Fig. 7C, F, G). OTs-2 can extend below the disk whether or not the jaws are open and can project directly into the buccal cavity when the jaws are open, but when the jaws are closed, OPas *s.l.* on opposing jaws interdigitate and the edges of the teeth intermesh, separating the vTCt and proximal OSl [LACM 1962-239.4].

PROXIMAL ASPECT. The DP is a single ossicle, and the teeth are close set and compose a continuous, narrow column on the DP. They are thick, triangular in cross section, tapering to a blunt tip, and their adradial edges are beveled (Fig. 7 C, D). The dorsal pair of TPas abuts the sloping sides of the vT. The proximal edge of the OP projects well above the OPR and dTCt, but it is truncated ventrally. The proximal aspect of the jaw is dominated by the large orifices of the dTCts, separated by thick OPRs from the smaller vTCt orifices. The divergent angle of inclination of the dorsal and ventral TCts is apparent when the jaw is tilted (compare: Fig. 7C, D).

VENTRAL TENTACLE COMPARTMENT. Composed of, and circumscribed by, the flank of the OP and OPR, VAP-1, LAP-2, vCtP, AdSh, AdShSp, 2°AdShSps, and VAP-1 TScs. The vCtP does not abut the AdSh or AdShSp (Fig. 7F, G). The vTCt forms a deep cavity on the ventral surface of the jaw. The ventral surface of VAP-1 inclines dorsally at a shallow angle and narrows proximally. Its thick, curved apex angles steeply upward beside the vCtPs (Fig. 7D, G). The orifice of the vTCt appears to be shallow, and OT-2 is excluded from the OSl when the jaws are closed, because the apex of VAP-1 and a vCtP block the connection between the vTCt and the proximal OSl (Fig. 7A, D, F, G). Nevertheless, this channel is confluent with the OSl, and OT-2 can project into the oral cavity (Fig. 7C, D). A groove beside the tentacle basin of OT-2 may accommodate a branch of the radial nerve cord that innervates the tentacle (Fig. 7F). *Stegophiura nodosa* lacks a foramen in the OP, which occurs in *Ophiura sarsii* and *Ophiocten sericeum* and was suggested to admit the tentacular nerve of OT-1 (Fig. 7F).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, OPR, and a dorsally tapering dCtP with a broad base, which may be surmounted by a smaller, dorsally tapering plate. A tapering FP abuts the dCtP, arching behind and above it, and extending to the dorsal edge of the OP (Fig. 7C, D, H).

PERRADIAL ARMATURE. The VAP-1 has a truncate, narrow projection on its stout, proximal edge, which arches upward toward the OPR, and blocks the ventral portion of the PG (Fig. 7D, G, I). LuOss that are laminar and composed of stereom with small pores, cover the dorsal portion of the PG and overlap the FP (Fig. 7C, D, H). A single foramen on the dorsal surface of each OP, resembling the dorsal foramen of *Ophiura sarsii and Ophiocten sericeum*, presumably leads to bifurcate intra-ossicular channels that terminate at the tentacle basins (compare: Figs. 4K, L and 7J).

Skeletal Ontogenesis and Homologies of Oral Armature

Skeletal ontogenesis of *Stegophiura* species has not been investigated. However, the development of confamilial *Amphiophiura sculpta* [=*Stegophiura sculpta*] was investigated by Murakami (1941). The youngest juvenile that he described (0.57 mm dd) had one rudimentary arm segment and TP, a tooth, and an AdShSp. A stage with four arm segments (<<1 mm dd) had an elliptical rudiment on the edge of the OP near VAP-1, which I regard as a BSc. However, Murakami (1941:70) presumed it was not a BSc, because it is small in comparison to BScs of Amphiuridae at a similar stage of development. Prior to their emergence from the brooding adult, juvenile *A. sculpta* (1.08 mm dd) developed a 2°AdShSp proximal to the AdShSp. The free-living juvenile (2.4 mm dd) had a wide BSc distal to the smaller IPa and 2°IPa, three VAP-1 TScs, an AdShSp, and two 2°AdShSps. Murakami (1941:75) stated that "distal scales appear earlier than the proximal ones" in the rows of VAP-1 TScs, and 2°AdShSps, and he noted that the four oral papillae (one of which evidently is a TPa) form "inwards to" the BSc. Also at this stage (2.4 mm dd), what appears to be a vCtP was figured between the BSc and VAP-1 (Murakami, 1941:fig. 9).

Diet, Feeding, and Operation of the Jaws

Information on the feeding biology of the genus *Stegophiura* is scarce and difficult to interpret. An unidentified northwest Pacific *Stegophiura* species was characterized as "a true carnivore, feeding on such highly active animals as Amphipoda and Nereididae," although only 5% of the specimens examined had stomach contents (Sokolova, 1959). The seemingly limited diversity of prey of this species was proposed as evidence that deep-sea carnivores have specialized feeding diets, with a caveat that "very limited data for the deep sea, together with the paucity of information on benthic carnivore feeding render any statements speculative" (Grassle and Sanders, 1973:650). The only other record indicates that the stomach of one specimen of *Stegophiura ponderosa* (Lyman, 1878), a bathyal species, was "filled with mud" (Lambert and Austin, 2007:90).

Buccal Morphology

Stegophiura species were characterized as having the OTPo-2 either "opening away from the mouth slit" or "opening partially into the mouth slit," but this disparity was not explained in terms of the skeletal structures composing the vTCts (Paterson, 1985:135; Kyte, 1987:249-250). A comparison among *S. nodosa* and several congeners showed that continuity of the vTCt and the proximal OSl varied according to the morphology of the OP and vCtP, deflecting OT-2 ventrally to a greater or lesser extent when the jaws are open. *Stegophiura nodosa* and *Stegophiura brachyactis* [LACM E.1998-177.2] have jaws with a ventrally truncate apex, a rudimentary vCtP, and an OPR that is dorsal to VAP-1. Their vTCt is confluent with the proximal OSl when jaws are opened, and OT-2 can extend directly into the buccal cavity (Fig. 7C, F, G). *Stegophiura sladeni* [LACM 70-302.1] and *Stegophiura sterea* (H.L. Clark, 1908) [LACM 64-233.1] have jaws with a ventrally protruding apex, a well-developed lamelliform vCtP, and a VAP-1 that is nearly level with the OPR. Their vTCt inclines ventrally and presumably would deflect the OT-2 in that direction. The latter two species have OPs and OSs that are enlarged distally and bulge ventrally, although the jaws of *S. sladeni* are considerably sunken proximally and swollen distally, in contrast to the jaws of *S. nodosa* and *S. brachyactis*, which have a relatively flat ventral surface. The diminutive *Stegophiura vivipara* Matsumoto, 1915 [LACM 40-339.1], may be an *Amphiophiura* species, because its arm spines are neither dimorphic nor arranged in multiple rows. Its jaw has an apex that does not protrude ventrally, a stout, rounded vCtP, and a vTCt that inclines ventrally and is blocked by the vCtP. As a result, its vTCt and OT-2 are isolated from the proximal OSl, even when the jaws are opened, and in this respect it resembles *Ophioplinthus gelida*, which has a bulky vCtP that completely separates the vTCt and OSl. Just as in the other *Stegophiura* species, the OT-2 is excluded from the mouth when the jaws are closed, because OPas *s.l.* borne on the OPR of opposing jaws block the OSl.

Ophioplinthus gelida (Koehler, 1901)
Fig. 8

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and on the basis of the ontogenesis of OPas *s.l.* in various species of Ophiurina discussed above, including *Ophiura sarsi*, *Ophiocten sericeum*, and *Amphiophiura sculpta*. Teeth, TPas, and other OPas *s.l.* are composed of labyrinthic stereom (Fig. 8A, I). The vT and 1–2 small, dorsoventrally compressed TPas are borne on the ventral apex of the DP. Ventral surfaces of the OSh, OP, and LAP-2 are depressed. A serried row of stout, angular OPas *s.l.* occupies the ventrolateral edge of the OP between the DP and VAP-1. Three large, proximal ossicles are tentatively identified as the IPa, 2°IPa, and BSc on the basis of their positions relative to one another. A larger ossicle, located between the BSc and VAP-1, is identified as a vCtP on the basis of its position beside the orifice of the vTCt, its connection to the OPR, and its overgrowth by a row of VAP-1 TScs (Fig. 8A, F, G). Small ossicles situated on the OP above and between the IPa, 2°IPa, and BSc are tentatively regarded as AOPas (Fig. 8A, G). Proximal OPas *s.l.* and AOPas are borne on ArtSs composed of sparsely perforate stereom, which are located beside small, irregular fossae in the OP (Fig. 8E). The small OPas *s.l.* beside the orifice of the vTCt are composed of the AdShSp and 2°AdShSps on the AdSh and OP, and VAP-1 TScs extending onto the vCtP (Fig. 8A). OT-2 can project ventrally through the orifice of the vTCt, but it is excluded from the OSl by the vCtP, BSc, and AOPas on the OPR (Fig. 8A, C, D, F, G). Similarly to the VAP-1 of *Sregophiura nodosa*, that of *O. gelida* abuts the vCtP and LAP-2 but not the AdSh (Fig. 8D). The oral frame is unified by connections of these plates with one another, and with the OShs and conjoined OPs

(Fig. 8A, D, H). When the jaws are closed, the ventrolateral OPas *s.l.* on adjacent jaws dovetail, and the AOPas and teeth on adjacent jaws intermesh, tightly sealing the OSl (Hunter, 2007:50, fig. E; [LACM E.1926-3.1]).

PROXIMAL ASPECT. Ventral teeth are compressed, triangular, and nearly as wide as the DP (Fig. 8B, F). Dorsal teeth are relatively slender or spiniform and are aligned in transverse pairs (Fig. 8H, I). The DP is a single ossicle that is shorter than the proximal edge of the jaw, and the dorsalmost spiniform teeth are attached to the DP and OP (Fig. 8H, I). The proximal end of the jaw projects well above the dTCts, but the ventral end is comparatively truncated (Fig. 8E, H, I). The vTCts are imperceptible in proximal view, and when the jaw is tilted upward the orifice of the vTCt is concealed by the vCtP, VAP-1 TScs, and 2°AdShSps (Fig. 8C, F, H). Tubercles above the OPas *s.l.,* borne on the massive OPR, are regarded as AOPas (Fig. 8G, H).

VENTRAL TENTACLE COMPARTMENT. Forms a deep pit on the ventral surface of the jaw, which is delimited by the OP and OPR, VAP-1, LAP-2, vCtP, VAP-1 TScs, AdShSp, and 2°AdShSps. The orifice of the vTCt is obstructed by the bulky vCtP, AOPas, and the OPR, which isolate it from the proximal OSl (Fig. 8A, D, E, G).

DORSAL TENTACLE COMPARTMENT. The heavily armored compartment is composed of the flank of the OP and OPR, and stout dCtPs abutting the BSc and vCtP. The dCtPs buttress a cylindrical collar of irregularly shaped, rugose, imbricating CtOss and CoOss, which are embedded in integument (Fig. 8G, H, I). This collar directs the OT-1 dorsally and abradially (Fig. 8B, G, H). An FP arching over the dTCt is concealed by LuOss (Fig. 8E, H, I).

PERRADIAL ARMATURE. The thick, wedge-shaped proximal tip of VAP-1 blocks the ventral portion of the PG and the OSl (Fig. 8E, F, H). The remainder of the gap is covered by clusters of squamous, imbricate LuOss that extend above the OPR and arch over the dTCt. LuOss cover much of the buccal cavity and adjoin a dense layer of ossicles embedded in the circumoral esophageal ligament (Fig. 8B, F, H). Numerous squamous ossicles are embedded in the integument that covers the water ring and perioral nerve ring (Fig. 8B). A single foramen on the dorsal surface of each OP, resembling the dorsal water ring foramen of *Ophiura sarsii*, presumably leads to bifurcate intra-ossicular channels that terminate at the tentacle basins (compare: Figs. 4K, L and 8B).

Diet, Feeding, and Operation of the Jaws

Ophioplinthus gelida has been considered a predator, because its stomach contents comprise invertebrates, predominantly polychaetes and euphausiids, and also foraminiferans, bivalves, gastropods, and ostracods. However, diatoms can be an important constituent of the species' diet. It also consumes sediment and fecal material, and individuals have been captured in baited traps, showing that its "feeding habits . . . include scavenging on larger particles of flesh and very likely seal feces as well" (Dearborn and Fell, 1974; Dearborn, 1977:314; Dahm, 1996). The ability of the stout jaws and oral armature to securely interlock and seal the OSl may enable *O. gelida* to tear and crush items of food held fast by its arms, and could help it retain fine material in the buccal cavity. The sturdy skeleton may also protect *O. gelida* from its confirmed predator *Glyptonotus antarcticus* Eights, 1852, a "giant" isopod with crushing jaws (Dearborn, 1967).

Buccal Morphology

The so-called "second tentacle pore" of *Ophioplinthus gelida* was characterized as "nearly completely enclosed by the jaw" in consequence of the jaw's "triangular shape" (Martynov and Litvinova 2008:88), but the orifice of the vTCt is walled off from the proximal OSl by the vCtP and AOPas, rather than by the OP itself (Fig. 8D, E, G). The species' vT was previously referred to as an "infradental papilla at the apex of the jaw," and its OPas *s.l.* were described as "soldered together," although these ossicles are separate (*contra* Hunter, 2007:47). Dimorphic teeth that occurred in the single specimen of *O. gelida* that was dissected in the present study, resemble the teeth of some individuals of *Ophioplinthus inornata* (Lyman, 1878b) [=*Ophiurolepis inornata*]. However, *O. inornata* may also have a single, vertical row of teeth (Bartsch, 1982:figs. 50, 54, 55). A confamilial ophiopyrgid, *Ophiura* (*Ophiuroglypha*) *lymani* [=*Ophiuroglypha lymani*] and an ophiacanthid, *Ophiotreta larissae* (Baker, 1979) were reported to have dimorphic, spiniform dorsal teeth, and in the present study an atypical individual of *Ophiacantha bidentata* (Bruzelius, 1805) was found which had aberrant, paired dorsalmost teeth (Fig. 16D; Bartsch, 1982:fig. 59; Martynov, 2010b:fig. 78C). It is not clear whether multiple, dimorphic dorsal teeth are a stable feature or an anomaly in *O. gelida* and other species in which they were observed.

Confamilial *Ophioplinthus gelida* and *Stegophiura nodosa* had an AdSh abutting LAP-2, which was separated from VAP-1, distinguishing them from other ophiuroids dissected in the present study, which had AdShs abutting VAP-1 as well as LAP-2. Notably, AOPas were only found in *Ophiurolepis gelida*, *S. nodosa*, *Ophiomusa lymani*, *Ophiura sarsii*, and debatably in *Gorgonocephalus arcticus*, and among the a limited number of taxa that were examined herein, AOPas occurred exclusively in Euryophiurida.

