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

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## CONTENTS

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**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 related to their similar diet of plant fragments, sediment, and small benthic items. Both species have teeth that are rhombic in cross section and are capped with resistant, imperforate stereom. Their teeth intermesh when the jaws are closed. Both species also have prominent chevrons of LuOss shielding the PG. However, *O. echinata*, which is more typical of microphagous suspension feeders and benthic deposit feeders, has a well-developed buccal funnel, a large abradial muscle fossa on the OP, well-developed jaw and tooth musculature, and papillose tube feet. In contrast, the diminutive IPas and teeth of *O. porrecta* [LACM E.1957-302.1] and *Ophionereis reticulata* [LACM 86-383.2] compose a comparatively shallow buccal funnel that is abruptly truncated by intermeshed tips of the first or second vT. *Ophionereis* species have a moderate-sized abradial muscle fossa on the OP, and they have dorsal teeth that are positioned by muscles that penetrate foramina in the DP and attach to the OP (Table 1, herein; Murakami, 1963:pl. 12 figs. 19–23, pl. 7 figs. 5–8; Medeiros-Bergen, 1996:fig. 2a, b,). *Ophionereis porrecta*, *O. schayeri*, *O. reticulata*, and other congeners, have relatively smooth, annulate tube feet, rather than the papillose tube feet that characterize specialized suspension-feeding ophiuroids (Fig. 22C; Byrne, 1994:fig.32A, B; Keogh and Keegan, 2006).

### Ontogenesis and Skeletal Homologies of Amphilimnidae and Ophiopsilidae

Species of *Amphilimna* and *Ophiopsila* originally were considered "Amphiurae" (Lyman, 1882:159; Koehler, 1907), and later were classified as Ophiacanthidae and Ophiocomidae, respectively, in part because of their buccal armature (Verrill, 1899a; Matsumoto, 1917:340; H.L. Clark, 1918; Thomas, 1967; Paterson, 1985). Subsequently, Murakami (1963:30) concluded that the dental and oral plates of *Ophiopsila* were "more closely related to the Ophionereididae than to those of the Ophiocominae," and Martynov (2010:123) proposed that *Amphilimna* and *Ophiopsila* are "aberrant amphiurids with unique jaw and dental plate morphology, but typical amphiurid disk and arm appearance and shape of the arm spine articulations." A morphological phylogenetic analysis recovered *Ophiopsila guineensis* Koehler, 1914b, in a clade "containing all amphiurid, ophiactid, ophiotrichid, and amphilepidid taxa sampled, also including … *Ophienigma spinilimbatum*" Stöhr and Segonzac, 2005 (Thuy and Stöhr, 2016:9). Similarly, a phylogenomic analysis of the Ophiuroidea showed equal support for Ophiopsilidae as a sister to the Gnathophiurina and the Ophionereidina, and dismissed the historical alignment of Ophiopsilidae and Ophiocomidae based on "arrangements of oral and tooth papillae" because "it has become apparent that papilla characters are plesiomorphic" (O'Hara et al., 2017:427). Nevertheless, consideration of the ontogenesis and homologies of their buccal armature may illuminate the relationships among Amphilimnidae, Ophiopsilidae, and other Amphilepidida.

Because of the similarity of the buccal armature of Amphilimnidae and Ophiopsilidae, Verrill (1899a) and Koehler (1926) identified Ljungman's "*Ophiocnida* (?) *caribea* " (1872:636, pl. 4, fig. 7) as an *Amphilimna* species, and Thomas (1967:127, fig. 9) assigned it to *Ophiopsila* . His conclusion was based on the species' diagnostic tentacle scales, with a caveat that "two dental papillae at the tip of each jaw, and…oral papillae…borne on the half jaws rather than on the adoral plate" set it apart from an adult *Ophiopsila vittata* H. L. Clark, 1918. With that in mind, I examined the holotype of *Ophiopsila caribea* (Ljungman, 1872), and found that the putative "dental papillae" of the 2.5-mm-dd juvenile are a pair of spiniform IPas borne on the ventral apex of the OP, rather than TPas on the DP. Its so-called "oral papillae" were an AdShSp on the AdSh and a 2°AdShSp on the OP, which both had distinctively large-pored stereom. The specimen also had an opaque, spiniform ossicle that projects from the OP between and above the IPa and 2°AdShSp, which was previously described as an "oral tentacle scale," and that I tentatively suggest is a BSc (Koehler, 1926:pl. 4, fig. 7; Thomas 1967:125). Thus, *Ophiopsila* appears to have the same sequence of OPas *s.l.* typical of many Amphilepidida: an IPa, BSc, 2°AdShSp, and AdShSp.

Surprisingly, adult *Ophiopsila riisei* Lütken, 1859, examined using SEM, has two spiniform ossicles on the adradial surface of the OP, both of these below the OPR (Fig. 24B). However, a single spiniform ossicle is present in *Ophiopsila californica* A.H. Clark, 1921 [LACM E.1941-365.5], and a specimen of *Ophiopsila vittata* [LACM E.1976-749.1] had a single spiniform ossicle on all but one jaw, which bore two spiniform ossicles on one OP. Tentatively, I presume that the ventralmost of these spiniform ossicles in *O. riisei* develops from a BSc, but the other spiniform ossicle cannot be characterized without additional information regarding its morphology and ontogenesis.

A juvenile *Ophiopsila californica* (1.7 mm dd) had the same configuration of IPa, BSc, 2°AdShSp, and AdShSp as adult *O. californica* and the juvenile holotype of *Ophiopsila caribea* (Fig. 24E; [LACM 96-42.1]). However, in adult *O. californica* (11.7 mm dd) the apex of the OPs jut ventrally and bear paired IPas that are well above the ventral apex of the jaw. Additionally, it has a small number of TPas on the DP immediately below the teeth, and a clump of papillae on the ventral protrusion of the jaw [LACM E.1941-365.5]. These latter ossicles were traditionally called "tooth papillae" or "apical papillae," and Lyman (1865:150, fig. 17) described them in *O. riisei* Lütken, 1859, as "tooth papillae in an irregular bunch, about nine in number; lowest ones smallest, and placed more outward" (see also A.H. Clark, 1921:110; Martynov, 2010b:122).

Remarkably, examination of *O. riisei* using SEM revealed that the clumped papillae on the ventral protrusion of the jaw are not homologous with TPas, because they are not borne on the DP. Herein, I refer to the protrusion as the crest of the jaw and designate the small, blunt papillae that it bears as "crest papillae" (CPas) (Fig. 24B, G–J). These are situated below a pair of IPas that are set in a constriction in the jaw that is immediately above the crest, whereas each IPa is attached to a fossa or foramen on the OP (Fig. 24B, F–J). Notably, Verrill (1899a:55–56:pl. 3, fig. 4) described *Ophiopsila maculata* (Verrill, 1899a) [=*Amphipsila maculata*] as lacking a "cluster of inner papillae, below the teeth…as in *Ophiopsila*," although his figure of the species shows what appear to be IPas and CPas (Fig. 24F–J). This is not to say that ophiopsilids typically lack TPas, since published figures of *Ophiopsila bispinosa* A.M. Clark, 1974, confirm that it has one or two pairs of presumptive TPas on the DP, which are situated below the teeth, although it may lack CPas (A.M. Clark, 1974:fig. 13b; Martynov, 2010b:122, fig. 38C–G). Moreover, *Ophiopsila riisei* has a 1–4 presumptive TPas between the IPas and the vT on several jaws, and the largest pairs of these TPas resembled small teeth (Fig. 24F–J). TPas may occur more consistently in some species of *Ophiopsila* than others. A specimen of *O. californica* had a pair TPas below the vT, on two of five jaws [LACM E.1941-365.5]. An individual of *Ophiopsila vittata* [LACM E.1976-749.1] appeared to lack TPas, although their absence was not confirmed by dissection.

An adult *Amphilimna olivacea* has buccal armature that is similar to *Ophiopsila* species. Although it lacks TPas and CPas, it has paired IPas on the apex of the OP, a 2°AdShSp proximal to an AdShSp on the AdSh, a presumptive spiniform BSc immediately above the 2°AdShSp, and an additional spiniform element closer to the OPR (Thomas, 1967:fig. 2; Thomas and Schoener, 1972:fig, 2A-D; Martynov, 2010b:figs, 37H, 38A, B; [LACM 1999-55.1]) An additional, small ossicle beside VAP-1 of this species may be a vCtOs (Martynov, 2016:fig. 37H, [LACM 1999-55.1]). Juvenile specimens of *A. olivacea* (3–3.8 mm dd) presented the same configuration of OPas *s.l.* as the adult, although the 2°AdShSp articulated on the AdSh instead of the OP, and the problematical, spiniform ossicle above the BSc was rudimentary (see Thomas and Schoener, 1972:fig.2D). The small size of the latter spine and its location near the OPR suggest that it arose independently from, and later than, the BSc.

Seemingly, the IPa, BSc, 2°AdShSp, and AdShSp of *Amphilimna olivacea* and *Ophiopsila* spp. might appear to be plesiomorphic characters of the Amphilepidida considered herein. However, the morphology of their jaws has not been closely examined, and the apical crest, TPas, and position of the IPa, not to mention the buccal funnel, set the Ophiopsilidae and Amphilimnidae apart from one another. Ophiopsilids are further distinguished by their CPas, although small, rounded apical ossicles on the OP of *Amphilimna tanyodes* Devaney, 1974, which somewhat resemble CPas (see Devaney, 1974:figs. 4, 5), indicate that CPas may not be a synapomorphy of Ophiopsilidae.

### Diet, Feeding, and Operation of the Jaws of Amphilimnidae and Ophiopsilidae

Despite similarities between the OPas *s.l.* of amphilimnids and ophiopsilids, the morphology of their jaws is not alike, which suggests that their modes of feeding may differ. *Amphilimna olivacea* lacks a buccal funnel. Teeth that are dorsal to the IPa and vT are of nearly equal length, and when its jaws are closed the columns of teeth intermesh. Proximal edges of the teeth form a thin, semicircular blade that, viewed with a stereomicroscope, appears to be composed of labyrinthic stereom, and the dorsal teeth have a broader, more spatulate proximal edge than the ventral teeth. Furthermore, the species' tube feet are smooth and annulate, unlike those of suspension feeders (Borges et al., 2002:fig. 22b; Borrero-Pérez et al., 2008:fig. 13B; Martynov, 2010b:figs. 37H, 38A; [LACM 1999-55.1]). In addition, *A. olivacea and Amphilimna polyacantha* Liao, 1983, have an OP with a moderately developed abradial muscle fossa, and their dental muscles occupy imperforate fossae on the DP (Thomas, 1967:figs. 4, 5; Liao, 1983:fig. 2b, e). Unfortunately, the feeding behavior of Amphilimnidae has not been examined, and "*Amphilimna* sp." was characterized without any evidence as a "filter feeding...burrowing brittle star," perhaps because of a seeming resemblance to Amphiuridae (Hecker et al., 1983:79, 91; Levin and Gooday, 1983:127). Nevertheless, it appears that amphilimnids are not specialized suspension feeders, because they lack a buccal funnel, strongly muscularized jaws, strongly muscularized teeth, and papillose tube feet.

In contrast with *Amphilimna* species, *Ophiopsila riisei*, *O. vittata*, and *O. californica* have a well-developed buccal funnel with an orifice circumscribed by CPas, IPas, and intermeshing teeth (compare: Martynov, 2010b: fig. 37G, fig. 37H). Their vT, which is dorsal to the CPas, is narrow, tapered, and recessed between protruding IPas on the DP. This configuration of CPas, IPas, TPas, and vT creates a concavity at the apex of the jaw (Figs. 11E, 24A, B, F, G). Dorsally, the next several teeth increase markedly in breadth. They have a concave proximal surface with a dorsomedial cusp, thick lateral edges, and a flanged, proximal edge that partially overlaps the base of the tooth above. Median depressions in these concave, partially imbricate teeth are aligned with the apical channel. The dorsal teeth grow longer and more narrow toward the upper edge of the jaw, and their blunt tips are capped with a rim of imperforate stereom (Fig. 24A, D).

When the jaws of *Ophiopsila* species are closed, the teeth on adjacent jaws intermesh, and the IPas and crest papillae on adjacent jaws abut (Figs. 11E, 24A, F). Concave surfaces of ventral teeth enclose an abruptly constricted, conical space that is blocked by the long, dorsal teeth (*Ophiopsila californica* [LACM E.1941-365.5; LACM E.1949-72.5]; *O. vittata* [LACM E.1976-749.1]). Because the lowest teeth are narrower than those above, their radial edges do not intermesh with counterparts on the adjacent jaws, which accounts for the short, radially positioned gaps on the ventral edge of the buccal funnel. The abradial muscle fossa of *Ophiopsila guineensis*, is well developed and the OP is wing shaped. Dental muscles controlling the dorsal teeth penetrate foramina in the DP and attach to the OP in this species, and also in *Ophiopsila seminuda* A.M. Clark, 1952 (A.M. Clark, 1974:fig. 12f; Wilkie, 1980:fig.1 D). Specimens of *O. riisei* have distal tube feet bearing numerous, slender papillae, and the density and size of papillae on the tube feet increase toward the tip of the arm. The spatulate, ciliated tentacle scales of *O. riisei* are extremely small and spiniform near the tip of the arm, and they become progressively larger toward the base of the arm (Hendler, prev. unpub.). The ciliated tracts on the VAPs and the spatulate TScs of *Ophiopsila* species drive a current of water proximally along the ventral surface of the arm (Hyman, 1955; Hendler, prev. unpub.).

Nocturnal *Ophiopsila* species erect their arms stiffly, with the ambulacrum directed toward the current and tube feet extended on either side in a nearly planar array (Massé, 1963; Warner and Woodley, 1975; Basch, 1985). They are primarily passive suspension feeders, and their stomach contents predominantly comprise diatoms, dinoflagellates, algal fragments, and fine sediment, and may also contain minute adult and larval crustaceans and other invertebrates (Massé, 1963; Basch, 1985). *Ophiopsila californica* was observed to feed on "suspended particles (plankton, seston, detritus, and resuspended sediment)... captured by sticky spines or mucus nets draped between adjacent spines and/or podia. At intervals, this accumulated material was wiped from the spines or podia and compacted into small boluses by adjacent podia, and then transferred down the arm by neighboring pairs of podia...at times of higher particulate flux, there were usually several boluses moving down the arm(s) at any one time" (Basch, 1985:46–47). It is not known whether coordinated waves of tube feet transport boluses as they do in *Ophiothrix* species (e.g., see Austin, 1966; Warner and Woodley, 1975).

Historical investigations of *Ophiopsila* speculated that the ciliated tentacle scales cleaned the surface of the arm or were involved in feeding or respiration (Mangold, 1907; Reichensperger, 1908; Gislén, 1924). I surmise they do facilitate respiration, having observed in Belize that individuals of *Ophiopsila riisei* extend their arms at night to collect food. However, during the day individuals are interred in separate, cramped fissures in coral and mangrove peat, with their arms tightly wound around the disk and immobile. When these individuals are excavated and exposed to daylight, their arms rapidly unfold and extend. Thus, it is possible that the ciliated arm segments and tentacle scales draw oxygenated water through the diurnal refuge.

The phylogenetic position of Ophiopsilidae is unresolved, and its relationship with Amphilimnidae is not clear (O'Hara et al., 2017, 2018). It is evident that both families have striking similarities and significant differences in the configuration of their OPas *s.l.* and the morphology of their jaws. However, it is not known how these structures evolved and whether they are adaptive for particular modes of feeding.

### *Amphioplus abditus* (Verrill, 1871)

Figs. 11D, 25

**VENTRAL ASPECT.** Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their ontogenesis in *A. abditus* and confamilials (described below).Teeth and OPas *s.l.* are composed of labyrinthic stereom, and the teeth are capped with a discontinuous layer of imperforate stereom (Fig. 25A–C). A pair of stout, wedge-shaped IPas borne on the apex of the OP overlaps the DP and sloping adradial edges of the vT (Fig. 25A, B). There is a series of OPas *s.l.* on the OP, distal to the IPa, which consists of the BSc, 2°AdShSp, and AdShSp, in that order. The BSc is elevated, above the others, on the adradial surface of the OP. A blunt, papilliform 2°AdShSp seamlessly abuts the larger AdShSp and is attached to the ventrolateral edge of the OP. The AdShSp is borne on, or beside, the proximal end of the AdSh. A narrow gap separates the IPa and 2°AdShSp, and there is a diastema between the AdShSp and several "accessory papillae" (*sensu* Hendler, 1978, 1988) on proximal edges of the AdSh and VAP-1. These papillae, which are embedded in integument surrounding the orifice of the vTCt, are provisionally identified as vCtOss. VAP-1 has a tapering, medially depressed proximal lobe that inclines steeply upward into the OSl and abuts the OPR. The distal lobe of VAP-1 is barely in contact with VAP-2, and is joined by integument to the flanking 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. 25A).

**PROXIMAL ASPECT.** Teeth are aligned in a column. Bases of teeth are large and nearly touch one another. Shafts of the teeth are tapering and have compressed lateral edges. The proximal edge of the tooth is capped with a discontinuous layer of imperforate stereom (Fig. 25C, D). Adjacent teeth are separated by wedge-shaped gaps. The vT is triangular in cross section and is recessed between the IPas. Its shape conforms to the abutting IPas and tooth. Ventral teeth are subtriangular in cross section, and they have a concave proximal edge and a dorsomedial cusp that partially overlaps the tooth above (Fig. 25D). Dorsal teeth are rhombic in cross section and have a truncate tip. DP is a single ossicle. TPas and teeth increase in length dorsally (Fig. 25C, D). When the jaws are closed, the adjacent columns of teeth intermesh, and the IPas and concave proximal edges of the teeth surround a conical space. This central aperture is gradually constricted between the dorsalmost teeth, blocking the opening of the mouth (Fig. 11D). OTs can extend beneath the closed jaws or retract and block the OSls. The proximal edge of the OP protrudes considerably farther above the dTCt than below the vTCt (Fig. 25C). Orifices of the dTCt and the somewhat larger vTCt are directed proximally and are separated by a narrow OPR (Fig. 25D).

**VENTRAL TENTACLE COMPARTMENT.** Composed of the flank of the OP, OPR, VAP-1, vCtOss, and the AdSh. In addition to the vCtOss, there may be minute, squamous ossicles embedded in the integumental sheath encircling the orifice of the vTCt (Fig. 25D). There is a single water ring foramen on the dorsal surface of the OP, which presumably merges with channels to the tentacle basins (Hendler, 1973:fig. 8A, B; 1978:fig. 6).

**DORSAL TENTACLE COMPARTMENT.** Composed of the flank of the OP, OPR, and an angular FP that arches between the OPR and an adradial protuberance of the OP (Fig. 25C, D). There is a gap that is immediately below the juncture between the FP and OP and above the tentacle basin. It is possible, but unconfirmed, that this opening accommodates a branch of the circumoral nerve to OT-1. Based on the shape and position of the FPs, it is evident that they developed from the "thin, boomerang-shaped elements" that were previously identified as "first buccal tube-foot scales" in juvenile *A. abditus* (≥0.8 mm dd; 8 ASs) (*contra* Hendler, 1978:87, fig. 6).

**PERRADIAL ARMATURE.** The proximal lobe of VAP-1 abuts the OPRs of adjacent jaws and covers the ventral portion of the PG. The dorsal portion of the gap above the OPR is covered by the overlapping FPs of adjacent jaws. The FPs and the gaps between these plates and the circumoral esophageal ligament are covered by a layer of integument. LuOss appear to be lacking (Fig. 25C, D).

### Skeletal Ontogenesis and Homologies of Oral Armature

BScs develop in the advanced larval stage of *A. abditus*, before AdShSp rudiments appear beside the AdSh (Hendler, 1978:fig. 2B–D). A tooth develops in the 0.3-mm-dd postlarva, and IPas form at the DP/OP juncture in the 0.7mm-dd (5 ASs) juvenile (Hendler, 1978:fig. 3A–C). Although an IPa of *Microphiopholis atra* (Stimpson, 1852) was interpreted to "unquestionably arise from the dental plate," its rudiment appears to be equidistant between the OP and DP (Turner and Miller, 1988:502, fig. 5). Inferences that IPas form on the DP and are homologous to teeth appear to be unsubstantiated (*contra* Hendler, 1988:27; Martynov, 2010b:31; O'Hara et al., 2018:5). A 2°AdShSp is present on the proximal edge of the AdShSp of the 1.1-mm-dd (17 ASs) juvenile (Hendler, 1978:fig. 4B). This ossicle was previously designated the "oral plate papilla" (Hendler, 1988:21), but herein it is inferred to be a serial homologue of the AdShSp. In more advanced juveniles, the BSc is converted, presumably by negative allometric growth, from a relatively large, opercular plate on the OPR to a small, blunt papilla below the OPR. Concurrently, the AdShSp is displaced from the AdSh to the OP, and the IPa overlaps the vT. These alterations in position are effected by differential growth of the OP and other elements of the oral frame, including the OPas *s.l.* themselves (Hendler, 1978, 1988, 1998).

A.M. Clark (1970:5–6) directed attention to "a few species of *Amphioplus* in which the . . . distalmost oral papilla is partly based on the first ventral arm plate." This is the situation in advanced juveniles of *A. abditus* (≥3.5 mm dd, with 82 ASs) that have OPas *s.l.* beside the AdSh and VAP-1, which have been referred to as "accessory papillae" or "outer oral tentacle-scale[s]" (Verrill, 1899b:314; Verrill, 1899a:25; Hendler, 1978:91). However, these are not TScs because they are not attached to an ArtSs, and they vary in number and size. *Amphioplus lucyae* Tommasi, 1971, has one such "minute adoral shield scale" abutting the VAP-1 and/or AdSh, which appears in the advanced juvenile (2.7–3.4 mm dd) (Brogger and O'Hara, 2015:436, fig. 2B, D, F). Individuals of *Amphiura filiformis* (O.F. Müller, 1776) >1.6 mm dd have a similar single ossicle (Madsen, 1970:fig. 13a; Stöhr, 2005:fig 13K). However, it has not been determined if the multiple presumptive vCtOss of *A. abditus* are homologous with what may be similar ossicles in these other Amphiuridae.

### Ontogenesis and Skeletal Homologies of Amphiuridae

Traditionally, three characteristic configurations of buccal armature, "oral formulae" *sensu* A.M. Clark, 1970, have been recognized among Amphiuridae. Each "formula" is produced by a different pattern of skeletal ontogenesis, and the several different configurations are exemplified by species of *Amphiura*, *Amphipholis*, and *Amphioplus* (Hendler 1978, 1988, 1998). The Amphiura-type configuration arises when an IPa and a BSc develop on the OP, which are separated by a diastema from an AdShSp, and this pattern of ontogenesis was documented in *Acrocnida brachiata* (Montagu, 1804), *Amphiura borealis* (G.O. Sars, 1872), *Amphiura chiajei* Forbes, 1843, *Amphiura constricta* Lyman, 1879, *Amphiura filiformis*, and *Amphiura stimpsonii* Lütken, 1859 (Hendler, 1978, 1988; Webb and Tyler, 1985; Stöhr, 2005; Falkner and Byrne, 2006). Although it was reported that the AdShSp disappeared in juvenile *A. borealis*, it is present in the adult (H.L. Clark, 1915a:pl. 4, fig. 4; Mortensen, 1927:fig. 122a; Stöhr, 2005:561). The Amphipholis-type configuration arises when an IPa and a 2°AdShSp develop on the OP, the BSc is resorbed, and an AdShSp maintains contact with the AdSh or is shifted to the OP. This pattern of ontogenesis was documented in *Amphiodia craterodmeta* H.L. Clark, 1911, *Amphipholis squamata* (Delle Chiaje, 1828), *Microphiopholis atra*, *Ophiocnida scabriuscula* (Lütken, 1859), and *Ophiophragmus filograneus* Lyman, 1875 (zur Strassen, 1901; Hendler, 1988; Turner and Miller, 1988; Martynov et al., 2015). The Amphioplus-type configuration arises when an IPa, BSc, and 2°AdShSp develop on the OP, and an AdShSp remains in contact with the AdSh or is shifted to the OP. Additionally, presumptive vCtOss may develop beside the vTCt. This pattern of ontogenesis was reported in *Amphioplus abditus*, *Amphioplus* *lucyae*, and *Amphioplus macilentus* (Verrill, 1882) (Hendler 1978, 1988; Brogger and O'Hara, 2015). The precise sequence in which all the OPas *s.l.* develop was not determined in most of these species, but the 1°T, BSc, and AdShSp consistently developed before the IPa and 2°AdShSp in *Acrocnida brachiata*, *A. abditus*, and *M. atra* (Hendler, 1978; Webb and Tyler, 1985; Turner and Miller, 1988).

Amphilepididae, comprising *Amphilepis* and *Ophiomonas* species, is sister to Amphiuridae, and ontogenetic studies confirmed that the buccal armature of *Amphilepis* and *Amphiura* species comprise the IPa, BSc, and AdShSp. The smallest documented juvenile *Amphilepis ingolfiana* Mortensen, 1933a (0.6 mm dd) had a 1°T, a BSc, and a prominent AdShSp that was approximately 0.17 mm in length, but in a 1.5-mm-dd juvenile the AdShSp was only 0.12 mm, and may have been partially resorbed (these estimates of AdShSp length are based on Sumida et al., 1998:fig. 11B, F). The AdShSp is lacking in *A. ingofiana* >3.0 mm dd, and also in *Amphilepis norvegica* (Ljungman, 1865) (Mortensen, 1933a:fig. 32; Schoener; 1967; Sumida et al., 1998:fig. 11B, F; Schoener, 1967). However, the AdShSp can persist in *Amphilepis patens* Lyman, 1869, as one of several papillae on the AdSh [LACM 1993-75.19]. However, ontogenesis of OPas *s.l.* on the AdSh and VAP-1 have not been examined and it is not clear which particular ossicles are homologues of the AdShSp, 2°AdShSps, VAP-1 TScs, vCtOss, or vCtPs. Adults of *Ophiomonas* spp. may retain an AdShSp, since three nominal species were described as having 1–2 OPas *s.l.* on the adoral shield (Koehler, 1904:pl. 23, fig. 9; Koehler, 1922a:pl. 69, fig. 8; Djakonov, 1952:fig. 3).

According to a revisionary phylogenetic analysis of Ophiuroidea, the genera *Amphiura*, *Amphipholis*, and *Amphioplus* "appear to be polyphyletic" on the basis of a subsample of amphiurid species (O'Hara et al., 2017:427). Some amphiurid clades predominantly comprised species with Amphiura-type dental formulae (e.g., species of *Amphiura*, *Ophiocentrus*, *Acrocnida*) or species with Amphipholis-type dental formulae (e.g., species of *Amphipholis*, *Microphiopholis*, *Ophiophragmus*, *Amphistigma*) (O'Hara et al., 2017:fig. S3). However, nominal *Amphioplus* species were distributed among lineages that were primarily composed of species with Amphiura-type or Amphipholis-type dental formulae, suggesting that *Amphioplus* is polyphyletic and/or that the three configurations of amphiurid buccal armature ("oral formulae") are homoplasious and phylogenetically uninformative. Even so, nominal species of *Amphioplus* may have been misclassified and/or their oral formulae may have been misinterpreted. A potential source of error are the species of *Amphioplus* (*Unioplus*), formerly classified as *Amphiura*, which appear to have an IPa, BSc, AdShSp, and a distal ossicle at the juncture between the AdSh and VAP-1 (e.g., A.M. Clark, 1970:fig. 8p, q, r). These may be *Amphioplus* species that lack a 2°AdShSp, or Amphiura-type species that develop a vCtOs, or they might represent several different taxa. The classification of species with "intermediate" dental formulae "illustrating the close relationship of *Amphiura* and *Amphioplus*" may also have been misconstrued (A.M. Clark, 1970:44, 23). Furthermore, particular OPas *s.l.* of Amphiuridae, such as the BSc and AdShSp, may be homologous even if the oral formulae are homoplasious. Resolving these potential discrepancies, and elucidating the biology and evolutionary relationships of Amphiuridae, will require further investigation of their morphology, ontogenesis, and skeletal homologies, and more extensive phylogenomic sampling "of the most speciose of all ophiuroid families" (O'Hara et al., 2017:427).

## Diet, Feeding, and Operation of the Jaws

Infaunal amphiurids occupy mucus-lined burrows from which they extend one or more arms to feed, to irrigate the burrow, and to dispose of waste. The Amphiuridae that have been studied are microphagous and generally consume waterborne and benthic particles. When *Amphiura filiformis* suspension feeds, "Particles are passed from one podia [sic] to another down the arm till the group of particles gradually assumes the appearance of a compact bolus which is added to by other podia in its progress downwards" (Buchanan, 1964:569; Loo et al., 1996). "The bolus is clasped by adjacent pairs of tube-feet which hug it to the belly of the arm and, with apparent reluctance, push it onward to be held by their neighbours" (Woodley, 1975:42). Amphiurids also can ingest subsurface material, and they can transfer large items to the mouth in a loop of the arm. Their OTs reject or select material that "can then enter the mouth either by adhering to these tube-feet or by transport in the ciliary currents of the surfaces adjoining the mouth" (des Arts, 1911; Buchanan, 1964; Fricke, 1970; Pentreath, 1970; Woodley, 1975:41; Gielazyn et al., 1999). Unfortunately, the functions of different amphiurid OPas *s.l.* have not been examined nor has the manner in which the OTs and jaws process food.

The diminutive, cryptic species *Amphipholis squamata* [=*Axiognathus squamata*] uses OTs to "pick up material directly from the substrate and thrust it into the mouth" (Martin, 1968:75). *Amphioplus abditus*, a microphagous deposit feeder, rarely elevates its arms above the substrate, and its stomach contents largely comprise sediment, plant fibers, diatoms, and fecal pellets, and may include algal fragments, pollen grains, and intact and fragmentary foraminiferans, nematodes, crustaceans, gastropods, and polychaetes (Hendler, 1973). Microphagous suspension feeders, for example *Amphiura filiformis* and *Amphioplus polymorphus* Cherbonnier, 1972, direct the ambulacral surface of their extended arms into the current to capture "non-living suspended particulate matter and phytoplankton" (Buchanan, 1964:575; Fricke, 1970). Particles and aggregates may be captured as they stream towards the ventral side of the arm and from attached vortices on the dorsal side of the arm (Loo et al., 1996). Information is virtually nil regarding the feeding biology of Amphilepididae, sister to Amphiuridae. *Amphilepis patens* was described as "infaunal but it is unknown if they feed directly on settling detritus or prey on other infaunal organisms" (Booth et al., 2008:934).

## Buccal Morphology

*Amphioplus abditus* has a buccal funnel resembling that of other long-armed, microphagous amphiurids (Fig. 11D). Its teeth increase in length dorsally. The small, triangular vT is recessed between a pair of protuberant IPas, and other ventral teeth have a beveled, concave proximal edge and a dorsomedial cusp that partially overlaps the tooth above. Dorsal teeth are compressed and rhombic in cross section. When the jaws are closed, the IPas approximate and the teeth intermesh, bounding a central, conical space that is progressively constricted and blocked by the dorsalmost teeth. The small OPas *s.l.* bordering the OSls do not curtail movement of OTs-2, which can extend from the spacious OSls, even when the jaws are closed. Tube feet of deposit-feeding amphiurids such as *A. abditus* are relatively smooth and annulate compared to the papillose tube feet of suspension-feeding species (Buchanan, 1964; Pentreath, 1970). *Amphioplus* species have a well-developed abradial muscle fossa and wing-shaped OP, and have dental muscles that penetrate paired foramina in the DP and attach to the OP (Murakami, 1963:pl. 1, figs. 40–41, 44-45; pl. 4, figs. 49–52; pl. 5, figs. 1–4). The teeth of *A. abditus* are capped with a discontinuous layer of imperforate stereom, and those of *Amphipholis squamata* have a thick, imperforate cap (Fig. 25C–E; Medeiros-Bergen, 1996:fig. 2e).