Ophiocoma echinata (Lamarck, 1816a)
Figs. 9, 11N

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *Ophiocoma wendtii* Müller and Troschel, 1842 (described below). Teeth, TPas, and OPas *s.l.* are composed of dense labyrinthic stereom, and teeth are capped with imperforate stereom (Fig. 9A–D). A cluster of TPas below the teeth occupies the apex of the DP. The smallest, youngest teeth and TPas are ventralmost on the DP. OPas *s.l.* on the ventrolateral edge of the jaw are separated from one another by small gaps (Fig. 9A, E). IPas project from the ventral apex of the OP, below the TPas (Fig. 9C). An AdShSp abuts the AdSh, and a 2°AdShSp occupies the ventrolateral edge of the OP, between the IPa and AdShSp. A truncate, tuberculate OPRSp protrudes from the OSl above the AdSh (Fig. 9A, B, F). LyOs inserts tightly between the AdSh and VAP-1, behind the AdShSp (Fig. A, B). The IPa, AdShSp, and 2°AdShSp have similar shapes and microstructure, in contrast with the coarse, striate stereom of the LyOs and VAP-1 (Fig. 9B). Microscopic, linear ridges on the ventral surface of LyOs and VAP-1, similar to striations found in *Ophioderma rubicunda* Lütken, 1856 and *Ophiolepis impressa* Lütken, 1859, may support tracts of cilia (Figs. 9A, B, 12E, 18C). Microscopic particles are carried by water currents across these ossicles in living *O. echinata* (Hendler, unpubl. obs.). VAP-1 is joined to flanking LyOss, LAPs-2, and AdShs, and the oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs.

PROXIMAL ASPECT. Three to four pairs of close-set, blunt, papilliform TPas surrounding a medial TPa are directly below a column of teeth (Fig. 9C–E). The shaft of a tooth is rhombic in cross section, and the broad bases of adjacent teeth nearly touch. The dorsalmost tooth may be long and tapering (Fig. 9D, G, H). The IPa, 2°AdShSp, and AdShSp are laterally compressed and project at an oblique angle from the ventrolateral edge of the OP (Fig. 9C). The anvil-shaped OPRSp is tightly attached to the proximal edge of the OPR, and abuts its counterpart on the adjacent jaw OP when the jaws are closed. Stereom on the contact surface of the OPRSp appears to be worn (Fig. 9F), suggesting that the OPRSps may function to align and brace the retracted jaws. However, additional study is required to confirm that presumptive signs of wear were not artefactual. DP is a single ossicle. The proximal edge of the jaw extends nearly symmetrically below and above the OPR (Fig. 9C). The proximally directed orifice of the vTCt is noticeably larger than the obliquely angled orifice of the dTCt (Fig. 9C, D, H). ArtSs of the OPas *s.l.* on the ventrolateral edge of the OP were not examined in *O. echinata*. However, the ArtSs in this location, which are composed of sparsely perforate stereom and have associated fossae, were figured in several species of *Breviturma* (Stöhr et al., 2013:figs. 3G2, 5A2, B2, C2). TPas are of approximately equal length and markedly shorter than the vT, but the teeth gradually increase in length dorsally (Figs. 9A, D, 10A). When the jaws are closed, a buccal funnel is formed by clusters of TPas surrounding a cylindrical space; the tapered edges of the teeth intermesh and abruptly block the dorsal end of the cylinder (Fig. 11N; [LACM E.1939-217.10]).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP and OPR, AdShSp, LyOs, vCtP, and CtOss (Fig. 9B–E). LyOs projects ventrally between the AdSh and VAP-1 and extends dorsally to the vCtP (Fig. 9C–E). An elliptical vCtP extends from the OPR to the dorsal edge of LyOs and the VAP-1, and a panel of thin, irregularly shaped CtOss projects from the proximal edge of the vCtP (Fig. 9C–E). This panel borders the vTCt and encloses the base of OT-2. A small vCtOs protrudes from the ventral edge of the OPR (Fig. 9E). A notch or foramen, which is between the OPR and the vCtP, may be the entry point for a branch of the radial nerve cord that innervates OT-2 (Fig. 9E).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP and a collar of squamous, irregularly shaped, imbricating CoOss, which surround the base of OT-1 (Fig. 9D, E, H). This collar is anchored to the dorsal edge of the OPR and directed abradially and above the OPRSp. A curved FP, set at right angles to the collar, arches above the tentacle basin and adjoins the flank of the OP (Fig. 9D, E, H). The abradial articulation surfaces of the OP form a conspicuous tongue-and-groove joint at the base of the arm (Fig. 9G).

PERRADIAL ARMATURE. The tapering proximal lobe of VAP-1 terminates below the OPR and abuts a column of imbricating LuOss (Fig. 9C–E). The dorsal LuOss are large, thin, tapering plates composed of smooth stereom with large perforations. They are positioned in a chevron pattern, forming a column of ossicles that bifurcates above the dTCt, and the diverging branches overlap the FPs (Fig. 9C–E). A sheath of integument covering the LuOss extends to the dorsal surface of the jaw, where it is embedded with numerous, minute, squamous ossicles (Fig. 9G). The radial water canal and nerve cord emerge dorsally, from behind the perradial armature, where they merge with the nerve and water rings (Fig. 9E, G, H). A single water ring foramen on the dorsal surface of each OP, distal to the PP, which resembles the dorsal foramen of *Ophiura sarsii*, presumably leads to bifurcate intra-ossicular channels that terminate at the tentacle basins (compare: Figs. 4K, L and 9G).

Skeletal Ontogenesis and Homologies of Oral Armature

A juvenile specimen of *Ophiocoma wendtii* (1.96 mm dd) had a prominent pair of TPas below the vT (Fig. 10A, B). Three of its jaws also carried a rudimentary, medial TPa, foreshadowing the alternating arrangement of single and paired TPas in the adult. Evidently, TPas arise near the ventral edge of the DP, and the largest and oldest TPas are closest to the teeth. The teeth on adjacent jaws of the individual intermeshed, and tips of the teeth were capped with nearly imperforate stereom (Fig. 10A). As it seems unlikely that these small individuals are suspension feeders, these reinforced teeth may not serve a specialized function in the juvenile. However, it may be necessary to intensify calcification in the juvenile stage, in order to generate an imperforate calcite cap in the adult. A slender ossicle on the ventral apex of the OP is inferred to be an IPa, because of its proximity to the DP/OP juncture. Two comparatively broad, dorsoventrally compressed papillae with large stereom pores were situated distal to the IPa, on the ventrolateral edge of the OP (Fig. 10B). Although neither was attached to an AdSh, the ossicle closer to the AdSh was inferred to be an AdShSp and the smaller more proximal ossicle a 2°AdShSp, on the basis of their position, size, and stereom structure. There is a possibility that the distinctly enlarged pores in the AdShSp enclose ducts of mucous glands that are comparable to the glands in the arm spines (Buchanan, 1963; Pentreath, 1970; Byrne, 1994:fig. 12A–B). However, in adult *O. echinata* the microstructure of the IPa and AdShSp is superficially similar and does not appear to be specialized for mucus secretion.

The rudiment of LyOs was discernible between the VAP-1 and the AdSh on several jaws, and rudimentary OPRSps were apparent above the vCtP and within the OSl (Fig. 10B, C). Close association of the vCtP and OPRSp on the OPR at this stage indicates that the OPRSp may be a specialized dCtP. The AdSh protruded below the broad, distal lobe of VAP-1, and both these ossicles overlapped LAP-2 (Fig. 10B, D). The tapering proximal lobe of VAP-1 curved upward into the OSl to the OPR. A fragile layer of small-pored stereom at the periphery of the VAP-1, AdSh, and OSh is evidence of the appositional growth on the edges of these plates (Fig. 10B). Ventral interradial scales of the disk were thin and circular with rather few, minute perforations, and they resembled the scales of juvenile *Ophiomyxa flaccida* (Say, 1825) (compare: Figs. 10D, 15A). A 2.0-mm-dd juvenile of confamilial *Ophiomastix annulosa* (Lamarck, 1816a) possessed TPas and an AdShSp but had not yet developed a 2°AdShSp (Hendler et al., 1999:fig. 5B). Juveniles of both these species lacked a BSc, corroborating the absence of the BSc in ophiocomids and among Ophiacanthida in general.

Diet, Feeding, and Operation of the Jaws

Indo-Pacific and Caribbean *Ophiocoma* species such as *Ophiocoma echinata, Ophiocoma wendtii*, and *Ophiocoma scolopendrina* (Lamarck, 1816a) extend or elevate their arms in order to collect particles in suspension and on the benthos. Stomach contents of field-collected *O. echinata* were composed of sand particles in the 0.1–0.3-mm range and pieces of fleshy algae, and individuals in aquaria could capture living brine shrimp with their distal tube feet (Sides and Woodley, 1985:710, 712). Seven species of Indo-Pacific *Ophiocoma* spp. consumed sand, algae, and algal detritus, although "stomachs of species inhabiting the reef floor occasionally contained foraminiferans, sponge spicules, crustacean (e.g., isopod) skeletal parts, nematodes and juvenile snail shells" (Chartock, 1983:140). Mean diameters of particles which were ingested ranged from 0.04–0.09 mm (Chartock, 1983:140). These *Ophiocoma* species tended to be primarily suspension feeders or deposit feeders, but they all employed more than one mechanism to capture food. *Ophiocoma scolopendina* (Lamarck, 1816a) skimmed food from the air-water interface, and *Breviturma dentata* (Müller and Troschel, 1842), was observed "rasping with the oral papillae" to ingest material on the substrate (Magnus, 1967; Chartock, 1983:142). Gut contents of three Caribbean *Ophiocoma* species contained particles ranging from <0.1 to >0.3 mm, which were of 70–90% organic material and typically included fragments of algae or *Thalassia* (Sides and Woodley, 1985:712).

Ophiocoma species use their tube feet to gather particles adhering to the mucus-coated arm spines, from the surface of the water, or from benthic substrate, consolidating this material into a mucus-bound bolus. Successive pairs of contralateral tube feet contribute to the bolus as they roll it toward the mouth (Chartock, 1983; Sides and Woodley, 1985). According to Sides and Woodley (1985:709) "this movement of the bolus appears to be very similar to that described for *Ophiothrix fragilis*" (Abildgaard in O.F. Müller, 1789). Chartock (1983:142) observed that "a podium with food on or near its tip would bend toward the mouth to the next adjacent podium; the next podium would flex and wipe material from the first podium and again bend toward the mouth for a subsequent transfer." Surprisingly, he found that in *Ophiocoma anaglyptica* Ely, 1944, "food would collect in the area of the mouth as it was passed down the arms. With the mouth pressed against the substrate, the particle laden mucus would collect in the area between the mouth and the substrate, below the oral frame. The buccal tentacles would compact the bolus. After several hours of accumulation, the food bolus was ingested (Chartock, 1983:144). Notably, *Ophiocoma wendtii* on Belizean coral reefs frequently were encountered that had several boluses of green-brown, mucus-bound particulate material covering 1–2 ventral arm plates or with a clump of similar material between the jaws. This pattern of behavior suggests that *Ophiocoma* species may accumulate a number of food boluses prior to transferring them to the buccal funnel, in a manner similar to Ophiotrichidae (Sides and Woodley, 1985:711; Hendler, prev. unpub.).

Buccal Morphology

Jaws of Ophiocomidae have a characteristic buccal funnel with close-set, blunt TPas of approximately equal length, forming level clusters of ossicles rather than the concave clusters that are typical of some microphagous ophiuroids (compare Fig. 11 A and N). Dorsalmost TPas are markedly shorter than the vT, and the teeth gradually increase in length dorsally. When the jaws are closed, the clusters of TPas surround a cylindrical space, and intermeshed edges of the teeth sharply obstruct the buccal funnel (Figs. 10A, 11N). The buccal funnels were alike in *Ophiocoma echinata* (Fig. 11N) [LACM E.1939-217.10], and other Ophiocomidae examined in the present study (Table 4), including ophiocomas of the "Scolopendina species-group" (*sensu* Devaney, 1970), "Pica species-group," "Pumila species-group," and species of *Breviturma*, *Ophiocomella*, *Ophiomastix* and *Ophiarthrum*. However, *Ophiarthrum elegans* Peters, 1851[LACM 1986-478.1], *Ophiocomella ophiactoides* (H.L. Clark, 1901) [LACM E.1939-210.10], and *Ophiocomella sexradia* (Duncan, 1887a) [LACM 1924-6.1] have a very shallow funnel with few TPas and only the vT is truncated. Notably, *Breviturma brevipes* (Peters, 1851) [LACM E.1947-54.1], which Chartock (1983) confirmed was a deposit feeder, also had an abbreviated buccal funnel with only a few, short TPas. In comparison, species that he characterized as suspension feeders, such as *Ophiocoma scolopendrina* and *Ophiocoma erinaceus* Müller and Troschel, 1842, had well-developed buccal funnels, signifying that morphology of a species buccal funnel may be related to its mode of feeding.

Ophiocoma, *Ophiomastix*, and *Ophiarthrum* species have, in addition to a buccal funnel, a suite of related adaptations that are characteristic of microphagous feeders. These species have papillose tube feet with numerous mucous-secreting glands (Sides and Woodley, 1985:figs. 6, 7). They also have well-developed dental muscles that move the teeth and penetrate pairs of foramina in the DP and connect with the OP (Murakami, 1963:pl. 3, figs. 1–14; pl. 7, figs.11–34). Their teeth are capped with imperforate stereom that resists abrasion. In addition, microphagous species have a well-developed abradial muscle fossa on a wing-shaped OP, and in ophiocomids the surface of fossa is banded with alternating zones of fine-pored and coarse-pored stereom to which are attached muscle and connective tissue, respectively (see Fig. 9B>, E; Murakami, 1963: pl. 7; Devaney, 1970:fig. 44).

The anvil-shaped OPRSps of ophiocomids were not described prior to this study. Although OPRSps were previously illustrated in *Ophiocoma echinata*, they were omitted from a figure of *Ophiocoma* sp. (Lyman, 1882: pl. 42, fig. 13; Spencer, 1925:text-fig. 187B). Nonetheless, OPRSps were discernible in undissected specimens of the ophiocomid species examined in the present study (specimens listed in Table 4), including ophiocomas of the "Scolopendina species-group" (*sensu* Devaney, 1970), "Pica species-group," "Pumila species-group," and in species of *Breviturma*, *Ophiocomella*, *Ophiomastix* and *Ophiarthrum*. The opposing OPRSps of these species make contact when the jaws close, but it is doubtful that the OPRSps crush food, since they are outside the buccal funnel. However, it is conceivable the OPRSps buttress or align the jaws as they are drawn together by massive abradial muscles of the OPs. Impact between these ossicles might account for signs of wear on the contact surface of the OPRSp (Fig. 9F).