Buccal morphology of the Amphiuridae is quite different from Amphilepididae, as exemplified by *Amphilepis patens* and *Amphilepis neozelandica* Mills and O'Hara, 2010. These species lack a buccal funnel. When their jaws close, the OSls are obstructed and the OTs-2 are blocked by the OPas *s.l.*, OPR, intermeshing teeth, and possibly by CtPs or CtOss. Teeth of *A. patens* are compressed and have a broadly rounded proximal edge that is not capped with imperforate stereom (Mills and O'Hara, 2010:fig. 2B; [LACM 1993-75.19]).

The OTPo-2 (i.e., vTCt) of amphilepidids was described as occupying a "superficial position…opening outside the mouth" and the jaw was characterized as flattened compared to, for example *Amphioplus* (A.M. Clark, 1970:70; Mills and O'Hara, 2010:50). Although the orifice of an amphilepidid vTCt is conspicuous and shallow, the vTCt of *Amphilepis* opens into the OSl and the VAP-1 inclines steeply upward, abutting the OPR (e.g., in *Amphilepis neozelandica*; Mills and O'Hara, 2010:fig. 2). Apparently, ventralward growth of the vTCt is truncated and the BSc of *Amphilepis* remains on the OPR throughout ontogenesis, whereas development of the dTCt is not hampered. As a consequence, OT-2 can protrude into the buccal cavity when the jaws are open, but when the jaws are closed OT-2 is excluded from the OSl by the BSc and OPR, a similar circumstance as in many Ophiurina.

### *Ophiothrix spiculata* Le Conte, 1851
Figs. 11A, 26

**VENTRAL ASPECT.** Homologies of buccal skeletal elements were inferred on the basis of their position in the adult and their pattern of ontogenesis in *Ophiothrix* spp. (described below). Remarkably, *Ophiothrix spiculata* and confamilials have a naked vTCt without any OPas *s.l.* on the OP and AdShSp. Teeth and TPas of *O. spiculata* are composed of labyrinthic stereom. The teeth and large TPas are capped with a discontinuous layer of imperforate stereom, and the proximal edge of the small TPas is composed of dense stereom with comparatively small stereomic pores (Fig. 26A, C, D). The tentacle basin of OT-2 is bordered by the OPR, AdSh, and VAP-1, and OT-2 is exposed within the broad OSl. VAP-1 is arched and medially depressed. Its tapering, proximal lobe inclines steeply into the OSl and inserts beside the OPR, and its smaller distal lobe usually overlaps the edge of VAP-2 and sometimes abuts the AdSh, but it does not contact LAP-2 (Fig. 26B, D). VAP-1 is linked to these surrounding ossicles by integument, and the oral frame is unified by connections of these plates with one another and with the LAPs-2, the OShs, and the conjoined OPs (Fig. 26A, D). A conspicuous ventral fossa is enclosed between the OPs of *O. spiculata*. This opening is characteristic of ophiotrichids and was previously characterized as "…a hole, from a want of perfect union between the two pieces of the mouth frame" (Fig. 26A; Lyman, 1882:213).

**PROXIMAL ASPECT.** Teeth are aligned in a column on the dorsal lobe of the DP, and they increase in length and width dorsally (Fig. 26C, D). Bases of teeth are large and nearly touch one another. Shafts of teeth are tapering, compressed, and rhombic in cross section. The truncate tip of the tooth is beveled, with an angular, dorsomedial cusp (Fig. 26D). Adjacent teeth are separated by wedge-shaped gaps. The vT is noticeably longer than the dorsalmost TPa. TPas occupy the ventral lobe of the DP and comprise two columns of larger, tapering, adradial ossicles flanking a medial series of short ossicles that are grouped in irregular triads. These three vertical bands of dimorphic TPas form a convex channel on the ventral apex of the jaw (Fig. 26A, C). When jaws are closed, the edges of adradial TPas abut, the teeth intermesh, and the columns of TPas and teeth surround a conical space. This central cavity is constricted by the dorsal teeth, blocking the opening of the mouth (Fig. 11A). OTs-2 can protrude from the OSl or block the OSls between closed jaws. DP is a single ossicle. Dental muscles that move the teeth penetrate foramina in the DP and attach to the OP (Fig. 26C). The proximal edge of the OP extends well above the dTCt and below the vTCt. The orifice of the vTCt is directed ventrally, that of the dTCt is directed proximally, and the TCts are separated by a thick OPR.

**VENTRAL TENTACLE COMPARTMENT.** Delimited by a depression in the OP and OPR surrounding the OT-2 basin, and by the proximal edges of the AdSh and VAP-1. The vTCt lacks any associated OPas *s.l.* (Fig. 26A, C, D). Murakami (1963: pl. 5 figs. 36, 38, 40, 44, 46, 48, 50, 52) depicts an external foramen in the OPR of ophiotrichids, which may open beside the ventral tentacle basin and potentially could accommodate a branch from the radial nerve cord that innervates OT-2. There appears to be an internal opening of this orifice beside the ventral tentacle basin of *O. spiculata* (Fig. 26D). An analogous foramen was documented beside the ventral tentacle basin of *Ophiura sarsii*, *O. luetkenii*, and *Ophiocten sericeum* in the present study.

**DORSAL TENTACLE COMPARTMENT.** Delimited by a depression in the OP and OPR surrounding the OT-1 basin and by a FP that extends between the OPR and an adradial protuberance of the OP (Fig. 26B–D). A gap between this protuberance, the FP, and the tentacle basin may accommodate a branch from the circumoral nerve cord, which innervates OT-1 (Fig. 26B, C, D).

**PERRADIAL ARMATURE.** The tapering proximal lobe of VAP-1 inserts between OPRs of adjacent jaws, covering the ventral portion of the PG. The overlapping FPs of adjacent jaws, and the integument in which they are embedded, cover the portion of the gap above the OPR. This perradial integument merges with the circumoral esophageal ligament. LuOss appear to be lacking (Fig. 26B–D).

### Skeletal Ontogenesis and Homologies of Oral Armature

Early postlarval stages of *Ophiothrix fragilis* have been described, and the smallest juvenile that was figured, 0.35 mm dd (2ASs), lacks OPas *s.l.* apart from a 1°T. A 0.55-mm-dd juvenile has two teeth; one pair of TPas is present in a 1.1-mm-dd juvenile, and there are several more TPas in a 1.3-mm-dd individual (Stöhr 2005: fig. 16C, D, G, K, M). It was conjectured that in this species "teeth appear to divide and shorten to form the tooth papillae, beginning with the ventralmost tooth. This must be a highly derived condition," such that new teeth developed "on the DP dorsal to the first," and that "In adults…all teeth have been replaced by papillae" (Stöhr, 2005:569, 574). However, teeth and TPas co-occur on the DPs of adult *O. fragilis* and of other Ophiotrichidae, and there is no evidence that the teeth divide or are replaced by TPas (Duncan, 1887b; Matsumoto, 1917:215; Hoggett, 1991, 2006; [LACM E.1948-100.1] ). Moreover, H.L. Clark (1914:115, pl. 3, figs. 15, 16) established that in *Ophiothrix angulata* (Say, 1825) the final "number of teeth…is 4 or 5, while the number of dental papillae [TPas] increases throughout growth…The first dental papillae arise in a pair, side by side, below the lowest tooth; beneath them the growing torus [DP] expands a little and a new papilla forms near the margin on each side." Teeth develop on the ventral edge of the plate as do the TPas, but TPas begin to develop only after all the teeth have formed. The teeth and TPas increase in length dorsally, because their size is directly related to the sequence in which they develop. Teeth form singly, but TPas develop in transverse pairs or in triplets. Each tooth is linked to the OP by a dental muscle that passes through 1–2 large foramina in the DP, but each TPa is connected to a single, small foramen or fossa (Duncan, 1887b, pl. 10, figs. 2, 8; Murakami, 1963:pl. 2, figs. 8–16).

### Ontogenesis and Skeletal Homologies of Ophiactoidea

Ophiactoidea, comprising Ophiactidae, Ophiopholidae, Ophiotrichidae, and their sister Ophiothamnidae, is sister to the Amphiuroidea (Amphiuridae and Amphilepididae), and these six families compose the Gnathophiurina (O'Hara et al., 2018). Components and configurations of buccal armature among the taxa in this suborder. *Amphioplus* species exhibit a relatively complex oral formula comprised of five types of OPas *s.l.* on the OP and AdSh, and buccal armature is drastically abridged in Ophiotrichidae, which only have OPas *s.l.* on the DP.

Ophiothamnids have a diminutive, rudimentary IPa, and their OPas *s.l.* can develop in the same sequence and have the same configuration as Amphiuridae. Juveniles of *Histampica duplicata* (Lyman, 1875), which are 1.5 mm dd and 2.9 mm dd, develop a BSc and AdShSp before the IPa and 2°AdShSp arise (Stöhr, 2005:fig. 14B, D). Adults with 3–5 oral papillae have been reported, and specimens examined in the present study had an Amphioplus-type configuration with a reduced IPa, a BSc that is elevated in the OSl, a 2°AdShSp, an AdShSp, and a prominent ossicle between the AdSh and VAP-1, possibly a vCtOs, as well as a supplementary perradial ossicle between the AdShs, which was referred to as part of a "transversely divided" VAP-1 (Lyman, 1875:19; Lütken and Mortensen, 1899:142; Paterson, 1985:80; [LACM 1967-136.1]). *Histampica umbonata* (Matsumoto, 1915) is reported to have the same number of OPas *s.l.* as *H. duplicata*, although specimens examined in the present study possess 1–2 additional OPa *s.l.* on some jaws, possibly 2°AdShSps [LACM 76-638.1]. Both these species of *Histampica* lack a buccal funnel, and their vT on opposing jaws intermesh.

According to O'Hara et al. (2017:427), Ophiactidae comprises two clades that "appear to be distinguished by the presence of one…or two distal oral papillae," but it is not clear whether the family is "monophyletic or paraphyletic with respect to the ophiotrichids/*Ophiopholis*." Ophiactids lack an IPa, and their buccal armature is reduced compared to Amphiuridae and Ophiothamnidae. They have a BSc and an AdShSp, and those species with two distal oral papillae develop a 2°AdShSp (Fig. 11C). The smallest juvenile *Ophiactis abyssicola* examined (0.4 mm dd) had a BSc and AdShSp, and a more advanced juvenile (0.9 mm dd) also had a 2°AdShSp (Sumida et al., 1998:fig. 12). *Ophiactis resiliens* Lyman, 1879, (0.36–1.5 mm dd) develops OPas *s.l.* in this same sequence (Falkner and Byrne, 2006), and adults of *O. abyssicola and O. resiliens* have a BSc, a 2°AdShSp, and an AdShSp on the OP. However, *Hemipholis cordifera* (Bosc, 1802) [=*Hemipholis elongata*] (0.42 mm dd), a member of the ophiactid clade with "one distal oral papilla," has a BSc and an AdShSp, but fails to develop a 2°AdShSp (Turner and Miller, 1988:figs. 5C, 7A, B; Hendler, 2011:fig. 1).

Ophiopholids usually develop three OPas *s.l.* on the AdSh and OP, although there may be as many as six OPas *s.l.* in adult *Ophiopholis bakeri* McClendon, 1909, and *Ophiopholis aculeata* (Linnaeus, 1767) (Serafy, 1971; McClendon, 1909). The youngest *O. aculeata* described (0.7 mm dd) had an AdShSp rudiment, and a 2.0-mm-dd juvenile had three similar, spiniform ossicles beside the AdSh, but it lacked a BSc and TPas (Duncan, 1880:fig. 2 [=*Polypholis echinata*]; Sumida et al., 1998:fig. 13F, G). Juvenile specimens of *Ophiopholis bakeri* (1.5–1.8 mm dd) [LACM E.1977-283.3, LACM E.1977-288.1] and *O. aculeata* (3.1 mm dd) [LACM E.1968-490.6] have 1–2 spiniform OPas *s.l.* on the proximal edge of the AdSh, and three OPas *s.l.* were present in a 4.7-mm-dd *O. aculeata* [LACM 1968-488.1]. The OPas *s.l.* of this species form a serried row, and in juvenile individuals the proximalmost papillae are generally the smallest. In adults, the proximalmost OPas *s.l.* articulate with the OP at considerable distance from the DP/OP juncture. Thus, the ophiopholid OPas *s.l.* appear to comprise an AdShSp and 2°AdShSps, rather than an IPa, BSc, or LOPas. Adults have OPas *s.l.* that are petaloid, and the proximalmost is aligned nearly perpendicular to those on the AdSh (Fig. 11D).

Species of sister taxa Ophiopholidae and Ophiotrichidae are the only Gnathophiurina that develop TPas. However, homology of TPas in these two families is problematic because their TPas differ morphologically and appear to develop at different stages of ontogenesis (see "Buccal Morphology of Ophiactoidea" in the treatment *O. spiculata*). Interestingly, the phylogenetic distributions of the IPa, BSc, AdShSp, and 2°AdShSp among the Ophiactoidea suggests a possibility that specific OPas *s.l.* occurring in the Ophiothamnidae were sequentially lost in later-branching taxa of this superfamily. It is also notable that TPas evolved in the latter groups. Among the Ophiactoidea, Ophiothamnidae develop the most diverse armature on the OP and AdSh comprising four OPas *s.l.* (IPa, BSc, AdShSp, 2°AdShSp), compared with the Ophiactidae that have 2–3 OPas *s.l.* (BSc, AdShSp ± 2°AdShSp) but lack the IPa, Ophiopholidae that have two OPas *s.l.* (AdShSp, 2°AdShSps) but lack the IPa and BSc, and Ophiotrichidae that have a naked OP and AdSh. Simplification of the buccal armature on the OP and DP, the occurrence of TPas on the DP, and differences in the morphology of buccal funnels among Ophiactoidea may be functionally related to their diet and mode of feeding, but in a manner that is not well understood (see "Buccal Morphology of Ophiactoidea" in the treatment of *O. spiculata*).

### Diet, Feeding, and Operation of the Jaws

Ophiotrichidae and other Ophiactoidea are primarily microphagous, and commonly suspension feeders. Dense populations of *Ophiothrix fragilis* inhabit subtidal locales swept by strong currents, and individuals consume waterborne diatoms, coccoliths, detritus, and small numbers of fecal pellets, foraminiferans, and crustacean exuviae (Allen, 1998; Warner and Woodley, 1975). However, this species reportedly can feed on "worms and crustaceans…small mussels, echinoderms, compound Ascidians, Foraminifera, etc." (Mortensen, 1927:175). Massive numbers of *Ophiothrix spiculata* occur at deepwater sites with strong currents, and fewer numbers occupy protected, shallow habitats (Austin, 1966; Lewbel et al., 1981). Individuals in aquaria can capture diatoms, zooea larvae, and copepods from the water column; collect small, active organisms and carrion from the benthos with their tube feet; and secure larger objects in an arm-loop (Austin, 1966). *Macrophiothrix variabilis* (Duncan, 1887a) and *Macrophiothrix longipeda* (Lamark, 1816a) gather suspended material and benthic carrion, and deposit-feeding *Ophiothrix lineata* consumes material adhering to the surface of its sponge host (Hendler, 1984; Emson and Mladenov, 1992; Marin et al., 2005).

*Ophiothrix fragilis* orients the ambulacral surface of the arm toward the current, extending its tube feet beyond the arm spines. Contralateral tube feet, which gather particulate material on mucus-secreting papillae, sweep past proximal pairs of tube feet, simultaneously cleaning themselves and molding a bolus of food. This action initiates a wave of activity proceeding from the tip of the arm toward the mouth, as successive groups of tube feet add material to the bolus and roll it along ambulacrum toward the mouth. Warner and Woodley (1975:204) state that "On reaching the mouth, the bolus is pushed in by the proximal tube-feet without any pause." However, Austin (1966:58) found that OTs of *O. spiculata* accumulate multiple boluses below the mouth before pushing the mass between the opened jaws. The jaws open and close 30–40 times at intervals of 7-10 seconds, repeatedly compressing the mass into a "truncated cone" that is bounded by TPas and intermeshing teeth. Following each compression, the OTs-1 push the compacted food mass farther up the cone until both sets of OTs push the mass into the stomach.

Duncan's (1887b:110–111) investigation of *Macrophiothrix variabilis* [=*Ophiothrix variabilis*] drew attention to a "truncated cone" within the ophiuroid's mouth. He "noticed…that on turning the animal on its back a very-decided funnel-shaped space exists leading…to the true teeth," and he erroneously deduced that "The tooth papillae do not therefore form any part of what has been inelegantly termed a 'chewing-apparatus,' because they do not touch "their opposite and similar structures" when the jaws are closed. Contrariwise, Boos (2012:115–117) suggested "the rough surface provided by the clusters of dental papillae [of *Ophiothrix fragilis*] …seem most appropriately applied as grinding instruments…the arrowhead shaped edges of the teeth…serve as knives in processing food prior to digestion." However, based on

Austin's (1966) findings regarding *Ophiothrix spiculata* it appears that the proximal surfaces of the TPas compress and consolidate boluses, rather than "grinding," and that "teeth dorsal to the dental papillae may also contribute to compaction of the bolus. . .[although] their mode of operation has not been observed" (Austin, 1966:59).

Ophiactidae such as *Ophiactis resiliens* and *Ophiactis savignyi* (Müller and Troschel, 1842) are rheophilic suspension feeders much like ophiotrichids, directing the ventral surface of their upraised arms into the current, and collecting food with their papillose tube feet (Pentreath, 1970; Emson and Mladenov, 1992). At regular intervals, "podia on both sides of the arm [of *O. resiliens*] suddenly collapse in a wave from near the arm tip in a proximal direction" compacting food in a mucus-bound bolus that is transferred to the mouth. Its stomach contents consist "almost entirely of phytoplankton, usually spherical diatoms" (Pentreath, 1970:404, 406). *Ophiactis savignyi* also was described as a suspension feeder that collects current-borne particles and directs them to the mouth with its tube feet. However, benthic items impinging on the arm of *O. savignyi* can rapidly be secured in coils of the arm, and this behavior may account for the presence of sediment, detritus, and the remains of small animals in its stomach contents (Pentreath, 1970; Boffi, 1972; Emson and Maldenov, 1992). The diet of *Ophiactis abyssicola* appeared to consist of "planktonic prey and resuspended organic material" such as crustacean fragments and "flocculent organic material" (Pearson and Gage, 1984:250). *Hemipholis cordifera* [=*Hemipholis elongata*], a burrowing species, is a selective deposit feeder that is also capable of capturing zooplankters (Hazzard et al., 2000; Bentley et al., 2006). In contrast with the burrowing Amphiuridae, *Hemipholis* does not ventilate a burrow by undulating its arms (Woodley, 1975; Hajduk, 1992; Beardsley and Colacino, 1998). Instead, individuals extend their arms from the sediment, and at regular intervals their papillose tube feet "contract in a wave, beginning at the most distal end of the arm and travelling towards the disc" (Beardsley and Colacino, 1998:324). These contractions promote gas exchange by circulating hemoglobin-filled coelomocytes through the water vascular system. Thus, the pulsed contractions of its tube feet are not related to feeding, although individuals do "use the tube feet to make a bolus and transport it to the mouth" (Ana B. Christensen, pers. comm).

*Ophiopholis aculeata*, the most intensively studied ophiopholid species, directs the ambulacral surfaces of its extended arms toward the current and gathers suspended particles with its papillose tube feet (Roushdy and Hansen, 1960; LaBarbera, 1978). It was reported for *O. aculeata* and *Ophiopholis kennerlyi* Lyman, 1860, that "distal tube feet bent proximally and were wiped by the more proximal tube feet; this process continued down the arm, forming a bolus of particles embedded in mucus," which was transferred to the mouth by the oral tentacles (LaBarbera, 1978:1148; Lambert and Austin, 2007:117). Alternatively, these species can secure food using "arm-loop capture" (Litvinova, 1980; Lambert and Austin, 2007:112). *Ophiopholis aculeata* mainly feeds on planktonic and resuspended benthic material, and its stomach contents are primarily organic detritus, microcrustacean remains, algal fragments, diatoms, copepods, and tintinnids (Wright, 1987). However, despite its propensity for microphagous suspension feeding, the presence of unidentifiable organic material and assorted invertebrates in stomach contents led authors to describe *O. aculeata* as a carnivore or detritivore (Eichelbaum, 1910; Turpaeva, 1953; Litvinova, 1979).

## Buccal Morphology of Ophiactoidea

Ophiotrichids have a conspicuous medial cavity on the ventral surface of each jaw, which opens proximally to the aboral muscle between the OPs. This cavity was described as ". . .a hole, from a want of perfect union between the two pieces of the mouth frame" (Figs. 11A, 26A; Lyman, 1882:213). Intriguingly, the aboral muscle in the jaws of *Ophiothrix spiculata* and *O. fragilis* encloses extensions of the respiratory bursae (Smith, 1940; Austin, 1966:155–156). Consequently, seawater that flushes the medial cavity and circulates in the bursal extensions might oxygenate the large abradial muscle of the OP, which activates repetitive feeding movements of the jaw. This hypothesis has not been tested ophiotrichids or in amphiurids that also have a medial jaw cavity, such as *Amphiura* (*Ophionema*) *hexacantha* Nielsen, 1932, and *Amphiura* (*Ophionema*) *intricata* Lütken, 1869 (Nielsen, 1932:fig. 6). However, it is known that primary respiratory bursae in the disk are lined with ciliated epithelium that circulates seawater, and seawater may be flushed from the bursae by compressions of the disk (Duncan, 1887b; MacBride, 1906:485; Austin, 1966; Hendler, 1991, prev. unpub.).

A buccal funnel is present in the Ophiotrichidae, Ophiopholidae, and Ophiactidae, but not in their sister Ophiothamnidae that have ventral teeth that intermesh and block the mouth (Fig. 11A–C). The Ophiactoidea with buccal funnels share a suite of features that are characteristic of microphagous suspension feeders, including well-developed adradial OP muscles and dental muscles, teeth with reinforced stereom, and papillose tube feet. However, the morphology of the buccal funnel, and the types of ossicles of which it is composed, vary among these three different families.

Ophiotrichids such as *Ophiothrix spiculata* [LACM 1939-117.14] have a buccal funnel composed of TPas and teeth. Its orifice is bounded by concave clusters of TPas, which are composed of short, truncate, medial TPas flanked by columns of longer, compressed, tapering TPas that increase in length dorsally. When the jaws close, the funnel is gradually constricted by columns of teeth that are compressed, rhombic in cross section, have a slight median cusp, and progressively increase in length and decrease in width toward the dorsal edge of the DP. Their teeth and TPas are capped with imperforate or reinforced stereom. Most ophiotrichids, including *Ophiocnemis marmorata* (Lamarck, 1816a) [LACM E.1948-99.1] and *Ophiomaza cacaotica* Lyman, 1871 [LACM E.1948-95.2] have a buccal funnel similar to *O. spiculata* [LACM 1939-117.14]. However, *Ophiolophus novarae* Marktanner-Turneretscher, 1887, has only two columns of TPas below the tapered, irregularly shaped teeth, and this exceptional morphology may be related to the species' diet and its commensal relationship with comatulid crinoids (Deheyn et al., 2006 [LACM 94-126.1]). Generally, Ophiotrichidae species have a well-developed abradial muscle fossa on a wing-shaped OP. Their DP is widened dorsally and ventrally and constricted between the TPas and teeth, and their dental muscles penetrate foramina in the DP and attach to the OP (see Smith, 1940:text-fig. 2; Murakami, 1963:pl. 2 figs.8–16 pl. 5, figs. 33–52).

Buccal funnels are present in both sister clades of Ophiactidae recognized by O'Hara et al. (2017:427). In *Ophiactis quinqueradia* Ljungman, 1872 [LACM 1939-213.10] and *Ophiactis savignyi* [LACM E.1936-29.9], members of the clade with "two distal oral papillae," the funnel is bounded by columns of teeth that narrow toward the dorsal and ventral ends of the DP. The vT is the smallest tooth and the succeeding teeth increase in breadth and length to a point, beyond which teeth continue to increase in length but progressively decrease in breadth. The broad, ventral teeth are imbricate, and have thickened lateral edges. Their concave proximal surface forms a flange that partially overlaps the base of the tooth above and often bears a dorsomedial cusp. The relatively long, narrow dorsal teeth are compressed and may have a rhombic cross section, and their convex proximal tip is capped with imperforate stereom. When the jaws are closed, the teeth on adjacent jaws intermesh. The concave, imbricate, ventral teeth enclose a conical space that narrows dorsally and is constricted and blocked by the long dorsal teeth. Because several ventral teeth are narrower than those above, their radial edges do not intermesh with teeth on the adjacent jaws, leaving radially positioned gaps along the ventral edge of the buccal funnel. Members of the clade characterized by "one distal oral papilla" (*sensu* O'Hara et al., 2017:427) typically have buccal funnels like those of the sister clade (e.g., *Ophiactis carnea* [LACM E.1933-215.1], *Ophiactis asperula* (Philippi, 1858) [LACM E.1927-3.1], *Ophiactis profundi* Lütken and Mortensen, 1899 [LACM 74-207.2], *Hemipholis cordifera* [LACM 1974-264.1], and *Hemipholis gracilis* Verrill, 1867 [LACM 1937-143.1]) (see Bartsch, 1982:fig. 44 *O. asperula*; Hendler, 2011:fig. 1B, E *Hemipholis* spp.). However, *Ophiactis abyssicola* [LACM E.1896-1.1] has an extremely shallow buccal funnel composed of only 2–3 ventral teeth with abruptly tapering, acutely beveled tips, and dorsal teeth with a broad, rounded proximal edge. I could not discern the dorsalmost teeth within intact specimens of *Hemipholis* species, *Ophiactis simplex* (LeConte, 1851) [LACM E.1954-9.8], and *O. asperula* [LACM E.1927-3.1], but *O. asperula* has teeth that are capped with compact stereom (Brogger et al., 2015:fig. 2C). Furthermore, its teeth are configured similarly to *O. quinqueradia* and *O. savignyi*, its OP has a well-developed abradial muscle fossa, and its tooth muscles penetrate foramina in the DP and extend to the OP (see Murakami, 1963:pl. 1 figs. 31–34, pl. 4 figs. 35-42; Bartsch, 1982:figs. 42–47). *Ophiactis resiliens* and *Hemipholis cordifera* [=*Hemipholis elongata*], which are suspension feeders, are known to have papillose tube feet (Pentreath, 1970:figs. 8–11; Hajduk, 1992:figs. 11–14).

According to O'Hara et al. (2017:427) the monogeneric Ophiopholidae are sister to the Ophiotrichidae, and *Ophiopholis* "has generally been considered an ophiactid, however, it does show features characteristic of the Ophiotrichidae, including the incipient fragmentation of the external tooth into a cluster of dental papillae (Martynov, 2010b: pl. 15O)." Nevertheless, ophiotrichid teeth are not fragmented, as noted above, and neither are those of ophiopholids. Specimens of *Ophiopholis* that were examined in the present study have few TPas, and these typically occur in large individuals with numerous, unfragmented teeth (e.g., *Ophiopholis aculeata* [LACM 1965-343.1]). On the basis of their size and position, it appears that ophiopholid TPas develop from minute ossicles on the ventral margin of the DP. TPas of *O. aculeata* are flat [LACM 1965-343.1, E.1937-244.1], and those of *Ophiopholis brachyactis* H.L. Clark, 1911, are globose with an acute projection [LACM 70-303.1]. Teeth of Ophiopholidae that were examined resemble those of Ophiactidae. The broadest teeth occupy the middle of the DP and the longest teeth are at the top of the DP. Ventral teeth are imbricate, broad, concave, and compressed, and their flanged proximal edge partially overlaps the base of the tooth above. Dorsal teeth are narrow and tapering, with a convex tip. They are longer than the imbricate teeth and increase in length dorsally. All but a few of the smallest, ventralmost teeth intermesh in the specimens with closed jaws. Teeth examined with a stereomicroscope appear to lack a cap of imperforate stereom, but it is possible that the stereom is compact. TPas of *O. aculeata* [LACM 1965-343.1] are minute and flat; those of *O. brachyactis* [LACM 70-303.1] are small, globose, and sharply pointed. The proximal edges of ventral teeth lack a medial flange in the species mentioned above and in *Ophiopholis mirabilis* (Duncan, 1879) [LACM 79-227.2], but ventral teeth of *Ophiopholis longispina* H.L. Clark, 1911 [LACM E.1964-297.1] have up to several cusps, and some columns of teeth have pairs of ossicles side by side in place of a single tooth. *Ophiopholis* species have a well-developed abradial muscle fossa, and the dental muscles penetrate foramina in the DP and attach to the OP, and *O. aculeata* has tube feet with numerous mucous secretory papillae (Murakami, 1963:pl. 1, figs. 35–37, pl. 4, figs. 43–46; Wright, 1987:fig.1A; Byrne, 1991:fig. 33).

## DISCUSSION

In the present study, OPa *s.l.* and PeSk ossicles were inferred to be homologous if they were morphologically similar and developed at equivalent skeletogenic sites. Ossicles deemed serially homologous were morphologically similar and developed in a unidirectional sequence, each ossicle arising beside its predecessor. Conceivably, a characteristic spatiotemporal pattern of gene might regulate the sequential development of a row of serially homologous ossicles (Gao et al., 2015; Halfon, 2017). In the discussion below, ophiuroid skeletal morphology, skeletal ontogenesis, and morphogenesis of buccal armature and the jaw are considered. Presumptive homologies of buccal skeletal elements are assessed in the light of previously published literature and results of the present study. The phylogenetic distributions of OPas *s.l.* and PeSk elements are evaluated. Configurations of buccal armature in different ophiuroid taxa are compared and related to functional morphology and feeding behavior.

### ELEMENTS OF ORAL PAPILLAE *sensu lato*

#### Infradental Papilla (IPa), Secondary Infradental Papilla (2°IPa), and Putative "Apical Papillae"

Ljungman (1867) coined the phrase "*papillae orales...infradentalis*." Yet he and subsequent authors who referred to "infradental papillae" at the "proximal angle of the jaw, just below the teeth," failed to consider precisely where IPas originate or where they connect to the jaw (e.g., Mortensen, 1927:199, 206; Thomas. 1962:631; A.M. Clark, 1970:5). As a result, the term "infradental papilla" has been applied to ossicles that are not IPas and are not necessarily homologous (e.g., Matsumoto, 1917:257, fig. 70b, *re* TPas of *Stegophiura vivipara*; Mortensen, 1927:199, *re* vT of *Ophiactis* spp.; Downey, 1967:43, *re* jaw spines of *Astronebris tatafilius* Downey, 1967; Bartsch, 1982:221, *re* vT of *Ophiomyxa vivipara*; Hunter, 2007:47; *re* vT of *Ophiuroglypha* spp.).