Anvil-shaped OPRSps are either inconspicuous or lacking in several families of Ophiacanthina, which in the past were regarded as Ophiocomidae, including the Ophiopteridae (*Ophiopteris papillosa* (Lyman, 1875) [LACM E.1960-313.3]), Clarkcomidae (*Clarkcoma bollonsi* (Farquhar, 1908) [LACM E.1951-79.1], *Clarkcoma pulchra* (H.L. Clark, 1928) [LACM E.1972-450.1]) and Ophiotomidae (*Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789) [LACM E.887]). I examined the buccal cavity of undissected specimens of these species with a stereomicroscope, and all appeared to have a flat-edged ossicle on the adradial face of the OP, which may be homologous with ophiocomid OPRSps or ophiacanthid dCtPs (e.g., Figs. 9C, 16D, 17B). Furthermore, as was mentioned herein, in the treatment of *Ophiocoma wendtii*, the anvil-shaped, ophiocomid OPRSp may itself be a modified dCtP (see "Skeletal Ontogenesis and Homologies of Oral Armature" in the treatment of *Ophiocoma echinata* and Phylogenetic Distribution of the Elements of Buccal Armature in the Discussion). These unresolved questions regarding homology of CtPs and OPRSps might be clarified by a more comprehensive comparative study of the skeletal ontogenesis and buccal morphology among Ophiacanthida.

Stereomicroscopic examination of these species also revealed that in Ophiacanthida with buccal funnels, the vCtOs, vCtP, and dCtP on each OP typically align in a vertical column. When the jaws close, the opposing columns of ossicles on adjacent jaws abut, and surround a small, vertical channel between the columns and VAP-1. For example, in *Clarkcoma pulchra*, tips of the pincer-like vCtOs and vCtPs on either side VAP-1 converge when the jaws close, enclosing a circular space at the distal end of the OSl (Fig. 11K). It is not clear what function, if any, these channels might perform. In Ophiocomidae such as *O. echinata* the ventral opening of the channel is covered by LyOss, and the vertical columns of ossicles are discontinuous because of a difference in size between the OPRSps and vCtPs (Fig. 11N).

Examination of living *Ophiocoma cynthiae* Benavides-Serrato and O'Hara, 2008, *Breviturma dentata*, *Ophiocoma pica* Müller and Troschel, 1842, and *Ophiocoma macroplaca* (H.L. Clark, 1915b) revealed that as the OT-2 extends from the mouth, it pushes aside the proximal OPas *s.l.* until they are perpendicular to the ventral plane of the jaw. When the OTs-2 are retracted, these OPas *s.l.* remain erect or slowly drop against the oral plate. They could also lock in an erect position when contacted with forceps. LyOss were not displaced by the OTs, but when they were tapped with fine forceps the LyOs, VAP-1, VAP-2, AdSh, and OSh tightened against one another, bracing the oral frame.

Ophioderma rubicunda Lütken, 1856
Figs. 12, 13

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *O. rubicunda* (described below). Teeth, TPas, and OPas *s.l.* are composed of compact, labyrinthic stereom (Fig. 12A, C; Medeiros-Bergen, 1996:fig.1c). TPas are larger than the IPas and project from the DP, below or beside the vT. The TPa articulates with a circular ArtS composed of sparsely perforate stereom surrounding a central fossa (Fig. E). The row of OPas *s.l.*, on the ventrolateral edge of the OP, behind the

TPa, comprises an IPa, 2–3 LOPas, 2–3 2°AdShSps, and a broad AdShSp beside the AdSh (Fig. 12A). These ossicles connect to ArtSs on the lateral edge of the OP, and the ArtSs of IPas and LOPas are associated with small fossae (Fig. 12E–G). LyOs protrudes ventrally between the AdShSp, AdSh, and VAP-1. It abuts the vCtP and may overlap VAP-1 (Fig. A, C–E). Microscopic, linear ridges on the ventral surface of LyOs and VAP-1 may bear tracts of that are similar to ciliated structures described in *Ophiura texturata* (Stubbs and Cobb, 1982). Water currents carry microscopic particles across these ossicles in living *O. rubicunda* (Fig. 12E; Hendler, unpubl. data). One or two prominent OPRSps are evident within the OSl (Fig. 12A–D). The proximal lobe of VAP-1 inclines dorsally into the OSl and abuts the vCtP, but terminates below the OPR (Fig. 12C, D, F). VAP-1 adjoins the LyOss, AdShs, and LAPs-1. The oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs (Fig. 12A, E). When the jaws are closed, teeth on adjacent jaws intermesh, OPas *s.l.* abut or intermesh and obstruct the OSl, and OPRSps on adjacent jaws crisscross or interdigitate (Figs. 12B, 13Q; [LACM 97-137.4]).

PROXIMAL ASPECT. Teeth are aligned in a column and are separated from one another by substantial gaps. The numbers of teeth vary between different jaws. Teeth are dorsoventrally compressed and wedge shaped, with a broad, beveled, proximal edge composed of labyrinthic stereom. However, the dorsalmost tooth is lanceolate (Figs. 12B, C, H, 13J–M). The DP is composed of multiple elements that each bear 1–2 teeth, except the ventralmost ossicle bearing teeth and TPas (Fig. 12B, C). The multi-element DP is similar to that of *Ophiarachnella gorgonia* (Müller and Troschel, 1842) and *Ophioderma* sp. (Fig. 12B; Murakami, 1963:fig. pl. 2, fig. 54; Martynov, 2010b:fig. 14N). IPas and LOPas are laterally compressed and project at an oblique angle from the ventrolateral edge of the OP, in contrast with the broad, dorsoventrally compressed AdShSp and 2°AdShSps (Fig. 12A, B, C). One or two tapering OPRSps project from the proximal edge of the OPR (Fig. 12A-D, H). The dTCt has a more restricted orifice than the vTCt (Fig. 12B, D).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP and OPR, AdShSp, 2°AdShSp, LyOs, vCtP, and vCtOss (Fig. 12B–D, F). The vCtP extends from the OPR to VAP-1, and LyOs extends below the vCtP and beneath VAP-1 (Fig. 12A, D, E, G). A tessellated panel of irregularly shaped, compressed CtOss, which is connected to the LyOs and vCtP, protrudes above the AdShSp and below the OPR, enclosing the adradial edge of the vTCt and the base of OT-2 (Fig. 12B–D). A branch of the radial nerve cord that innervates OT-2 may enter the tentacle basin through a notch between the OPR and the vCtP (Fig. 12F, G).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, in addition to several small dCtPs and several overlapping CtOss, which extend from the OPR and support a cylindrical collar of irregularly shaped, imbricating, squamous CoOss (Fig. 12B–D>, H). The collar encloses the base of OT-1 and is directed abradially and dorsally (Fig. 12D, H). A short, bar-shaped, weakly curved FP extends behind the collar and between the OPR and the dorsal surface of the OP (Fig. 12F).

PERRADIAL ARMATURE. VAP-1 covers part of the PG, and its tapering proximal lobe terminates below the OPR. The dorsal edge of VAP-1 is overlapped by a column of tapered, squamous LuOss that are composed of smooth stereom with large perforations, which imbricate in a chevron pattern (Figs. 12C, D, F). The column widens dorsally, covering the PG and overlapping the FPs. The single water ring foramen on the dorsal surface of each OP, which is distal to the PP, resembles the dorsal foramen of *Ophiura sarsii*, and presumably merges with intra-ossicular channels that enter the dorsal and ventral tentacle basins (Figs. 12H, 4H, K).

Skeletal Ontogenesis and Homologies of Oral Armature

Ophioderma rubicunda is the only ophiodermatid species whose skeletal ontogenesis has been investigated. The smallest individual examined was a 1.3-mm-dd "ophiocryptus stage," *viz.*, a juvenile ophiodermatid with granule-covered ossicles on the disk and arms (*sensu* A.H. Clark 1939:452; Parslow and Clark, 1963:48). The granules of juvenile *O. rubicunda*, which were shaped like a chess rook and had a triradiate core (Fig. 13A), are distinctly different from the dome-shaped granules of adult Ophiodermatidae, but they resembled the granules of juvenile *Ophiopeza spinosa* Ljungman, 1867 (Turner, 1984:fig. 1C–D; Irimura, 1998:pl. 3; Byrne et al., 2008:6, fig. 4F). At this early stage, the sloping, ventral surface of the jaw inclined upward from VAP-1 to the vT. There was a pair of TPas below the vT on the DP, an IPa beside the DP/OP juncture, a LOPa distal to the IPa, and a 2°AdShSp and AdShSp on the AdSh. Both of the latter ossicles had three blade-shaped ridges, and they were separated by a diastema from the proximal OPas *s.l.* The OTPo-2 and AdShSp adjoined an incipient OSl that extended from VAP-1 to the buccal cavity. Notably, a BSc was lacking in this individual and in more advanced developmental stages of *O. rubicunda*. A 1.1-mm-dd juvenile of *Ophioderma wahlbergii* Müller and Troschel, 1842, also lacked a BSc, but possessed a tooth and AdShSp (Landschoff and Griffiths, 2015:fig. 2D).

At the 1.7-mm-dd stage, the ventral surface of the jaw sloped more steeply into the buccal cavity because the base of the jaw and the arm had increased in height and breadth (compare: Fig. 13A, B). The AdShSp and two 2°AdShSps, one of which was newly formed, were spiniform and had stereom with larger pores than the IPa and LOPa (Fig. 13B, D). Furthermore, the AdShSp and 2°AdShSps had been shifted to the growing, adradial edge of the OP, and were beside the midpoint of an AdSh that had increased in length distally. Rudiments of LyOs, vCtP, and OPRSp, barely perceptible in the previous stage, were evident inside the OSl of 1.7–2.1-mm individuals (Fig. 13D, E, J). In the 2.1-mm-dd juvenile, LyOs was beside VAP-1 and abutted the vCtP (Fig. 13E). The arms of a 2.2-mm-dd individual were nearly devoid of granules, and at this stage the OPas *s.l.* were disposed in a continuous row and the diastema between 2°AdShSp and LOPa was minimized (Fig. 13C). The vTCt was concealed by the increased height of the jaws and depth of the OSl, and by the enlarging OPas *s.l.* (compare: Fig. 13A–C). At this stage, the IPa and LOPa appear to have developed in a proximal-to-distal sequence, and were tapered in comparison with the broader, more compressed AdShSp and 2°AdShSps. The LyOs, vCtP, FP and OPRSp were visible within the buccal cavity (Fig. 13J).

Individuals between 2.9 and 6.2 mm dd gradually acquired dome-shaped granules and an adult buccal morphology (Fig. 13F–I). During this transformation, TPas always exceeded the size of IPas, and the AdShSp and 2°AdShSps enlarged allometrically, forming imbricate, leaf-like structures overlapping the vTCt (Fig. 13F–I). VAP-1 and LuOss merged near the OPR, covering the PG, and the FP, CtPs, and LyOs framed the TCts (Fig. 13J–Q). CtOss arose beside the dCtP, CoOss developed around OT-1, and LyOs enlarged and emerged between the VAP-1, AdSh, and AdShSp (Fig. 13J–P). In a 3.9-mm-dd juvenile, it is evident that adjacent jaws have different numbers of teeth, and that opposing teeth intermesh when the jaws close (Fig. 13Q).

The growth series of *O. rubicunda* demonstrates that as the height of the jaw increased, the growing distal lobe of VAP-1 overlapped VAP-2 on the ventral surface of the arm, while the proximal lobe of VAP-1 grew toward the OPR. However, a gap between the OPR and VAP-1 is bridged by LuOss in the adult. In step with these developments, growth of the OP above and below the OPR increased the depth of the OSl. The latter expanded in step and enlarged the vTCt. VAP-1 did not "rotate" into the OSl nor did the orifice of the vTCt "migrate" into the OSl as described in previous literature on ophiuroid skeletogenesis (see "Ossicle Migration and Ontogenesis of the Oral Plate" in the

Discussion). Morphogenesis of the VAP-1 and vTCt was initiated by and coupled with changes in the size and shape of the OPs and other plates composing the oral frame (Figs. 12A, D, 13A–O).

Further significant aspects of skeletal development were clarified by the ontogentic series. The DP of the 2.9-mm-dd juvenile, which was a single element with three teeth, transformed into a two-element DP with four teeth in the 6.2-mm-dd juvenile, and into a four-element DP in the adults with five teeth, as a result of the growth and subdivision of the original plate (compare: Figs. 13K, O; 11B, C). As a result, teeth that co-occur on one plate in the juvenile are distributed on separate elements of the DP in the adult (Fig. 12C). A LOPa arose distally to the IPa at the 1.3-mm-dd stage, whereas 2°AdShSps developed proximally to a preexistant 2°AdShSp and the AdShSp (compare: Fig. 13B, F, I). LyOs of *O. rubicunda* developed below the vCtP rather than alongside the OPas *s.l.*, similarly to LyOs of *Ophiomyxa flaccida* and *Ophiocoma wendtii*, which are described below.

Diet, Feeding, and Operation of the Jaws

Although the diet of *Ophioderma rubicunda* is not known, *Ophioderma brevispina* (Say, 1825), a sympatric congener, is an omnivorous predator and scavenger that primarily feeds on small crustaceans and also on mollusks, polychaetes, other invertebrates, algae, and detritus (Hendler, 1982b). However, it was reported to pursue *Ophiothrix oerstedii* Lütken, 1856, and consume its severed arms (Aronson and Harms, 1985). *Ophioderma cinerea* Müller and Troschel, 1842, and *Ophioderma appressa* (Say, 1825), which co-occur with *O. rubicunda*, feed on injured animals, carrion, and "faeces just released by passing fish" (Hendler, et al., 1995:136; Queiroz, 2018). These *Ophioderma* species carry small items of food to the mouth with series of tube feet, and snare larger items in a coil of the arm that is rapidly flexed toward the mouth (Reimer and Reimer, 1975; Hendler, 1982b).

The oral frame of *Ophioderma longicauda* (Bruzelius, 1805) was "dilated very widely to allow the ingestion or egestion of large food objects," which "passed rapidly into the stomach by movements of the buccal tube-feet…without any masticatory movements of the jaws" (Deschuyteneer and Jangoux, 1978; Candia-Carnevali et al., 1994:388). Candia-Carnevali et al. (1994:390, 392) emphasized that "stereom present in the non-articular regions of the teeth and oral papillae is the common galleried type…which does not have the characteristics of hardness and resistence of abrasion of chewing surfaces" and that integument covering the tooth is a "feature untypical of true teeth." From this they inferred that the oral frame of *Ophioderma* "is not a true masticatory apparatus in the sense that its primary function is not the grasping and mechanical disruption of food items…this species would seem to be a detritivore and to be adapted only secondarily for carnivorous feeding." However, *Ophioderma brevispina* appeared to use the OPRSps, OPas *s.l.*, and teeth to grip food between the closed jaws and to retain items in the buccal cavity. Individuals of *O. brevispina* that were offered pieces of polychaetes did not pulverize the tissue, and the "ingested pieces…retained their normal color and showed muscular contractions through the second hour after ingestion." These items were completely digested after 10 hours (Hendler, 1982b:24).

Buccal Morphology

Buccal armature of *Ophioderma rubicunda* resembled that of *Ophioderma* sp., *Ophioderma longicauda*, and other ophiodermatids that were figured in the literature (Matsumoto, 1917:pl. 6, fig. 6; Cuénot, 1948:fig. 278; Murakami, 1963:pl. 2, figs. 50–51, 54; Candia-Carnevali et al., 1994:389, fig. 2; Martynov, 2010b:fig. 14N, Q). These species have in common a multi-element DP, intermeshing teeth, similar ArtSs on the DP and on the OP, OPRSps, and well-developed CtOss and CoOss. Also, as Lyman (1882:19) noted, in *Ophioderma* [=*Ophiura*] "the first mouth tentacle is enclosed in a tube of lime scales." Large individuals of *Bathypectinura heros* (Lyman, 1879) have up to 10 TPas on the DP, which were referred to as "apical papillae" (Madsen 1973:141).

Ophiomyxa flaccida (Say, 1825)
Figs. 14, 15

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in juvenile *O. flaccida* (described below). The disk, arms, and oral frame are embedded in thick integument (Byrne and Hendler, 1988). Teeth, IPa, and two LOPas are flabelliform and are capped with a serrate crest of imperforate stereom (Fig. 14A, B). An IPa on the apex of the OP slants obliquely toward the vT, and LOPas with twisted shafts are borne on the ventrolateral edge of the OP, distal to the IPa (Fig. 14A, B). These OPas *s.l.* are separated from one another by substantial gaps. A small, tapering, blunt-tipped AdShSp, which is composed of labyrinthic stereom, lies between the distal LOPa and a LyOs (Fig. 14A, B). LyOs is set close to the AdSh and abuts the AdShSp and VAP-1. VAP-1 inclines dorsally into the OSl and nearly abuts the OPR (Fig. 14A–C). It is coupled by integument to the flanking LyOs, AdShs, and LAPs-1, and the oral frame is unified by connections of these plates with each other, and to the OShs and conjoined OPs. Small, blunt OPRSps are visible above the LOPa, inside the OSl (Fig. 14A–C). Teeth, IPa, and LOPas on adjacent jaws overlap or intermesh and cover the OSls when the jaws of *O. flaccida* are closed [LACM 89-119.9, LACM 67-333.1]. Teeth of *Ophiomyxa vivipara* Studer, 1876, also intermesh (Bartsch, 1982:fig. 17).

PROXIMAL ASPECT. Teeth, IPa, and LOPas are dorsoventrally compressed and bowed. Teeth are aligned in a column and are separated from one another by gaps (Fig. 14B). They are borne on ArtSs on the DP, which are composed of a ring of sparsely perforate stereom surrounding a central fossa, and these resemble equivalent structures in *Ophiomyxa australis* Lütken, 1869 (Fig. 14C; Martynov, 2010b:23, fig. 1R). Serrations on the ventral teeth are dorsally recurved; dorsal teeth are smaller and lack serrations (Fig. 14B, C). Two to three short, blunt OPRSps protrude from the proximal edge of the OPR (Fig. 14B, C). The DP is composed of multiple elements, each bearing one tooth, except for a ventral element that carries four (Fig. 14B). The DP and its armature dominate the proximal aspect of the jaw. The proximal edge of the jaw extends farther below the OPR than above it, and the vTCt is noticeably larger than the dTCt (Fig. 14B, C). ArtSs of OPas *s.l.* on the OP were not exposed in preparations of *O. flaccida*, but the OPs of *Ophiomyxa pentagona* (Lamarck, 1816a) and *O. australis* had ArtS composed of sparsely imperforate stereom, which were associated with microscopic fossae (Murakami, 1963:pl. 3, fig. 16; Martynov, 2010b:23, fig. 1S, T).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP, AdShSp, LyOs, a vCtP set at an oblique angle on the OPR, several stout vCtOss, and imbricate CoOss. The vCtOss and numerous squamous CoOss with minute stereom perforations compose a semicylindical collar enclosing the base of OT-2 (Fig. 14B–D).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, a dCtP set at an oblique angle on the OPR, several small dCtOss, and imbricate CoOss. The dCtOss and numerous squamous CoOss with minute stereom perforations compose a semicylindical collar enclosing the base of OT-1. A broad, stout FP arches from the dCtP to the dorsal edge of the OP (Fig. 14B, C).

PERRADIAL ARMATURE. The large VAP-1 nearly reaches the OPR, and it covers the ventral portion of the PG. The LuOss, which are irregularly shaped, flat, imbricating plates, cover the remainder of the gap and overlap VAP-1 and the FPs (Fig. 14B–D). The water ring foramen was not examined in *O. flaccida*. However, *Ophiomyxa pentagona* has a single water ring foramen near the adradial edge on the dorsal side of the OP, which is similar to the foramina described in *Ophiura sarsii* and *Ophioderma rubicunda* (Figs. 4H, K; 12H; Martynov, 2010b:23, fig. 1S, T).

Skeletal Ontogenesis and Homologies of Oral Armature

Juvenile *Ophiomyxa vivipara* of 1.2 and 2.4 mm dd reportedly had 1–2 and 4 mouth papillae (“Mundpapillen”), respectively, compared to 4–5 on each side of the jaw in the adult, but these ossicles were not described in sufficient detail to gauge their homologies (Ludwig, 1898:774). However, a juvenile *Ophiomyxa flaccida* (2.1 mm dd) (Fig. 15A, B) has a vT with a flabelliform crown that is composed of imperforate stereom, which terminates in slender serrations. The IPa articulates on the apex of the OP and overlaps the DP, and behind it there are two LOPas with compressed, serrated tips; the smaller, more distal element presumably developed after the larger one. An OPa on the AdSh, which is pointed and lacks serrations, is presumed to be an AdShSp. Several jaws have a small, compressed, rounded LyOs protruding between VAP-1 and the AdSh, which usually is separated from the latter by a gap. The ventral interradial scales have stereom perforations that are remarkably small and few in number, and they resemble the disk scales of juvenile *Ophiocoma wendtii* (compare: Figs. 10D, 15A). Although Lyman (1874:264) did not describe the skeleton of juvenile *O. flaccida*, he stated “the secretion of lime is stopped in the disk integument at an early period and, in the adult, nothing is to be found but a few minute grains buried in the skin, while the general surface of the disk is smooth and fleshy.” However, the ontogenesis of the “minute grains” has not been examined, and it is not known if they are identical to the ovoid, sparsely perforate scales in the juvenile.

Ontogenesis and Skeletal Homologies of Ophiomyxidae and Ophioscolecidae

Buccal armature in *Ophiomyxa flaccida* was markedly different from species of Ophioscolecida that were formerly regarded as ophiomyxids. On the basis of the development of their buccal armature, I infer that *Ophioscolex* and *Ophiolycus* spp. lack IPas, BScs, and flabelliform teeth. Aside from teeth and TPas, their OPas *s.l.* are borne on the OPR rather than on the ventrolateral edge of the OP like the LOPas of Ophiacanthida. The first-formed OPa *s.l.* of *Ophioscolex glacialis* Müller and Troschel, 1842 (1.7 mm dd), and *Ophiolycus purpureus* Düben and Koren, 1846 (0.9 mm dd), were a 1°T, a TPas on the DP, and an AdShSp. The AdShSp was retained in adult *O. glacialis*, but lost during the ontogenesis of *O. purpureus* (Lyman, 1882:pl. 42, fig. 3; Stöhr, 2005:fig. 3C, E, G; Martynov, 2010b:fig. 73B, E). Small specimens of *Ophioscolex corynetes* (H.L. Clark, 1911; [LACM 85-353.1, LACM E.1941-205.4]) had AdShSps, but those few AdShSps remaining in large individuals were very small. Interestingly, the base of this species' AdShSp was enlarged like that of a typical ASp, but the ArtS of the spine of the AdSh was rudimentary, appearing to lack the characteristic articular lobes, fossa, and canal that occur on a LAP (Wilkie, 2016).

A spiniform OPa *s.l.* was present on the lateral edge of the OP in juvenile *O. glacialis* (3.0 mm dd) and *O. purpureus* (0.9 mm dd), and several similar spines occur in the adult. This ossicle is not an IPa or BSc, since it is spiniform and develops distal to the apex of the OP (see Mortensen, 1927:fig. 95; Mortensen, 1933a:fig. 4; Stöhr, 2005:figs. 2–3; Martynov, 2010b:fig. 73B). In the adult, these spines either occupy the OPR or sit above the vTCt. In this respect, the configuration of the jaws of Ophioscolecida, Asteronychidae, and Ophiurina are similar, since OT-2 is situated beneath a series of OPas *s.l.* that appear to obstruct its entry into the OSl when the jaws are closed. Furthermore, adult *Ophioscolex glacialis* and *O. corynetes* have a slender ossicle on either side of VAP-1, which is attached to the OPR and seems to be a CtP [*O. glacialis* LACM E.1928-4.1, LACM 1978-265.7; *O. corynetes* LACM E.1941-205.4, LACM E.1977-204.3]. It appears that Lyman (1882:pl. 42, fig. 47) depicted these ossicles as spinous processes of the VAP-1 of *O. glacialis*, but they are not noticeable in photomicrographs of juvenile or adult *O. glacialis* (Stöhr, 2005:fig. 2), and their ontogenesis is enigmatic. When the jaws of *O. corynetes* are closed, these ossicles on the OPRs abut and enclose a slot at the distal edge of the OSl.

Diet, Feeding, and Operation of the Jaws

Ophiomyxa flaccida can loop its arms around large items of food, and sponge, algae, and detritus were found in its stomach contents (Hendler et al., 1995). *Ophiomyxa serpentaria* and *Ophiomyxa brevirima* H.L. Clark, 1915a, are considered to be carnivores because small ophiuroids, amphipods, decapod crustaceans, and benthic material, sponge spicules, and foraminiferans occur in their stomach contents (Mortensen, 1933a; Pentreath, 1970). The latter species employed its arms to push food into the gaping buccal cavity, where items were “grasped by the teeth, which are serrated, as are the oral papillae, and then passed into the mouth by the buccal podia” (Pentreath, 1970:418–419). *Ophiarachna incrassata* (Lamarck, 1816a), a strikingly large ophiomyxid, traps small fishes between its intertwined arms, and individuals “swallow their prey whole” (Morin, 1988:404). It also entraps invertebrates such as active decapods beneath the disk and arms, and it uses the arms to position prey in its buccal cavity. Individuals apply the OTs to gradually push large items upward into the stomach, periodically closing their jaws to secure the prey (based on video of feeding behavior provided by Gerritt Meinen).

Buccal Morphology

Although *Ophiomyxa flaccida* examined in the present study had teeth capped with imperforate stereom, the teeth of *Ophiomyxa vivipara* were described as “completely fenestrated.” Nevertheless, there is a consensus that in both species “the [tooth's] distal stereom microstructure is quite different from that found proximally” (Figs. 14A–C, 15B; Medeiros-Bergen, 1996:215, fig. 1; Brogger et al., 2015:357, fig.2A). Hence, it appears that *Ophiomyxa* spp. are macrophagous feeders that have specialized, resistant teeth. This interpretation is at odds with the hypothesis that “all ophiuroids classified as macrophagous possess uniform (i.e., fenestrated) teeth,” whereas microphagous feeders “grind” food between teeth capped with resistant, imperforate stereom (Medeiros-Bergen, 1996:218). Nevertheless, reinforced and imperforate stereom could safeguard the teeth of ophiomyxids feeding on armored prey. That said, it should be noted that *Ophiomyxa vivipara*, *O. pentagona*, and *O. flaccida* have OPRSps that might serve to restrain prey, but in the latter species the OPRSp is not composed of imperforate stereom (Fig. 14B, C; Bartsch, 1982:fig. 17; Martynov, 2010b:fig. 1P). The tube feet of adult ophiomyxids may be protected from abrasive food items by a “fleshy barrel surrounding the podia stem” that is supported by “sheath plates” or so-called “tentacle scales,” which do not articulate on the LAP like typical TScs (Fig. 14A; Mortensen, 1933a:fig. 3; Pentreath, 1970:419, fig. 28; Byrne, 1994:296, fig. 34B; Stöhr, 2004:101, fig. 4F). The homology of “sheath plates” with TScs is problematic, and it is not known if they develop on the tube foot, or arise on the LAP and detach during ontogenesis. Although OTs of *Ophiomyxa brevirima* reportedly lack a “surrounding barrel of the arm podium” (Pentreath, 1970:420), it is possible that they may occupy a tube of CoOss similarly to OTs of *O. flaccida* (Fig. 14B, C).

Ophiacantha bidentata (Bruzelius, 1805)
Fig. 16

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in Ophiacanthidae species (described below). Teeth and OPas *s.l.* are composed of labyrinthic stereom (Fig. 16A, B, I). OPas *s.l.* on the ventrolateral edge of the OP of *O. bidentata* usually comprise an apical IPa, LOPa, and an AdShSp that overlaps the orifice of the vTCt. The IPa and LOPa are tapered and elliptical, and the AdShSp is spatulate and has a concave ventral surface (Fig. 16A, B, J). These OPas *s.l.* have a concave ArtS composed of sparsely perforate stereom, and each one attaches to a convex ArtS on the OP, which is distal to a small fossa (Fig. 16J). VAP-1 abuts vCtPs within the OSl and adjoins the AdShs (Fig. 16A, B, D, E). The oral frame is unified by connections of these plates with one another and with the LAPs-2, OShs, and conjoined OPs (Fig. 16A, B, G). When the jaws are closed, teeth and OPas *s.l.* intermesh with their counterparts on adjacent jaws, although gaps remained between these intercalating ossicles in the preserved specimens examined in the present study ([LACM 1978-263.1]; Martynov and Litvinova, 2008:fig. 8I, Martynov, 2010b:fig.2P, O).

The orifice and a cavity on the dorsal side of the madreporites of *O. bidentata* and *Astrobrachion constrictum* probably house the ampulla vesicle and part of the axial complex (Fig. 16G; Stewart, 2000:figs. 3B, 5C). The convoluted orifice may enclose what Hamann (1889:265) described a spiral whorl ("spiralige Windung") in the stone canal as it passes into the madreporite of *Ophiura albida* Forbes, 1839 [=*Ophioglypha albida*], and the cavity may hold the vesicle that was described to unite with the pore canal inside the madreporite (Ferguson, 1995; Ezhova et al., 2015, 2016).

PROXIMAL ASPECT. Teeth are aligned in a column, separated from one another by narrow gaps, and some are set obliquely to the vertical axis of the DP (Fig. 16B, D, E). They are dorsoventrally compressed, with a beveled proximal edge composed of compact stereom that has pores considerably smaller than the stereom at the base of the tooth (Fig. 16B, I). Teeth are of similar length to one another, except for the long, tapered dorsalmost tooth (Fig. 16A, B). The IPa and LOPa project at an oblique angle from the lateral edge of the OP, and the AdShSp projects horizontally. DP is a single ossicle. Orifices of the dTCt and vTCt appear to be of approximately equal size, and the dorsal and ventral CtPs may be nearly mirror images of one another (Fig. 16B, D, E).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP, AdShSp, and vCtP; vCtOs also may be present (Figs. 16B, D–F). A blunt, tapering lobe of the vCtP is attached to the OPR, and a larger ventral lobe abuts VAP-1 but does not contact the AdSh or AdShSp (Fig.16C–E). The vCtP of *O. bidentata*, which is visible within the OSl (Fig. 16A), was identified by Verrill (1899b:322) as "a vertical process…not moveable" beside VAP-1 of this species. Ventral CtOss are usually lacking but occasionally occur (compare: Fig. 16B, D *versus* E).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, a dCtP, and a flared, dorsally tapering FP that arches between the dCtP and the OP (Fig. 16B, D–G). There may be 1–2 dCtOss beside the dCtP. The base of the dCtP overlaps the OPR, and the dorsal lobe of the plate is set at right angles to the FP (Fig.16F, G).