Herein, ossicles that are identified as IPas develop on and project from the OP, despite their ostensibly "intimate relationship to the dental plate in the adult" (H.L. Clark, 1914:121; Matsumoto, 1917:166, 377). The notion that IPas form on the DP is rejected (*contra* Martynov, 2010b:31; Stöhr et al., 2012a:5; O'Hara et al., 2018:5). Analyses of ophiuroid skeletogenesis, which were reviewed and described in the present study, indicate that IPas typically develop after the AdShSp and BSc. They form near the DP/OP junction, impinge on the DP and OP in juveniles, and ultimately articulate with the OP and project below the teeth (Hendler, 1988:22, 27, fig. 2B, E). Available information regarding the ontogenesis and placement of IPas is consistent with the interpretation that "infradental papillae are genuine oral papillae," and that they are not homologous with TPas and teeth on the DP (Matsumoto, 1917:377). My previous assertions that IPas "originate on the dental plate and transfer to the tips of the oral plates" and are "homologous with dental papillae or teeth" were based on a misinterpretation of these structures which overlap the DP and OP (Hendler, 1988:22, 27). Turner and Miller (1988:502, fig. 5B) also proposed that IPas "unquestionably arise from the dental plate" in a 0.4-mm-dd juvenile *Microphiopholis atra*. However, at this stage the rudimentary IPa was situated between the BSc, OP, and DP, whereas in a 0.89-mm-dd individual it projected from the OP and beneath the DP (Turner and Miller, 1988:fig. 6B).

The paired IPas of *Amphioplus abditus* (Gnathophiurina: Amphiuridae) have a prismatic shape and overlap a modified, triangular vT. This triad of vT and IPas is strikingly similar to the homologous OPas *s.l.* of *Ophioplocus januarii* (Ophionereidina: Hemieuryalidae) (compare: Fig. 25C, D and Bartsch, 1982:245, fig. 71). My interpretation of these structures is at odds with assertions that the triads consist of three teeth, and that the IPas "cannot strictly be called infradental since [they are] offset to the side of the tooth" (A.M. Clark, 1970:36, fig. 8a; Martynov 2010:31, fig. 15K–M).

Amphiurid IPas vary considerably in shape (see A.M. Clark, 1970:fig. 8), but they have typically been characterized as "block-like" (e.g., Thomas, 1962:631). Furthermore, IPas were regarded as an exclusive feature of Amphiuridae, and on this basis species in other families that have IPas were mistakenly identified as Amphiuridae (Thomas, 1967:123; Gondim et al., 2016:383). Ophiurida were not acknowledged to have IPas, even though they typically develop a pair of ossicles at the DP/OP juncture, after the tooth, AdShSp, and BSc have formed (e.g., Murakami, 1941; Webb and Tyler, 1985; Sumida et al., 1998; Stöhr, 2005). In striking contrast to the Amphiuridae, IPas of Ophiurida may not remain at the tip of the jaw throughout ontogenesis, because as the jaw increases in length a gap opens between the IPa and DP, in which a new ossicle develops beside the proximal edge of the initial IPa. Since this new ossicle develops at the DP/OP juncture and is borne on the OP, like the initial IPa, it was herein designated a secondary IPa (2°IPa). One or more 2°IPas may develop as the juvenile matures, arising in a unidirectional sequence, each one forming proximal to the previous 2°IPa. Although these serially homologous primary and secondary IPas form a serried row proximal to the BSc, their origin at the DP/OP juncture indicates they are not homologous with a BSc, tooth, or TPa.

A specious term, "apical papilla," has been applied to IPas, teeth, and TPas. It was ambiguously defined as "oral papilla at tip of jaw, often homologous to first tooth; may be single or in cluster" (Stöhr et al., 2012a:5). Application of this term to structures on the DP as well as on the OP has been a source of confusion. For example, the unequivocal IPas of *Amphiura complanata* Ljungman, 1867, were referred to as apical papillae (Borges et al., 2015:375). *Amphilepis neozelandica* was described as having a "cuspidate ventralmost tooth" on some jaws and "apical papillae" on other jaws, but these supposedly different types of ossicles were teeth at different stages of maturity (see Mills and O'Hara, 2010:fig. 2). Teeth and TPas on the DP of *Bathypectinura heros* [=*Bathypectinura gotoi*] were variously termed "apical papillae," "unpaired infradental papilla," and "cleft" teeth (Matsumoto, 1917:321; Madsen, 1973:141).

Ossicles have been identified as "apical papillae" because it was assumed there must either be an "unpaired infradental papilla" or "paired infradental papillae" at the ventral apex of an ophiuroid jaw (see Fell, 1960:6 couplet 22). However, ophiuroid OPas *s.l.* are arranged in a bilaterally symmetrical series on the jaw's OPs, and as a general rule have an unpaired ossicle at the apex of the jaw, which is either a tooth or a TPa borne on the DP. For example, *Ophioplinthaca grenadensis* John and Clark, 1954, was stated to have an "oral papilla...below the teeth, at the apex," but was figured as having a large vT on the DP (John and Clark, 1954:153, fig. 6). Likewise, the TPas and vT that were figured on the DP of *Ophiura albida*, were identified as "three apical papillae located at the proximal tips of the jaw" (Boos, 2012:114, fig. 1b). Plainly, the term "apical papilla" is imprecise, ambiguous, and a source of confusion. If its use were discontinued, ophiuroid oral armature could be described more consistently and accurately.

### Teeth and Tooth Papillae (TPas)

Historically, OPas *s.l.* borne on the DP were distinguished based on their size, shape, and position. Large ossicles aligned in a column were referred to as teeth ("Zähne") and clustered rows of smaller ossicles were called tooth papillae, mouth-angle papillae, or dental papillae ("Zahnpapillen" or "Mundeckpapillen") (Müller and Troschel, 1842:82; Müller, 1854:197; Lütken, 1858:13; Ljungman, 1867:328, 330; H.L. Clark,1914:115). Teeth range in shape from broad and blunt to slender and spiniform, occupy varied patterns on the DP, and connect to different types of ArtSs such as fossae, and single or paired foramina that may be surrounded by a raised rim (Cuénot, 1888; Smith, 1940; Murakami, 1963; Candia-Carnevali et al., 1994; Martynov, 2010b:114, figs.11–14). Teeth may be tipped with reinforced stereom and may have a cap composed of imperforate stereom (Mortensen, 1927; Devaney, 1970; Candia-Carnevali et al., 1994; Medeiros-Bergen, 1996; Brogger et al., 2015). The adaptive significance and specializations of TPas and teeth are considered below (see "Contrasting Modes of Macrophagous and Microphagous Feeding" and "Buccal Funnel" in the Discussion).

Among species examined in the present study, and possibly in all ophiuroids, teeth on opposing jaws form staggered series and may be unequal in number on different jaws. This has generally escaped notice, because dorsal teeth are concealed when ophiuroids are examined in the customary manner for purposes of identification. Staggered arrangement of teeth is established during ontogenesis and must involve adjustments in the sequence of development and the rate of growth of teeth on opposing jaws, as noted herein in the treatment of *Ophioderma rubicunda*. Movements of the teeth are effected by dental muscles that penetrate the DP and insert on the OP (Cuénot, 1888). On account of their mobility and because of the alternating arrangement of teeth on opposing jaws, the tapered proximo-lateral edges of opposing teeth interlock when the jaws close together. The functional consequence of this morphology is discussed below (see "Intermeshed and Opercular OPas *s.l.*" in the Discussion).

In early studies of Ophiuroidea, TPas were reported in Ophiocomidae and Ophiotrichidae and were presumed to be limited to these taxa. MacBride (1906:493) maintained that "tooth-papillae" are rare, and that "mouth-papillae and tooth-papillae are present at the same time...only in a restricted number of genera (*Ophiocoma* and its allies)." This interpretation persisted in contemporary literature, where TPas are defined as a "cluster of short, granule-like apical papillae on the dental plate in Ophiotrichidae and Ophiocomidae. [The TPas are] Not to be confused with the cluster of larger, pointed apical papillae in some Ophiacanthidae" (Stöhr et al., 2012a:5).

Nevertheless, the perception that TPas are limited to Ophiotrichidae and Ophiocomidae was contradicted by Verrill (1899a:36) who asserted that so-called "mouth papillae" of Ophiacanthida, which "stand on the dental plate...should be considered as true tooth-papillae." Although Lyman (1874:261) ventured that TPas are "quite wanting in *Ophiura*," Sumida et al. (1998:297) specified that "mouth papillae" of *Ophiura* spp., which "appear to originate from the dental plate... should be homologous with the teeth and not with the remaining mouth papillae. A more careful examination of the ontogenesis of these papillae is needed before a definite conclusion can be drawn." More recently, O'Hara et al. (2018:9) diagnosed Ophiurina as having a "cluster of teeth on ventral part of dental plate," but in the present study, the pairs of OPas *s.l.* that develop below the teeth on the DP of Ophiurida are considered TPas.

Some authors interpreted all the ossicles on the DP as homologues, whereas others distinguished between teeth "arranged in a single series" and TPas "in several series" (H.L. Clark, 1914:121; Mortensen, 1927:148; Martynov, 2010b:31, 118). H.L. Clark's (1914:115) assertion that "dental papillae are strictly homologous with the teeth" is debatable, because differences in their skeletal ontogenesis, morphology, position, and manner of articulation suggest that different genomic processes regulate the development of TPas and teeth. Disparate developmental programs may be involved in the sequential ontogenesis of TPas and teeth in *Ophiothrix angulata*. Its teeth develop in a linear series at the ventral extremity of the DP, forming a linear series, but it is only "after 4 or 5 teeth are formed, [that the] dental papillae...arise in double, then in triple series..." below the vT, producing a symmetrical cluster comprising multiple columns of small ossicles (H.L. Clark, 1914: 110). As noted above, the TPas of *Ophiothrix fragilis* do not develop from teeth that "divide and shorten… beginning with the vT," (Stöhr, 2005:574, fig. 16; see "Skeletal Ontogenesis of Oral Armature" in the treatment of *Ophiothrix spiculata*).

Accounts of skeletal ontogenesis and morphology that are reviewed and documented herein, indicate that TPas usually arise after teeth, BSc, IPa, and 2°IPas have formed, and that the groups of TPas that develop below the vT may be symmetrically or irregularly arranged. TPas may either develop in postlarvae (e.g., in *Ophiura* spp.) or in relatively large juveniles and adults (e.g., in *Ophiopholis* spp.), and they may be limited to a single pair of ossicles on the DP (e.g., in *Ophioderma* spp.) or become more numerous during ontogenesis (e.g., in *Bathypectinura heros*) (Madsen, 1973:141; present study).

Historically, it was thought that members of the Gorgonocephalidae have mouth spines ("spinae orales," "stachelartigen Papillen") rather than true teeth ("dentes verae") (Müller and Troschel, 1842: 85; Lütken, 1858:13; Ljungman, 1867:335). These spiniform ossicles subsequently were characterized as oral papillae, tooth papillae, and teeth (e.g., Matsumoto, 1917:59; Döderlein, 1927; Baker, 1980; Smith et al., 1995). However, the distinction drawn herein between gorgonocephalid TPas and teeth is problematic because these structures can intergrade and their placement is inconsistent. The dearth of information regarding their ontogenesis is also an impediment to understanding these structures.

In the present study, clustered, spiniform OPas *s.l.* on the ventral edge of the DP of gorgonocephalids were provisionally referred to as TPas, if they and the teeth appreciably differed in shape. It is noteworthy that gorgonocephalids may use these spiniform OPas *s.l.* to disentangle zooplankters from girdle hooklets on their arms (see "Diet, Feeding, and Operation of the Jaws" in the treatment of *Asteroporpa annulata*). In this regard, it is not surprising that Triassic *Aspiduriella streichani* (Kutscher, 1987), which is "a basal member of the euryalid clade," had "lateral arm plates, spine articulation morphology… and …hourglass-shaped vertebral articulation pegs [that] bear clear euryalid traits" (Thuy, 2015:186; Thuy and Stöhr, 2018:1). However, it had "five leaf-shaped ("blattartigen")" or "block-like…oral papillae" and appeared to lack buccal spines and girdle hooklets—quite unlike gorgonocephalids (Kutscher, 1987:704; Thuy, 2015:186–187; Thuy and Stöhr, 2018:6). Middle Triassic *Aspiduriella scutellata* (Blumenbach, 1804) had compressed, truncate "lateral oral papillae forming a continuous row" and what were described as "two to three block-like papillae" on the edges of VAP-1 (Thuy and Stöhr, 2018:5). Judging from their dissimilar buccal armature, it would seem the feeding habits of basal Euryalida were unlike modern Gorgonocephalidae. Remarkably, the shallow VAP-1 fringed with papillae (VAP-1 TScs), which was present in *A. scutellata* (Thuy and Stöhr, 2018:fig. 3B), is more similar to the structure in modern Ophiurina than in modern Euryalida.

### Buccal Scale (BSc)

Buccal scales were discovered in juvenile *Amphipholis squamata* [=*Ophiolepis squamata*] and described as spoon-shaped calcareous blades ("löffelförmige Kalkblätter") (Schultze, 1852:42). Ludwig's (1878, 1882) conjecture that they are ambulacral ossicles that develop into PPs was refuted by zur Strassen (1901), who demonstrated that there are PPs in adult *A. squamata*, even though "spoon shaped ossicles" are resorbed in the juvenile stage. Paradoxically, zur Strassen's discovery was disregarded, and Ludwig's interpretation of Asterozoan homologies persisted in the literature (e.g., Hyman, 1955). However, the rediscovery of a "spoon shaped ossicle" in juvenile *Amphioplus abditus* marked a turning point in this controversy. In the latter species, this ossicle was shown to develop into the OPa *s.l.* that had been erroneously regarded as a "tentacle-scale of the first oral tentacle," and it was renamed the "buccal scale" (compare: Hendler 1978, 1988, with Lyman 1874:263; Verrill, 1899a:25; A.M. Clark, 1970:4-5). Subsequent investigations revealed the occurrence of putatively homologous BScs in other ophiuroids (e.g., Hendler, 1988:355; Sumida et al., 1998:297; Stöhr, 2005:545).

BScs develop on the OPR, distal to the DP/OP juncture. In juvenile individuals, they are elongated and often curved, extending nearly the full length of the OSl, and opercular BScs on opposing jaws can block the OSl. Its function in the juvenile stage may be performed by other OPas *s.l.* in the adult (see "Feeding and Locomotory Adaptations of Juvenile Ophiuroids" in the Discussion). A suggestion that the BSc "splits into several smaller papillae" as it develops is unsubstantiated (*contra* Stöhr, 2005:573). BScs are among the first-formed OPas *s.l.* of *Amphioplus abditus* and *Amphipholis squamata*, but the BScs of *Amphiophiura sculpta* [=*Stegophiura sculpta*] do not appear until the juvenile has four arm segments (Ludwig, 1882; Murakami, 1940, 1941; Hendler, 1978). It is not known whether this distinction is typical of amphiurids and ophiopyrgids in general, because ontogentic processes in members of these families have not yet been systematically documented. The BSc arises near the middle of the jaw in both families, but it is displaced by the growth of the OP and by the development of additional OPas *s.l.*, which differ between amphiurids and ophiopyrgids. These disparities in the ontogenesis and position of BScs cast some doubt on the homology of BScs in Amphilepidida and Ophiurida.

The BSc has been described as the "distalmost oral papilla, wide and low, at the oral plate" (Stöhr et al., 2012a:2), but BScs are commonly proximal to a larger, operculate AdShSp in adult Ophionereidina. Although BScs were stated to "persist into the adult stage… in presumably paedomorphic taxa" (Martynov, 2010b:23), they are evident in non-paedomorphic adult Ophionereididae and Ophiolepididae and are less conspicuous in presumptively nonpaedomorphic, adult Ophiactidae, Ophiothamnidae, Amphiuridae, and Amphilepididae, owing to differential allometric growth of the BSc and OP during ontogenesis (Figs. 19, 23; examples in Hendler, 1988; Stöhr, 2005; Falkner and Byrne, 2006). Negative allometric growth and resorption may account for the loss of BScs during the ontogenesis of some species, for example, in *A. squamata* (Hendler, 1978, 1988).

### Lateral Oral Papilla (LOPa)

The term "lateral oral papilla" previously was applied to oral papillae in a general sense or more specifically to oral papillae on the ventrolateral edge of the jaw (e.g., Verrill 1899:206; Fell 1960:7; Martynov and Litvinova, 2008:98,108; Stöhr and Muths, 2010:833; Boos, 2012:114; Paim et al., 2015:2; Thuy et al., 2015:926; Thuy and Stöhr, 2016:16; Alitto et al., 2018). However, in the present study the term "LOPa" specifically refers to ossicles that develop on the OP and distal to the IPa, which are not a 2°IPa, BSc, AdShSp, or 2°AdShSp. Serially homologous LOPas develop in a unidirectional, linear sequence as each new ossicle arises distal to its predecessor. In the present study, this distalward, sequential pattern of skeletogenesis was detected in juvenile *Ophiomyxa flaccida* and *Ophioderma rubicunda*. In other species with multiple LOPas (e.g., *Ophiolimna bairdi*, *Ophiocomina nigra*) this ontogenetic pattern was not corroborated by the sizes of ossicles in the adult stage, because size and shape of LOPas could not be correlated with the order in which they developed.

LOPas of Ophiodermatina, such as *O. rubicunda* and *Ophiarachnella gorgonia* [LACM E.1959-317.1], are serried ossicles that cover and presumably protect the OSl and OTs. These species have dorsoventrally compressed, horizontally projecting TPas, slender, obliquely tilted LOPas, a dorsoventrally compressed, opercular AdShSp and 2°AdShSp, and a LyOs. When their jaws close, opposing TPas meet, IPas and LOPas interlock with their counterparts, lateral edges of AdShSps, 2°AdShSps, and LyOss abut, and vT overlap and intermesh. In contrast, the LOPas of *Ophiacantha* spp. are comparatively few in number and spiniform. LOPas may compose the distinctive cluster of OPas *s.l.* beside the vTCt of *Ophiocamax* spp. (see Martynov and Litvinova, 2008:fig. 16).

### Adoral Shield Spine (AdShSp), 2° Adoral Shield Spine (2°AdShSp), and Tentacle Scale of VAP-1 (VAP-1 TSc)

Müller (1846:299) discovered that the planktonic, newly metamorphosed *Ophiura albida* [=*Pluteus paradoxus*] could actively move a microscopic spine beside each of its OTs-2 ("Diese Stacheln kann das Thier willkürlich bewegen"), and a homologous spine later was found to articulate with the AdSh of newly metamorphosed *Amphipholis squamata* (Schultze, 1852; Ludwig, 1882). Because Fewkes (1887:134) established that the AdSh is homologous with the spine-bearing lateral arm plates, the spine borne on the AdSh was designated an "adoral shield spine" (Hendler, 1978). The present study shows that during ontogenesis, the spiniform AdShSp of juvenile *Ophioderma rubicundum* becomes compressed in shape like a TSc (Fig. 13A, H). In *Amphioplus abditus* juvenile AdShSps undergo a similar ontogenetic transformation (Hendler, 1978:Figs. 3A, 5B). However, adults of some ophiuroids, such as the ophiacanthid *Ophiomedea duplicata* Koehler, 1906, and the ophioscolecid *Ophioscolex glacialis*, have a long, tapering AdShSp that resembles an arm spine. The AdShSp of *O. glacialis* has a bulbous base, like the arm spine, but it has not been determined if the AdShSp and the arm spine have similar ArtSs (see Stöhr, 2005:fig. 2; Martynov, 2010:fig. 50).

The position of the AdShSp can change during ontogenesis, and ultimately it may remain on the AdSh (as in *Ophioderma rubicunda*: Fig. 13), overlap the AdSh and the OP (as in *Ophiolepis paucispina*: Fig. 19), or articulate with the OP (as in *Ophionereis olivacea*: Fig. 23) (Hendler, 1978, 1988, 1998; Martynov et al., 2015). Translocations of AdShSps are created by ontogenetic changes in the size and shape of the AdSh and OP, and probably involve alterations in the connective tissue around the base of the AdShSp. Although displacement of the AdShSp has been interpreted as "transforming" the spine into a "distalmost oral papilla" or a "mouth papilla" (e.g. Stöhr, 2005:545, 574; Martynov et al., 2015:38), this is a "transformation" in name only, because the AdShSp and 2°AdShSps are not homologous with other types of OPas *s.l.* that develop on the OP.

Typically, the AdShSp is located adjacent to the orifice of the vTCt and overlaps the OSl, but in various species it may be opercular or spiniform, and it may articulate with the OP or the AdSh. Because of these variations in their morphology and placement, the discrete homology of AdShSps was long overlooked. For example, in Ophiocomidae the AdShSp was simply referred to as the "outer oral papilla" (Devaney, 1970:2, fig. 1). The spine-shaped AdShSps of Ophioscolecidae and Ophiacanthidae have the appearance of potential defensive structures. In contrast, *Ophiomusa lymani*, *Ophioderma rubicunda*, and *Ophiolepis impressa* have a distinctly opercular AdShSp that overlaps the vCtP or LyOs, enclosing the vTCt and OSl. In these species, the obvious protective function of the AdShSp, LyOs, and vCtP could account for the increasing size of OPas *s.l.* toward the wide, distal end of the OSl, and their protective function may explain why "In different families oral papillae are differentiated, distalmost papillae often modified into wider and operculiform shape, proximal papillae narrower" (Martynov, 2010:23) (see "Intermeshed and Opercular OPas *s.l.*" in the Discussion). If the function of the AdShSp is defensive and protective, it would seem counterintuitive that many Ophiurina have a lightly armored, superficial vTCt orifice that is surrounded by very small OPas *s.l.* including a small AdShSp. Nevertheless, *Ophioplinthus gelida*, an ophiurine species, has homologous structures that completely seal the vTCt.

The strange, ephemeral AdShSps of *Ophiolycus purpureus*, *Ophioscolex corynetes*, *Amphilepis norvegica*, and *Amphilepis ingolfiana* are resorbed or autotomized during ontogenesis, and AdShSps fail to develop in Euryalida and Ophiotrichidae (Mortensen, 1912, 1933b; H.L. Clark, 1914; Bartsch, 1985; Stöhr, 2005; present study). *Asteronyx loveni*, a species of Euryalida, does not have spines on the AdSh and LAP-2, and its juvenile does not develop any arm spines until it has more than five ASs. At this stage, hooked ASps begin to form on distal arm segments, but development of ASps on proximal arm segments is greatly delayed, and ASps fail to develop on LAP-2 (Mortensen, 1912:pl.14, figs. 2–4). These manifestations of the postdisplacement of arm spine development, in *A. loveni*, hint that a similar heterochronic process might account for the pervasive absence of spines on the AdSh and LAP-2 among all Euryalida. The functional significance of this peculiar morphology is not known, but delayed development of hooked spines in *A. loveni* could conceivably be related to the drastic difference in body shape between the the postlarva and juvenile, and in *Gorgonocephalus* spp. the absence of basal ASps might be related to the symbiosis of juveniles within the gastrovascular cavity of Alcyonacea (Mortensen, 1912:pl. 14; Hendler, 1991:431). Notably, epizoic postlarvae and the adults of *Ophiothrix fragilis* also have hooked ASps lack AdShSps (see Stöhr, 2005:fig. 16A–C; "Feeding and Locomotory Adaptations of Juvenile Ophiuroids" in the Discussion).

Previously, OPas *s.l.* that develop beside the AdShSp of juvenile Amphiuridae and *Ophiomusa lymani* [=*Ophiomusium lymani*] were referred to as the "third oral papilla," "oral plate papilla," and "tentacle scales" (Hendler, 1978, 1988, 1998). In *O. lymani*, two of these elements are incorporated in the serried row of OPas *s.l.* on the OP of the adult. The distal ossicle abuts the AdShSp on the AdSh, and the proximal ossicle overlaps the OP of the adult, but both these ossicles abut the AdSh in the juvenile stage. In the present study, I have designated the serially homologous ossicles that are associated with the AdShSp as "2° adoral shield spines," although it is not clear whether they are homologous with arm spines or tentacle scales. In that regard, it may be significant that the shape of the 2°AdShSp is more similar to a TSc than to an ASp in juvenile *O. rubicunda* and *Ophiolepis paucispina* (Figs. 13F, 19A).

Murakami (1941:75, fig. 9) discovered that the distalmost 2°AdShSp develops before the other 2°AdShSps in *Amphiophiura sculpta* [=*Stegophiura sculpta*], and he found that the TScs develop on the abradial edge of VAP-1 before they form on the vCtP. In other words, each newly formed 2°AdShSp and VAP-1 TSc develops proximal to its precursor, thereby forming the serried rows of ossicles flanking OTPo-2. Although the series of 2°AdShSps are not homologous with the VAP-1 TScs, they have all been conflated as "oral tentacle scales" or "mouth papillae," and they have been described collectively as tentacle scales beside OTPo-2 or as "extra rows of papillae... not in line with ordinary lateral oral papillae-exclusively in the ophiurids" (e.g., Lyman, 1874:264; Paterson, 1985;56; O'Hara and Stöhr, 2006:63, 73; Thuy and Stöhr, 2016:16, fig. 5N). Similar ossicles as these occur in some Ophintegrida. TScs on the VAP-1 that could be homoplasious with their counterparts in Ophiurina occur in the amphilepidid *Amphilepis patens* [LACM 1993-75.19] and in *Ophiopristis axiologus* H.L. Clark, 1909 (H.L. Clark, 1909:pl. 53, fig. 1). The latter species is regarded as an ophiotomid (*vide* O'Hara et al., 2018:13, but its generic placement was queried by O'Hara and Stöhr (2006:73) and Martynov (2010:86).

## ELEMENTS OF PERIBUCCAL SKELETON (PeSk)

### Ventral and Dorsal Compartment Plate (CtP), Compartment Ossicle (CtOs), and Collar Ossicle (CoOs)

The "tentacle compartment" (TCt) enclosure, which surrounds and protects the base of an OT, comprises PeSk ossicles that are interconnected with one another and with the OP. In contrast to OPas *s.l.*, these ossicles do not moveably articulate with the OP. CtPs often are the largest elements of the TCt and usually attach to the OPR. Smaller CtOss that arise on the free edge of the CtP or OPR, and imbricate CoOss that adjoin the CtOss may form a tubular collar that encloses the base of the OT. In the present study, the vCtP was found to develop on the ventral edge of the OPR of juvenile *Ophioderma rubicunda*, *Ophiolepis paucispina*, *Ophionereis olivacea*, and *Ophiura luetkenii*. In the latter species, the dCtP arose on the dorsal edge of the OPR, and the vCtP was overgrown by VAP-1 TScs (Fig. 5).

Lyman was the first observer to mention components of the TCts, and he aptly described CtOss of *Ophiura*, *Ophiarachnella*, *Ophioderma*, and *Ophiolepis* as "a tube of lime scales" (Lyman, 1882:19). Although he failed to distinguish between LyOs and the vCtP in *Ophiocoma* and *Ophioderma*, he graphically described the vCtP as "the piece. . .which gives the forked look to the mouth-slit" of *Ophiura* (Lyman, 1874:223, 258, 264). This striking Y-shaped mouth structure of Ophiurina derives from a juxtaposition of the OSl with paired vTCts that are fringed by VAP-1 TScs, 2°AdShSps, and AdShSps (see "Clade-Specific Configurations of Buccal Armature" and "Putative Paedomorphic 'OTPo-2' of Ophiurina" in the Discussion).

Amazingly, apart from Lyman's writings and Mortensen's (1936:309, fig. 34a) perfunctory reference to "a small supplementary plate" abutting VAP-1 of *Ophiogona doederleini* (Koehler, 1901) (Ophiopyrgidae), the vCtP of Ophiurida seems previously to have escaped notice, even in instances where it was manifestly obvious, as in Madsen's (1956:fig. 2a, d) illustration of *Ophiura* (*Ophiuroglypha*) *irrorata loveni* (Lyman, 1878) [=*Ophiura loveni*]. A vCtP is figured—but not mentioned—in descriptions of Pliocene *Ophiura paucilepis* Stöhr et al., 2011, Late Cretaceous *Felderophiura vanderhami* Jagt, 1991, and extant *Spinophiura jolliveti* (Jagt, 1991:199, fig. 2B, D; Stöhr and Segonzac, 2006:16, figs. 2D, 4D; Stöhr et al., 2011:116, fig. 3K). Curiously, vCtPs were depicted as an extension of the OP or VAP-1, and they were implied in line drawings by several interconnected ossicles proximal to VAP-1 (e.g., Berry, 1934:pl. 3, fig. 14; Patterson, 1985:fig. 48). Lyman (1883:259, pl.6, fig. 82) remarked that the VAP-1 of *Ophiomitrella laevipellis* (Lyman, 1883), an ophiacanthid, "carries on its inner edge two scale-like papillae," and Verrill (1899a:43) astutely observed that these "special. . .tentacle-papillae" on VAP-1 ". . .could not be distinguished from the solid, immoveable, crest-like lobes, which are present on these plates in the same position in many species, including *O*[*phiacantha*] *bidentata*." Clearly, the structures to which Lyman and Verrill referred were vCtPs (see Fig. 16A, B).

Morphology of the vCtP bears directly on questions regarding the structure of ophiurid vTCts, and whether the "second oral tentacle pore" opens "superficially outside the mouth slit or . . .outside but entering the mouth slit via a furrow" (Paterson, 1985:102). A lack of agreement regarding the location and shape of these so-called "pores" and whether they open outside or inside the mouth is evident in the unresolved exchange between Koehler (1904; 1922a:353) and H.L. Clark (1908:295). Their impasse led Matsumoto (1917:247) to question the systematic value of the "second oral tentacle pores," and led (Fell 1960:6) to characterize "the second oral tentacle pores" of all ophiurids as "more or less entirely outside the oral slits." Other investigators asserted "The position of the second tentacle pore inside the mouth is evidently the developed state, its position outside the mouth in adult specimens is paedomorphic" (Martynov and Litvinova, 2008:88; Stöhr and Martynov, 2016:16). Surprisingly, the "OTPo-2" *per se* was never defined, and its boundary was never delineated. However, in postlarval ophiuroids the OTPo-2 may simply be viewed as the gap between VAP-1 and the AdSh through which OT-2 protrudes, whereas in adult ophiuroids, the "pore" is incorporated in a multi-element vTCt whose shape is molded by the morphogenetic changes in the OP, vCtP, LyOs, OPas *s.l.*, and PeSk (see "Ossicle 'Migration' and Ontogenesis of the Oral Plate," and "Putative Paedomorphic 'OTPo-2' of Ophiurina" in the Discussion).

### Lyman's Ossicle (LyOs)

LyOs abuts the vCtP and VAP-1, and may adjoin the AdSh in adult ophiuroids. It is stouter than the vCtP, protrudes from the distal edge of the OSl between the AdSh and VAP-1, and may overlap the latter plate. In the present study, LyOs was found to develop inside the OSl and in contact with the vCtP of *Ophioderma rubicunda*, *Ophiolepis paucsipina*, and *Ophionereis olivacea*, rather than on the OP or AdSh like an OPa *s.l.* Based on its morphology, development, and position, LyOs is deemed a PeSk element, and may be a homologue of a vCtP or vCtOs, but the shape and stereom microstructure of a LyOs can conform to that of adjacent OPas *s.l.* Because of this resemblance, LyOss previously were referred to as a "buccal tentacle scale," "distal oral papilla," "chilophiurid-type distal oral tentacle scale," or as a tentacle scale of OT-2 in taxonomic descriptions of Ophiomyxidae, Ophionereididae, and other families of Amphilepidida and Ophiacanthida (e.g., Ludwig, 1878:361, fig. 10; H.L. Clark, 1901:248; Matsumoto, 1917:233; A.M. Clark, 1970:70; Devaney, 1970:3; figs. 1–3, 7; Bartsch, 1974:101; A.M. Clark and Courtman-Stock, 1976:262; Madsen 1983:33; Vadon, 1990:172; Monteiro et al., 1992:46; Benavides-Serrato and O'Hara, 2008:52, fig. 1C).

LyOs was discovered in *Ophiarachnella gorgonia* [=*Pectinura marmorata*] and described as "...a long papilla which stretches upward into the mouth-slit, and embraces the second mouth-tentacle; its base rests on the side mouth-shield and on the first under arm-plate." It was also reported to occur ". . .in other genera, *Ophiocoma*, *Ophiura* [=*Ophioderma*], etc., and . . . reckoned among the true mouth-papillae" (Lyman, 1865:27; 1874:223). Matsumoto (1915:74) regarded LyOs as an "oral papilla" that is diagnostic of the order Chilophiurida Matsumoto (i.e., Ophiolepididae, Ophioleucidae, Ophiodermatidae, Ophiochitonidae, Ophiocomidae), and Madsen (1983:32) considered LyOss "scales of second oral tentacle pore within oral slit," and a diagnostic feature of Ophioleucidae.

LyOss of Ophiodermatidae, Ophiocomidae, Ophionereididae, and Ophiolepididae are robust, protuberant, and usually associated with a large, opercular AdShSp. Less conspicuous ossicles that resemble LyOss were observed in specimens of Ophioleucidae, Ophiopsilidae, Amphilimnidae, Clarkcomidae, and Ophiopteridae. However, their morphology and skeletogenesis have not been examined in sufficient detail to determine whether they are homologous with one another, with LyOss, or with vCtPs. *Ophiopsila californica* [LACM E.1941-365.5], *Amphilimna olivacea* [LACM 1999-55.1], *Ophioleuce seminudum* Koehler, 1904 [LACM E.1934-333.1], and *Ophiernus adspersus* Lyman, 1883[LACM 78-226.1] have a thin, arched ossicle abutting the VAP-1 and AdSh, and possibly adjoining the vCtP in the latter two species. In *O. adspersus*, the LyOs-like ossicles are strikingly similar in shape to the enlarged tentacle scales on the VAPs of the basal ASs (see Madsen, 1977:fig. 3f). *Clarkcoma bollonsi* [LACM E.1951.79.1] and *Clarkcoma pulchra* [LACM E.1972-450.1] had 1–2 small ossicles on the ventral edge of the vCtP, which abutted VAP-1. Previously, these LyOs-like ossicles were identified in *Clarkcoma pulchra* [=*Clarkcoma canaliculata*] as the "buccal tentacle scale" and "accessory oral papillae" (Devaney, 1970:fig. 1). *Ophiopteris antipodum* [LACM E.1964-298.1] and *Ophiopteris papillosa* [LACM E.1960-313.3] have a small ossicle on the ventral edge of the vCtP, which adjoins the VAP-1 but not the AdSh, and which somewhat resembles the vCtOss of *Ophiophthalmus normani* (Fig. 17A).

An ossicle that may be a LyOs or a vCtP, which abutted a "leaf-like" AdShSp, was figured in the Jurassic ophiolepidid, *Eozonella bergeri*. It was described as the "distalmost [oral] papilla pointed, slightly curved, sitting on the border between the adoral shield and the first ventral arm plate" (Thuy et al., 2013:421, fig. 7A, D). *Palaeocoma milleri* (Phillips, 1829), a Jurassic ophiodermatid, has a similar ossicle that was identified as the "scale of the second oral tentacle" (Jaselli, 2015:191, fig. 7; Thuy and Stöhr, 2016).

### Ludwig's Ossicle (LuOs)

LuOss are squamous ossicles that reinforce the integument covering the PG and form a partition between the gap and the buccal cavity. Ludwig (1878:363, pl. 24, fig. 9B1) discovered these eponymous structures in *Ophiarachna incrassata*, but he described them as rudimentarily developed VAPs that safeguard the radial water canal and nerve ("gegen die Aussenwelt abschliessen"). However, VAPs arise proximal to the TP, whereas the LuOss develop within the buccal cavity. Ludwig (1878:363, pl. 24, fig. 10B2) characterized the VAP-1 of *O. incrassata* as bent ("gebogen"), because its proximal lobe curves upward into the OSl. Typically, the ventralmost LuOss abut this tapering, proximal projection of VAP-1, and dorsal LuOss range toward, and may overlap, the FPs. The bent surface of VAP-1 follows the curvature of the water vascular canal, hemal and perihemal vessels, and nerve cord where they exit the arm and enter the oral frame. Just as VAPs protect the radial water vascular canal, hemal, and perihemal vessel, and nerve cord that are within the arm, VAP-1 and LuOss protect extensions of these structures within the PGs, forming a partition that separates them from the buccal cavity. VAP-1 and LuOss also shield the adradial muscles within the PG.

VAP-1 and LuOs have the same function in the juvenile as in the adult, judging from their ontogenesis in *Ophioderma rubicunda* (Fig. 13). In the earliest postlarval stage examined, VAP-1 extends between the OPR and the proximal edge of LAP-2, enclosing the rudimentary PG. As the juvenile grows, the OP enlarges, thereby increasing the depth of the OSl and the distance between OPR and LAP-2. Concurrently, VAP-1 lengthens, maintaining contact with the OPR and LAP-2 for some time, and LuOss proliferate dorsalward, covering the PG. Ultimately, VAP-1 encloses the ventral portion of the PG, and the LuOss, FPs, circumoral esophageal ligament, and buccal integument enclose the remainder of the gap (Fig. 12).

### Falcate Plate (FP)

Falcate plates arch over the OTs-1, between the OPR and the dorsal edge of the OP, and they demarcate the dorsal rim of the dTCt. It is noteworthy that the nerve ring, which occupies a groove encircling the OPs, is shielded by the FPs and PPs that overlap the neural groove. Adjacent FPs between adjacent jaws, which are sheathed in integument and may be overlain by LuOss, can form a continuous arch that spans adjacent dTCts (e.g., see *Ophiocoma echinata*, Fig. 9C–E; *Ophiophthamus normani*, Fig. 17G–L). FPs may be slender, stout, bar shaped, or broad and flat, and as their name indicates, they are typically crescentic and tapering at one or both ends. Adradial edges of the FPs on adjacent jaws abut perradially, and an abradial extension of the FP arches over OT-1 and toward the OP. Remarkably, overlapping FPs are the only substantial skeletal elements that buttress the dorsal portion of the PGs of *Ophiothrix spiculata* and *Amphioplus abditus*. The FP of *O. spiculata* frames a distinctive gap beside the tentacle basin of OT-1, which may be traversed by a branch of the radial nerve cord innervating the tentacle (Figs. 25C, D, 26B, C). Previously, FPs of juvenile *Amphioplus abditus* were misidentified as "thin, boomerang-shaped. . .buccal tube foot scales" beside OT-1 (Hendler, 1978:87). Similar ossicles in juvenile *Amphipholis squamata* and *Asteronyx loveni*, which were construed to be a VAP or rudiments of vertebrae, were probably FPs or LuOs (see zur Strassen, 1901:614, figs. 2, 4; Mortensen, 1912:288, pl. 15; Sollas and Sollas, 1912:228, fig. 5).

### Oral Plate Ridge Spine (OPRSp)

OPRSps project into the OSl and are rigidly attached, but not fused, to the proximal edge of the OPR (Fig. 9H). These PeSk elements were originally documented in *Ophiarachna incrassata* (Ophiomyxidae) and termed internal oral papillae ("inneren Mundpapillen") (Ludwig, 1878:362, pl. 24, figs. 8, 11). Similar spiniform structures were described as "a small pointed protuberance from the innermost foot pore extending obliquely into the mouth" of *Ophioderma variegata* (Lütken, 1856), and as "a conspicuous pointed papilla as large as the largest of the oral papillae" of *Ophioderma pentacantha* H.L. Clark, 1917 (Nielsen, 1932:330, Fig. 36A, B; H.L. Clark, 1917:444). In the present study, OPRSps on the proximal edge of the OPR were described in *Ophiomyxa flaccida* (Ophiomyxidae), *Ophiocoma echinata* (Ophiocomidae), and *Ophioderma rubicunda* (Ophiodermatidae). In the latter species, rudiments of OPRSps developed before a serried row of OPas *s.l.* formed on the ventrolateral edge of the OP (Fig. 13B, D).

Striking morphological differences between the OPRSps of ophiodermatids and ophiocomids imply that they have different functions, and at the same time suggest these ossicles in Ophiocomoidea and Ophiodermatoidea might not be homologous. The tapering, pointed OPRSps of *O. rubicunda* are positioned such that 1–2 spines on adjacent jaws cross or intermesh when the jaws close together. Presumably, these spines can restrain, retain, or even impale prey in the buccal cavity, facilitating the predatory and scavenging feeding behavior of ophiodermatids (Pentreath, 1970; Stancyk, 1974; Dearborn, 1977; Tewes, 1984; Hendler, 1982b). *Ophiocoma echinata*, like most of ophiocomids, consumes mucus-bound bundles of particulate material and fleshy algae plucked from rock surfaces (Chartock, 1983; Sides and Woodley, 1985). The OPRSps of *O. echinata* are tuberculate and anvil shaped, and their flat proximal surfaces occlude when the jaws close, which could account for signs of wear on the adradial face of the anvil (Fig. 9F). These OPRSps likely brace and align the retracted jaws. Presumably, they do not macerate food because they are outside the buccal funnel, but they might help to retain food in the buccal cavity.

Spiniform ossicles resembling OPRSps occur in taxa such as *Asteroporpa annulata*, which have rounded, spine-bearing protuberances on the OP (Fig. 2F, I). *Ophienigma spinilimbatum* (Amphilepidida *incertae sedis*, *sensu* O'Hara et al., 2017) has one or two indeterminate "additional papillae deep in [the] oral cleft," which have the appearance of TCtPs or OPRSps (Stöhr and Segonzac, 2005:389, fig. 4H). However, the "three spinelike papillae. . .at the edge of the first tentacle pore inside the mouth slit" of *Spinophiura jolliveti*, which were assumed to be unique to the species, appear to be the IPa, 2°IPa and BSc that characteristically remain on OPR throughout ontogenesis in Ophiurida (*contra* Stöhr and Segonzac, 2006:11, 20, figs. 2D; 3G, I; 4C, D).

## CHARACTERISTIC CONFIGURATIONS OF OPas *s.l.* AND PeSk OSSICLES OF MAJOR CLADES

### Phylogenetic Distribution of the Elements of Buccal Armature

In the present study, OPas *s.l.* and PeSk ossicles were characterized, and their presumptive homologies were inferred, on the basis of their shape, their position in relation to other jaw elements, and their ontogenesis. However, tentative inferences regarding skeletal homology, which were drawn from this evidence, were not assessed using a phylogenetic approach. This is because the small number of species examined in the present study and the restricted taxonomic sampling in recent phylogenomic investigations of ophiuroid phylogeny would limit the reliability of phylogenetic analysis. Nevertheless, available information regarding the phylogenetic distribution of OPas *s.l.* and PeSk ossicles is set forth below and in Table 1.

Teeth were ubiquitous among species examined in the present study and IPas are widespread in both superorders and most orders of Ophiuroidea. Thus, it is conceivable that teeth are synapomorphies or symplesiomorphies of living ophiuroids. Previously, IPas were mistakenly deemed lacking in Ophiodermatidae, Ophiolepididae, and Hemieuryalidae (Ljungman, 1867:303; H.L. Clark, 1908:290; Mortensen, 1927:206, 225, 228; A.M. Clark, 1970:5; Stöhr et al., 2012a:5). However, they occur in every family of Amphilepidida (Ophiothamnidae, Amphiuridae, Amphilepididae, Ophiopsilidae, Ophionereididae, Amphilimnidae, Hemieuryalidae, Ophiolepididae), in Ophiacanthida (e.g., Ophiacanthidae, Ophiocomidae, Ophiomyxidae) and Ophiurida (e.g., Ophiopyrgidae, Ophiuridae, Ophiomusaidae, Ophiosphalmidae), and probably in other taxa, although the skeletal ontogenesis of IPas has not been traced in Ophioleucida, Astrophiuridae, Ophiohelidae, and several families of Ophiacanthida in which they appear to occur (Ljungman, 1867; Mortensen, 1927:224; Thomas, 1967:123; Paterson, 1980:216; Hendler, 1998; O'Hara and Harding, 2015:51; present study). On the other hand, IPas are lacking and may have been secondarily lost in several families of Ophiactoidea (Ophiotrichidae, Ophiopholidae, Ophiactidae), in Ophioscolecida and Euryalida, and in some Ophiurida *incertae sedis* (see "Clade-Specific Configurations of Buccal Armature" in the Discussion). However, it is possible that putative IPas are homoplasious, which if confirmed could account for differences in the shape and position of IPas in various taxa.

TPas were identified in representative species of five ophiuroid orders, and they may also occur in Euryalida (Table 2). They were observed in representative species of every family of Ophiurida (5 families), Ophioscolecida (2 families), Ophiacanthida (10 families), and Ophioleucida (2 families). Among Amphilepidida, they occurred in four of the eight families that possess buccal funnels (i.e., Ophiotrichidae, Ophiopholidae, and Ophiopsilidae, and possibly in a hemieuryalid, *Ophiozonoida obscura*, but not in Ophiactidae, Amphiuridae, Ophionereididae, Ophiolepididae). TPas also were lacking in Ophiopsilidae and Hemieuryalidae, which are two of the eight families of Amphilepidida that develop IPas (listed in Tables 1 and 2). The sporadic occurrence of TPas in the Amphilepidida suggests that they are homoplasious in this order and possibly in other orders. Moreover, the presence of TPas in a family does not indicate they occur in every species. TPas are present in *Ophiarachna incrassata* [LACM E.1939-293.1], but not in confamilial *Ophiomyxa flaccida*, and they are present in *Ophiacantha diplasia* H.L. Clark, 1911 [LACM 38-158.2], but are lacking in *Ophiacantha bidentata*. Nevertheless, TPas are ubiquitous in clades such as the Ophiocomidae and Ophiotrichidae and presumably are homologous among members of each of these taxa.

BScs were identified in growth series of at least 38 species by virtue of their position and shape in juvenile stages, but they appear to be lacking in 20 species for which ontogenetic information is available (Table 3). Among ophiuroids for which data are available, BScs occur in the majority of Ophiurida (at least 15 of 16 spp.) and Amphilepidida (25 of 28 spp.), but were lacking in Ophiotrichidae (2 spp.), Ophiopholidae (1 sp.), and in *Abyssura brevibrachia* Belyaev and Litvinova, 1976 (Belyaev and Litvinova, 1976:fig.1), which is an Ophiurida *incertae sedis*. Published reports of BScs that were reported in several Ophiacanthida (3 of 15 spp.) are problematic, and BScs have not been found in the sister Ophioscolecida (0 of 2 spp.) (see "Clade-Specific Configurations of Buccal Armature" in the Discussion). It was suggested that "absence of the buccal scale may be ancestral for Ophiuroidea because it is lacking in the basal taxa Ophiomyxidae, Ophiacanthidae and possibly Euryalida," but phylogenetic analyses indicate that these taxa are not basal (compare: Stöhr, 2005:573; O'Hara et al., 2017, 2018). However, based on confirmed records of their phylogenetic distribution, BScs could conceivably be a plesiomorphy or synapomorphy of living Ophiuroidea, which was retained in Amphilepidida and Ophiurida and was secondarily lost in the Ophiacanthida, Ophioscolecida, and Euryalida. Conversely, homoplasious BScs might have evolved independently in Amphilepidida and Ophiurida, and ontogenetic differences between the BScs of these groups indicate this is a possibility. Nevertheless, BScs of species within each of these orders could be homologous.

In the present study, LOPas were found exclusively among Ophiacanthida (Table 4). They were identified on the basis of their development between the IPa and the 2°AdShSp or AdShSp, in the ophiacanthids *Ophiacantha bidentata*, *Ophiacantha kokusai*, *Ophiacantha rhachophora*, *Ophiolimna bairdi*, in an ophiotomid *Ophiocomina nigra*, and possibly in an Ophiacanthida *incertae sedis*, *Ophiolamina eprae* (Sumida et al., 1998:fig. 5; Stöhr, 2005:fig. 17; Stöhr and Segonzac, 2006:figs. 6–8; Martynov et al., 2015:fig. 22; see "Skeletal Ontogenesis and Homologies of Oral Armature of Ophiacanthida" in the treatment of *Ophiacantha bidentata*). Additionally, LOPas appeared to be present in Clarkcomidae (*Clarkcoma bollonsi* [LACM E.1951-79.1], *Clarkcoma pulchra* [LACM E.1972-450.1]) and Ophiopteridae (*Ophiopteris antipodum* [LACM E.1964-298.1], *Ophiopteris papillosa* [LACM E.1960-313.3]), on the basis of buccal morphology of adult individuals. LOPas also were identified among Ophiodermatoidea in ontogenetic series of an ophiomyxid (*Ophiomyxa flaccida*), and an ophiodermatid (*Ophioderma rubicunda*), and in adult of an ophiopezid (*Ophiopeza spinosa* [LACM E.1958-250.1]), and Ophiocomidae.

Among Ophiocomidae, a presumptive LOPa was documented between the IPa and 2°AdShSp in *Breviturma* species and in *Ophiocoma* species of the "Pica" species-group (*sensu* Devaney, 1970) excepting *Ophiocoma pusilla* (Brock, 1888) [LACM 1959-313.2] (Table 4). In contrast, LOPas were lacking in all 14 species of the "Scolopendrina" and "Pumila" species-groups of *Ophiocoma* (*sensu* Devaney, 1970) as well as in representative species of *Ophiocomella*, *Ophiomastix*, and *Ophiarthrum*. These disparate lineages of Ophiocomidae, one lacking and the other (except *O. pusilla*) possessing LOPas, correspond to the primary sister clades of Ophiocomidae delineated by O'Hara et al. (2017:S3), which suggests that ophiocomid LOPas may be homologous. However, information regarding the phylogenetic distribution of LOPas among the species of Ophiacanthida is insufficient to assess the homology of LOPas within and between other ophiacanthidan clades.

The suggestion that the AdShSp is a plesiomorphic character of Ophiuroidea (e.g., Stöhr, 2005:574) is corroborated by its nearly ubiquitous occurrence among the taxa examined herein. It was identified in juvenile stages of 21 of the 23 families for which information on postlarval ontogenesis is available, although it fails to develop in Ophiotrichidae, Gorgonocephalidae, and apparently in other Euryalida (based on species listed in Table 3). 2°AdShSps did not occur in any taxa lacking AdShSps, and they did not develop in all the species that have AdShSps. In the present study, 2°AdShSps were seen in exemplars of nine families, possibly 10 including Hemieuryalidae, but they were lacking in *Ophiomyxa flaccida*, *Ophiocten sericeum*, and *Ophiacantha bidentata*, which have AdShSps, and they may be lacking in some Ophiurina *incertae sedis* (see "Clade-Specific Configurations of Buccal Armature" in the Discussion). They previously were figured in juvenile stages of Amphiuridae (e.g., *Amphioplus abditus*), Ophiothamnidae (e.g., *Histampica duplicata*), and Ophiactidae (e.g., *Ophiactis resiliens*), although they were not referred to as 2°AdShSps by the authors (Hendler, 1978; Stöhr, 2005; Falkner and Byrne, 2006).

CtPs, which are the principal PeSk elements incorporated in dorsal and ventral TCts, were prevalent among species examined in the present study, and taxa with well-armored TCts had prominent CtPs bearing groups of CtOss and CoOss. CoOss occurred in fewer species and families examined than CtPs, and vCoOss occurred in fewer taxa than dCoOss (Table 1). However, taxa with an abridged vTCt or reduced PeSk had relatively small and/or few TCt elements. A dCtP and vCtP were lacking in exemplar species of *Asteronyx*, *Asteroporpa*, *Amphioplus*, and *Ophiothrix*. *Ophiocten sericeum* had a shallow vTCt lacking a vCtP, and *Stegophiura nodosa* had a reduced vTCt with a rudimentary vCtP. A panel of multiple vCtOss adjoined the vCtP and overlapped the vTCt of some Ophiacanthida (e.g., *O. echinata*) and Amphilepidida (e.g., *Ophionereis porrecta* and *Ophiolepis impressa*). *Ophiocoma echinata* was exceptional as it lacked a dCtP and dCtOss, but it had dCoOss and vCoOss. *Ophiomyxa flaccida* and *Ophioderma rubicunda* were distinguished by a well-developed tube of imbricate CoOss surrounding OT-1, and *O. flaccida* was the only species that exhibited vCoOss as well as dCoOss.

In the present study, LyOs was documented in exemplar species of Ophiacanthida (Ophiocomidae, Ophiodermatidae, Ophiomyxidae, and Ophiopezidae) and Amphilepidida (Ophiolepididae, Hemieuryalidae, and Ophionereididae), but it was lacking in Ophioscolecida, Ophiurida, and Euryalida. Species of Ophioleucidae, Ophiopsilidae, Amphilimnidae, Clarkcomidae, and Ophiopteridae were found that have LyOs-like ossicles. If future studies confirm that these are LyOs, then LyOs would be recognized in at least six of nine families of Ophiacanthida, five of 11 families of Amphilepidida, and two families of Ophioleucida. The Amphilepidida that appear to lack LyOs *sensu lato* are six families composing the suborder Gnathophiurina, at least several of which have a markedly reduced PeSk.

Among the species investigated herein, FPs were nearly ubiquitous among Ophiurida and Ophintegrida, but a more comprehensive survey is required to accurately ascertain their phylogenetic distribution. FPs were absent in Euryalida and abridged in *Ophiomusa*, which had tentacle compartments heavily covered with connective tissue that may have the same function as the FP. On the other hand, FPs were virtually the only PeSk ossicles in *Amphioplus abditus* and *Ophiothrix spiculata*, aside from PPs and putative vCtOss.

LuOss were widely distributed among the exemplar species of Euryophiurida and Ophintegrida which were examined although the occurrence, quantity, and morphology of LuOss were inconsistent, even among confamilial species. Species with prominent FPs and VAPs-1 had relatively few, irregularly arranged LuOs, for example, among Ophiacanthidae and Ophiuridae. Amphiuridae and Ophiotrichidae, which had prominent FPs but a reduced PeSk, lacked LuOss. On the other hand, exemplar species of Ophiodermatidae, Ophiocomidae, and Ophionereididae, which had a well-armored buccal cavity, presented well-developed columns of imbricating LuOss arrayed in chevrons. The drastic difference between the Ophiodermatina and Ophionereidina, compared to the Gnathophiurida, may be related to their diet, since the latter group, which had a relatively unfortified buccal cavity, has a comparatively fine-grained, non-abrasive diet. PeSk elements were also sparse in *Asteronyx longifissus*, which has FPs but lacks LuOss, and consumes small, soft food items.

Among the species examined herein, OPRSps were restricted to Ophiacanthida. However, OPRSps of ophiomyxids, ophiodermatids, and particularly ophiocomids are dissimilar. It is questionable whether they are homologous among these taxa, and their homology with respect to dCtPs is problematic. Furthermore, some Ophiacanthina (Clarkcomidae, Ophiopteridae, and *Ophiocomina nigra*, an ophiotomid) have truncate ossicles on the OP, which somewhat resemble the anvil-shaped OPRSp of Ophiocomidae, but further study is required to clarify their morphology (see "Buccal Morphology" in the treatment of *Ophiocoma echinata*). Irregularly arranged, spiniform ossicles borne on the OP of Euryalida might conceivably be homologous with OPRSps or with the AOPas that occur in some species of Euryophiurida (see "Clade-Specific Configurations of Buccal Armature" in the Discussion).

### Clade-Specific Configurations of Buccal Armature

On the basis of available information, it appears that Ophiurida, Euryalida, Ophiacanthida, and Amphilepidida have distinctive arrays of buccal armature, which are distinguished by their morphology, their pattern of ontogenesis, and location of their constituent ossicles (Fig. 27; Table 1). Ophiurida are the only ophiuroids with 2°IPas in addition to IPas and BScs, and they typically have an assemblage of papillae flanking the vTCt, which is composed of an AdShSp, and 2°AdShSp(s) that may encroach on the OP, and VAP-1 TSc(s) that may encroach on the vCtP (Fig. 27). The IPa develops near the DP/OP juncture, abutting the proximal tip of the BSc. As the OP lengthens during ontogenesis, 2°IPas arise near the DP/OP juncture in a unidirectional sequence, such that the oldest papillae lie closest to the BSc. 2°AdShSps and VAP-1 TScs develop in a similar, unidirectional sequence, by adding new papillae at the proximal end of the series. TPas may develop on the DP, usually after the 2°IPas have formed, and AOPas may arise between other OPas *s.l.* on the flank of the OP.

Atypical, miniaturized, or paedomorphic deep-sea species that are currently allocated to Ophiopyrgidae and Ophiurida *incertae sedis* (*sensu* O'Hara et al., 2017) typically have a shallow vTCt that remains exposed to view when the jaws are closed, but which may be completely isolated from the OSl (see "Putative Paedomorphic 'OTPo-2' of Ophiurina" in the Discussion). The adults may exhibit a typical array of OPas *s.l.* including an IPa, 2°IPa, BSc, VAP-1 TSc, and AdShSp (e.g., *Uriopha ios*: Paterson, 1980:fig. 3b). But their buccal armature can be abbreviated, and species may lack the vCtP, IPa, and 2°IPa (e.g., *Ophiopyrgus biocalae*: Vadon, 1991:fig. 8); the IPa, 2°IPa, and VAP-1 TSc (e.g., *Bathylepta pacifica*: Belyaev and Litvinova, 1972:fig. 5; *Aspidophiura cherbonnieri* Vadon, 1991:fig. 10); and even the vCtP, IPa, 2°IPa, BSc,VAP-1 TSc, and AdShSp (e.g., *Abyssura brevibrachia*: Belyaev and Litvinova, 1976:fig. 1). The relationship between their buccal armature and their modes of development and feeding is not clear, because these species have not been reared and their feeding behavior has not been observed.

Amphilepidida typically have IPas, BScs, AdShSps, and 2°AdShSps, but the occurence, morphology, and position of these ossicles vary among different families (Fig. 27). In the present study, homologies of the OPas *s.l.* were inferred on the basis of their ontogenesis in *Amphioplus abditus* (Amphiuridae), *Ophionereis olivacea* (Ophionereididae), and *Ophiolepis paucispina* (Ophiolepididae). The same suite of OPas *s.l.* was found in juvenile Ophiopsilidae (*Ophiopsila vittata*), Hemieuryalidae (*Ophioplocus esmarki*), Amphilimnidae (*Amphilimna olivacea*), and Ophiothamnidae (*Histampica* spp.). IPas of *Histampica* spp. are rudimentary, and in some Amphiuridae, the BSc is resorbed during ontogenesis (e.g., *Amphipholis squamata*) or a 2°AdShSp fails to develop (e.g., *Amphiura stimpsonii*) (Hendler, 1988). Amphilepididae (e.g., *Amphilepis ingolfiana*) may resorb the AdShSp, Ophiactidae (e.g., *Hemipholis cordifera*) do not develop an IPa, Ophiopholidae lack IPas and BScs, and Ophiotrichidae lack OPas *s.l.* on the OP and AdSh (Mortensen, 1933a:fig. 32; Thomas, 1967:127, fig. 9; Schoener, 1967:fig. 8; A.M. Clark, 1970:fig. 11D, E, K; Thomas and Schoener, 1972:fig. 2; Turner and Miller, 1988:figs. 5C, 7A–B; Hendler, 1988, 2007:pl. 467, fig. A2; present study). Thus, one or more types of OPas *s.l.* can be lacking in some Amphilepidida, particularly among late-branching Ophiactoidea. LyOs occurs in Ophionereidina and Ophiopsilidae but is lacking in Gnathophiurina (e.g., Amphiuridae and Ophiotrichidae) that have an abridged PeSk. Regarding the two latter families, Matsumoto (1917:378) erroneously contended that other Gnathophiurina lack oral papillae "which arise from the adoral shields," but he astutely observed that "in these forms, in which the masticatory apparatus is well developed, the oral papillae are liable to reduction," and that "*Ophiotrichidae* entirely lack the oral papillae."

The OPas *s.l.* of Ophiacanthida may be block-like or spiniform, and serried as in *Ophioderma rubicunda* or form discontinuous series as in *Ophiacantha bidentata* (Fig. 27). Ophiacanthida may have TPas, IPas, LOPas, 2°AdShSps, and AdShSps, whereas sister Ophioscolecida develop TPas, AdShSps, and an indeterminate series of spiniform ossicles on the dorsolateral surface of the OP (see "Ontogenesis and Skeletal Homologies of Ophiomyxidae and Ophioscolecidae" in the treatment of *Ophiomyxa flaccida*). LOPas might be a unique feature of Ophiacanthida, but based on currently available information it is not clear whether they occur in the sister Ophioscolecida or if they are restricted to Ophiacanthida. In the present study, LOPas were identified in five families of Ophiacanthina and in four families of Ophiodermatina including the Ophiocomidae, but they appear to be lacking in a primary clade of latter family (Table 4). A preponderance of available ontogenetic data suggest that the sister groups Ophiacanthida and Ophioscolecida do not develop BScs. BScs were lacking in postlarval stages of seven species of *Ophiacantha* (Ophiacanthidae), *Ophiocomina nigra* (Ophiotomidae), *O. flaccida* (Ophiomyxidae), and *O. rubicunda* (Ophiodermatidae), but it is not certain that all Ophiacanthida lack a BSc (see Table 3; "Skeletal Ontogenesis and Homologies of Oral Armature in Ophiacanthida" in the treatment of *Ophiacantha bidentata*). *Ophiolimna bairdi* (Lyman, 1883), which is considered to be a "divergent" basal ophiacanthid (*sensu* O'Hara at al., 2017), reportedly has a BSc, but the homology of this ossicle is problematic (Stöhr, 2005:200, fig. 5D, F; see "Skeletal Ontogenesis and Homologies of Oral Armature in Ophiacanthida" in the treatment of *Ophiacantha bidentata*). *Microphiura decipiens* Mortensen, 1910, which is putatively an Ophiacanthida *incertae sedis* (*sensu* O'Hara et al., 2017), was reported to have "one mouth-papilla...occupying the whole side" of each jaw (Mortensen, 1910:204), but there is no evidence that this "oral papilla is completely soldered together" (*contra* Matsumoto, 1917:375) and its homology is undetermined. *Ophiolamina eprae* Stöhr and Segonzac, 2006, which is *incertae sedis* among Ophiacanthida (*sensu* O'Hara et al., 2017), was alleged to generate oral papillae by "division of the buccal scale" (Stöhr and Segonzac, 2006:28). However, splitting of this ossicle and its homology with a BSc was not substantiated.