PERRADIAL ARMATURE. The long, tapering proximal lobe of VAP-1 covers the ventral portion of the PG and may project dorsally beyond the OPR (Fig. 16B, D, E). The dorsal portion of the PG is covered by abutting pairs of FPs and a sheath of integument (Fig. 16B, D–F). LuOss were not observed, but may have been concealed in perradial integument. There are dual water ring foramina above the adradial and abradial muscle fossae of each OP. Only the adradial foramen is visible in dorsal aspect, and only the abradial foramen is evident on the flank of the OP (Fig. 16F, G; Martynov, 2010b:fig. 2S, T). A channel between the foramina was demonstrated by inserting an eyelash through the channel connecting them (Fig.16F, G). This channel is traversed by the water ring that presumably sends out bifurcating canals within the OP, which terminate in OT-1 and OT-2. A single PP, which bridges the dorsal surface of each jaw, superficially appears to have a characteristically compressed morphology (Fig. 16E, G). However, it possesses a remarkable ventrally projecting peduncle that protrudes between the nerve ring and the abradial muscle of the jaw, penetrating the medial gap between the OPs (Fig. 16F, H). The proximal rim of the PP overlies the dorsal nerve groove of the OPs and likely shields the nerve ring. Nervous, hemal, or perihemal tissue might traverse the enclosed channel running beneath the rim, near the apex of the PP. However, the functions of the peduncle and channel are uncertain (Fig. 16H). PPs were not previously reported to have these structures, and it is not known whether they occur in other species.

Variable numbers of supernumerary OPas *s.l.* were found in specimens of *O. bidentata* from off the coast of Oregon (Fig. 16C), and were previously documented in Icelandic specimens by Koehler (1914a:81, pl. 8, figs. 3, 4). In addition, Koehler (1914a) and Martynov (2010:fig. 2P) described and illustrated specimens with "supplementary tooth papillae…near the terminal tooth papillae." However, a supplemental dorsalmost tooth was observed in one specimen dissected in the present study (Fig. 16D).

Although authorship of *O. bidentata* is usually attributed to Retzius, it is correctly ascribed to Bruzelius according to Mortensen (1925a).

Ontogenesis and Skeletal Homologies of Ophiacanthida

In the smallest (3.0 mm dd) juvenile *Ophicantha bidentata* examined, an IPa projects from the OP and overlaps the DP, and an AdShSp protrudes below OTPo-2, near the midpoint of the AdSh (Sumida et al., 1998:fig 3D). The other OPa *s.l.* on the OP is tentatively inferred to be a LOPa on account of its greater proximity to the IPa than to the AdShSp in this juvenile and in adult *O. bidentata*, and because it differs in shape from the AdShSp (Fig. 16A; Sumida et al., 1998:fig. 3D). However, this hypothesis should be evaluated by examining a comprehensive growth series of this species. According to Sumida et al. (1998:274) "ventral development" of juvenile *O. bidentata* is "very similar to that of *O. abyssicola*." These authors observed a tooth and an AdShSp in the smallest (0.4 mm dd) available juvenile of *Ophiacantha abyssicola* G.O. Sars, 1872 (Sumida et al., 1998:fig. 2B), and stated that a 0.66-mm-dd juvenile (not illustrated) has a spiniform papilla, which I infer is an IPa on the basis of its shape and location "near the base of the DP" (Sumida et al., 1998:273, fig. 2B). In a 2.0-mm-dd individual the AdShSp was on the OP, and an additional papilla that is equidistant between the IPa and AdShSp might either be a LOPa or a 2°AdShSp (Sumida et al., 1998:fig. 2D). The "thorny" AdShSp of juvenile (<1 mm dd) *Ophiacantha rhachophora* H.L. Clark, 1911, is at least partially shifted to the OP during ontogenesis, but a similarly "thorny" AdShSp remains permanently on the AdSh in *Ophiacantha kokusai* Martynov et al., 2015, and the adult of *O. kokusai* appears to have an IPa, 1–3 LOPas, 0–1 2°AdShSs, and an AdShSp (Martynov et al., 2015:figs. 1B, F, 22C–F).

Ontogenesis of the buccal armature of ophiacanthids such as *O. bidentata*, which appear to have an IPa, LOPa, and AdShSp, differs in some respects from the pattern in species of other families of Ophiacanthina. Juvenile (0.7-mm-dd) *Ophiocomina nigra* (Ophiacanthina: Ophiotomidae) have 1–2 TPas below the vT, in addition to IPas near the DP/OP juncture and an AdShSp on the AdSh (Stöhr, 2005:fig. 17C, E). A 0.9-mm-dd juvenile has what appears to be a LOPa behind the IPa, and a 1.6-mm-dd individual has a 2°AdShSp abutting the AdShSp (Stöhr, 2005:fig. 17E, I). The order in which OPas *s.l.* developed seems to vary between jaws of an individual and among juvenile individuals of *O. nigra* (1.4–3.2 mm dd) that were examined in the present study [LACM 86-400.1]. Smaller individuals had a TPa, IPa, and AdShSp, and larger individuals had a presumptive LOPa and a 2°AdShSp. In an adult *O. nigra* [LACM E.887], groups of TPas on the DP formed a medial column of small, spiniform ossicles flanked on either side by a column of longer, compressed ossicles.

Ophiolimna bairdi (Lyman, 1883) was suggested to be a member of "a divergent lineage within the Ophiacanthidae possibly deserving of subfamily status" (O'Hara et al., 2017:426). Its 1.0-mm-dd juvenile stage has an unambiguous IPa and AdShSp and was described as having "a wide low BSc" that is replaced by a "a single conical mouth papilla" in a 1.6-mm-dd juvenile (Stöhr, 2005:552, compare: fig. 5D, G). However, a BSc was not clearly figured and the manner in which it might have been replaced was not described. Nevertheless, the 1.6-mm-dd juvenile appears to have an IPa and a LOPa on the OP and an AdShSp and 2°AdShSp on the AdSh, and adults appear to have an additional LOPa (Martynov, 2010b:fig 81B; [LACM E.1967-116.1, LACM 1991-235.5, LACM E.1964-296.1, LACM E.1962-283.1]). Thus, *O. bairdi* lacks the TPas that develop in *O. nigra*, but the configuration and ontogenesis of its buccal armature are comparable to *Ophiacantha* species such as *O. rhachophora*.

Ophiolamina eprae Stöhr and Segonzac, 2006, which is classified among Ophiacanthida *incertae sedis* (*sensu* O'Hara et al., 2017, 2018), has peculiar OPas *s.l.* and a problematic mode of ontogenesis. A juvenile of 0.7 mm dd was described as having an AdShSp on the AdSh and a putative BSc near the DP/OP juncture. A 0.8-mm-dd individual has an additional papilla near the DP/OP juncture, which may be an IPa. A 1.0-mm-dd juvenile has a 2°AdShSp on the AdSh and proximal to the AdShSp, and a newly formed TPa is present on the DP of a 1.4-mm-dd juvenile. However, I am not able to infer homologies of OPas *s.l.* on the OP of adult *O. eprae*, on the basis of published photographs, and it does not appear that one of the OPas *s.l.* "forms by division of the buccal scale" as was suggested to occur (*contra* Stöhr and Segonzac, 2006:26, 28, figs. 7B, D, F, H, 8B, C). The holotype was described as having "five lateral mouth papillae." However, a sixth papilla appears to be present, which might be an auxiliary 2°AdShSp (Stöhr and Segonzac, 2006:22, fig. 6E). The "proximal three mouth papillae" with a "blade-like shape and a vertical orientation" were stated to be "unique for this species among all ophiuroids" but somewhat resemble the compressed, proximal OPas of *Ophioderma rubicunda*, which also are vertically oriented (Fig. 11B–D).

Diet, Feeding, and Operation of the Jaws

Surprisingly little is known regarding the feeding behavior and diet of the prolific, diverse, and predominantly deep-water species of *Ophiacantha*, although available evidence indicates their feeding habits are diverse and flexible. It was conjectured that *Ophiacantha* spp. "fall on the borderline between the carnivorous and microphagous groups of ophiuroids" (Warner, 1982:170). *Ophiacantha pentactis* Mortensen, 1936, *Ophiolimna antarctica* (Lyman, 1879) [=*Ophiacantha antarctica*], and *Ophiacantha fraterna* Verrill, 1885 [=*Ophiacantha bidentata*], were described as epizoic suspension feeders that spread their arms to collect planktonic crustaceans, diatoms, foraminiferans, radiolarians, and resuspended benthic material, and to opportunistically collect benthic material (Dearborn, 1977; Pearson and Gage, 1984; Martynov and Litvinova, 2008). Copepods were "the principal food" of *Ophiacantha pentactis*. However, *Ophiacantha bidentata* was thought to "switch from deposit-feeding to suspension-feeding, depending upon resource availability," and the species' stomach contents consisted of pieces of amphipods, shrimp, nauplii, foraminifera, diatoms, plant material, detritus, and sand (Turpaeva, 1953; Litvinova, 1980; Dearborn, 1977:320; Gallagher et al., 1998; Brooks et al., 2007:308).

Buccal Morphology of Ophiacanthina

Ophiacantha bidentata lacks a buccal funnel, and the specimens studied herein had tube feet with a smooth shaft [LACM 1978-263.1]. These attributes indicate that it is not a microphagous suspension feeder. However, several families of Ophiacanthida, namely Ophiocomidae, Ophiotomidae, Ophiopteridae, and Clarkcomidae, include microphagous suspension-feeding species that have jaws with the same suite of features as occur in suspension-feeding Amphilepidida. They have buccal funnels that comprise clusters of TPas and columns of teeth that increase in length dorsally (Fig.11; see "Buccal Funnel" in the Discussion). Typically, these clusters are concave and comprise a medial column of TPas that are shorter and less stout than the column of TPas on either side. When their jaws close, the TPas and teeth surround a conical space that is centered between five spindle-shaped OSls. Some species of suspension-feeding Ophiacanthina are known to have tube feet with numerous glandular papillae that collect particles of food (Smith, 1937; Fontaine, 1964, 1965; Pentreath, 1970; Ball and Jangoux, 1990). They can also have OPs with well-developed abradial muscles and DPs that are penetrated by dental muscles.

Ophiopteris antipodum E. A. Smith, 1877 (Ophiopteridae), maintains its lowered arms at right angles to the current and accumulates particles that adhere to the arm spines. This material is compacted into a bolus by individual tube feet, and multiple boluses are relayed simultaneously along an ambulacrum between ipsilateral tube feet, rather than being carried proximally in coordinated waves of contralateral tube feet as in most other suspension feeders. When the OTs-2 of *O. antipodum* accept an incoming bolus, they "appear to scrape the bolus on to [sic] the tooth papillae…from where it is finally passed to the mouth by the first pair of buccal podia" (Pentreath, 1970:410, fig. 15). *Ophiopteris papillosa* collects particles of food on erect, mucus-coated arm spines and tube feet, which were "passed down the arms to the mouth by the tube feet." Individuals in aquaria can feed on "larger food items…in a manner similar to *Ophioderma panamense*" (Austin and Hadfield, 1980:153–154).

Ophiopteris papillosa [LACM E.1960-313.3] and *Ophiopteris antipodum* [LACM E.1964-298.1] have similar buccal funnels (Fig.11L; Devaney, 1970:fig. 7; Pentreath, 1970:fig. 15; Hendler, 2007:pl. 468, fig. A2). They have OPas *s.l.* on the ventrolateral edge of the OP and a large, elliptical cluster of TPas below each column of teeth, rather than "several columns of small papilliform teeth all over dental plate, no regular teeth" (*contra* O'Hara, et al., 2018:13). The TPas are regularly arrayed, and they are more densely crowded in *O. antipodum* than *O. papillosa*. Each cluster is concave, because the small, spiniform medial TPas are flanked by larger, blunt TPas that increase in length dorsally. The teeth are compressed and elliptical in cross section with a convex tip. Ventralmost teeth are slightly longer than the dorsalmost TPas, and the teeth modestly increase in length and narrow dorsally. Although TPas and teeth are not capped with imperforate calcite, stereom at the proximal edge is compact in specimens examined herein (see Medeiros-Bergen, 1996:fig. 2d). When the jaws are closed, lateral TPas and teeth intermesh with their counterparts on adjacent jaws. They form a funnel that has an orifice that is framed by the TPas, and which is constricted between the dorsal teeth. Small notches in the ventral edge of the funnel separate adjacent clusters of TPas. The OP of *O. papillosa* has a moderately well-developed abradial muscle fossa, and well-developed dental muscles that position the dorsal teeth, which penetrate foramina in the DP and attach to the OP (Wilkie, 1980:fig. 1B).

Ophiocomina nigra (Abildgaard in O.F. Müller, 1789) (Ophiotomidae) spreads and lifts its arms to suspension feed, and uses its papillose tube feet to collect material adhering on the arm spines. Groups of tube feet amalgamate particles in mucus and augment the bolus as they relay it toward the mouth. "Nearing the mouth, these pellets are about 2–3 mm in diameter and consist of greenish brown masses of organic detritus, planktonic algae and minute zooplankton organisms cemented together by mucus. . .Each bolus is held by the oral tube-feet for a few seconds and then passed into the mouth" or rejected. This species also employs tube feet or the entire arm to convey large food items to the mouth (Fontaine, 1965:377–378; Ball and Jangoux, 1990). The buccal funnels of *O. nigra* and *Ophiopteris* spp. are similar, although the clustered TPas of *O. nigra* are less evenly spaced. Its lateral columns of TPas are more blunt, and thicker and longer than the spiniform medial TPas. TPas increase in length dorsally, and the dorsalmost are almost as long as the vT. The teeth are compressed, with a convex proximal edge. They increase somewhat in length proceeding dorsally, and they narrow dorsally more noticeably than those of *Ophiopteris* (Fig. 11M; Koehler, 1922a:pl. 75, figs.1–6; [LACM 2007-125.2, LACM 86-401.1]). TPas and teeth of *O. nigra*, which were examined with a stereomicroscope, did not have a noticeable cap of imperforate stereom (Medeiros-Bergen, 1996; [E.887, 86-401.1, 2007-125.2]). The OP has a moderate sized abradial muscle fossa, less prominent than that of *O. papillosa*, and its DP lacks perforate foramina (see Wilkie, 1980:fig. 1A, B; Martynov, 2010b:fig. 14I). The presence of a buccal funnel in *O. nigra* may be atypical among the ophiotomids. *Ophiomitra valida* Lyman, 1869, and also *Ophiotreta lineolata* (Lyman, 1883) that were examined lacked buccal funnels. Their teeth were all of similar length, and their compressed, spiniform TPas were not arranged in symmetrical, concave clusters.