As a rule, Euryalida lack TScs, AdShSps, and 2°AdShSps on the jaw and lack arm spines on the first arm segment (Mortensen, 1933b:2; present study). Aside from the teeth, homologies of the OPas *s.l.* of Euryalida are indeterminate. In the present study, dissections of *Asteroporpa annulata* and *Asteronyx longifissus* indicated that Euryalida have LuOss and CtOss and that they lack LyOss and FPs. The OPas *s.l.* of Euryalida are usually spiniform or tuberculate. Within a species, the shapes of OPas *s.l.* intergrade, and the number and position of the ossicles are inconsistent. These characteristics make it difficult to homologize the OPas *s.l.* of Euryalida with those of Ophiurida and Ophintegrida. Another obstacle to comparison is a lack of information regarding the skeletal ontogenesis of Euryalida. Postlarval *Asteronyx loveni*, *Gorgonocephalus arcticus*, and *G. eucnemis* did not develop a BSc, AdShSp, or 2°AdShSps, and the OPas *s.l.* on the ventrolateral edge of the OP did not arise in the same sequence or positions as the IPas, 2°IPas, LOPas, OPRSps, and LyOss of other ophiuroids (Mortensen, 1912; Litvinova, 1998; Stöhr 2004, 2005; present study).

Differences in morphology of their teeth distinguish families of Euryalida (Okanishi and Fujita, 2013:577-578), and these contrasting features may be related to the modes of feeding in different taxa. *Asteroporpa annulata* and *Asteronyx longifissus*, which were examined herein, had spiniform teeth and putative TPas, which intergraded to an extent, but were still distinguishable on the basis of their size and shape. Asteronychidae and Gorgonocephalidae were characterized as having "acute and spiniform teeth arranged at the top of each jaw and spiniform (sometimes rudimentary or no) oral papillae on the lateral side of each jaw...a number of rounded and projecting articulation sites for teeth scattered on fragmented dental plates." In contrast, Euryalidae exhibit "triangular...stout and large teeth forming a single ventral [vertical?] row on the dental plate; pavement-like domed oral papillae on the sides of the jaws... one (rarely two) rounded and projecting articulation sites for teeth on fragmented dental plates" (Okanishi et al., 2011:398; Okanishi and Fujita, 2013:577–578, fig. 2A–F).

Feeding behavior of Asteronychidae is incompletely understood, and has not been directly observed. They may capture prey using hooked spines on the terminal arm segments, or use tube feet to collect material from the host or the benthos. Limited information on simple-armed Euryalidae indicates that they collect suspended material and ingest unconsolidated material and boluses of food, which are conveyed to the mouth by the tube feet. In contrast, gorgonocephalids capture active plankters such as copepods using girdle hooklets, and it appears that they ingest prey by combing the arm tendrils through the clusters of spiniform teeth (see "Diet, Feeding, and Operation of the Jaws" in the treatment of *Asteroporpa annulata*).

## FORAMINA OF THE WATER RING AND OF PODIAL NERVES IN THE ORAL PLATE

Traditionally, it was presumed that all Ophiuroidea have a water ring that "occupies a groove on the aboral surface of the jaw apparatus, immediately to the outside of the nerve rings" which "supplies the buccal podia directly, giving off 10...branches that bifurcate, passing through the main jaw ossicle" (Spencer, 1925:266; Hyman, 1955:611; Shackleton, 2005:111). This view was based on studies of ophiuroids that have one water ring foramen in each OP, which admits a branch of the water ring that bifurcates within the plate and produces a pair of OTs (see Müller, 1854:217, pl. 6, fig. 12, pl. 7, fig. 6, *re Ophiura ophiura* [=*Ophiolepis ciliata*]; Simroth, 1876:pl. 31, fig. 10, 12, 13; pl. 32, figs. 15, 16, 20, *re Ophiactis virens* (M. Sars, 1859); Ludwig, 1878:361, pl. 24, figs. 8, 9, 12, *re Ophiarachna incrassata*; Cuénot, 1948:246, 256, figs. 278, 290, *re Ophioderma longicauda* and *Ophiothrix* sp.). Specimens of *Ophiura sarsii* examined herein had a single, dorsal water ring foramen in the OP, like the aforementioned species. I found that an eyelash inserted in this foramen bypassed a channel to OT-1 and entered a channel to OT-2. Thus, water canals to both OTs of an OP arise from a single, bifurcate branch of the water ring (Fig. 4H, K, L; Martynov, 2010:fig.65R, S). Additional species of ophiuroids have a single foramen and similar morphology of the OP, including *Ophiocoma echinata* and *Ophioderma rubicunda* examined herein (see Lyman, 1882:pls. 37–42; "Buccal Morphology" in the treatment of *Ophiura sarsii*). The proximal and distal edges of the PPs overlapped the nerve and water rings, respectively (Figs. 9G, H, 12H). These structures were overlain by an integument embedded with microscopic ossicles, and presumably the PPs and integument protect the nervous and water vascular structures. The same position of PPs, in relation to the water vascular and nervous systems, was noted by Müller (1854:199) in *Ophioderma longicauda* and *Ophiura ophiura* [=*Ophiolepis ciliata*].

Unexpectedly, several species dissected in the present study were discovered to have OPs pierced by two foramina that are penetrated by the water ring. Although shape of the OP and positions of these dual foramina varied somewhat among *Asteroporpa annulata, Ophiomusa lymani*, *Ophiacantha bidentata,* and *Ophiophthalmus normani* that were examined, these openings were always positioned near the dorsal surface of the OP, with one situated above the adradial muscle and beside the radial water canal, and the other above the abradial muscle. The presence of a channel in the OP, connecting the dual foramina, was verified by passing an eyelash through both foramina (*A. annulata*, Fig. 2D, H, J, K; *O. lymani*, Fig. 3I, L–P; *O. bidentata*, Fig. 16F–G; *O. normani*, Fig. 17F, J, H, K). In contrast with species that have a single water ring foramen, these species with dual foramina lack a continuous water ring groove encircling the OP, since their water ring passes through the OPs rather than above the dorsal surface of the OPs. Also, the interradial portions of their water ring, which pass between the jaws, extend across the adradial muscles of the OPs. The interradial sections of the water ring, which are not enclosed in the OPs, are sheathed in integument that is embedded with microscopic ossicles. The nerve ring of these species with dual foramina is partially shielded by the PPs but the PPs do not cover the water ring. The nerve and water rings of *A. annulata* are covered by a continuous ring of perradial and interradial PPs (see "Buccal Morphology" in the treatment of *Asteroporpa annulata*). However, PPs partially overlie the water ring and nerve ring of Ophiurida and Ophintegrida that have a single water ring foramen in the OP.

The presence of an internal water ring within ophiuroid OPs is quite remarkable, because the water rings of other extant echinoderms are always external to the oral skeleton. The water ring is peripheral to the radial plates of crinoids, to the calcareous ring of holothuroids, to the mouth angle plates of asteroids, and to the Aristotle's lantern of echinoids. Although evidence of dual water ring foramina is limited to the results of the present study and indications in several published figures, and it is evident that these structures occur in several major ophiuroid clades, the phylogenetic distribution of single and dual water ring foramina is unclear. It is not known if single or dual water ring foramina are predominant among Ophiuroidea, how these dissimilar morphologies develop during ontogenesis, and how or why they evolved.

Dual water ring foramina occur in both orders of Euryophiurida, Euryalida and Ophiurida. They are present in an asteronychid, *Asteronyx loveni*, in gorgonocephalids including *Asteroporpa annulata*, *Astroclon propugnatoris* Lyman, 1879, *Astrotoma agassizii*, and *Gorgonocephalus chilensis* (Philippi, 1858), and in a euryalid, *Astroceras annulatum* Mortensen, 1933b (Murakami, 1963:fig. 1; pl. 3, figs. 21–40; pl. 4, figs. 1–2; Bartsch, 1982:figs. 2, 3, 9, 10; 1985:figs. 15–16). However, the seeming absence of an adradial water ring foramen in a presumptive member of the Euryalida stem-group, *Aspiduriella scutellata*, could well be a preservational artifact, considering the condition of the fossil (see Thuy and Stöhr, 2018:fig. 3e). Dual foramina are present in Ophiurida including *Ophiomusa lymani* and *Ophiosphalma armigerum* (Bartsch, 1983b:figs. 4–5, 13–14), and thus they occur in both families of Ophiomusina. Additionally, they occur in *Aspidophiura uniumbonata* Murakami, 1942, an ophiopyrgid, and in *Uriopha ios*, an Ophiurida *incertae sedis*, although the ophiurids *Ophiura ophiura*, *Ophiura sarsii*, and *Ophiura luetkenii* only have one water ring foramen (Müller, 1854:217, pl. 6, fig. 12, pl. 7, fig. 6; Murakami, 1963:pl. 6, figs.7–8; Paterson, 1980:figs. 1d, e; Hendler, herein and prev. unpub.).

Dual foramina were observed and figured in all four orders of Ophintegrida. They were depicted in a species of Ophioscolecida, *Ophiocymbium tanyae* Martynov, 2010 (Martynov, 2010:fig. 12C, D), and in species of sister Ophiacanthida, including *Ophiacantha bidentata* and *Ophiophthalmus normani* as reported herein, *Ophiacantha abyssicola* (Bartsch, 1987:figs. 8–9), *Ophiocanops fugiens* Koehler, 1922a (Hendler, prev. unpub.), and *Ophiolamina eprae*, which is an Ophiacanthida *incertae sedis* (*sensu* O'Hara et al., 2017) (Stöhr and Segonzac, 2006:fig. 6G, H). However, the Ophiodermatina species *Ophiarachna incrassata* (Ophiomyxidae) and *Ophioderma rubicunda* (Ophiodermatidae) have a single OP foramen (Ludwig, 1878:pl. 24, fig.9; present study). Among Ophioleucida, dual water ring foramina were illustrated in *Ophioleuce seminudum* [=-*Ophioleuce charischema, Ophiocirce mabahithae*] (Murakami, 1963:pl.6, figs. 47–48; Bartsch, 1983a:figs. 12–13). Dual foramina also were found among Amphilepidida, in the primary sister clades of Hemieuryalidae exemplified by *Actinozonella texturata* and *Hemieuryale pustulata* (Stöhr, 2011:fig. 20 F, G; Gondim et al., 2015:fig. 5A, B).

There are indications in the literature of variant morphologies of water ring foramina. Devaney (1970:31, fig. 43) described and illustrated "an opening near the center of the adradial muscle scar…thought to lead to the water vascular system" of *Ophiocomella* species (Ophiacanthida: Ophiodermatina). He mentioned a similar structure in an ophiactid, *Ophiactis savignyi* and suggested that the foramen might be related to the fissiparous reproduction of these phylogenetically disparate species. Neither this proposal nor the occurrence of dual foramina in these species have been assessed. There is also a possibility that species that have been depicted as lacking a dorsal water ring foramen have instead a cryptic adradial or abradial foramen (e.g., Lyman, 1882:pls. 37–42). Dual, interconnected foramina could be advantageous, if enclosure of the water ring within the OP protects the water-vascular system from mechanical trauma. In addition, movements of the jaws and contractions of the abradial muscles of the OP might compress the interradial sections of the water ring and drive fluid through the water-vascular canals.

It seems significant that species with a single foramen have relatively enlarged abradial muscle fossae, in comparison with species that have dual foramina. For example, species of Amphiuridae, Ophiotrichidae, and Ophiocomidae possess a single water ring foramen, and characteristically have an expansive, wing-shaped abradial muscle fossa that covers an area of the OP, which in the species with dual water ring foramina is pierced by an abradial foramen. This suggests that the "wing" of the OP, develops, it may displace or preclude formation of an abradial foramen resulting in a single, dorsal water ring foramen. This hypothesis should be evaluated by comparing the morphogenesis of the jaws of species with single and dual water ring foramina.

Two Paleozoic ophiuroids were depicted with a single foramen in the water ring groove of the OP, namely a Devonian species, *Furcaster* n. sp. B Haude and Thomas, 1983, and a Carboniferous species, *Onychaster flexilis* Meek and Worthen, 1868 (Bjork et al., 1968:text-fig. 1; Haude and Thomas, 1983:fig. 6A). These species were referred to a clade comprising Furcasteridae and Onychasteridae, characterized as *incertae sedis* among Paleozoic ophiuroids (Hotchkiss and Glass, 2012).

Several Paleozoic species had pairs of water ring foramina that were not interconnected. These foramina were set close together in the water ring groove on the dorsal surface of the OP, and they opened into separate channels leading to OTs on the ventral surface of the OP. These were illustrated in "archaic" Oegophiurida species, *Protaster groomi* (Spencer, in Spencer and Groom, 1934), *Bohemura jahni* Jaekel, 1903, *Klarasterina klara* Petr, 1989b (Ordovician), *Lapworthura miltoni* (Salter, 1857) (Silurian), and *Strataster ohioensis* Kesling and Le Vasseur, 1971 (Mississippian). They also occurred in an Ordovician ophiuroid, *Stenaster obtusus* (Forbes, 1848), whose ordinal relationship is "unknown" (*sensu* Blake, et al., 2016). Similar foramina were present in "modern-type" Devonian ophiuroids, *Stephanoura belgica* Ubaghs, 1941, and *Ophiaulax decheni* (Dewalque, 1881) (Spencer, 1925:fig.

191A; Kesling and Le Vasseur, 1971:322, fig. 8b; Petr, 1989a:text-fig. 5, 1989b:text-fig. 3B; Haude and Thomas, 1983:133, 135, fig. 10B, C; Shackleton, 2005:fig. 9B). These unconnected, paired foramina were depicted as penetrating the penultimate element of the OP in *P. groomi*, *L. miltoni*, *S. ohioensis*, and *O. decheni,* and passing between the penultimate element of the OP and its adjoining ossicles in *S. obtusus* (Dean, 1999: fig. 5). Notably, the OTs of these ophiuroids may issue from the water ring, in contrast with the tube feet of asteroids, which issue from the radial canal.

Previously, it was thought that the ophiuroid nerve ring occupies a groove in the dorsal surface of the OPs and "supplies a nerve directly to each of the buccal podia," or that the nerve to OT-2 branches from the radial nerve. But in neither case was the tentacular nerve thought to "perforate the substance of the ossicle [OP]" (Hyman, 1955:607, 609; Spencer, 1925:268). Consistent with this view, several species examined in the present study had a groove beside the podial basin of OT-2, which may accommodate a branch of the radial nerve cord (i.e., in *Ophiomusa lymani*, *Asteroporpa annulata*, *Stegophiura nodosa*, *Ophioderma rubicunda*, and *Ophiacantha bidentata*). In *Amphioplus abditus* and *Ophiothrix spiculata* there was a notch in the OPs below the FP and beside the tentacle basin of OT-1, which presumably accommodated a branch of the nerve ring innervating the tentacle. Suprisingly, several species of Ophiurida that were examined had buccal tentacles that may be innervated by nerves that penetrate the OP. *Ophiura sarsii*, *Ophiura luetkenii*, *Ophiocten sericeum,* and *Ophiosparte gigas* Koehler, 1922b, have a foramen situated near the radial nerve cord, which penetrates the OPR and opens in the tentacle basin of OT-2, and through which a podial nerve could reach the tentacle (Martynov, 2010:fig. 65U; present study). Analogous foramina have been figured in an ophioleucid, *Ophioleuce seminudum* [=*Ophiocirce mabahithae*], and in *Ophiothrix exigua* Lyman, 1874 [=*Ophiothrix marenzelleri*] and several other Ophiotrichidae. In the present study, a foramen on the adradial surface of the OPR was found to open beside the tentacle basin of OT-2 of *Ophiothrix spiculata* (Fig. 26C; Bartsch, 1983a:fig. 13; Murakami, 1963:pl.5, figs.36, 38, 40, 44, 46, 48, 52).

## OSSICLE FUSION AND FRAGMENTATION

Traditionally, authors presumed that ophiuroid ossicles can merge by "fusion" and subdivide by "fission," although these processes were not confirmed. DPs composed of multiple elements, which customarily were described as "fragmented" or "broken by fissures," have been reported in Asteronychidae, Euryalidae, Gorgonocephalidae, Ophiacanthidae, Ophiodermatidae, Ophiomyxidae, Ophionereididae, and Amphilimnidae (e.g., Murakami, 1963:5; Martynov, 2010:117). Thuy and Stöhr (2016:16, supplemental file 1) deemed *Ophiomyxa*, *Ophioderma*, and *Ophiarachna* to have "unambiguously fragmented dental plates" and regarded the "fragmented" DPs of *Gorgonocephalus* and *Euryale* as convergent structures, but did not specify how they differed and how they developed.

Multi-element DPs may bear one or more teeth and/or TPas on each element, and the margin of an element may either fall between or across a dental ArtS. Instances of bisected dental ArtSs suggest, but do not prove, that the abutting elements separated after the ArtS developed (e.g., Fig. 17E; Murakami, 1963:pl. 1). In the present study, the DP of *Ophioderma rubicunda* was shown to comprise a single ossicle in juveniles 2.1–4.6 mm dd (with 3–4 teeth), an evenly divided, two-element DP in a 6.2-mm-dd juvenile (with 4 teeth), and a four-element DP in the adult (with 5 teeth) (Figs. 13K, O, 12B, C). Evidently, the original DP ossicle cleaved as it developed, dividing the column of teeth. This mechanism could be corroborated by examining a DP under crossed nicols, since the elements arising from a single ossicle would be expected to have an identical angle of extinction, and elements developing from several independent ossicles would have different angles of extinction. The multi-element DP of *Ophiophthalmus normani* may develop similarly to that of *O. rubicunda*, although divisions in the DP pass through, rather than between, its dental foramina (Fig. 17E; Murakami, 1963:pl. 1, fig. 20). Subdivision of the DP might be accomplished through the resorption of stereom by phagocytes, as occurs during the cleavage of primary spines of *Eucidaris tribuloides* (Lamarck, 1816b), and the resorption of pedicellarial stalks of *Sphaerechinus granularis* (Lamarck, 1816b). Resorption surfaces of ossicular trabeculae in these echinoids are etched during this process, exposing microscopic pits and concentric lamellae (Märkel and Röser, 1983; Bureau et al., 1991). The DP of *Ophioderma rubicunda* and other putative, "fragmented" ophiuroid ossicles could be examined for comparable microstructural evidence of phagocytic resorption. The adaptive significance of the multi-element DP is perplexing, since the individual elements are "reciprocally immovable" and presumably function like an undivided DP (Candia Carnevali et al., 1994:390). Nevertheless, Thuy and Stöhr (2016:16) suggested that subdivided plates evolved because of unspecified "biomechanical constraints" that are related to the dimensions of the DP.

Although there is strong evidence that each TPa develops from a separate rudiment, authors have suggested that TPas are produced by the fission of teeth. Teeth of *Ophiothrix fragilis* were posited to "divide and shorten to form the tooth papillae," and the "external tooth" of *Ophiothrix* and *Ophiopholis* was stated to undergo "incipient fragmentation...into a cluster of dental papillae" (Stöhr 2005:574; O'Hara et al., 2017:427). TPas of *Ophiopholis* species were also construed as divided lowermost teeth ("underste Tænder ere delte i flere") or "an irregular apical papilla, which may be single, double or triple" (Lütken, 1858:20; Martynov, 2010:123). However, the asymmetrical clusters of TPas of *Ophiopholis* spp. appear to develop late in ontogenesis from separate ossicular rudiments that arise below the teeth on the ventral edge of the DP (see "Buccal Morphology of Ophiactoidea" in the treatment of *Ophiothrix spiculata*). TPas of *Ophiothrix* also develop independently of the teeth, rather than by fragmentation (H.L. Clark, 1914:115; present study).

Contemporary investigations of skeletal ontogenesis have invalidated the claims that oral papillae of Ophiurida differentiate from the edge of the oral plate and "separate from one another," and that supernumerary ophiacanthid oral papillae "are due to a splitting of the external papillae" (Koehler, 1914a:81; Tyler et al., 1995:983; compare: Paterson, 1980:215–216, and Sumida et al., 1998:fig. 7). The statement that the BSc of *Ophiozonella novaecaledoniae* "divided in two parts" was based on misidentifications of the developing 2°AdShSp and AdShSp (*contra* Vadon, 1990:174; see "Ontogenesis and Skeletal Homologies of Hemieuryalidae and Ophiolepididae" in the treatment of *Sigsbeia murrhina*). Assertions that the developing BSc "divides" in *Ophiopleura borealis* (Ophiopyrgidae) and *Ophiolamina eprae* Stöhr Segonzac, 2006 (Ophiacanthida *incertae sedis*) were founded on problematical, discontinuous growth series (e.g., Stöhr, 2005:555–557, 573; Stöhr and Segonzac, 2005:395; 2006:28).

Dorsal arm plates (DAPs) and oral shields have been described, without consideration of their morphogenesis, as "fragmented" or "divided" (e.g., Ziesenhenne, 1955; Hunter, 2007; Stöhr et al., 2012a:2). For example, so-called "fragmented" DAPs frequently occur on basal arm segments of adult *Ophioderma panamensis* Lütken, 1859, but they are rare on distal arm segments of adults and in juveniles. However, on the basis of this pattern of occurrence it cannot be confirmed whether "fragmented" arm plates were produced by the fission of ossicles or arose from multiple, independently developing ossicles. Mosaic DAPs of *Hemieuryale pustulata*, *Ophioplocus huttoni* Farquhar, 1899, and *Ophioplocus imbricatus*, which bear a resemblance to the "accessory dorsal arm plates" of Ophionereididae, comprise bilaterally symmetrical arrays of ossicles that arise at the edges of a primary DAP. It is entirely possible that each component ossicle develops independently, even though the multi-element DAPs have been presumed to form by a process of "fragmentation" or "division," (e.g., Thomas, 1974:fig. 2 d, e, f; Cherbonnier and Guille, 1978:fig. 77C–F; Baker and Devaney, 1981:figs.18–21; Gondim et al., 2015:350, fig.11).

Authors have asserted that wide or bar-shaped oral papillae are composed of "fused" or "soldered together" ossicles in *Ophiotypa simplex* Koehler, 1897, *Ophiomusa* [=*Ophiomusium*] spp., *Ophiotrochus longispinus* H.L. Clark, 1911, *Perlophiura profundissima* Belyaev and Litvinova, 1972, *Aspidophiura* spp., and *Microphiura decipiens* (Lyman, 1869:322, 1882:83; Koehler, 1897:281; H.L Clark, 1911:95; Matsumoto, 1917:250, 252, 287, 375; Paterson 1980:214; Stöhr et al., 2012a:5; Ishida et al., 2015:211). The BSc of Kirk's ophiuroid (misidentified as a "peristomial plate") was reported to develop from "scattered spicules," but this observation is completely contrary to other studies of ophiuroid skeletogenesis (Fell, 1941:428). It has also been alleged that fused oral papillae are a "typical juvenile character," characteristic of Ophiolepididae, and a distinctive feature of "paedomorphic ophiuroids" (Matsumoto, 1917:382, 375, 379; Paterson, 1980:214; Vadon, 1990:165; Tyler et al., 1995:983; Martynov, 2012:845; Stöhr et al., 2012a:5; Martynov and Stöhr, 2013:262). However, these assertions do not withstand close scrutiny. The description of fused oral papillae in *P. profundissima* was equivocal and seemingly inaccurate (compare: Belyaev and Litvinova, 1972: fig. 2, and Glover et al., 2016:fig. 23C). OPas *s.l.* of *Aspidophiura forbesi* (Duncan, 1879) are clearly demarcated from one another [LACM 65-311.1]. The ostensibly fused oral papillae of *Ophiomusa* remain as separated ossicles throughout ontogenesis, and this is evident when integument binding the ossicles is removed from juvenile and adult individuals (Hendler, 1998:353). *Microphiura decipiens* has a single oral papilla (compare: Mortensen, 1910:204, and Matsumoto, 1917:375). Likewise, *Ophiotrochus longispinus* (H.L. Clark, 1911:95), was thought to have oral papillae "completely fused into a low, but very wide plate," but the holotype [USNM 25538] has a single BSc that is incised with shallow, microscopic grooves (H.L. Clark, 1911:95; Hendler, prev. unpub.).

The notion that basal arm spines of *Amphilimna* species fuse together "to form peculiar flanges occupying genital slits" is widely accepted, and the putative occurrence of "basal arm spines fused into a flap" is thought to distinguish Amphilimnidae from Ophionereididae (Thomas, 1967:125, fig. 3; Devaney, 1974; Liao, 1989; O'Hara and Stöhr, 2006; Martynov, 2010a:238; O'Hara et al., 2017:427). However, it has not been confirmed that the trabeculae of these overlapping spines interlock or fuse, and microscopic fissures that are discernible between the modified arm spines of *Amphilimna olivacea* suggest that they may be solely connected by soft tissue [LACM 1999-55.1].

It was thought that radial shields of the Early Carboniferous *Aganaster gregarius* (Meek and Worthen, 1869) are fused together, and that radial shields of ophiuroids are "derived from fusion of scales on the edge of the disc" (Spencer, 1925:287; 1966:U20). However, Hotchkiss and Haude (2004:428) determined that radial shields of *A. gregarius* are separated, and studies of ophiuroid skeletogenesis have shown that the pairs of radial shields are discrete ossicles that develop side by side (e.g., Sumida et al., 1998; Hendler, 1998; Stöhr, 2005; Borges et al., 2015), except in the case of teratological individuals. The radial shield of *Astrobrachion constrictum*, a euryalid, was thought to consist of a "riblike" ossicle coupled to a series of scales, some of which are enmeshed in connective tissue and others that "appear to be cemented to the solid portion of the radial shield" (Stewart, 1996:324). Furthermore, authors proposed that the radial shields of Asteronychidae, Euryalidae, and Gorgonocephalidae are "laminar secondary plates, which overlap and fuse together," and it was suggested that these compound radial shields are a trait of Euryalida (Lyman, 1882:251, 258, 285; Matsumoto, 1917:29; Stewart, 1996:327; Okanishi et al., 2011). Nevertheless, radial shields of various Ophintegrida, such as *Ophiocoma aethiops* Lütken, 1859, *Ophioderma elaps* Lütken, 1856, *Ophioplocus imbricatus*, and *Sigsbeia murrhina* are overlapped by imbricate series of large scales that may be equivalent to the laminar elements of Euryalida (Lyman, 1882:pl. 37, figs. 1, 10; pl. 42, fig. 9; pl. 43, fig. 4). At present, there is no conclusive evidence to suggest that they are fundamentally different from scales on the radial shields of Euryalida or that the imbricate ossicles are fused.

Ophiuroid vertebrae are generally considered to be "fused" ossicles (Hyman, 1955:603), and Ludwig (1882:184) established that each vertebra is composed of two ambulacral ossicles that gradually become intimately connected ("immer innigere Verbindung schliessen") during ontogenesis. Even after connective tissue is removed from the vertebrae, the ambulacral ossicles may remain attached by interlocking stereomic trabeculae. These connections create a "suture line" on the midline of vertebrae, which has been documented in SEM images of many species, and it resembles the connection between the elements of ophiuroid OPs, and between some echinoid coronal plates (Lyman, 1874:257; Ludwig, 1882:193; Murakami, 1963:4; Hendler, 1978:84; Smith, 1984:fig. 2.5; Irimura and Fujita, 2003).

The vertebral suture constitutes an immobile joint designated a "gomphoid synarthrosis" and interpreted as "evidence of the incomplete fusion of separate ossicles" (Irimura and Fujuta, 2003:163; Croce and Turner, 2013:E44; Stöhr and Martynov, 2016:10). Sutured ambulacral ossicles and OP ossicles, which were examined with a polarizing microscope under crossed nicols, were distinguishable as separate crystal structures (Becher, 1914:pl. 12, fig. 5c, pl. 14, fig. 11b). However, some vertebrae lack a continuous suture line, and it appears that trabeculae of the ambulacral ossicles have coalesced or that the ambulacral ossicles are connected by a callus of imperforate stereom uniting the articular facet (e.g., Irimura and Fujita, 2003:fig. 5; Stöhr et al., 2012a:fig. 6; Pearse et al., 1998:fig. 7). In order to explain the connection between such seamlessly united vertebrae or of the so-called "fused" genital plates and compound test plates of echinoids, it will be necessary to examine their ultrastructure (Gordon 1929a:318, 1929b:318; Kier, 1974:7, 36).

## OSSICLE "MIGRATION" AND ONTOGENESIS OF THE ORAL PLATE

During ontogenesis, structures of the ophiuroid jaw may radically change in size, shape, and relative position. Some of the most remarkable alterations have been mistakenly attributed to independent movements of the VAP-1, OPas *s.l.*, and so-called OTPo-2. VAP-1 and the "pore" were presumed to "migrate into," "move into," "withdraw into," "move closer to," or to be "pushed into" the OSl (Ludwig 1878:366; Murakami, 1940:27; Schoener, 1967:652, 659; Hendler, 1978:87; Vadon 1990:173; Stöhr 2005:563, 566; Martynov, et al., 2015:13). It was supposed that the OT-2 is "pushed into the oral slit" by the AdShSp, or that "The distal ends of the oral plates ascend into the disc…creating a shallow trough…. The first ventral arm plate moves into the buccal cavity by rotating its proximal margin upward; the second oral podium migrates with it into the buccal cavity. The spine of the adoral plate follows the second oral podium and migrates…onto the oral plate" (Murakami, 1940:27; Turner and Miller, 1988:499–500). However, as explained below, these morphogenetic changes are brought about by differential allometric growth of the OPs and adjoining ossicles, rather than independent movements of skeletal elements on the surface of the jaws.

The OTPo-2 of the juvenile is not a skeletal element, but rather a gap between the AdSh and VAP-1 through which OT-2 emerges. OT-2 is a modified tube foot, and OTPo-2 is a tentacle pore in a modified arm segment compromising the OP (a modified vertebra), VAP-1 (a modified VAP), and the AdShs (modified LAPs). The orifice of the vTCt remains between VAP-1 and the AdSh throughout ontogenesis, but as the shapes and sizes of these plates change, OTPo-2 merges into the vTCt and OSl. An impression that OTPo-2 "migrates," "withdraws," or is "pushed" from a "superficial" position into the buccal cavity is evoked by modifications of the ossicles surrounding the vTCt (e.g., Hendler, 1978, 1988, 1998; Vadon, 1990:173; Sumida et al., 1998; Stöhr, 2005; Borges et al., 2015). The present study revealed that orientation of the orifice of the vTCt, with respect to the OSl of the adult, is established by morphogenetic alterations of the OP, AdSh, VAP-1, OPas *s.l.*, and PeSk elements. In some species, these processes produce a vTCt described as a "slit shaped tentacle pore" and having a "superficial placement" in the adult. However, the so-called "superficial OTPos-2" of adults, which have been interpreted as a juvenile feature (*sensu* Stöhr et al., 2012b:1199; Stöhr and Martynov, 2016:16, table 3), are multi-element vTCts that are fundamentally different from of a juvenile OTPo-2.

In the present study, morphogenesis of the OP and the jaw were examined in growth series of *Ophioderma rubicunda*, *Ophiolepis paucispina*, *Sigsbeia conifera*, and *Ophionereis olivacea* (e.g., Figs. 23A–F). In these species, the OP and jaw grow in step with the arm and disk, and VAP-1 grows in step with the OP. The jaw of a juvenile initially has a level ventral surface (Fig. 23A), but as the individual grows the jaw becomes wedge-shaped; its apex inclines dorsally into the mouth and its distal edge protrudes ventrally (Fig. 23B). Subsequently, the vTCt expands and the OSl deepens as a result of ventralward enlargement of the distal portion of the OP below the OPR, accompanied by expansion of the proximal and distal lobes of VAP-1 (Fig. 23C). Concurrently, enlargement of the OS, AdSh, and LAP-2 creates a ventral protrusion at the distal end of the jaw, further increasing the depth of the OSl (Fig. 23C, D). Finally, the proximal portion of the OP increases in height, protruding ventrally and bringing the apex of the jaw into register with the bulging distal edge, and the serried OPas *s.l.* and LyOs create a ridge around the OPs (Fig. 23 D–F).