Clarkcoma bollonsi and *Clarkcoma pulchra* (Clarkcomidae) have large clusters of TPas that increase in length dorsally and occupy nearly one-half of the DP (Fig. 11K; Devaney, 1970:figs. 1, 2). These clusters are each composed of a broad medial group of small, closely spaced TPas, which is flanked by narrow columns of larger TPas. Their teeth, which are compressed, blunt, and elliptical in cross section, gradually increase in length and decrease in width dorsally. The dorsalmost TPas are markedly shorter than the ventralmost teeth. The teeth are capped with imperforate stereom, but TPas are not. When the jaws are closed, lateral TPas and teeth intermesh with their counterparts on adjacent jaws, and the TPas circumscribe a shallow buccal funnel that is abruptly constricted by ventral teeth. *Clarkcoma* spp. have wing-shaped OPs, well-developed, ear-shaped abradial muscle fossae, and well-developed dental muscles that penetrate foramina in the DP and insert on the OP (Devaney, 1970:figs.4, 5, 8, 14; Rowe, 1985). Neither feeding behavior of *Clarkcoma* species nor the morphology of their tube feet has been investigated (*C. bollonsi* [LACM E 1951-79.1]; *C. pulchra* (H.L. Clark, 1928) [LACM E.1972-450.1]).

Ophiacantha bidentata was found to have OPs with dual water ring foramina that are traversed by the water ring. Within each OP, a bifurcate branch of the water ring gives rise to the OTs (Fig. 16F, G). Previously published figures of this species revealed only one foramen above the abradial muscle fossa (Martynov, 2010b:fig. 2S, T; Stöhr et al., 2012a:fig. 5D). OPas *s.l.* on the OP of *O. bidentata* occupy ArtSs that are adjacent to minute fossae, and this morphology is similar to that figured in other Ophiacanthina such as *Ophiophthalmus normani*, *Ophiolimna bairdi*, and *Ophioplinthaca rudis* (Koehler, 1897) (Fig. 17C; Martynov, 2010b:fig. 82D; Okanishi, 2017:fig. 25.1g).

Ophiophthalmus normani (Lyman, 1879)
Fig. 17

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *Ophiacantha bidentata* and *Ophiophthalmus normani* (described below). Teeth and OPas *s.l.* are composed of labyrinthic stereom (Fig. 17A, B). An IPa at the apex of the OP, which projects beneath the DP, is bluntly pointed, dorsoventrally compressed, and aligned with the ventral plane of the jaw. Distal to the IPa there is a laterally compressed 2°AdShSp and an AdShSp, and some individuals have 1–2 supernumerary OPas *s.l.* The OPas project obliquely from the ventrolateral edge of the OP, and each one has a concave ArtS that adjoins a convex ArtS on the OP, the adjoining ArtSs are composed of sparsely perforate stereom (Fig. 17A, C). There is a small fossa in the OP proximal to each ArtS, and a small fossa is present near the base of the OPa *s.l.*, indicating that the fossae enclose muscular, neural, or connective tissue spanning the OPa and OP (Fig. 17A, C). The vCtPs, and up to several vCtOss, are visible within the OSl (Fig. 17A). The latter ossicles are embedded in integument surrounding the orifice of the vTCt, and they may be isolated or abut the vCtP, AdSh or VAP-1. VAP-1 adjoins the flanking vCtPs, AdShs, and LAPs-2 (Fig. 17A, D, G, J). The oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs (Fig. 17A). When the jaws are closed, the teeth and OPas *s.l.* intermesh with their counterparts on adjacent jaws, but gaps remained between the OPas *s.l.* in OSls of the specimens that were examined [LACM 1965-139.2].

PROXIMAL ASPECT. Teeth are aligned in a column. They are separated from one another by substantial gaps and are positioned obliquely to the vertical axis of the DP (Fig. 17B, C). Dorsal teeth are only slightly larger than the ventral teeth. They are dorsoventrally compressed, with a beveled proximal edge. The edge is composed of compact stereom that has pores that are considerably smaller than those at the base of the tooth (Fig. 17B, C). The DP can comprise multiple elements, and a DP examined in the present study was composed of three pieces, separated from one another by a jagged, slender fissure that bisected a dental foramen (Fig. 17E; Murakami, 1963:pl.1, fig. 20). Another DP had a hairline fissure that was just above the ventralmost dental foramen (Fig. 17C). Orifices of the vTCts and dTCts are fairly similar in size (Fig. 17B, G, J). Dorsal and ventral CtPs abut at the horizontal midline of the OPR (Fig. 17B, G, J).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP, AdSh, and VAP-1, a thick, curved vCtP and vCtOss that are embedded in the integument covering the vTCt and the base of OT-2 (Fig. 17A, B, D). The long, narrow proximal lobe of VAP-1 terminates beside the OPR (Fig. 17G). Ventral and dorsal lobes of the vCtP are nearly perpendicular to one another. The ventral lobe abuts VAP-1 and angles abradially toward the OT-2, but it is separated by a sizeable gap from the AdSh and AdShSp (Fig. 17A, B, D). A branch of the radial nerve cord that innervates OT-2 may enter the tentacle basin via a notch in the OPR, immediately above the vTCt (Fig. 17D).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, a bar-shaped dCtP, and a T-shaped FP composed of a dorsal column and diverging arms (Fig. 17B, G-L). FPs on adjacent jaws abut one another, as do the adjacent dCtPs, and both these pairs of opposing plates, and integument in which they are embedded, cover the PG. Several microscopic LuOss were found embedded in integument near the dTCt and FP of one dissected specimen. A small, perradial ossicle that is composed of delicate, spinose stereom, connects and supports the short, adradial arms of adjoining FPs (Fig. 17G–L).The vertical column of the FP abuts the dCtP, broadens dorsally, and gives rise to the adradial arm as well as a tapering abradial arm that extends toward a protuberance on the OP. A short gap between the abradial arm and OP is spanned by a slender supplementary ossicle (Fig. 17I, L).

PERRADIAL ARMATURE. The narrow proximal lobe of VAP-1 nearly covers the ventral portion of the PG, and the dorsal portion of the gap is closed by the dCtPs and FPs of adjacent jaws (Fig. 17B, G, J). A sheath of integument envelops the VAP-1, FPs, dCtPs, and OPs and closes the gaps between these ossicles. An abradial water ring foramen was previously figured by Murakami (1963: pl.4, figs. 15–16). However, dual water ring foramina penetrate each OP. A channel between these was demonstrated by passing an eyelash through foramina above the adradial and adradial muscle fossae (Fig. 17F). The water ring traverses this channel, and emits a bifurcating branch within the OP, which gives rise to OT-1 and OT-2 (Fig. 17F, J).

Skeletal Ontogenesis and Homologies of Oral Armature

Several dried juvenile specimens of *Ophiophthalmus normani* were examined with a stereomicroscope [LACM E.1976-257.2, LACM E.1977-286.2]. A 0.9-mm-dd individual had two teeth, an IPa at the DP/OP juncture, and an acutely pointed AdShSp on the distal end of the AdSh. Two specimens <2.5 mm dd (=approximate size of distended disks) had three teeth, an IPa at the DP/OP juncture, an AdShSp on the AdSh, and a shorter, more slender papilla on the OP, abutting the AdShSp. A dCtP and vCtP were present, and VAP-1 adjoined the OPR of these juveniles. LuOss had formed in a 3.4-mm-dd individual, and a vCtOs had formed on the vCtP of a 4.4-mm-dd individual. Its vCtOs was embedded in a collar of integument enclosing the vTCt and barely in contact with VAP-1, but it did not abut the AdSh.

I surmise that the OPa *s.l.* between the IPa and AdShSp is a 2°AdShSp, on account of its proximity to the AdSh and AdShSp. The same configuration of OPas *s.l.* was illustrated in a 2-mm-dd specimen examined with SEM (Martynov et al., 2015:fig. 23F). In a 3.4-mm-dd specimen examined herein, the DP, IPa, 2°AdShSp, and AdShSp were separated from one another. At this stage, as well as in a 7.1-mm-dd individual with four teeth, the vCtP, dCtP, and FP were distinguishable, as were several conspicuous, irregularly shaped LuOss embedded in integument above VAP-1. The vCtP of the latter individual had a broad ventral edge that curved beneath OT-2 and was embedded in integument covering the vTCt.

Diet, Feeding, and Operation of the Jaws

Ophiophthalmus normani is a bathyal, epibenthic species that rapidly responds to experimental bait falls by forming aggregations that "covered tens of square meters and involved thousands of individuals" (Smith, 1985:429). It has been described as "a generalized scavenger," because it consumes carrion, gleans material in submerged parcels of kelp, and feeds on invertebrates including Euphausiacea, Porifera, and moribund scyphozoans (Shepard and Marshall, 1975; Litvinova, 1979; Smith, 1985:436).

Ophiolepis impressa Lütken, 1859
Fig. 18

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *Ophiolepis paucispina* (Say, 1825) (described below). Teeth and OPas *s.l.* are composed of labyrinthic stereom (Fig. 18A, B). A pair of IPas, on the apex of the OP, overlaps the DP and the sloping sides of the vT (Fig. 18A, B). On the ventrolateral edge of the OP there is a row of OPas *s.l.* comprising a BSc that overlaps the IPa, a 2°AdShSp, and a large, ovate AdShSp that tangentially overlaps the AdSh (Fig. 18A). The BSc and 2°AdShSp are borne on separate, small ArtSs composed of sparsely perforate stereom, which are alongside small fossae in the OP (Fig. 18C). The AdShSp is borne on an elongated ridge composed of sparsely perforated stereom (Fig. 18A). A conspicuous LyOs, which inserts between the AdSh and VAP-1, has a tapering, ventral flange that meets the AdShSp and a dorsal flange that abuts the vCtP (Fig. 18A, B, C). Microscopic striations on the ventral surface of LyOs, which are similar to striated ossicles found in *Ophioderma rubicunda* and *Ophiocoma echinata*, may support tracts of ciliated epithelium (Figs. 9B, 12E, 18B). Edges of LyOs, 2°AdShSp, and AdShSp conform in shape to one another. The AdShSp articulates with the OP and closes the vTCt by retracting against LyOs (Fig. 18A, B). The tapering, wedge-shaped, proximal lobe of VAP-1 juts steeply upward in the OSl and abuts the OPR (Fig. 18B-D). Beveled edges of VAP-1 are joined to the flanking LyOss, AdShs and LAPs-1, and the oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs (Fig. 18A, B).

PROXIMAL ASPECT. Teeth are aligned in a column, and separated from one another by substantial gaps (Fig. 18B, D). They are dorsoventrally compressed and wedge shaped, except for the lanceolate, dorsalmost tooth (Fig. 18D). The beveled proximal edge of each tooth is composed of compact stereom that has considerably smaller pores than stereom at the base of the tooth (Fig. 18B, D). DP is a single ossicle. The IPas overlap the sloping sides of the vT, forming a tight triad of ossicles at the apex of the jaw (Fig. 18A, B). The IPa, BSc, and 2°AdShSp are attached at an oblique angle to the ventrolateral edge of the OP. They are close together and their shapes conform to one another (Fig. 18A, B). The orifice of the vTCt is ventrally and abradially directed, and appears to be somewhat smaller than the dorsally and abradially directed orifice of the dTCt (Fig. 18B). The DP and proximal edge of the OP protrude above the dTCt to a greater extent than below the vTCt. Preserved specimens of *Ophiolepis impressa* examined in the present study had jaws that were agape, but some specimens of congeners had closed jaws with intermeshed teeth and OPas *s.l.* that sealed the OSl (e.g., *Ophiolepis superba* H.L. Clark, 1915b [LACM E.1948-98.2] and *Ophiolepis crassa* Nielsen, 1932 [LACM E.1940-23.16]).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP, LyOs, vCtP, a narrow panel of several squamous, tesselate CtOss, and an opercular AdShSp (Fig. 18C–E). The vCtP is lamelliform and slightly arched, and it extends from the OPR to LyOs and the VAP-1. The panel of CtOss may extend between the vCtP and LyOs (Fig. 18E).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, and up to several flat, irregularly shaped dCtPs attached to the OPR, which support a semicylindical collar of imbricated CtOss encircling the base of the OT-1 (Fig. 18B, D, E). This collar was first described by Lyman (see "Buccal Morphology" in the treatment of *Ophioderma rubicunda*). A prominent FP, which arches between the dCtPs and the dorsal edge of the OP, is oriented nearly perpendicularly to the collar of CtOss (Fig. 18E).

PERRADIAL ARMATURE. The PG below the OPR is covered by the large proximal lobe of VAP-1, and much of the gap above the OPR is covered by the FPs on adjacent jaws and by integument in which they are imbedded (Fig. 18B, D, E). LuOss appear to be lacking. I observed a single water ring foramen on the dorsal surface of the OP, distal to the PP.

Skeletal Ontogenesis and Homologies of Oral Armature

A growth series of brooded and free-living juveniles of *Ophiolepis paucispina* was studied, because specimens of juvenile *Ophiolepis impressa* were not available. The earliest stage examined, a 0.7-mm-dd juvenile, had at least one tooth on the DP, an IPa extending from the apex of the OP onto the DP, and an elongated BSc on the OPR, which reached from VAP-1 to the IPa (Fig. 19A, B). A broad, blunt AdShSp, which overlapped OTPo-2, resembled the tentacle scale on LAP-2. It occupied a densely calcified ArtS on the AdSh. At this and later growth stages, OSls were covered by intermeshing teeth and the abutting OPas *s.l.* on adjacent jaws (Fig. 19A–H). In a 1.5-mm-dd juvenile, the rudiment of a 2°AdShSp had developed proximally to the ovate AdShSp (Fig. 19C, D). In a 1.72-mm-dd individual, the BSc, as well as the IPa, articulated with the edge of the OP instead of the OPR, and the 2°AdShSp overlapped the BSc and vCtP. The AdShSp, now at the distal end of an enlarged OSl, overlapped an emergent LyOs that abutted the AdSh, VAP-1, and vCtP (Fig. 19E, F). At this stage, the AdSh had grown beneath the VAP-1. VAP-1, which had previously been level with the AdSh, was partially engulfed within the OSl, which had expanded due to growth of the OP and the rest of the jaw (compare: Fig. 19D, F). In a 4.4-mm adult, further enlargement of the OP and AdSh had augmented the OSl and expanded the distal end of the jaw, and the LyOs, AdShSp, 2°AdShSp, BSc, and IPa formed a serried row on a level with ventral edge of the jaw (Fig. 19G, H).

Ophiolepis impressa and *Ophiozonella novaecaledoniae* Vadon, 1990, are Ophiolepididae and Hemieuryalidae, respectively, yet they have homologous OPas *s.l.* (i.e., IPa, BSc, 2°AdShSp, AdShSp, and LyOs) that develop in an identical ontogenetic sequence. This similarity between the species may be a plesiomorphic feature of the superfamily Ophiolepidoidea, as noted below in the treatment of *Sigsbeia murrhina* Lyman, 1878a.