Initially VAP-1 bridges the ventral surface of the arm and the OPR, but as the OP enlarges and the OSl increases in depth the narrow proximal lobe of VAP-1 grows toward the OPR and the broad distal lobe expands toward LAP-2. As a result, the gap widens between the ventral surface of the arm and the OPR, VAP-1 develops an arched shape, with its proximal lobe curving dorsally in the OSl and its ventral lobe curving toward VAP-2. However, VAP-1 does not "move. . .into the buccal cavity by rotating its proximal margin upward" (*per* Turner and Miller, 1988:499–500).

The AdSh grows in step with VAP-1. Its proximal lobe lengthens while maintaining contact with the OP, and its distal lobe extends alongside the OS while maintaining contact with LAP-2. Initially, the AdShSp is situated on the distal edge of the AdSh, and subsequently near the midpoint of the elongating AdSh. Although proximal and distal growth of the AdSh creates an impression that the AdShSp moved independently, the AdShSp remains in place on the lengthening AdSh, beside the orifice of the vTCt. The AdShSp may ultimately be displaced to the ventral surface of the OP, and it appears that during this transition the base of the spine overgrows the edge of the AdSh, onto the OP, and that subsequent growth of the OP separates the AdShSp from the AdSh (compare: Fig. 23I, K).

Throughout ontogenesis, OT-2 remains on a level with the ventral edge of the OPR, and between VAP-1 and the AdSh. The "OTPo-2" does not "migrate" or "move," and it is not "pushed into" the OSl. Rather, the increasing length of the OP, and enlargement of the OP above and below the OPR, coupled with the growth of adjoining OPas *s.l.* and LyOs, expand the length and depth of the OSl, and ossicles bordering the OSl overtop and enclose the tentacle basin of OT-2. As a result, OT-2 of the early postlarva projects distally, between the AdSh and VAP-1 and toward the edge of the disk, but in advanced juvenile stages with a well-developed disk and arms, the orifice of the vTCt remains on the ventral surface of the jaw and extends toward the OSl. This functionally adaptive change in the orientation and position of OT-2 attends the transformation of the tentacle from a locomotory to a feeding structure.

Ontogenetic changes in growth vectors of the OP can create an impression that OPas *s.l.* migrate upward on the OP and into the OSl. For example, in *Amphiura chiajei*, the BSc was described as having "moved deeper on the oral plate" (Stöhr, 2005:563). However, in *Amphiura filiformis* it is apparent that the BSc develops beside the OPR and remains there. Growth of the OP itself, which expands ventralward beneath the OPR and the BSc, makes it appear that the BSc moves independently "deeper on the oral plate" during ontogenesis (Hendler, 1988:fig. 3; Stöhr, 2005:fig. 13). The BSc and 2°IPas of many *Ophiura* species form a descending row on the edge of the OPR (Fig. 4A, B). They align in this configuration because differential growth of the OP produces an OPR that slants ventralward, and as a result the distal BSc is dorsal to the youngest in the series of 2°IPas, which is closer to the ventral apex of the jaw (compare: Fig. 4A, B; Sumida et al., 1998:fig 5H).

A recent synoptic account of ophiuroid skeletogenesis stated that "During development the adoral shields shorten and in their most advanced state they are completely removed from the lateral arm, only bordering the proximal edges of the oral shield. The second tentacle pore is in young stages far from the mouth, but moves closer during ontogeny." This account also indicates that the OP of the postlarva is "proportionally longer than in adults, confirming that growth occurs at first lengthwise, later widthwise" (Stöhr and Martynov, 2016:4, 10). However, the OTPo-2 is incorporated in the vTCt and it remains at the ventral juncture between VAP-1 and the AdSh in the juvenile and the adult (e.g., see Sumida et al., 1998:figs. 5, 12). Furthermore, the AdSh lengthens during ontogenesis rather than shortening, and it maintains contact with the OSh and augments its attachment to VAP-2, rather than detaching from the arm. Throughout ontogenesis, the distance between the orifice of the vTCt and the mouth remains negligible compared to its distance from the edge of the disk. A misimpression that the OTPo-2 "moves" toward the mouth may be created by the increasing distance between the vTCt and the outer edge of the disk, as the developing disk overgrows the base of the arms. Furthermore, rudiments of OPs and vertebrae bear little resemblance to the mature ossicles, and their growth is three-dimensional and accretive, rather than "at first lengthwise, later widthwise" (e.g., Hendler, 1978:figs. 2–5; Dahm and Brey, 1998:fig. 1; Stöhr and Martynov, 2016:figs. 4A–B, 5A–B).

## PUTATIVE PAEDOMORPHIC "OTPo-2" OF OPHIURINA

The concept that adult ophiuroids present juvenile features was broached by Lyman (1880:3), who described skeletal elements in Ophiohelidae, which have a putative "embryonic character." Subsequently, the diminutive holotype of *Ophiotypa simplex* (Ophiolepididae *sensu* O'Hara et al., 2017) was construed as an adult whose morphological development was interrupted at a juvenile stage (Koehler, 1897). Matsumoto (1917:234, 378, 382) questioned whether other small, seemingly juvenile, deep-sea ophiuroids were archaic forms, but he concluded that they are "embryonal, that is, paedomorphic." He erected a subfamily distinguished by "second oral tentacle pores opening outside of the oral slits," which purportedly comprised an "almost unbroken series of paedomorphism, of which the terminal members are such genera as *Astrophiura*, *Ophiophycis*, *Ophiomisidium*, *Ophiotypa*, *Ophiomastus*, *Anthophiura*, *Aspidophiura*, *Ophiopyrgus*, &c." Vadon (1990:175, 176) directed attention to the "emergence" of the so-called OTPo-2 "outside the mouth slit" of adult Ophiuridae and putatively juvenile Ophiolepididae such as *Ophiozonella novaecaledoniae*, and she enquired whether "paedomorphic" Ophiurinae evolved from Ophiolepidinae by paedomorphosis or if Ophiolepidinae evolved from Ophiurinae by peramorphosis. Although these taxa were considered sisters at that time, they were elevated to family status and allocated to different superorders of Ophiuroidea (*per* O'Hara et al., 2017), which effectively nullifies both alternative evolutionary scenarios, at least with respect to Ophiozonella and Ophiura. Details of the evolution of sister *Ophiomusina* and *Ophiurina*, and the possibility that some deep-sea Ophiurida are paedomorphic, are unresolved.

Since the 19th century, certain skeletal characteristics suggestive of juvenile morphology, such as a restricted number or size of arm spines, tentacle scales, or disk ossicles, were assumed to evolve through paedomorphosis, and species exhibiting these characters were identified as paedomorphic (e.g., Paterson, 1980, Vadon, 1990, Stöhr and Martynov, 2016). It was suggested "that the whole family Ophiuridae has a paedomorphic origin," because "the position of the second tentacle pore inside the mouth is evidently the developed state, its position outside the mouth in adult specimens is paedomorphic" (Stöhr and Martynov, 2016:16). These authors referred to Ophiuridae *sensu* Smith et al. (1995), encompassing species that are currently allocated to Ophiurina (comprising Ophiuridae, Ophiopyrgidae, Astrophiuridae) and Ophiurida *incertae sedis* (*sensu* O'Hara et al., 2017). This proposal concerning the putative "paedomorphic origin" of Ophiuridae implies that, during their evolution, the timing of developmental processes shifted such that adult Ophiuridae *sensu lato* "resemble the juveniles of their ancestors" and that "all interspecific differences are explicable in terms of rate or timing differences along the trajectory of ontogenetic shape change" (Raff and Wray, 1989:413; Webster and Zelditch, 2005:356). Stöhr and Martynov (2016:6–7) gauged the paedomorphosis of Ophiuridae *sensu lato* based on subjectively assigned ontogenetic stages and character states, and they arbitrarily calibrated character states on the basis of their presumptive resemblance to juvenile features of *Ophiura sarsii*, *Ophiomusa lymani*, and *Amphipholis squamata*, in comparison with the adult features of a phylogenetically and morphologically disparate species, *Breviturma krohi* Stöhr et al., 2013. This approach falls short of confirming that Ophiuridae are more or less "paedomorphic" and have a "paedomorphic origin." Rigorously substantiating the role of heterochrony in the evolution of Ophiuridae *sensu lato* is impracticable at present, because the staging and timing of skeletal ontogenesis have not been accurately established in extant and ancient Ophiuridae *sensu lato*, and the anatomy, ontogenetic shape change, and evolution of the species from which they were derived have not been ascertained.

Certain features of Ophiurina species may be paedomorphic, but the mode of developmental reprogramming by which they evolved is unknown, and may have involved heterotopy, heterotypy, heterometry, and allometric repatterning (*sensu* Webster and Zelditch, 2005). Webster and Zelditch (2005:355) argued there is a "strong bias in favor of recognition of some modes of change (particularly heterochrony), in the confounding of heterochrony with other kinds of modification of development, and in a tendency to oversimplify the evolution of ontogeny." Even so, the "paedomorphic origin" hypothesis raises pertinent questions that are considered below. Do features that are regarded as paedomorphic confer a selective advantage on Ophiurina? What was the morphology of the putative "OTPo-2" in the most recent common ancestor of Ophiurina? What distinguishes the morphologies of vTCts that have been characterized as "inside" and "outside the mouth" and how do they develop? Is the vTCt of Ophiurida invariably paedomorphic?

Regarding the adaptive and ecological significance of paedogenesis among Ophiuridae, Vadon (1990:177) speculated that small size, "abbreviation of development," and dense populations found in some deep-sea species imply that they are progenetic. The presumption was that they undergo rapid sexual maturation and have high reproductive output, which enables them to successfully colonize new habitats. However, their population dynamics and reproductive biology are unknown. Similarly to other "miniaturized" organisms, they may have "a complex combination of ancestral and derived traits" that are "the outcome of a complex interplay of size, developmental mechanisms, functional demand, and historical contingency" (Hanken and Wake, 1993:501). The supposedly "juvenile" features of deep-sea Ophiurina (*sensu* O'Hara et al., 2017) may comprise morphological adaptations and innovations related to small body size. Their buccal morphology may be specialized for a particular mode of locomotion and feeding, rather than the consequence of a global heterochronic process. For example, the limpet-shaped Astrophiuridae have enlarged, ventrally directed OTs-2 and basal tube feet that are distal to the OSl, and which could facilitate adhesion on the hard substrate occupied by these bizarrely shaped, deep-sea ophiuroids (see "Feeding and Locomotory Adaptations of Juvenile Ophiuroids" in the Discussion).

It was theorized that "hypothetical non-paedomorphic ancestral taxa" of paedomorphic ophiuroids "can be expected in the upper size range of *Ophiura*" (Stöhr and Martynov, 2016:19). However, "modern type" Paleozoic ophiuroids from which extant Ophiurida may have evolved are of modest size. *Aganaster gregarius*, which was characterized as "a most recent crown group ancestor" of Ophiuroidea and as "a basal crown group ophiuroid," was 4–6 mm dd, *Aganaster jagiellonicus* Thuy et al., 2015, was 9 mm dd, *Ophiaulax decheni* was 3–4 mm dd, and *Stephanoura belgica* was 6–7 mm dd (Ubaghs, 1941; Haude and Thomas, 1983:figs. 9C, 10C, 12H; Jell, 1997:fig. 6-4, 6-5; Hotchkiss and Haude, 2004:428, fig. 1H, I, K; O'Hara et al., 2014; Thuy et al., 2015; Thuy and Stöhr, 2016:5).

*Aganaster gregarius*, *A. jagiellonicus*, and *S. belgica* were stated to have an OTPo-2 "opening into the mouth" and "within the buccal slit," with a caveat that "criteria for deciding whether the second oral tentacle pore is outside the oral slit is itself a topic for study" (Jell, 1997:fig. 6-1, 6-4, 6-5; Hotchkiss and Haude, 2004:426-428, 430, fig. 1H, I, K; Thuy et al., 2015:926, fig. 2$C_1$, $C_2$). In published figures of *A. gregarius* and *A. jagiellonicus*, the tentacle basin of OT-2 appears to be set on a shallow OPR near the ventral surface of the jaw. Although VAP-1 is not discernible in figures of *A. gregarius*, VAP-1 of *A. jagiellonicus* appears to be horizontal, which is indicative of a shallow vTCt. However, it is not clear whether its "lateral oral papillae" are above or below the vTCt. Thus, it is not clear whether the OT-2 and vTCt of *Aganaster* were separated from the OSl. Aside from this, it is difficult to say how similar *Aganaster* may be to the most recent common ancestor of the Ophiurina or Ophiurida.

Stöhr and Martynov (2016:8) compared features of Ophiuridae and Ophiolepidae with those of a non-paedomorphic ophiocomid that presumably has an OTPo-2 (i.e., vTCt) "far from [the] oral slit" of the postlarva, "superficial" in a juvenile, and "inside [the] oral slit" of an adult. On the basis of these subjective criteria, OTPo-2 of postlarval *Ophiura sarsii* was scored as "far from oral slit." In comparison, adult *O. sarsii* was deemed to have a "superficial" OTPo-2 like a juvenile ophiuroid, but the vTCt of an adult *O. sarsii* is unlike the OTPo-2 of a juvenile *O. sarsii*, which suggests that the criteria used to characterize OTPo-2 and its "paedomorphic score" (see Stöhr and Martynov, 2016:12, tables 3, 4) were not suitable (compare: Fig. 4A; Sumida et al., 1998:fig. 5H). In the postlarva, OTPo-2 is an opening between LAP-1 (=AdSh) and VAP-1 through which OT-2 emerges from the oral frame. This opening remains on the ventral surface of the jaw throughout the ontogenesis of putatively "paedomorphic" and "non-paedomorphic" species. However, the orifice of the vTCt is a more complex structure than the postlarval OTPo-2, and it is composed of ossicles that change in number and structure during ontogenesis.

The vTCts of adult *O. sarsii* and of *Ophiolepis impressa* are part of the OSl, and are not "on the same plane as the ventral surface of the corresponding oral plates" (*contra* Koehler, 1922a:353; compare: Figs. 4I, 18C, herein). The vTCt of *O. impressa* is covered by opercular OPas *s.l.*, whereas that of *O. sarsii* is bordered by much smaller OPas *s.l.* However, the vTCts of both species constitute the distal section of the OSl, and they are delimited by the OPR, vCtP, AdSh, VAP-1, and associated elements. The OT-2 of both species can extend directly into the mouth when the jaws are open, but when the jaws are closed the OT-2 of *O. sarsii* is isolated from the proximal OSl by the IPa, 2°IPas, and BSc on the OPR. When the jaws of *O. impressa* are closed the OSl is not obstructed, because IPa, BSc, 2°AdShSp, and AdShSp are aligned on the ventral edge of the OP, which is below the OPR and OT-2. In contrast with the adult, the vTCt of juvenile *O. sarsii* is not incorporated in an OSl, and OT-2 of the juvenile cannot extend directly into the mouth even when the jaws are open (compare: Figs. 4A, C, 5A, B, and Sumida et al., 1998:figs. 5, 6). Thus, the orifice of the vTCt of adult *O. sarsii* is neither "outside the mouth" nor "paedomorphic" (*contra* Stöhr and Martynov, 2016:16). Nevertheless, the buccal morphology of Ophiurina differs markedly from other Ophiuroidea, because of evolutionary innovations in the morphology of the OP, OPas *s.l.*, and PeSk, which are described below (see also "Clade-Specific Configurations of Buccal Armature" in the Discussion).

Pioneering students of ophiuroid morphology called attention to the uniquely Y-shaped OSl of Ophiurina, and later authors invoked a dichotomy between species with a putative OTPo-2 "entering the mouth slit via a furrow" or opening "directly on to the ventral surface" (e.g., Lütken, 1858:12, 23; Lyman, 1874:223, 258, 264; Koehler, 1904:37-38; 1922a:353; Matsumoto, 1917:247; H.L. Clark, 1908:295). Koehler (1922a:354) admonished that "these differences must be stated in precise and correct terms. Thus not only will serious errors be avoided, but also differences in opinion and uncertainties in interpretation." Regrettably, the "second oral tentacle pore" was not defined, and it was characterized in equivocal terms such as "superficial," "extending towards the mouth," "opening into the mouth," "opening more or less outside the series of oral papillae," or opening "more or less entirely outside the oral slits" (e.g., Fell 1960:6; Clark and Rowe, 1971:128; Paterson, 1980:213–214;1985:102, 119, 122, 125).

Martynov and Litvinova (2008:88) drew a distinction between *Ophiura* species that "have the second tentacle pore rather opened inside the mouth" and *Ophioplinthus* species that have a "second tentacle pore [that] does not open inside the mouth." They inferred that the differences "correspond to the shape of the jaws: in the genus *Ophiura* the jaws have nearly parallel edges distally and rounded edges proximally, whereas in *Ophioplinthus*… the jaws are triangular." However, in the present study, dissections of the ophiurids *Ophiura sarsii* and *Ophiocten sericeum*, and of the ophiopyrgids *Ophioplinthus gelida* and *Stegophiura nodosa*, revealed that the "opening of the second tentacle pore (i.e., morphology of the vTCt) is contingent on the shape and configuration of the OP, PeSk, and OPas *s.l.* composing the vTCt, and is not defined by the profile of the jaw. The orifice of the vTCt of *Ophiura sarsii* lies within the OSl, and the orifices are separated from the OSl to different degrees in the other three species.

Jaws of *O. sarsii* and *S. nodosa* have similar contours with "nearly parallel edges distally and rounded edges proximally" (*per* Martynov and Litvinova; 2008:88). The relatively spacious vTCt of *O. sarsii*, which composes the distal portion of the OSl, forms a "channel" or "furrow" that authors have described as "outside the oral slit" or "rather close to these slits" (Matsumoto, 1917:234; Koehler, 1922a:352). This vTCt is demarcated by a prominent vCtP and the OPR, which are elevated in the OSl, and well above the ventral surface of the OP (Fig. 4A, C; see Murakami, 1963:pl. 6, fig. 40). Pairs of vTCts that converge on VAP-1, which are bordered by VAP-1 TScs, 2°AdShSps, and the AdShSp, impart a "forked" appearance to the adjoining OSl. However, the shallow orifice of the vTCt of *S. nodosa* is nearly isolated from the OSl by a vestigial vCtP and a stocky, tapering VAP-1 that overlaps the OPR (Fig. 7A, C, D, F).

In contrast with *O. sarsii* and *S. nodosa*, the jaws of *Ophiocten sericeum* and *Ophioplinthus gelida* have a "triangular" shape (*sensu* Martynov and Litvinova, 2008:88), and the orifices of their vTCts are isolated from the OSl. The vTCt of *O. sericeum* is shallow, because of the proximity of the OPR and of the tentacle basin of OT-2 to the ventral surfaces of the OP, AdSh, and VAP-1. The orifice of the vTCt is fringed by several OPas *s.l.*, but lacks a vCtP and other PeSk armature. OT-2 of *O. sericeum* can extend above VAP-1 and across a shallow groove on the ventral surface of the OP toward the proximal OSl, from which it is blocked by a bar-shaped BSc when the jaws are closed (Fig. 6A, C). The vTCt of *O. gelida* sits on a massive OPR that is nearly on a level with the ventral surface of the OP. The orifice of the vTCt is entirely surrounded by the AdSh, VAP-1, vCtP, and an unbroken ring of OPas *s.l.* Its OT-2 can extend ventrally between these OPas *s.l.* But OT-2 cannot extend proximally into the OSl because it is obstructed by a very bulky vCtP (Fig. 8A, D, E G).

There is negligible similarity between the jaws of adult and juvenile *O. sarsii*, because the configurations of their buccal armature and the components and morphology of their vTCts are quite dissimilar. The vTCt is incorporated in the OSl of the adult but excluded from the OSl of the juvenile (compare: *O. sarsii*: fig. 4A, I, and Sumida et al., 1988:fig. 5H). When the jaws of an adult are open OT-2 can extend directly into the proximal OSl, but the orifice of the vTCt of the juvenile is blocked by the AdSh and VAP-1. The orifice of the vTCt of adult individuals of *Ophiocten sericeum* has a constricted connection to the proximal OSl, compared with adult individuals of *O. sarsii*, but OT-2 of juvenile of *Ophiocten gracilis* is excluded from the OSl by VAP-1 (compare *O. sericeum* in Figs. 6A, B, C, with *O. gracilis* in Sumida et al., 1998:fig. 10F). The adult and juvenile jaws of *Ophiocten* are similar to one another, in comparison with the adult and juvenile jaws of *Ophiura*, and have a relatively "paedomorphic" appearance. Nevertheless, the morphology of the oral frame and OPas *s.l.* of the juvenile and adult are different. Regardless of whether *Ophiocten* species are paedomorphic, which remains to be determined, it seems the genus may be a late-branching lineage in a clade of Ophiuridae that have a relatively complex vTCt morphology (see O'Hara et al, 2017:fig. S3).

The OPs of Ophiurida, which have been described as "chisel-shaped in lateral view" are elongated, and have expanded proximal and distal extremities, and a relatively shallow ventral OPR and vTCt (Murakami, 1963:34). Their "chisel shape" results from restricted ventralward growth below the OPR relative to the growth of the OP dorsal to the OPR. The truncated OP restricts the depth of the OSl and vTCt and abridges the connection between the vTCt and the proximal OSl, and the morphology of the VAP-1, AdSh, and buccal armature also affect the dimensions of the vTCt. The relatively large vTCt of *O. sarsii* and the increasingly smaller vTCts of *Stegophiura nodosa*, *O. gelida*, and *O. sericeum* are related to the degree that ventralward growth of the OP is truncated, and species with a relatively unobstructed connection between the vTCt and OSl have an OPR and vTCt that are elevated above the ventral surface of the jaw and VAP-1. *Ophiura maculata* (Ludwig, 1886) has OPas *s.l.* on the ventrolateral edge of the OP, instead of on the elevated OPR, and its OT-2 can extend into the proximal OSl, even when its jaws are closed (see Mortensen, 1933a:fig. 45 [LACM 1976-731.2]). *Ophiura sarsii* has OPas *s.l.* on the edge of an elevated OPR, which obstruct OT-2 when the jaws are closed, but not when they are open. However, the vTCt and proximal OSl of Ophiurina may also be completely separated from one another by the AdSh, VAP-1, or vCtP. For example, in *Ophioplinthus gelida* the OT-2 is excluded from the OSl, even when the jaws are open.

## FUNCTIONAL MORPHOLOGY OF THE BUCCAL ARMATURE OF JUVENILE AND ADULT OPHIUROIDEA

At one time, ophiuroid jaws were deemed a "chewing apparatus" and their buccal armature was regarded as "doubtless directly correlated with important differences in their mode of feeding and nature of their food" (Lyman, 1874:254; Verrill, 1899b:306). Since these ideas were based almost entirely on questionable "details afforded by dead specimens," a modern overview of ophiuroid feeding biology recommended that "a study of functional anatomy combined with knowledge of diet, behavior, and changes which take place in the food during ingestion, seems likely to be a fruitful line of enquiry" (Spencer, 1925:263;Warner, 1982:181). This suggestion notwithstanding, functional mechanics and feeding behavior of ophiuroids have attracted scant attention (e.g., Candia-Carnevali et al., 1994; Medeiros-Bergen, 1996; Boos, 2012). Nevertheless, relevant literature was marshaled in the present study, in order to illuminate the connection between structure and function of ophiuroid jaws.

## INTERMESHED AND OPERCULAR OPas *s.l.*

A staggered arrangement of the teeth on alternating jaws was encountered in most exemplar species dissected in the present study (e.g., Figs. 13Q, 23K). In this configuration, opposing teeth alternate and their edges can intermesh when the jaws close. The same organization of teeth is evident in published figures of ophiuroid jaws, but was not remarked upon in previous literature (e.g., Devaney, 1970:fig. 45 *re Ophiocoma erinaceus*; Bartsch, 1982:figs. 44, 71 *re Ophiactis asperula*, *Ophioplocus esmarki*; Candia-Carnevali et al., 1994:fig. 2a *re Ophioderma longicauda*; Thuy et al., 2013:fig. 7b *re Eozonella bergeri*). Although the bases of teeth on a jaw may be either loosely or closely spaced, their shafts have tapered or faceted edges that permit the teeth to intermesh or interlock (e.g., Figs. 3F, 18B, 20C, 26C). Presumably, this configuration is established by the sequence in which teeth develop and their rate of growth. In addition, their size, number, and arrangement might conceivably be regulated by reciprocal interactions between the teeth on opposing jaws. This modality could account for lock-and-key docking between notched, opposing teeth, and between the oral papillae, on adjacent jaws of *Ophiomusa lymani* (Figs. 3B, D, F).

The arrangement of ophiuroid teeth on the jaw must affect their performance in feeding, just as the type of occlusion—opposition, grinding, shearing, or alternation—dictates the function of mammalian teeth (Simpson, 1933). Ophiuroid teeth that alternate and interlock when the jaws close likely have the same function as alternating mammalian teeth, "primarily that of grasping or piercing, secondarily that of breaking" (Simpson, 1933:130). TPas and teeth may not "chew," grind, or shear food, because they lack opposing crests that could grate or slice food, and because they travel in the horizontal plane rather than performing alternating, vertical movements. Therefore, the likely function of teeth in macrophagous ophiuroids is to briefly clench food items before they are swallowed. Microphagous species have TPas that do not contact one another directly but can compress boluses of particulate material. Their opposing teeth, which can repeatedly strike a bolus, might crush material before it is swallowed, but the effect of their movements has not been assessed (Austin, 1966).

Austin (1966:119) "never observed the jaws moving up and down" in living individuals of *Ophiura luetkenii* or *Ophiothrix spiculata*," and this undercuts proposals that TPas of microphagous *Ophiothrix fragilis* are "grinding instruments," that the teeth of *O. fragilis* and macrophagous *Ophiura albida* are used for "crushing and cutting," and that food "within the jaws is . . .masticated" by teeth that . . ."saw by an 'up and down' movement" (Spencer, 1925:265; Candia Carnevali, et al., 1994:390; Boos, 2012:117). Although a "grinding edge" or "cutting edge" was ascribed to ventrolateral papillae on the jaws of ophiuroids with buccal funnels (e.g., *Ophiocoma*, *Ophiostigma*, *Ophiactis*, and *Ophionereis*), they are more likely compressive and crushing instruments (Fig. 11C, F, N; Lyman 1865:58, 81, 103, 108, 145).

Martynov (2010:23) observed that "In different families. . .distalmost [oral] papillae [are] often modified into wider and operculiform shape, proximal papillae narrower. Wide distalmost papillae are characteristic for some ophiacanthids. . . and for all genera of the families Ophionereididae, Ophiocomidae and Ophiodermatidae." Ophiomusaidae, Ophiosphalmidae, Hemieuryalidae, and Ophiolepididae present a similar aspect. The presence of opercular distal papillae was construed to be a derived feature, in contrast with the "numerous, long, spiniform oral papillae" that exhibit "homogeneity and similarity in size and shape from the distal to the proximal jaw area." This latter morphology was suggested to be the "ancestral. . .plesiomorphic state of the oral papillae," on account of its occurrence in Euryalidae and Ophiomyxidae (Martynov, 2010:23). Other authors asserted "the primitive form of oral-papillae" is "scale-like, flat with rounded tip," on the basis of purportedly scale-like OPas *s.l.* of juvenile *Amphipholis squamata*, an amphiurid (H.L. Clark, 1914:121; Spencer, 1925:276). Nevertheless, these taxa that allegedly have plesiomorphic OPas *s.l.*, Euryalidae, Ophiomyxidae, and Amphiuridae, are not "ancestral" (see O'Hara et al., 2017, 2018).

Interestingly, relatively large distal OPas *s.l.* and contrastingly smaller proximal ossicles, rather than homogeneous, spiniform papillae, occur in Paleozoic "modern-type" ophiuroids. These forebears had enlarged, distal oral papillae beside the orifice of the vTCt and smaller, narrower proximal OPas *s.l.* The Early Carboniferous *Aganaster jagiellonicus*, which is regarded as a "crown group. . .modern-type ophiuroid," had a "leaf-like lateral papilla. . .sitting on the adradial edge of the adoral shield" and leaf-like papillae of different sizes on the lateral edge of the jaw (Thuy et al., 2015:926; fig. 2C$_1$, C$_2$; Thuy and Stöhr, 2016:5). "Triassic *Aspiduriella streichani* and *Aspiduriella scutellata* had a pair of comparatively large, leaf-like papillae on the AdSh, which may be a AdShSps and 2°AdShSp, and several smaller, leaf-like papillae on the OP, which decreased in size toward the apex of the jaw (Kutscher, 1987:704, fig. 6; Thuy and Stöhr, 2018:13). Mesozoic ophiacanthids, *Leadagmara gracilispina* Thuy et al., 2012, and *Ophiosternle crinitum* (Quenstedt, 1876), also had "leaf-like papillae" covering the orifice of the vTCt, which may be AdShSps, and slender spiniform papillae on the edge of the OP (Thuy et al., 2012:521, fig. 4E; Thuy and Schulz, 2013:526, fig. 1D, E).

The progressive increase in the size of OPas *s.l.* from the apex of the OP to the distal edge of the OSl in ancient and modern ophiuroids may be related to protective and defensive functions of the papillae, to the wedge shape of the jaw, and to the distalward increase in the width of the OSl. OPas *s.l.* can form parallel rows of "double doors" on opposing jaws, which block the OSl when the jaws close, and progressively larger ossicles between the IPas and the AdShSps can seal the OSl. Large, opercular AdShSps and 2°AdShSps can cover the orifice of the vTCt and, together with LyOs and the vCtP, can shield the vTCt and protect the OT-2.

The morphology of the OPas *s.l.* of Ophiomusina species, which precisely dovetail when the jaws close, demonstrate that OPas *s.l.* can completely seal the OSl. The capacity of these OPas *s.l.* to shield the OTs, and to sequester food in the buccal cavity, is advantageous in bathyal ecosystems that these animals inhabit, where their rate of mortality is high and food is scarce (Gage, 1982; Baker, 2016). The antithesis of ophiomusine buccal armature is exemplified by Ophiactoidea such as *Ophiothrix* species in which OPas *s.l.*, except teeth and TPas, are lacking. Matsumoto (1917:378) remarked that members in this superfamily group also have a well-developed "masticatory apparatus," and "This fact probably has a certain biological meaning." It is argued below that their reduced buccal armature and their muscularized jaws, which form a buccal funnel, are adaptive for microphagous feeding.

## BUCCAL FUNNEL

The closed mouth of *Ophiothrix spiculata* circumscribes a complex feeding apparatus that, in the present study, was designated a "buccal funnel" (see "Diet, Feeding, and Operations of the Jaws" in the treatment of *Ophiothrix spiculata*). The buccal funnel comprises a graduated series of OPas *s.l.* borne on the proximal edges of the jaws, and it is surrounded by radiating, spindle-shaped OSls between the jaws (Fig. 11). Columns of teeth that progressively increase in length dorsally, gradually constrict or block the funnel, and small apical ossicles, such as TPas, CPas, and IPas, may encircle the funnel's orifice. Suggestions that this structure is a "grinding instrument," or that it is not a "chewing apparatus" at all (Duncan, 1887b:111; Boos, 2012:115–117), were refuted by Austin's (1966:59) discovery that TPas and teeth in the "truncated cone" of *O. spiculata* may "contribute to compaction of the bolus."