Diet, Feeding, and Operation of the Jaws

Ophiolepis impressa is a deposit feeder that lives in sandy habitats, under slabs of coral rubble. Its stomach contents consist of algae, scavenged feces, and mucus-bound sediment (Sides, 1985; Hendler et al., 1995). *Ophiolepis elegans* Lütken, 1859, which occupies comparatively deep, sandy habitats, also appears to be a scavenger that consumes small invertebrates, since its stomach contents comprise shell fragments, dead coralline algae, organic detritus, and occasional small mollusks, crustaceans, and the remains of polychaetes (Stancyk, 1970).

Buccal Morphology

Eozonella bergeri Thuy et al., 2013, a Late Jurassic ophiolepidid, appears to have a prominent, tapering LyOs (vCtP?) that was described as a "distalmost papilla pointed, slightly curved, sitting on border between the adoral shield and the first ventral arm plate." This presumptive LyOs and an operculate AdShSp resemble equivalent structures in *Ophiolepis impressa*. But this interpretation is speculative, because a vCtP is not distinctly discernible in the published figures of the fossils (Thuy et al., 2013:421, figs. 6b, 7b). Figures of *E. bergeri* show that its teeth on adjacent jaws intermesh, like those of confamilial *Ophiolepis superba* [LACM E.1948-98.2], *Ophiolepis crassa* [LACM E.1940-23.16], and *O. impressa* [LACM E.1969-416.1].

Sigsbeia murrhina Lyman, 1878a
Fig. 20

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *Sigsbeia conifera* Koehler, 1914a (described below). Teeth and OPas *s.l.* are composed of nearly uniform, labyrinthic stereom, although stereom pores are somewhat smaller at the proximal edge than at the base of the tooth (Fig. 20B, D). A pair of IPas, which are borne on the apex of the OP, overlap the DP and may abut the vT (Fig. 20A, B). Distal to the IPa, armature on the OP includes an ossicle of indeterminate homology, a dolabriform AdShSp, and a large LyOs that inserts between the AdSh and VAP-1 (Fig. 20A). One of six specimens examined had two indeterminate ossicles. Whether these represent a BSc, 2°AdShSp, or something else could not be established on the basis of the ontogenesis of OPas *s.l.* in *S. conifera*. The vT and the adjacent ossicles on the ventrolateral edge of the OP conform in shape to one another but are separated by slender gaps (Fig. 20A, C). The edge of LyOs overlaps the ventral edge of VAP-1 (Fig. 20A). The VAP-1 is joined to the flanking LyOss, AdShs, and LAPs-1, and the oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs (Fig. 20A). When the jaws are closed, the OPas *s.l.* on adjacent jaws abut and teeth intermesh, blocking the OSls (Lyman, 1882:pl. 43, fig. 4).

PROXIMAL ASPECT. Teeth are aligned in a column, on a DP that appears to be a single ossicle like that of *Hemieuryale pustulata* von Martens, 1867 (Gondim et al., 2015; fig. C). Teeth are bluntly pointed, with angular, tapered lateral edges. The edges of adjacent teeth are separated by wedge-shaped gaps, but the bases of adjacent teeth are nearly in contact (Fig. 20B, C, D). The OPas *s.l.* are stout, their adradial edges are bluntly beveled, and they overlap the ventrolateral rim of the OP (Fig. 20C, D). The dorsally directed orifice of the dTCt is smaller than the proximally directed orifice of the vTCt, and these compartments are separated by a massive OPR (Fig. 20C). In proximal view, it is evident that LyOs is a tall, lamelliform plate, and that its dorsal edge adjoins the OPR and may abut 1–2 small vCtPs (Fig. 20D–G). The tapering, wedge-shaped proximal lobe of VAP-1 slots into the OSl nearly to the OPR (Fig. 20A, C, G).

VENTRAL TENTACLE COMPARTMENT. Primarily composed of the flank of the OP and OPR and the prominent LyOs, in addition to a vCtP or vCtOs (Figs. 20C–G).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, and a small dCtP and/or dCtOs on the OPR, which are attached nearly at right angles to a short, stout FP that arches between the OPR and the dorsal surface of the OP (Fig. 20C, D, E).

PERRADIAL ARMATURE. The VAP-1 blocks the ventral portion of the PG, and the narrow dorsal segment of the gap is covered by integument and by LuOss lodged between the OPs and above the FP (Fig. 20C, D, E, G).

Skeletal Ontogenesis and Homologies of Oral Armature

A growth series of brooded and free-living juvenile stages of *Sigsbeia conifera* was examined, because juvenile *Sigsbeia murrhina* were not available for study. The brooded embryo resembled a vitellaria larva with a prominent pre-oral lobe, which had what appeared to be remnants of ciliary tracts that were damaged during preservation. It had primary disk plates, OPs, and TPs that were covered with integument, an OT-1, and a much smaller OT-2 and terminal tentacle (Fig. 21A, B). A brooded 0.7-mm-dd juvenile had a tooth on the DP, an IPa projecting from the OP and below the DP, and a blunt, spiniform AdShSp at the distal end of the AdSh. Teeth on adjacent jaws intermeshed, and IPas covered part of the OSl (Fig. 21D). An AdShSp beside the OTPo-2 of a 1.2-mm-dd individual occupied the midpoint of the AdSh, and at this stage the AdSh and VAP-1 had grown distally, beyond the AdShSp and the OTPo-2 (Fig. 21E). Typically, juveniles approximately 2 mm dd had developed OPas *s.l.* in contact with an IPa or with an AdShSp, or in an intermediate position on the OP (Fig. 21F, G). Although it is conceivable that these might be BSs or 2°AdShSs, their homology is indeterminate because the numbers of these ossicles, the order in which they develop, and their size, shape, and position varied on single jaws, among jaws of individuals, and between individuals (Fig. 21F). In larger individuals, the indeterminate OPas *s.l.* occupied the adradial edge of the jaw, and the IPa overgrew the DP and vT. Concurrently, the AdShSp enlarged, connected to the growing edge of the OP, and became detached from the AdSh. Additionally, a PeSk rudiment developed in the OSl beside VAP-1 (Fig. 21G), which subsequently protruded from the OSl in juveniles approximately 3–5 mm dd (Fig. 21H, I). It was inferred to be LyOs, because of its proximity to the AdSh and VAP-1, because it developed below the OPR and protruded from the OSl, and because its stereom had larger pores than the OPas *s.l.* In adult individuals the number and positions of the indeterminate OPas *s.l.* varied. Ultimately, the OPas *s.l.* grew large enough to occupy the entire edge of the jaw, and they attained to a larger size on jaws with fewer papillae (Fig. 21H, I).

It is striking that in juveniles ~2 mm dd the AdShs overtopped the distal corners of the enlarging VAP-1, thereby expanding the length and depth of the OSl such that it enclosed the proximal tip of VAP-1 (compare: Fig. 21E, F). In 3–5-mm-dd juveniles the distal edge of VAP-1 had overtopped LAP-2, and the proximal tip of VAP-1 was wedged in the OSl, which had deepened on account of ventral expansion of the OP and AdSh (compare: Fig. 21H, I). Thus, ontogenetic transformation of the jaw resulted from differential allometric growth of the OPs and associated ossicles, rather from independent movement of the OTPo-2 and AdShSp or "rotation" of VAP-1 into the mouth.

Ontogenesis and Skeletal Homologies of Hemieuryalidae and Ophiolepididae

Hemieuryalidae *sensu* O'Hara et al. (2017) incorporates several genera previously classified as ophiolepidids and comprises *Hemieuryale*, *Sigsbeia*, *Ophioplocus*, *Ophiozonoida*, and *Ophiozonella* species with 1–2 arm spines; *Actinozonella*; and four additional genera, whereas Ophiolepididae is limited to *Ophiolepis*, *Ophioteichus*, and *Ophiotypa*. Nevertheless, on the basis of the patterns of skeletal ontogenesis in *Ophiolepis paucispina*, which was described in the present study, and in *Ophiozonella novaecaledoniae*, a hemieuryalid which was described by Vadon (1990) and reinterpreted and rectified below, in addition to information on *Ophioplocus esmarki* Lyman, 1874, it is clear that Ophiolepidiae and Hemieuryalidae develop an IPa, a BSc, a 2°AdShSp, an operculate AdShSp, and a LyOs, which are aligned identically on the jaw and arise in a similar ontogenetic sequence in species of both families (Vadon, 1990; Hendler, 1988:335; Hendler, 2007:pl. 467, fig. A2; *O. esmarki* [LACM E.1954-14.16]).

The smallest individual of *O. novaecaledoniae* (0.80 mm dd) was stated to have a 1°T (="apical papilla"), BSc (="bar-like papilla"), and an AdShSp (="arm spine") (Vadon, 1990:173). An IPa was present at the 1.12-mm-dd stage, and a 2°AdShSp was present at the 1.35-mm-dd stage (compare: Fig. 19A, C; Vadon 1990:173, figs. 3, 9, 25). However, Vadon (1990) overlooked the 2°AdShSp of *O. novaecaledoniae*, and misinterpreted the 2°AdShSp and AdShSp, which overgrew and concealed the BSc in a 1.50-mm-dd individual, as an "oral bar [BSc]…divided in two parts" (compare: Fig. 19C, E, G; Vadon, 1990:174, figs. 8, 12, 25–27). Furthermore, an ossicle misidentified as "the remains of the second oral tentacle scale" (i.e., AdShSp) of a 1.50-mm-dd juvenile of *O. novaecaledoniae*, was actually a LyOs protruding from the OSl (compare: Fig. 19C, E, G; Vadon, 1990:172–173, figs. 12, 15, 21, 26, 27). Accordingly, OPas *s.l.* previously identified as an apical papilla, IPa, divided "bar-like papilla," and "remains of the second oral tentacle scale" of *O. novaecaledoniae*, were the vT, IPa, (BSc + 2°AdShSp + AdShSp), and LyOS, respectively.

It was thought that "Ontogenesis [of *O. novaecaledoniae*] involves migration of the second oral tentacle pore from a position outside the oral slit to a position within the slit" (Vadon, 1990:173). However, during development of *O. novaecaledoniae* and *Ophiolepis paucispina* the orifice of the vTCt remains at the juncture between the AdShSp and VAP-1. It is overtopped by growth of the OP, AdSh, and VAP-1, and thereby incorporated in the enlarging OSl.

The presence of an IPa, BSc, 2°AdShSp, and AdShSp in species of Ophionereidina described herein, which are *Ophiolepis paucispina*, *Ophiolepis impressa*, *Ophiozonella novaecaledoniae*, *Ophioplocus esmarki, Ophionereis olivacea* H.L. Clark, 1901, and *Amphilimna olivacea* (Lyman, 1869), suggests that homologues of these structures may have occurred in the common ancestor of Ophiolepidoidea (Ophiolepididae, Hemieuryalidae) and Ophionereidoidea (Amphilimnidae, Ophionereididae) (see phylogenetic tree of O'Hara et al., 2017:fig. S3). Although *Hemieuryale pustulata* appears to have an IPa, BSc, 2°AdShSp, and AdShSp, this typical pattern of ontogenesis is disrupted in *Sigsbeia conifera* and *S. murrhina*, which are closely related to *Hemieuryale.* These *Sigsbeia* species develop an IPa and AdShSp, but the number and shape of their other OPas *s.l.* is erratic, as is the sequence in which they develop (see Gondim et al., 2015:figs. 2, 3, 9; O'Hara et al., 2017:fig. S3). Another problematical hemieuryalid, *Ophiozonella falklandica* Mortensen 1936, had a ~1.1-mm-dd juvenile stage with a tooth and AdShSp, and the adult had three serried papillae on the jaw, which may be an IPa, a BSc, and an AdShSp. Mortensen (1936:303) concluded that the AdShSp (="tentacle scale at the first ventral plate") of the juvenile "disappeared in the adult," but his figures do not corroborate this interpretation or clarify homologies of the other OPas *s.l.*

Diet, Feeding, and Operation of the Jaws

Virtually nothing is known about the diet and feeding habits of epizoic Hemieuryalidae. Individuals of *Sigsbeia conifera* coil their arms around branches of hydrocoral (*Stylaster* spp.) during the day, unfurling some arms and extending the tube feet at night. They might capture waterborne items, or collect material that is entangled on the host or appropriate prey captured by the host, but their stomach contents have not been examined (Hendler et al., 1995).

The morphology and behavior of *Sigsbeia* spp. differ from *Ophioplocus januarii* (Lütken, 1856), an epibenthic hemieuryalid, which is a microphagous, passive suspension feeder and an "unselective omnivorous species" (Brogger et al., 2015:355, 357). Individuals of *O. januarii* "raised two or three arms into the passing currents. Small particles were trapped by the tube feet and collected into a bolus that was passed down along the arm to the mouth." Their stomach contents were primarily "macroalgal fragments, mainly from filamentous algae" most of which were less than 0.5 mm in size and unidentifiable material, in addition to "cuticular animal structures," and rarely small animals (Brogger et al., 2015:355). Interestingly, the tube feet of *O. januarii* bear numerous papillae, similarly to other suspension feeding species (Brogger, 2010:fig. 3.3C).

Buccal morphology of *Sigsbeia* and *O. januarii* are markedly different, because the latter species has a buccal funnel (Fig. 11I). Furthermore, *O. januarii* has specialized teeth and well-developed dental and jaw muscles similar to unrelated, suspension-feeding Ophintegrida. The jaws of *O. januarii* bear a small, triangular vT recessed between a pair of tall, tapering IPas. This triad of ossicles forms a concave structure on the apex of the jaw. Successive teeth immediately above the triad increase in width and height dorsally, and the broadest teeth each have a deeply concave proximal face and a beveled edge with a dorsomedial cusp that partially overlaps the tooth above (Thomas, 1975:fig. 1B; Bartsch, 1982:fig. 71; Brogger et al., 2015:fig. 1C, D; [LACM 87-290.1]). The upper dorsal teeth have truncate tips and are compressed and rhombic in cross section. They are longer than the broader, imbricate teeth, and they increase in length and decrease in width dorsally. When the jaws of *O. januarii* are closed, the concave triad, intermeshed ventral teeth, and intermeshed edges of longer dorsal teeth, circumscribe a gradually constricting, conical space (Fig. 11I). The teeth, when examined with a stereomicroscope, do not appear to be capped with imperforate stereom, but the edges of teeth are reinforced with "compacted" minutely perforate stereom (Medeiros-Bergen, 1996; Brogger at al., 2015:355). Also, the OP of *O. januarii* has a large abradial muscle fossa, and its moveable dorsal teeth have well-developed muscles that penetrate paired foramina in the DP and attach to the OP (Bartsch, 1982:figs.70–72). In comparison, *Ophioplocus imbricatus* (Müller and Troschel, 1842) and *Ophioplocus japonicus* H.L. Clark, 1911, which lack buccal funnels, have abradial muscle fossae of modest size and DPs with imperforate tooth fossae (Murakami, 1963: pl. 2, figs. 29–30; pl. 6, figs. 17-20l).