Previous authors remarked on the particular ossicles that compose buccal funnels, for example teeth, TPas, and IPas. However, they did not consider the buccal funnel in its entirety as a complex adaptation for microphagous feeding, or examine its phylogenetic distribution. For example, Lyman (1865:127) described, in amphiurids, the "innermost pair" of "mouth papillae [IPas]. . .extending upwards towards the teeth, and thus partly holding the place of tooth-papillae," without considering the resemblance between these amphiurid IPas and ophiotrichid TPas. He described IPas of a hemieuryalid, *Ophioplocus januarii* [=*Ophioceramis januarii*], as "tooth-papillae. . .diverging upwards, leaving a triangular space, which is filled by the lowermost tooth. . .[that] might almost as well be termed [a] *mouth-papilla*," and he noted that "The innermost papillae in *Amphiura* are similar, but descend, so as to form part of the row of mouth-papillae, among which they are included" (Lyman, 1865:63). Perhaps he viewed differences among OPas *s.l.* of ophiotrichid, amphiurid, and hemieuryalid species to be more significant than their remarkable similarities.

In the present study, one or more species with buccal funnels were noted in 12 of the 25 families of superorder Ophintegrida (Table 1; Fig. 11). These species belong to both suborders (i.e., Ophiodermatina and Ophiacanthina) and to four of the nine families of Ophiacanthida, but buccal funnels appear to be lacking in the sister Ophioscolecida. Buccal funnels occur in the three suborders of Amphilepidida (i.e., Ophionereidina, Ophiopsilina, and Gnathophiurina) and in eight of the 10 families, but appear to be lacking in the sister order Ophioleucida. On the other hand, buccal funnels, and other morphological adaptations associated with microphagous feeding, are lacking in the primarily macrophagous species of Ophiurida, Ophiodermatidae, and Ophiomyxidae. Members of superorder Euryalida also lack buccal funnels, which is not surprising considering their distinctive feeding habits (see "Diet, Feeding, and Operation of the Jaws" in the treatments of *Asteronyx loveni* and *Asteroporpa annulata*).

Species that possess buccal funnels, and for which dietary information is available, prove to be microphagous (see "Diet, Feeding, and Operation of the Jaws" and "Buccal Morphology" in the treatments of *Ophiacantha bidentata* and *Ophiothrix spiculata*). Most of these species are facultative, passive suspension feeders or benthic deposit feeders, which relay mucus-bound particles to the mouth with their tube feet. It is likely they process food in a manner similar to *O. spiculata*, by using repetitive movements of the jaws and the buccal funnel to compact, and perhaps crush, food boluses. Furthermore, limited evidence suggests that *Ophiocoma* species consolidate and ingest multiple boluses similarly to *O. spiculata*. However, Ophionereididae that facultatively suspension feed but exhibit generalized feeding habits, have abbreviated buccal funnels.

Many species with buccal funnels have in common a suite of morphological specializations, namely wing-shaped OPs, perforate DPs, blunt tapered teeth capped with dense or imperforate stereom, and papillose tube feet, which are presumptive adaptations for microphagous and suspension feeding (see "Diet, Feeding, and Operation of the Jaws of Amphilimnidae and Ophiopsilidae," and "Buccal Morphology" in treatments of *Ophiocoma echinata*, *Ophiacantha bidentata*, *Ophionereis porrecta*, *Amphioplus abditus*, and *Ophiothrix spiculata*). Lyman (1882:168) remarked on the "quasi-enamelled grinding end" of the teeth of *Ophiocoma*, which is a characteristic feature occurring in other microphagous taxa with buccal funnels, and reinforced teeth of other Ophiocomidae were noted by Mortensen (1920:52). In addition, he recognized that "powerful muscles attached to these wings [on the first vertebrae of *Ophiocoma*] must enable it to [make] very active movements with its jaws, and the enamel point of the teeth. . .bear witness of an exceptional masticating power" (Mortensen, 1920:52). Likewise, Matsumoto (1917:4) emphasized that "forms with quadrangular and stout teeth have oral frames with well developed lateral wings [on the OP] for the attachment of voluminous masticatory muscles, for example, *Amphiuridae* mihi; *Ophiotrichidae*; *Ophioceramis*; *Ophionereidinae* mihi; and *Ophiocomidae*."

Curiously, these members of Gnathophiurina and Ophiacanthida, which have well-developed lateral wings on the OP, and perforated DPs that signify well-developed dental muscles, were previously described as having "gnathophiurine jaws" that might function "as a respiratory pump, involved in the circulation of water through the bursae." It was deemed that "not even a convergence of habit could explain the extraordinary similarities between the jaws of Ophiocomidae and Ophionereididae on the one hand and the Amphiuridae, Ophiactidae, and Ophiotrichidae on the other," and thus it was concluded that these similarities must "unite a distinct monophyletic group" of families (Pentreath, 1970:410; Wilkie, 1980:154). However, judging from an up-to-date phylogeny and classification of Ophiuroidea (O'Hara et al., 2017, 2018), it appears that a conjunction of buccal funnels, muscularized jaws, perforate dental plates, reinforced teeth, and papillose tube feet, may have evolved repeatedly and in unrelated microphagous taxa. Among members of the order Ophiacanthida, buccal funnels occur in a single family of Ophiodermatina (Ophiocomidae), but in several families of the sister Ophiacanthina (Table 1). Morphological differences between the buccal armature of these two suborders suggest that their buccal funnels evolved independently (see "Buccal Morphology" in the treatment of *Ophiocoma echinata*, and see "Buccal Morphology of Ophiacanthina" in the treatment of *Ophiacantha bidentata*. Disparities among key skeletal components of the buccal funnels in the order Amphilepidida, such as CPas in Ophiopsilidae, IPas in Amphiuridae, and TPas in Ophiotrichidae may signify that buccal funnels evolved separately in their respective superfamilies.

Buccal funnels of Ophiacanthida are composed of clusters of TPas below columns of teeth that increase in length dorsally. The TPas of Ophiacanthina (e.g., *Ophiocomina nigra*, *Ophiopteris* spp., and *Clarkcoma* spp.) increase in length dorsally and form a concave cluster composed of shorter medial and longer lateral TPas, whereas TPas of Ophiodermatina (i.e., Ophiocomidae) are of nearly equal length. In contrast, buccal funnels of Amphilepidida, except Ophionereididae and Ophiotrichidae, have dimorphic teeth that somewhat resemble the tapering, compressed, blunt teeth of Ophiacanthida. However, their distinctive ventral teeth typically have a wide, concave proximal surface with a dorsomedial cusp, thick adradial edges, and a flanged, proximal edge that partially overlaps the base of the tooth above. These characteristic amphilepididan teeth sometimes were described as a "tricuspid" ventral tooth or apical papilla (e.g., A.M. Clark, 1970:36, 39, 62; Paterson, 1985:80; Stöhr and Segonzac, 2005:390; Falkner and Byrne, 2006:1202; Martynov, 2010:123).

The families of Amphilepidida with buccal funnels are distinguished by characteristic types of ossicles below the teeth, namely CPas and/or IPas on the OP or TPas on the DP. Ophiactoidea and Ophiopsiloidea are the only Amphilepidida with TPas. Ophiotrichidae lack OPas *s.l.* but have well-developed, concave clusters of TPas, that somewhat resemble those of Ophiacanthina. However, their long adradial TPas are capped with imperforate stereom and are controlled by muscles that penetrate foramina in the DP, which suggests they may actively interlock with adjacent counterparts when the jaws are fully closed (Fig. 26C; Martynov, 2010:fig. 14M). In contrast, Ophiopholidae, which are sister to Ophiotrichidae, have a buccal funnel dominated by dimorphic teeth, larger and concave ventrally and smaller dorsally, and comparatively few TPas that are not aligned in vertical columns. Ophiactidae too have dimorphic teeth, but entirely lack TPas. Ophiopsilidae (Ophiopsiloidea) have a relatively complex buccal funnel composed of dimorphic teeth and TPas, in addition to subapical IPas and apical CPas on the OP.

Aside from Ophiactoidea and Ophiopsiloidea, there are three other families of Amphilepida in different superfamilies, which have buccal funnels with IPas rather than TPas. Ophionereididae (Ophionereidoidea) lack concave ventral teeth and have an abridged buccal funnel comprising small IPas and dorsal teeth capped with imperforate stereom. Amphiuridae (Amphiuroidea) and several species of Hemieuryalidae (Ophiolepidoidea) examined in the present study have a buccal funnel comprising dimorphic teeth and IPas. However, *Ophiozonoida obscura*, a hemieuryalid, may have both IPas and TPas in its buccal funnel.

Most species with buccal funnels have a concave cluster of small ossicles at the apex of the jaw, and although the types of ossicles that compose the buccal funnel in various species are not necessarily homologous (e.g., IPa, TPa, and CPa), the buccal funnels may be functionally analogous. A strikingly similar triad of ossicles comprising paired IPas and a recessed vT, which occurs in some Amphiuridae (e.g., *Amphioplus abditus*) and Hemieuryalidae (e.g., *Ophioplocus januarii*), raises the question whether buccal funnels of these species are homologous. Interestingly, *O. januarii* is nested in a hemieuryalid lineage that is otherwise composed of species lacking buccal funnels, but which have IPas and vT, suggesting that buccal funnels of *O. januarii* and the Amphiuridae are homoplasious. Based on the tree in O'Hara et al. (2017:fig. S3), Ophiolepidoidea consist of an ophiolepidid clade that appears to lack species with buccal funnels, and a hemieuryalid clade that is composed of a mixture of species with and without buccal funnels. However, despite the seeming absence of a buccal funnel among the 16 ophiolepidid taxa represented in the tree, *Ophiozonella oedilepis*, an ophiolepidid, was found to have a buccal funnel in the present study (Fig. 11G), suggesting that buccal funnels evolved independently in both clades of Ophiolepidoidea (see "Diet, Feeding, and Operation of the Jaws" in the treatment of *Sigsbeia murrhina*). Moreover, differences in the types of ossicles that compose the buccal funnels of other Amphilepidida (e.g., Amphiuridae, Hemieuryalidae, and Ophiolepididae), and dissimilarities between buccal funnels of Ophiodermatina and Ophiacanthina, suggest that buccal funnels may have evolved convergently among these lineages of Ophiacanthida.

## CONTRASTING MODES OF MACROPHAGOUS AND MICROPHAGOUS FEEDING

Two principal feeding modes of ophiuroids, macrophagy and microphagy, are distinguished according to the type of food consumed and the manner in which it is acquired (reviewed by Warner, 1982). Generally, macrophagous species are carnivores and carrion feeders that grasp prey in loops of their arms, whereas microphagous species are deposit feeders and passive suspension feeders that gather particulate material with their tube feet. Although "there is much overlap between the groups" (Warner, 1982:161), a preponderance of the literature indicates that macrophagous and microphagous species constitute separate feeding guilds. Each group comprises taxa that are phylogenetically diverse but have similar feeding behaviors and use similar, specialized body structures to collect, transport, and process food (Simberloff and Dayan, 1991).

### Feeding Adaptations of Macrophagous Ophiuroids

The feeding behavior of *Ophiura luetkenii* is illustrative of other macrophagous species (Austin, 1966; Pentreath, 1970; Dearborn et al., 1996; see "Diet, Feeding, and Operation of the Jaws" in treatments of *Ophiura sarsii*, *Ophioderma rubicunda*, and *Ophiomyxa flaccida*). The arm of a feeding individual is coiled around a large item of food and folded beneath the disk, and the OTs reject the item or push it into the mouth. Although small objects may be transferred to the mouth by successive pairs of contralateral tube feet, *O. luetkenii* does not feed on suspended particles. Food is ingested with the mouth agape, and the jaws close infrequently and briefly on an object before OTs thrust it toward the gut. Large objects may be swallowed gradually, alternately clamped in the jaws and pushed upward by the OTs, and items too large to swallow may be secured in the jaws and torn by the arms. However, prey can be captured with alacrity and virtually undamaged. *Ophiura ophiura* [=*Ophiura texturata*] was observed to bound ahead "jump, and land with the food below its mouth. . .once food was within the oral field, only seconds were usually required for material to be transferred to the stomach. . .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" (Feder, 1981:224). *Ophiura robusta* fed in a similar manner, and used the hooked spines on distal arm segments to snag food items (Litvinova, 1980). The food of *Ophiura albida* [=*Ophioglypha albida*] consisted of small invertebrates and "bottom material," indicating that its pointed teeth and TPas are not "carnassial instruments. . .thrusting into the flesh of a prey organism and tearing off pieces" (Eichelbaum, 1910; Boos et al., 2010:180; *contra* Boos, 2012:111). It was suggested that teeth of *O. luetkenii* might "partially break up or crush material before it enters the gut," but the teeth of this species and other macrophagous ophiuroids have not been directly observed to macerate food (Austin, 1966:66). Macrophagous *Ophioderma* species transfer undamaged items of food to the stomach "without any masticatory movements of the jaws" (Deschuyteneer and Jangoux, 1978; Hendler, 1982b; Candia-Carnevali et al., 1994:388). *Ophiomyxa brevirima* uses its serrated teeth merely to "grasp" items that are en route to the stomach, and individuals of *Ophiarachna incrassata*, a formidable, predaceous ophiomyxid, "swallow their prey whole" (Pentreath, 1970:419; Morin, 1988:404).

Jaws of macrophagous ophiuroids have a buccal apparatus that is more serviceable for grasping than for mastication. Their teeth, which intermesh when the jaws close, are typically composed of stereom that is not strongly reinforced, presumably because they do not strike against refractory food items or opposing ossicles (e.g., Figs. 12B, 13Q). Their OPs have moderate-sized muscle fossae and therefore are not highly muscularized, presumably because protraction and retraction of the jaws is not forceful or repetitive. The moderate size of these muscle fossae accounts, in part, for the low-profile, "chisel-shaped" OPs of Ophiuridae and "axe-shaped" OPs of Ophiodermatidae and Ophiomyxidae (*sensu* Murakami, 1963:34, 37). DPs of Ophiurida, Ophiomyxidae, and Ophiodermatidae lack large foramina, presumably because their relatively weakly developed dental muscles insert on the DP, instead of the OP (Duncan, 1889:pl. 10, fig. 3; Murakami, 1963:pl. 1, figs. 1–2; pl. 2, figs. 32-44, 53–55; Candia-Carnevali et al., 1994:390). The buccal cavity of the predatory macrophagous species *Ophiomyxa flaccida* and *Ophioderma rubicunda* has a comparatively well-developed PeSk comprising CtPs, CtOss, CoOss, and LuOss that might shield the OTs and PG from unwieldy, injurious food items that are swallowed intact.

Some macrophagous feeders, such as *Ophiarachna incrassata*, an ophiomyxid, and the ophiodermatids *Ophiochasma nitida* Hertz, 1927, and *Ophioderma* species, have one or more prominent, spiniform OPRSps that could restrain or impale prey in the buccal cavity (Fig. 12B; Matsumoto, 1917:pl. 6; Clark and Courtman-Stock, 1976:fig. 276). OPas *s.l.* of some ophiomyxid species such as *Ophiomyxa vivipara* and *O. flaccida* are fringed with serrations or recurved spikes composed of imperforate stereom (Fig. 14A, C; Medeiros-Bergen, 1996:fig. 1d; Brogger et al., 2015:fig. 2A). In contrast with *Ophioderma rubicunda*, which has well-developed OPRSps and smooth-edged teeth, *O. flaccida* has rudimentary OPRSps, but its spinose teeth might be used to pinion prey (Figs. 12B, C, 14B, C).

Ophiurids typically have jaws with a lower profile than those of ophiodermatids and ophiomyxids. Their OP has a "chisel-shaped" profile, because of its truncated apex, small abradial muscle fossa, and shallow OPR, and the truncate vTCt that is fringed by small OPas *s.l.* Their OT-2 can be deployed when the jaws are tightly closed. The OT-2 can rotate in a >90° arc beneath the disk, which may augment the ability of ophiurids to detect and gather food. "Gulping" behavior of *Ophiura* spp., and the rapidity with which they convey food to the stomach, might be facilitated by the abridged height of the jaws. It might be expected that *Ophioplinthus gelida* manipulates food items differently than *Ophiura* spp. because its OT-2 is sequestered from the OSl within a heavily armored vTCt, but both species have similar stomach contents. However, *O. sarsii* is an active, versatile predator, and *O. gelida* appears to be a scavenger (see "Diet, Feeding, and Operation of the Jaws" in the treatments of *O. gelida* and *Ophiura sarsii*).

Amphilepididae, like Ophiuridae, have low-profile jaws with a truncated apex, a shallow, abridged vTCt, and OPas *s.l.* on the OPR (Figs. 4C, 6A; A.M. Clark, 1970:fig. 1A; Mills and O'Hara, 2010:50, fig. 2C, D). The orifice of the vTCt of *Amphilepis* spp. has been described as "opening outside the mouth," although the vTCt extends into the mouth between the upcurved VAP-1 and the OPR (Mills and O'Hara, 2010:50; Thuy and Stöhr, 2016:16). The amphilepidid OT-2 can extend directly in the mouth when the jaws are open, and when the jaws are closed it is blocked by OPas *s.l.* on the OPR. The striking similarities between amphilepidids and ophiurids raise questions as to how their distinctive morphology evolved in different superorders, and whether it is adaptive for the same function in Amphilepididae and Ophiurina. Unfortunately, a comparison between these taxa is not feasible because the feeding biology of Amphilepididae is an enigma. Individuals of *Amphilepis patens* are reportedly "infaunal but it is unknown if they feed directly on settling detritus or prey on other infaunal organisms" (Booth et al., 2008:934). Living individuals of the miniaturized, cave-dwelling amphilepidid, *Amphicutis stygobita* Pomory et al., 2011, have been studied, but were not seen to feed (Pomory et al., 2011:52, 63).

### Feeding Adaptations of Microphagous Ophiuroids

The feeding behavior of *Ophiothrix spiculata* is typical of microphagous, suspension-feeding ophiuroids (see "Diet, Feeding, and Operation of the Jaws," "Buccal Morphology of Ophiactoidea," and "Diet, Feeding and Operation of the Jaws of Amphilimnidae and Ophiopsilidae" in the treatments of *Amphioplus abditus* and *O. spiculata*, and *Ophionereis porrecta*, respectively, and the discussion of the "Buccal Funnel"). *Ophiothrix spiculata* erects its arms, directing the ambulacral surface toward the current and extending the tube feet in two comb-like rows. The tube feet accumulate particulate material that they bind in mucus and compact into a bolus. This mass accrues additional material as it is propelled by contralateral pairs of tube feet, from the tip of the arm toward the mouth, in a rapid, coordinated wave of tube-foot activity (Austin, 1966). Boluses reaching the jaws are tested by the OTs, and may be retained or rejected (Austin, 1966; Pentreath, 1970). *Ophiothrix fragilis* has a similar feeding behavior, and was described to transfer boluses into the mouth "without any pause" (Warner and Woodley, 1975:204). However, Austin (1966) observed that OTs-2 of *O. spiculata* accumulated incoming boluses beneath the closed jaws until the mass was large enough to fill the mouth opening. At this juncture the jaws opened, and the mass was forced into the buccal funnel by the OTs and basal tube feet (Austin, 1966:58). In the ensuing ~5-minute interval the jaws opened and closed on the clump 30–40 times. OTs pushed the clump higher in the buccal funnel each time the jaws opened, before both sets of OTs propelled the compacted mass into the stomach.

The buccal funnel of *Ophiothrix spiculata* comprises clusters of TPas and columns of teeth on the proximal edge of the DP, which increase in length dorsally. When the jaws draw together, the teeth and TPas intermesh with counterparts on the adjacent DPs, forming a funnel-shaped cavity that is constricted by the dorsalmost teeth. The ventral orifice of the cavity, which remains agape when the jaws are closed, is framed by five concave clusters of TPas, each of which is composed of a medial column of short papillae flanked by successive columns of increasingly longer papillae. The clusters of TPas compress and consolidate boluses, and "teeth dorsal to the dental papillae may also contribute to compaction of the bolus…[although] their mode of operation has not been observed" (Austin, 1966:59). Whether the teeth of *Ophiothrix* spp. can crush food could be tested by analyzing stomach contents of individuals after they had ingested particles of a known, uniform size.

*Ophiothrix* species have specialized OPas *s.l.*, OPs, DPs, and tube feet, as well as the buccal funnel, which distinguish them from macrophagous taxa. Their teeth and some TPas are capped with imperforate stereom that is thought to "provide a tough grinding surface for food particles, and may reduce frictional wear from abrasion from teeth located on adjacent jaws" (Medeiros-Bergen, 1996:219; Brogger et al., 2015). The teeth are dorsoventrally compressed, and gaps separate the edges of successive teeth. Owing to these gaps and the staggered positions of teeth on adjacent jaws, opposing teeth intermesh when the jaws are closed. Furthermore, as the jaws move, teeth can be positioned by dental muscles that extend through foramina in the perforate DP and insert on the OP (Simroth, 1876; Duncan, 1887b; Murakami, 1963; Wilkie, 1980:fig. 2B). The jaw has a tall, proximal blade, and large, splayed, wing-shaped abradial muscle fossae. Well-developed sets of abradial, adradial, and interambulacral muscles on the OPs drive the jaws. The large OTs of *Ophiothrix* species are accommodated in spacious dorsal and ventral TCts on opposite sides of the OPR, and they fill the OSls of the ophiuroid. The absence of OPas *s.l.* on the vTCt may facilitate the mobility of the OTs. Delicate FPs are the sole PeSk elements in the PG, presumably because the buccal cavity is not liable to damage from the ophiotrichid from a diet of particulate matter. The tube feet, which can extend beyond the arm spines, bear numerous glandular papillae that secrete mucus that collects and binds particles of food (Smith, 1937; Buchanan, 1962; Warner and Woodley, 1975:pl. 1, fig. B).

## FEEDING AND LOCOMOTORY ADAPTATIONS OF JUVENILE OPHIUROIDS

Muus (1981:165) described the ability of postlarval ophiuroids to ingest remarkably large prey, and she commented that for a juvenile *Amphiura filiformis* "...with no arms, only ten tube-feet, and a very primitive mouth apparatus it must involve a considerable effort to overcome a disc-shaped foraminiferan of about its own size. This fact excludes the possibility that they use unsorted bottom material as their only source of nourishment. They must be classified as facultative predators and scavengers." She found that over 40% of newly settled juveniles (0.3–0.5 mm dd) had food in their stomach, and she saw some individuals that were ball-shaped, having gorged on foraminiferans, ostracods, or particulate benthic material (Muus, 1981:165). Similarly to postlarval *A. filiformis*, postlarval *Ophiocten gracilis* (0.5–1.5 mm dd) capture foraminiferans, polychaetes, and phytodetritus (Sumida et al., 2000:625).

Juvenile *Amphiura filiformis* (0.5 mm dd) must use the OTs-2 to push food into the stomach, since at this stage the only OPas *s.l.* that could be brought to bear on prey are teeth and opercular BScs (Stöhr, 2005:fig. 13D). During this crucial phase of development, the vT, BSc, and AdShSp are the only buccal armament, since other IPas do not develop until *A. filiformis* is ~1 year old and until *Amphioplus abditus* is ~5 months old (Hendler, 1978; Muus, 1981; Stöhr, 2005:fig. 13F). The BScs alone seal the OSl and shield the buccal cavity at this stage. Juvenile ophiuroids have BScs that are proportionally much larger than those in adults, and they are functionally equivalent to multiple OPas *s.l.* that are present in the adult stage. Correspondingly, the AdShSp, FP, vCtP, and TP are proportionally larger in the juveniles than in adults with a fully developed skeleton (compare figures of successive ontogenetic stages: e.g., in *Ophioderma rubicunda* Figs. 12A, C, 13A, C, K; *Ophionereis olivacea* Figs. 23A, F). The hooked terminal arm spines of pelagic, postlarval *Ophiothrix fragilis* and *Ophiopholis aculeata* are enormous relative to the terminal arm spines of the adult. They exemplify the adaptive importance of hypertrophied juvenile structures, since newly settled young of these species use the terminal spines to cling to adult conspecifics and other hosts, whereas postlarvae that settle on sediment, such as *Ophiura* species, have small, unspecialized distal spines (Klitgaard, 1995; Medeiros-Bergen et al., 1998:figs. 2, 3; Sumida et al., 1998; Turon et al., 2000; Morgan and Jangoux, 2004).

Juvenile *Amphioplus abditus*, *Amphiura filiformis*, *Ophioderma brevispina*, *Ophiolepis elegans*, and *Ophionereis squamulosa* use OTs-2 to adhere on substrate and perambulate, whereas adults use OT-2 to select and ingest food (Grave; 1900:96; Mortsensen, 1920:139; Stancyk, 1973:8; Hendler, 1977:57, 1988:28; Muus, 1981:164). Accordingly, Vadon (1990:176) postulated that "migration of the second oral tentacle pore within the buccal slit suggests a possible change in the mode of nutrition and locomotion of the ophiuroid during its growth." Indeed, newly settled individuals of *A. filiformis* utilize OTs-2 to cling to hard substrate and to move on or below the surface of fine sediment, and juvenile *A. abditus* with fewer than two ASs use the OTs-2 for locomotion (Hendler, 1977:57; 1988:28; Mortensen, 1920:139). Juveniles of *A. abditus* with eight ASs move using their tube feet rather than arm flexion, and as their OT-2 is still isolated from the OSl it might be employed for feeding and locomotion (Hendler, 1977:57; 1978:fig. 4A). At this stage they perambulate like the diminutive adult of *Amphicutis stygobita*, which "mainly uses podial walking for locomotion" (Pomory et al., 2011:63). In contrast, adult *A. abditus* employ arm flexion and tube foot flexion to crawl, feed, and to maintain and irrigate their mucus-lined burrow. The OTs of the adult are not locomotory structures. They are morphologically distinguishable from the tube feet and are used exclusively for feeding (Hendler, 1977, 1978, prev. unpub.).

## CONCLUSIONS

1. Oral papillae in the broad sense (OPas *s.l.*) comprise ossicles that are distinguishable as (1) teeth and tooth papillae (TPas), which develop on the dental plate (DP); (2) buccal scales (BScs), infradental papillae (IPas), crest papillae (CPas), secondary infradental papillae (2°IPas), lateral oral papillae (LOPas), and accessory oral papillae (AOPas), which develop on the oral plate (OP); (3) adoral shield spines (AdShSps) and serially homologous secondary adoral shield spines (2°AdShSps), which develop on the adoral shield (AdSh) and/or OP; and (4) serially homologous tentacle scales (VAP-1 TScs) that develop on the first ventral arm plate (VAP-1) and ventral compartment plate (vCtP).
2. The peribuccal skeleton (PeSk) comprises ossicles distinguishable as (1) compartment plates (CtPs), compartment ossicles (CtOss), and collar ossicles (CoOss), which enclose the tentacle basins and oral tentacles (OTs); (2) falcate plates (FPs) of the dorsal tentacle compartment (dTCt), which arch over the first oral tentacle (OT-1); (3) Lyman's ossicles (LyOss) of the ventral tentacle compartment (vTCt), which abut the vCtP, VAP- 1, and AdSh; (4) Ludwig's ossicles (LuOss), which may occupy the perradial gap (PG) between the adjacent jaws; (5) oral plate ridge spines (OPRSps), which are rigidly borne on the adradial oral plate ridge (OPR); and (6) peristomial plates (PPs) that overlap the dorsal surface of the jaw.
3. The orders Ophiurida, Euryalida, Ophiacanthida, and Amphilepidida each have a characteristic suite of OPas *s.l.* and PeSk ossicles (Fig. 27). Ophiurida typically exhibit an IPa, one or more 2°IPas, a BSc, an AdShSp, and they may have one or more 2°AdShSps and VAP-1 TScs bordering the vTCt. 2°lPas occur exclusively in Ophiuridae. The vTCt and vCtP of Ophiurida may be abbreviated or lacking, and Ophiurida lack LyOs but may develop AOPas. Ophiacanthida have an IPa and an AdShSp, and may have 2°AdShSps, but they characteristically lack a BSc. They are the only ophiuroids that bear LOPas and OPRSps. Amphilepidida typically have an IPa, BSc, AdShSp, and 2°AdShSp, although in some taxa one or more of these ossicles are rudimentary or resorbed. Ophiotrichidae, for example, lack OPas *s.l.*, except for teeth and TPas. Homologies of OPas *s.l.* of the Euryalida are indeterminable on the basis of available information. Euryalida lack VAP-1 TScs, AdShSps, and 2°AdShSps, and they do not develop spines on the first arm segment. Their OPas *s.l.* typically are homogeneous (tuberculate or spiniform), and the number and location of their OPas *s.l.* can be unpredictable. The occurrence of leaf shaped OPas *s.l.* in "modern-type" fossil *Aganaster* spp. that are presumptive "basal crown group ophiuroid[s]," and in *Aspiduriella* spp. that are "basal member[s] of the euryalid clade," suggests that uniformly spiniform OPas *s.l.* may have originated in Recent crown group taxa (Martynov, 2010:23; Thuy, 2015:186-187; Thuy and Stöhr,

2016:5; Thuy and Stöhr, 2018:1). Additionally, morphological and ontogenetic distinctions among OPas *s.l.* suggest that "oral papillae" are not "merely groove spines carried by the mouth-angle plate" as was previously suggested (Spencer, 1925:276).