In contrast with *O. januarii*, *Ophioplocus esmarki* Lyman, 1874, captures "moribund or slow-moving small [benthic] animals" (Austin and Hadfield, 1980:152). It irrefutably lacks a buccal funnel, and its tube feet are not papillose (compare Fig. 11I and J; [LACM E.1954-14.6, LACM 2009-36.1]). The species' IPas project directly below a protuberant vT, and its teeth are compressed, elliptical in cross section, and have rounded tips. When the jaws are closed, the teeth intermesh and OPas *s.l.* on adjacent jaws abut, covering the OSls. Teeth of *O. esmarki* do not seem to be capped with imperfortate stereom when viewed with a stereomicroscope, but they have not been examined for compact stereom using SEM and neither have teeth of the following two species.

Ophiozonella longispina (H.L. Clark, 1908) has two arm spines and therefore is a hemieuryalid *sensu* O'Hara et al. (2017:427). Although considerably smaller than *O. januarii*, it too has an unequivocal buccal funnel, suggesting it is microphagous and perhaps is a passive suspension feeder or a benthic deposit feeder (Fig. 11H; [LACM 74-207.3]. Its concave, triangular vT is flanked by IPas that incline upward in the OSl. Its 1–2 short, relatively wide, concave ventral teeth bear, on their flanged proximal edge, a slight medial cusp that partially overlaps the base of the tooth above. The other teeth, which lengthen and narrow dorsally, are compressed and have a truncate tip with a medial point. When the jaws are closed and the teeth intermesh, ventral teeth circumscribe a shallow buccal funnel, dorsal teeth constrict the funnel, and opercular OPas *s.l.* on the edge of the jaw seal the OSl. *Ophiozonella oedilepis* (Murakami, 1942), which has four arm spines and therefore is an ophiolepidid *sensu* O'Hara et al. (2017:427), has a buccal funnel similar to *O. longispina* (Fig. 11G; [LACM 78-227.2]. Both these nominal *Ophiozonella* species have dental muscles that penetrate foramina in the DP and attach to the OP, and *O. longispina* has an abradial muscle fossa of moderate size (Murakami, 1963:pl. 2, figs. 24, 25; pl. 6, figs. 9–10).

The unanticipated presence of buccal funnels in Ophiolepididae and Hemieuryalidae raised the question as to how this complex feature evolved in these families. To clarify this issue, those species of Ophiolepidoidea, which were included in the phylogenetic analysis of O'Hara et al. (2017), were examined to map the phylogenetic distribution of buccal funnels. This survey was based on available museum specimens, previously published figures, and photographs provided by T. Pineda-Enríquez. The 17 species of Ophiolepididae in the tree appeared to lack buccal funnels, but a buccal funnel was found in specimens of *Ophiozonella oedilepis* (Fig. 11G) [LACM 78-227.2], a species that was not included in the phylogeny

Two clades of Hemieuryalidae were represented in the phylogeny of O'Hara et al. (2017), one of which consisted of *Actinozonella* spp. lacking a buccal funnels. The other clade comprised two lineages, one of which included *Ophioplocus januarii* and seven congeners, as well as *Sigsbeia conifera* and *Hemieuryale pustulata*. Among these nine species, only *O. januarii* had a buccal funnel. The other lineage included 12 species in the genera *Astrogymnotes*, *Ophioplocus*, *Ophiozonoida*, and *Ophiozonella*. Based on specimens of *Ophiozonella longispina* (Fig. 11H; [LACM 74-207.3]) and images of the other species, there appeared to be a buccal funnels in *O. longispina*, *Ophiozonella stellata* (Lyman, 1878b), *Ophioplocus declinans* (Koehler, 1904), and *Ophiozonoida obscura* Koehler, 1922a, all of which had a central, cylindrical opening between the closed jaws, a reduced vT flanked by large IPas, and columns of teeth that increased in length dorsally. Surprisingly, *O. obscura* appeared to have one pair of truncate TPas above the vT, and since TPas did not occur among other hemieuryalids that were examined, this observation should be substantiated by dissection. Thus, available evidence indicates that buccal funnels occur sporadically among different clades of Ophiolepidoidea, seemingly more frequently in Hemieuryalidae than in Ophiolepididae, and they may have evolved repeatedly in both families.

Buccal Morphology

An isolated OP of *Sigsbeia* spp. has not been figured in the literature. However, the OPs of confamilial *Hemieuryale pustulata* and *Actinozonella texturata* (Lyman, 1883) evidently have dual water ring foramina located above the abradial and adradial muscle fossae of the OP (Stöhr, 2011:fig. 20J, K; Gondim et al., 2015:fig. 5A, B). Both these species have very small abradial muscle fossae compared to *Ophioplocus januarii* [=*Ophioceramis januarii*], which has a single, dorsal water ring foramen. It also has a large muscle fossa on the adradial surface of the OP, which may preclude development of an adradial foramen (Bartsch, 1982:fig. 72; Lyman, 1882:pl. 37, fig. 16).

Postlarvae of benthic ophiuroids typically have a moveable AdShSp that may serve in locomotion, but an AdShSp does not develop in Euryalida and Ophiotrichidae, which are typically epizoic and use hooked arm spines to cling to a host (Hendler, 1988:28; present study). In contrast, the juvenile stage of *Sigsbeia conifera*, which is an obligate epizoic symbiont, has ASps with acute terminal spurs, as well as a short, tapered AdShSp that acquires an opercular shape in the adult (Fig. 21C, D). It appears that the ASps could be used to cling to the host and that the AdShSps are not locomotory, but too little is known about the biology of *Sigsbeia* to accurately infer the adaptive significance of these features.

Ophionereis porrecta Lyman, 1860
Fig. 22

VENTRAL ASPECT. Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *Ophionereis olivacea* (described below). Teeth and OPas *s.l.* are composed of labyrinthic stereom, and the teeth are capped with imperforate stereom (Fig. 22B, D, E). IPas are the smallest OPas *s.l.* on the OP, and they articulate on the ventral apex of the jaw, overlapping the DP and vT (Fig. 22A, B, D; Stöhr, 2011:fig. 16E, G). A row of OPas *s.l.* on the ventrolateral edge of the OP and distal to the IPa, comprises a BSc, a 2°AdShSp, and a markedly wider AdShSp (Fig. 22A). Adjoining edges of the laterally compressed IPa, BSc, and 2°AdShSp conform to one another in shape (Fig. 22A, B, F, H). OPas *s.l.* on the proximal, ventrolateral edge of the OP, are borne on separate ArtSs composed of sparsely perforate stereom, which are situated beside small fossae (see Stöhr, 2011:fig. 16J). Large, atypical individuals can have an additional 2°AdShSp, and one specimen examined in the present study had two 2°AdShSps and an undersized AdShSp on both sides of the jaw, in contrast to most specimens that have been illustrated (Lyman, 1865:fig. 15; Ely, 1942:fig. 13; Stöhr, 2011:fig. 16E; Okanishsi, 2017:fig. 25.). LyOs, which inserts at the juncture between the AdSh and VAP-1, has a tapering, ventral flange extending alongside the AdShSp, and an incurvate, dorsal flange that angles steeply upward within the OSl (Fig. 22B, D, H). VAP-1 adjoins the flanking LyOs, AdShs, and LAPs-1, and the oral frame is unified by connections of these plates with one another and with the OShs and conjoined OPs (Fig. 22A).

PROXIMAL ASPECT. Teeth are aligned in a column and increase in length dorsally. They are dorsoventrally compressed, tapering, truncate, and capped with imperforate stereom (Fig. 22B, D, E). The broad bases of the teeth are nearly in contact, but shafts of the teeth are somewhat rhombic or triangular in cross section, creating wedge-shaped gaps between adjacent teeth (Fig. 22C). DP is a single ossicle (Stöhr, 2011:fig. 16E, H). The IPa, BSc, and 2°AdShSp are laterally compressed and project at an oblique angle to the ventrolateral edge of the OP, and the edges of adjacent OPas *s.l.* are separated by slender gaps (Fig. 22B, F–H). The small IPas do not cover the adradial edges of the vT (Fig. 22A, B, D, F). The orifice of the vTCt faces proximally and appears slightly larger than that of the dTCt, which is directed dorsally and abradially (Fig. 22B, D, F, H). The proximal edge of the OP protrudes only slightly below the vTCt but relatively farther above the dTCt (Fig. 22B; see Stöhr, 2011:fig. 16I, J). As the jaws are closed the teeth intermesh, and a broad, shallow, buccal funnel is circumscribed by the TPas and teeth on opposing jaws (Fig. 11F; [LACM E.1957-302.1]). At the same time, OPas *s.l.* on adjacent jaws partially cover the OSl, and the dCtPs of adjacent jaws nearly touch. Teeth of *Ophionereis olivacea* Koehler, 1914a, and *Ophionereis reticulata* (Say, 1825) intermesh when the jaws close, forming a shallow buccal funnel (Fig. 23K; Lyman, 1882:pl. 40, fig. 14).

VENTRAL TENTACLE COMPARTMENT. Composed of the flank of the OP, OPR, AdShSp, LyOs, two vCtPs, and a panel composed of several tesselate CtOss (Fig. 22B, F–H). The upper vCtP has a large, rounded dorsal lobe attached to the OPR, which is nearly perpendicular to a smaller, angular ventral lobe adjoining the elliptical, lower vCtP (Fig. 22B, F–H). The lower vCtP abuts LyOs, and proximal edges of the vCtPs and LyOs support a narrow panel on the edge of the vTCt, consisting of several CtOss (Fig. 22B, H).

DORSAL TENTACLE COMPARTMENT. Composed of the flank of the OP, OPR, dCtP, and a semicylindrical collar consisting of several CtOss and squamous, imbricating CoOss (Fig. 22B, E, F, H). The collar, which encloses the base of OT-1, arises from the dorsal edge of the dCtP and arches above the tentacle basin toward the OP. The dorsal edge of the collar connects at right angles to a broad FP that extends from the OPR to the dorsal surface of the OP (Fig. 22B, E, F, H).

PERRADIAL ARMATURE. The tapering proximal lobe of VAP-1 terminates below the OPR, and its dorsal edge is overlapped by a distinctive, campanulate LuOs that, in turn, overlaps a column composed of small, flat, elongated LuOss, which reaches the OPR (Fig. 22B, F, G). Near the OPR, where the column widens, the LuOss form a chevron pattern. Above the dTCt, the column bifurcates into two diverging rows of scales which overlap the FPs on adjacent jaws (Fig. 22B, E, F). The sheath of tissue in which the LuOss are embedded merges with a layer of integument that is embedded with squamous ossicles and that covers the circumoral esophageal ligament (Fig. 22E). I examined a dissected skeleton of *O. porrecta* with a stereomicroscope and observed one water ring foramen in each OP, within which there were two discernable channels leading to the dorsal and ventral tentacle basins.

Skeletal Ontogenesis and Homologies of Oral Armature

Mortensen (1921:175, fig. 96) reared vitellaria larvae of *Ophionereis squamulosa* Koehler, 1914a, and he depicted a 12-day-old juvenile stage that had developed a 1°T, an AdShSp, and a pair of crescentic ossicles in each OSl, which he identified as "the adoral plates." He noted "This interpretation is not in conformity with that usually adopted; I cannot, however, enter here on a discussion of the morphology of the oral skeleton of Ophiurids." However, on the basis of their shape and location, I am convinced these crescentic ossicles are BScs, and I regard as a VAP-1 the ossicle that Mortensen called the "second ventral plate." This interpretation is corroborated by the following analysis of the skeletal ontogenesis of *Ophionereis olivacea*.

The earliest stage of *O. olivacea* examined in the present study was a brooded, 0.4-mm-dd (2 ASs) postlarva with a 1°T, a rudiment of the IPa beside the DP/OP juncture, a BSc on the OPR, and a tapering, pointed AdShSp at the distal end of the AdSh (Fig. 23A). Judging from its much smaller size, the IPa develops after the BSc and AdShSp. At this stage, pairs of opercular BScs cover the OSl, and the apex of the OP protrudes below the DP. OTPo-2 is positioned between the AdSh and VAP-1, and it is separated from the OSl by the BSc. The smallest free-living stage examined herein, 1.1 mm dd (13 ASs), has a small newly formed vT on several jaws beneath an older, larger tooth (Fig. 23B). The IPa on the apex of the OP partially overlaps the DP and a triangular BSc on the OPR. A 2°AdShSp, which had developed at the proximal edge of the AdShSp, is semicircular and articulates beside the orifice of the vTCt, near the midpoint of the AdSh. By this stage, an increase in the height, depth, and breadth of the OP enlarges the OSl and creates a diastema between the 2°AdShSp and BSc. On account of ventralward growth of the distal element of the OP, the AdShSp protrudes considerably below the BSc, and the developing VAP-1 bridges a significant gap between the OPR and VAP-2 (Fig. 23B, G). However, in a 1.5-mm-dd (17ASs) juvenile, the proximal and distal ends of the jaw come into register with one another as a result of differential allometric growth of the OPs and associated ossicles, and the IPa, BSc, 2°AdShSp, and AdShSp align on the ventrolateral edge of the jaw, closing the former gap between the 2°AdShSp and BSc (Fig. 23C). Additionally, a triradiate rudiment of LyOs appears within the OSl, immediately below the developing vCtP (Fig. 23H). In larger 2.0–3.5-mm-dd (30 ASs) juveniles, the LyOs progressively enlarges and gradually emerges between the AdSh, AdShSp, and VAP-1 (Fig. 23D, E, F, I, J, K). Compact stereom that was already present on the proximal edge of the tooth of the 1.5-mm juvenile, becomes incorporated in a thick cap of imperforate stereom as the animal matures (Fig. 23C–F, H–K). Initially, the IPa, BSc, 2°AdShSp, and AdShSp had disparate shapes and dissimilar stereom microstructure, but these ossicles acquire an increasingly uniform morphology in advanced juveniles (compare: Fig. 23A–F). When the jaws of a large juvenile close, IPas on opposing jaws approximate and teeth intermesh, forming a rudimentary, shallow buccal funnel, and the OPas *s.l.* overlap the OSl and vTCts (Fig. 23I).

Diet, Feeding, and Operation of the Jaws

Ophionereis spp. are regarded as omnivorous scavengers and occasional predators that feed on benthic and suspended material and small invertebrates. *Ophionereis reticulata* primarily ingests diatoms, fragments of macroalgae, sediment, and entire or fragmentary small crustaceans, polychaetes, and echinoderms (May, 1925; Hendler et al., 1995; Yokoyama and Amaral, 2008). *Ophionereis schayeri* (Müller and Troschel, 1844) can "suspension and deposit feed" (Byrne and O'Hara, 2017). *Ophionereis fasciata* Hutton, 1872, was seen extending its arms from beneath stones, raising them slightly and moving them horizontally in response to moderate currents. Its tube feet removed "benthic detrital matter" from the mucus-coated arm spines, which they deposited on TScs and then shaped into a bolus. Contralateral tube feet on successive arm segments relayed food boluses toward the mouth, one arm segment at a time, until they were intercepted by OTs-2 that "scrape [the bolus] against the teeth and oral papillae." Individuals can also gather material from the benthos using their tube feet, and they can carry large items toward the mouth using their arms (Pentreath, 1969:414, 1970:398).

Buccal Morphology

Similarities between the buccal armature of *Ophionereis porrecta* (Amphilepidida) and *Ophiocoma echinata* (Ophiacanthida) may be