4. Regarding the species examined herein: The nearly ubiquitous occurrence of teeth and AdShSps suggests that these ossicles may be plesiomorphic features of living Ophiuroidea. TPas also are widespread, but their sporadic occurrence in families of Amphilepidida and among some Hemieuryalidae and Ophiolepididae indicates they may be homoplasious in Ophiuroidea, but that the TPas in certain clades may be homologous. The loosely used term "apical papilla" was traditionally applied to an ossicle on the DP, which should be referred to as a ventralmost tooth (vT). IPas have a considerably broader phylogenetic distribution than previously understood, but they do not appear to occur in the Euryalida, Ophioscolecida, and late-branching Ophiactoidea. So-called "paired infradental papillae" are IPas, and are not restricted to Amphiuridae. FPs, vCtPs, and LuOss appear to be nearly ubiquitous PeSk elements. Evidence for the homology of the BScs of Ophiurida and Amphilepidida is inconclusive, and reports of BScs in Ophiacanthida are problematic. LyOss are documented in five families of Ophiacanthida and three families of Amphilepidida, but appear to be lacking among Gnathophiurina. The homology of LyOs-like ossicles, and the homological relationship between LyOs and the vCtP are unresolved. LOPas are found exclusively in Ophiacanthida. Notably, one primary clade of Ophiocomidae lacks LOPas and all but one species in the sister clade develop LOPas that presumably are homologous. OPRSps are found exclusively in Ophiodermatoidea, and anvil-shaped OPRSps are characteristic of Ophiocomidae.
5. In the present study, morphologically similar OPas *s.l.* that arise in close proximity, and in a unidirectional linear sequence, are provisionally considered serially homologous. These rows of ossicles include the following: (1) IPa and 2°IPas of Ophiurida, which develop near the DP/OP juncture and proliferate proximally, with each new ossicle forming proximal to its predecessor; (2) VAP-1 TScs of Ophiurida, which proliferate proximally and may spread from VAP-1 onto the vCtP; (3) AdShSp and 2°AdShSps, which proliferate proximally and may spread from the AdSh onto the OP; (4) LOPas that arise on the OP, distal to the IP, and appear to proliferate distally; and (5) teeth and some TPas, which proliferate ventrally at the growing edge of the DP.
6. PeSk ossicles enclose OTs, and shield the PG and the circumoral neural and water vascular grooves, and link the arms and oral frame. The four tentacle compartments (TCts) on a jaw, which each enclose an OT, may be composed of CtPs, CtOss, CoOss, LyOs, and FPs. The water ring, hemal ring, and nerve and perihemal rings, which encircle the oral frame, give rise to radial branches that descend through the PG, between adjacent jaws and beside adradial muscles on the OPs, before entering the arm. These coelomic, nervous, and muscular structures within the PG are separated from the buccal cavity by the VAP-1, LuOss, FPs, and an integumental sheath in which they are embedded. VAP-1 bridges the arm and OP, shielding the ventral portion of the PG, and FPs and LuOss shield the dorsal portion of the PG. PPs may shield the water ring, and the FPs and PPs overlap the circumoral neural groove on the jaws, protecting the nerve ring. The discovery that the PP of *Ophiacantha bidentata* is pedunculate and has an intraossicular conduit, demonstrates that PPs can be morphologically and functionally more complex than previously thought.
7. A water ring overlies the radial plates of crinoids, the calcareous ring of holothuroids, Aristotle's lantern of echinoids, the mouth angle plates of asteroids, and the oral plates of the ophiuroids that have a single foramen in each OP. This foramen receives a branch of the water ring, which bifurcates within the OP an terminates in two OTs. Surprisingly, in the present study the OPs of some Euryalida, Ophiurida, Ophioscolecida, Ophiacanthida, Ophioleucida, and Amphilepidida were discovered to have an internal water ring that passes through two foramina in each OP and bifurcates within the OP. Typically, species with a single water ring foramen have OPs with splayed, wing-like abradial muscle fossae. During ontogenesis, growth of these wing-like structures may prevent the development of an abradial water ring foramen. However, species with dual water ring foramina have a relatively small abradial muscle fossa. Single water ring foramina have been described in extinct "modern-type" ophiuroids, but dual water ring foramina have not been reported in fossil taxa.
8. Traditionally, it was thought that the nerves innervating the oral tentacles "do not perforate the substance of the ossicle [OP]" (Hyman, 1955:607; Spencer, 1925:268). Consistent with this view, several species examined in the present study had a groove beside the tentacle basin of OT-2, which may enclose a branch of the radial nerve cord that innervates the tentacle (i.e., *Ophiomusa lymani*, *Asteroporpa annulata*, *Stegophiura nodosa*, *Ophioderma rubicunda*, *Ophiacantha bidentata*). Surprisingly, *Ophiura sarsii*, *Ophiocten sericeum*, and *Ophiosparte gigas* were found to have a foramen that pierces the tentacle basin of OT-2, through which a podial nerve can presumably reach the tentacle. An analogous, presumptive nerve canal that appears to penetrate the OPR of *Ophiothrix spiculata* was shown to open beside the tentacle basin of OT-2. *Ophiothrix spiculata* also has a gap between the FP and OP, through which a branch of the circumoral nerve may extend to OT-1.
9. Buccal structures such as the AdShSp, VAP-1, and the putative OTPo-2 seemingly change position during ontogenesis, and this phenomenon was attributed to the independent "migration" and "rotation" of these structures themselves. However, these ostensible movements are effected by differential allometric growth of the ossicles that bear the displaced structures. In the present study, analysis of skeletal ontogenesis of several species revealed that allometric growth of the OP increases the length and depth of the oral slit (OSl) and the distance between the VAP-1 and OPR. Concomitantly, VAP-1 grows proximally toward the OPR and distally toward LAP-2, developing an arched morphology that was previously interpreted as evidence of "rotation." Ontogenetic changes in the size and shape of the OP, AdSh, and AdShSp can bring the AdShSp into contact with the OP, which it overgrows. Subsequently, the AdShSp may be separated from the AdSh by the growth of the OP, rather than by independent "migration of the AdShSp." Authors have proposed that "the second tentacle pore is in young stages far from the mouth, but moves closer during ontogenesis," and that "during development the adoral shields shorten and in their most advanced state they are completely removed from the lateral arm, only bordering the edges of the oral shield" (Stöhr and Martynov, 2016: 4). However, the AdSh lengthens during ontogenesis, and as it grows it maintains contact with LAP-2, never separating from the arm. The distance between OT-2 and the edge of the disk increases markedly as the disk grows centrifugally across the base of the arms, whereas there is a relatively negligible increase in the distance between the vTCt and the mouth. OT-2 remains beside the mouth throughout ontogenesis, between the AdSh and VAP-1 during ontogenesis.
10. Typically, Ophiuridae have a Y-shaped OSl that incorporates a pair of vTCts, which constitute the distal portion of the OSl and extend

toward the proximal OSl. In the adult ophiurid, the vTCt is usually composed of an OPR, AdSh, VAP-1, vCtP, and a BSc and other types of OPas *s.l.* However OTPo-2 of a postlarva is simply a gap between VAP-1 and the AdSh. Because the ophiurid vTCt is truncated in comparison with the dTCt, the vTCt may sit close to the ventral surface of the oral frame, and OT-2 may be completely isolated from the proximal OSl by the structures that surround it, including the OP itself, the vCtP, and the OPas *s.l.*. Nonetheless, in species where the OPR is sufficiently elevated above the ventral surface of the oral frame, the vTCt is confluent with the proximal OSl, permitting OT-2 to extend directly into the mouth when the jaws are open. Nevertheless, when the jaws of many ophiurids are closed, OPas *s.l.* on the OPR obstruct the OSl and exclude OT-2 from the mouth.

11. Authors have proposed that Ophiurina are paedomorphic, in part because the so-called OTPo-2 of the adult, that is, the vTCt, was assumed to have the same morphology as the OTPo-2 of juvenile ophiuroid, and was perceived as simply "superficial and outside the mouth" (e.g., Vadon, 1990; Stöhr and Martynov, 2016; Thuy and Stöhr, 2016; O'Hara et al., 2018). Generally, however, the juvenile OTPo-2 is superseded by a complex vTCt during ontogenesis, and consequently the morphology of juvenile and adult vTCts are dissimilar. The proposal that Ophiurina have a paedomorphic origin implies that as a result of shifts in the timing of ontogenetic processes, the adult stage evolved a resemblance to the juvenile stage of ancestral Ophiurina. However, this scenario has not been confirmed because the ancestral species are unknown and their ontogenesis has not been examined. Furthermore, the timing of ontogenetic milestones has not been established for Ophiurina or other ophiuroids, and shifts in the timing of developmental processes that regulate their skeletal ontogenesis have not been accurately assessed.
12. The two principal ophiuroid feeding guilds comprise distinctive groups of macrophagous and microphagous species. Members of each guild are not necessarily phylogenetically related, although they exploit similar resources in comparable ways. Macrophagous ophiuroids use teeth, other OPas *s.l.* and OPRSps to temporarily grip large food items transported through the buccal cavity. Their OPas *s.l.* interlock when the jaws are completely closed, blocking the buccal cavity. Microphagous ophiuroids, exemplified by Ophiotrichidae, employ a suite of specialized structures to acquire and process food. Their papillose, mucus-secreting tube feet amass boluses of suspended particulate material, which they transport to the mouth. Their buccal funnel, wing-shaped OPs with well-developed abradial muscles, well-developed dental muscles and perforate DPs, and blunt, tapered teeth capped with compact or imperforate stereom, enable ophiotrichids to condense, and possibly crush, mucus-bound packets of particulate food. Microphagous ophiocomids have unique, anvil-shaped OPRSps that are may align and buttress their strongly muscularized jaws. OPas *s.l.* and PeSk ossicles are drastically reduced in size and number among microphagous Amphiuridae and Ophiotrichidae, presumably because the buccal cavity is not liable to damage from the ophiotrichid diet of innocuous particulate material. The feeding biology of Euryalida is poorly understood. Gorgonocephalidae are atypical suspension- feeding carnivores, which are thought to use spiniform OPas *s.l.* to extract prey ensnared by girdle hooklets and coiled arm tendrils.
13. A buccal funnel is comprised of a graduated series of elements on the DPs, which consist of small elements on the ventral apex of the jaw (e.g., TPas, CPas, and short, concave teeth) and progressively larger and longer dorsal teeth. When the jaws close, the small apical ossicles surround a circular orifice and the columns of teeth intermesh, forming a conical cavity. Buccal funnels occur in Amphilepidida (Ophiotrichidae, Ophiopholidae, Ophiactidae, Amphiuridae, Ophiopsilidae, Ophionereididae, and some Ophiolepididae and Hemieuryalidae) and in Ophiacanthida (Clarkcomidae, Ophiopteridae, Ophiocomidae, and at least one species of Ophiotomidae). Species that have buccal funnels are primarily microphagous and are typically passive suspension feeders or benthic deposit feeders. Their buccal funnels are suggested to function similarly to the structures in ophiotrichids. Microphagous species with generalized diets, which consume particles of assorted sizes, have weakly developed buccal funnels. Closely related microphagous taxa usually have buccal funnels composed of similar elements. However, buccal funnels of different families exhibit different types and configurations of OPas *s.l.* Furthermore, the phylogenetic distribution of buccal funnels suggests that they have evolved repeatedly, and that they are a homoplasious feature of Ophiuroidea.
14. Traditionally, Ophiopsilidae were described as having clusters of TPas on the ventral apex of the jaw. However, the presumptive TPas on their DPs are few in number. The number of TPas varies, even in a single individual, and TPas may be lacking in some ophiopsilid species. The present study shows that OPas *s.l.* on the apex of the ophiopsilid jaw are not TPas, because they are borne on a protuberant ventral crest formed by the conjoined projections of the OPs rather than on the DP. These newly recognized OPas *s.l.* are designated crest papillae (CPas). The IPas, in contrast, are each connected to a fossa in the OP, and embrace an indentation between the ventral crest and the ventral edge of the DP. Additionally, Ophiopsilidae are distinguished by their spiniform BScs that are elevated within the OSl. Another spiniform ossicle on the OP, of indeterminate homology, is set above the BSc of some species of *Ophiopsila*. Ophiopsilidae and Amphilimnidae have similar arrays of OPas *s.l.* composed of an IPa, BSc, 2°AdShSp, AdShSp, and an indeterminate spiniform ossicle. However, the jaws of Amphilimnidae do not form a buccal funnel and generally lack CPas.
15. The present study indicates that ophiuroid teeth move in a horizontal plane and that as the jaws retract, the teeth intermesh with their counterparts on opposing jaws. Authors have suggested that the teeth of macrophagous species are composed of fenestrated, labyrinthic stereom, whereas teeth of microphagous species are reinforced with compact or imperforate stereom (although macrophagous *Ophiomyxa* spp. may have teeth with a crown of imperforate calcite spikes). Authors have suggested compact and imperforate dental stereom in microphagous species forms an abrasion-resistant grinding surface. However, ophiuroid teeth do not execute vertical or circular movements that would be required to grind food. It is possible that the reinforced, occlusive teeth of microphagous species crush ingested boluses of particulate material, but this process has not been directly observed. The teeth of macrophagous feeders, usually have a comparatively weak stereom structure, and authors have contradictorily suggested that they are not used for mastication or that they are used to cut and tear food. Information reviewed herein indicates that the teeth of macrophagous feeders can temporarily restrain food items during ingestion, and that stereom on the edges of the teeth may be reinforced. Chisel-shaped jaws, shallow and the exposed, truncated vTCts, of Ophiurida may, facilitate the "gulping behavior" exhibited by *Ophiura* spp., and may enable their OTs-2 to manipulate food items, even while the jaws are tightly closed.

16. A progressive decrease in the size of the OPas *s.l.* towards the apex of the OP is related to the wedged shape of ophiuroid jaws, and to the proximally constricted shape of the OSl. This configuration of OPas *s.l.* enables the jaws to securely seal. Opposing OPas *s.l.* on adjacent jaws compose rows of "double doors" that abut, interlock, or interdigitate when the jaws are fully closed. Consequently, OPas *s.l.* can protect structures within the buccal cavity, yet their flexible articulation permits protraction and retraction of the OTs. In numerous species of ophiuroids, OPas *s.l.* on the ventrolateral edge of the OP are located beside small fossae and attached to ArtSs. However, the occurrence, structure, and function of ligaments, muscles, and nerves between these articulated ossicles has not been investigated.
17. Figuratively speaking, postlarval ophiuroids because they scaled-down macrophagous feeders because they can gorge on relatively large prey and masses of particulate material. Until their arms grow considerably longer than the disk, juveniles use OT-1 to manipulate food. They primarily use OT-2 and tube feet for locomotion, and possibly also for feeding. Components of buccal armature, such as the BSc, AdShSp, FP, vCtP, and TP, are disproportionately larger in the juvenile than in the adult stage, and each of these skeletal elements of the juvenile may serve the same role as multiple ossicles in an adult individual. Some precociously developing ossicles, such as the opercular BScs that cover the OSl of juvenile amphiurids, and the hypertrophied arm spines of postlarval ophiotrichids, may be resorbed or undergo negative allometric growth during ontogenesis. Moreover, evidence is marshalled herein, which suggests that juvenile and adult Euryalidae lack the AdShSp and an arm spine on LAP-2, as a result of heterochronic postdisplacement.
18. Certain types of ophiuroid skeletal ossicles were traditionally presumed to undergo fusion or fission during ontogenesis, but most of these claims are unsubstantiated. Pairs of ambulacral plates (i.e., vertebrae) can be united by intermeshed stereomic trabeculae and/or by a callus of imperforate stereom, but whether and to what extent the trabeculae have coalesced has not been examined on an ultrastructural level. Authors have claimed that teeth divide and form TPas, BScs divide and form multiple oral papillae, DAPs fragment into symmetrical arrays of ossicles, and OPas *s.l.* fuse, but confirmatory evidence is lacking, and contradictory evidence is presented herein. However, the present study established that DPs in *Ophioderma rubicunda* undergo fission. The smallest individual examined had a single-element DP bearing 3–4 teeth, a larger juvenile had a two-element DP with four teeth, and adults had a four-element DP with five teeth. However, the functional significance of a multi-element DP and the process by which the plate subdivides are not known.

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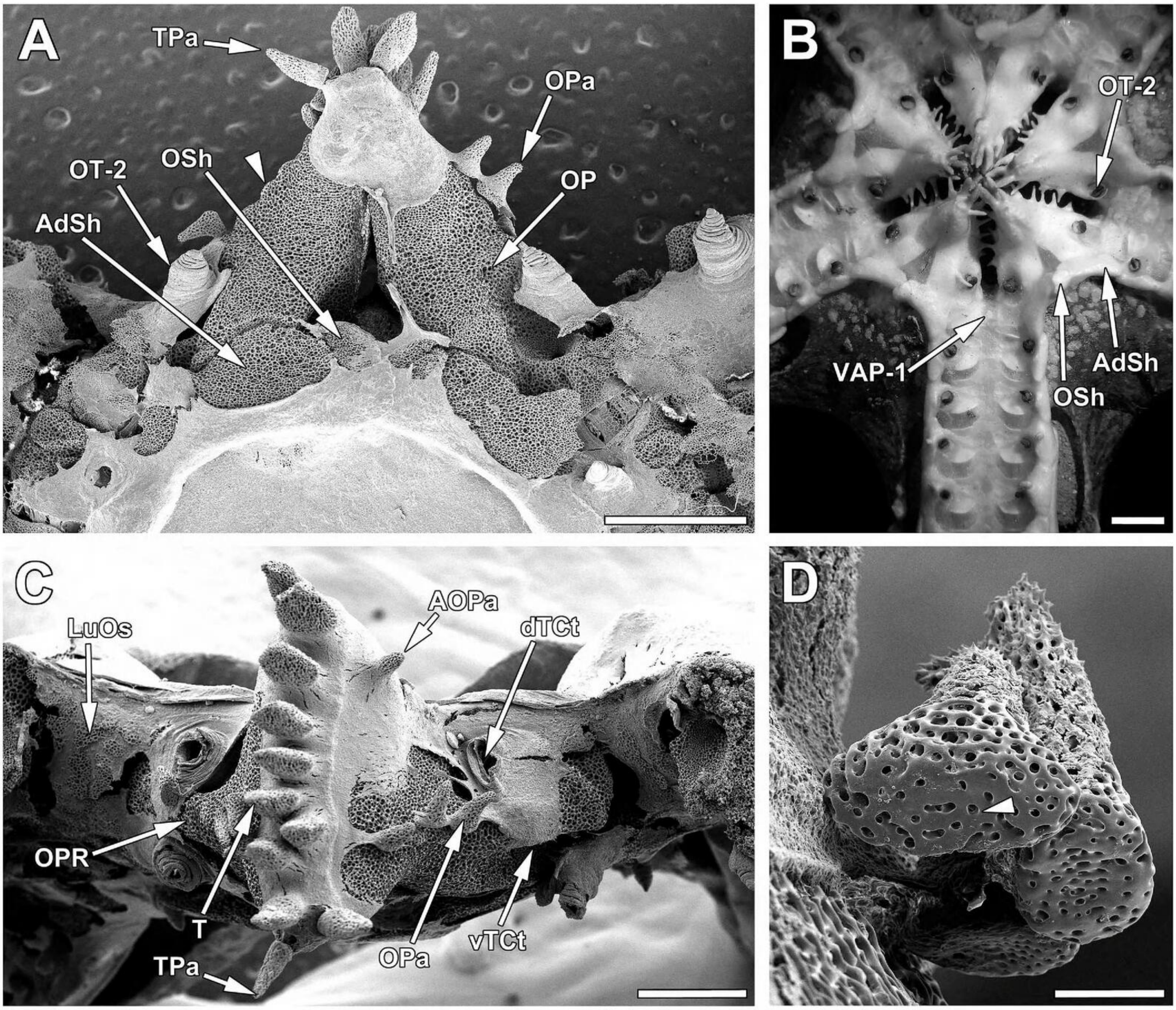

**Figure 1** *Asteronyx longifissus* Döderlein, 1927. **A**, ventral view of jaw. **B**, ventral view of disk and arm of a dried specimen; note that apices of the jaws form a ventally projecting cone. **C**, proximal view of jaw; note that the labeled TPa has an ArtS on the DP, which has a central fossa. **D**, detail of several detached OPas *s.l.*; arrowhead marks sparsely perforate stereom on the ArtS. A, C, D: SEM micrographs; LACM E.1988-214.2; 24.3 mm dd specimen. B: Stereomicroscope image; LACM 77-204.1; 21.8-mm-dd specimen. Scale bars: A=1.5mm; B, C=1.0 mm; D=150 µm.

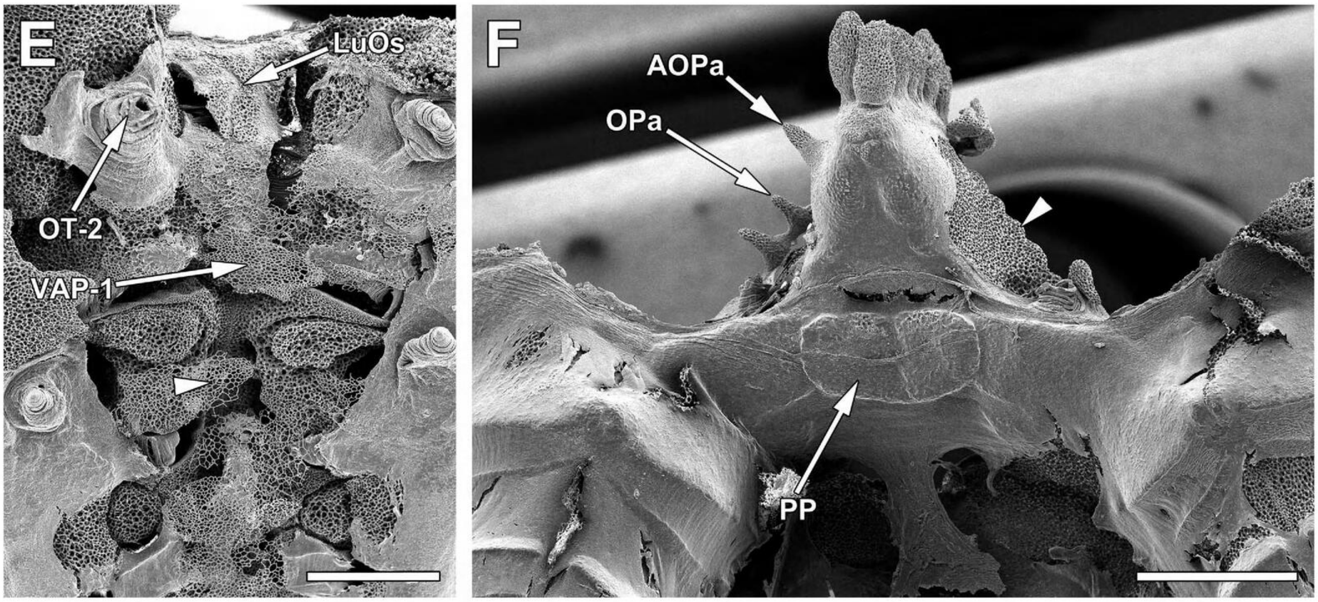

**Figure 1 cont.** *Asteronyx longifissus* Döderlein, 1927. **E,** ventral view of base of arm; arrowhead indicates open reticulate stereom of an accessory VAP. **F,** dorsal view of oral frame; arrowhead marks protuberance on which an OPa *s.l.* was attached. E, F: SEM micrographs; LACM E.1988-214.2; 24.3-mm-dd specimen. Scale bars: E=1.0 mm; F=1.5mm.

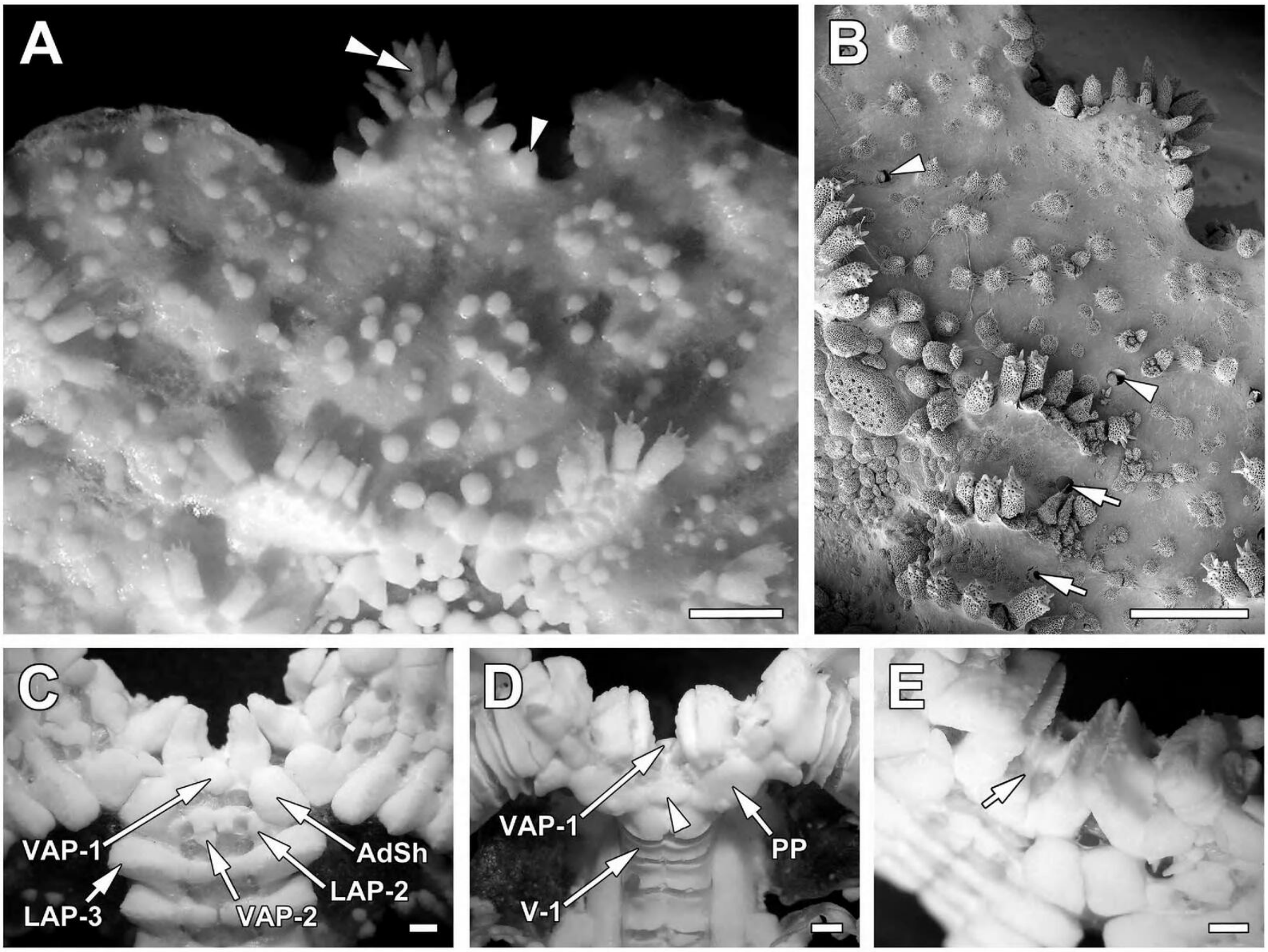

**Figure 2** *Asteroporpa annulata* Örsted and Lütken in: Lütken, 1856. **A,** ventral view of jaw and base of arm, arrowhead marks OPas on ventral adradial edge of OP; double arrowheads mark TPas on DP. **B,** ventral view of jaw and base of arm, arrowheads mark tentacle pore of first arm segment; arrows mark tentacle pores of second and third arm segments. **C,** ventral view of jaws and arm bases. **D,** dorsal view of oral frame and arm bases; arrowhead marks a small, perradial PP that abuts larger interradial PPs. **E,** oblique ventral view of jaws; arrow indicates ossicles between VAP-1 and OPR. B: SEM micrograph, LACM E.1982-166.1; 16.8 mm dd specimen. A, C–E: Stereomicroscope images of specimens with integument partially or almost completely removed; LACM E.1982-166.1; 16.8-, 20.2-mm-dd specimens. Scale bars: A=1.0 mm; B=1.5 mm; C–E=1.0 mm.

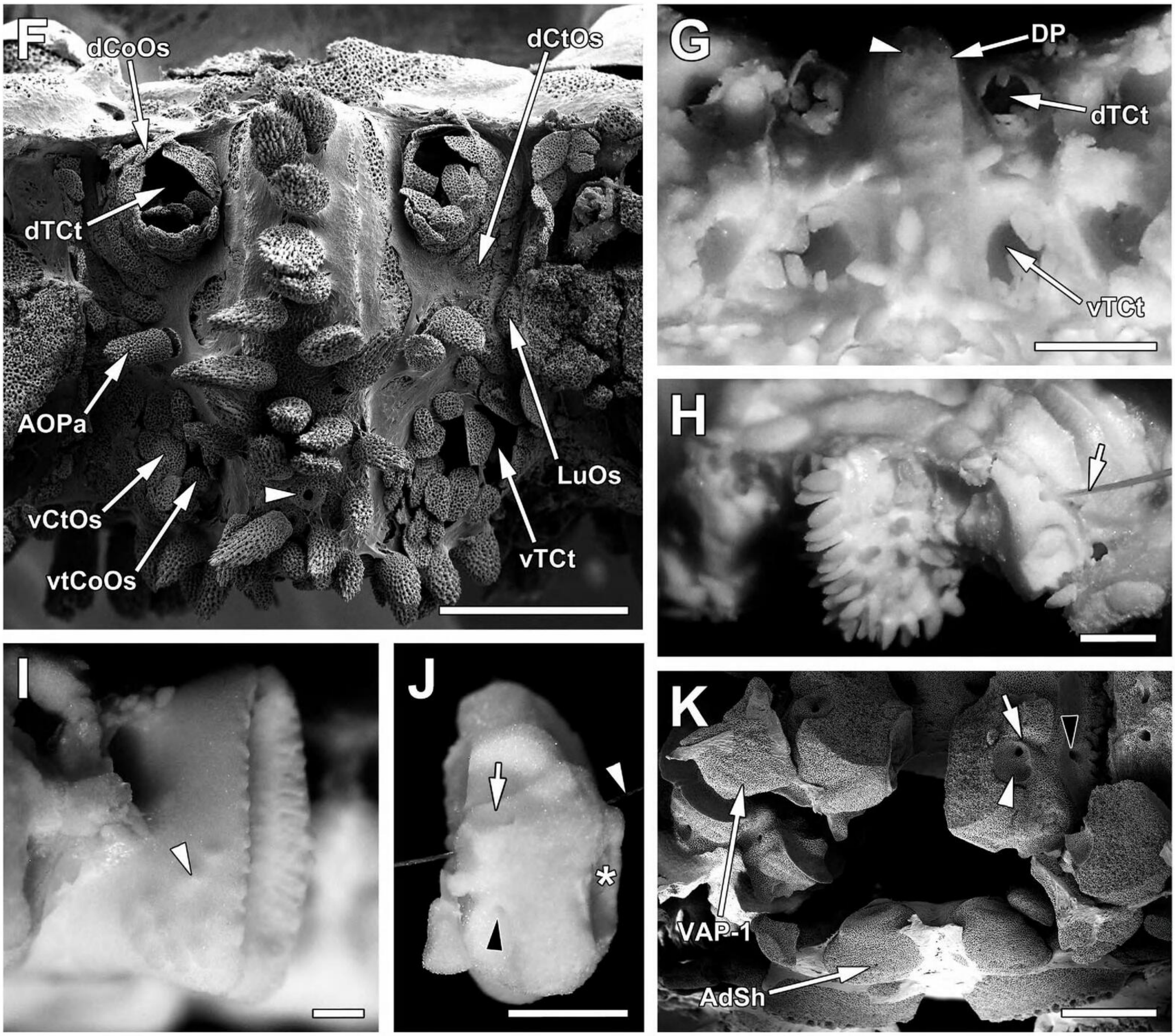

**Figure 2 cont.** *Asteroporpa annulata* Örsted and Lütken in: Lütken, 1856. **F, G,** proximal view of jaw; arrowhead indicates a round ArtS with a central fossa on which a T or TPa was borne. **H,** oblique view of jaw; arrow indicates eyelash inserted in an abradial water ring foramen. **I,** oblique view of jaw, dental plate removed; arrow marks imperforate protuberance on OP to which AOPa was attached. **J,** Isolated distal element of an OP; white arrow marks dorsal tentacle basin; black arrowhead marks ventral tentacle basin; asterisk marks abradial muscle fossa; white arrowhead indicates eyelash that has penetrated the paired water ring foramina of the OP. **K,** partially disarticulated oral frame; white arrowhead marks ventral OT basin in distal element of OP; white arrow marks groove between tentacle basin and OPR, which may accommodate a branch of the radial nerve cord innervating OT-2; black arrowhead marks adradial water ring foramen, located between adradial muscle fossa and adradial articular area of OP. F, K: SEM micrographs; LACM E.1982-166.1; 16.8, 20.2 mm dd specimens. G, H, I, J: Stereomicroscope images of specimens with integument partially or almost completely removed; LACM E.1982-166.1; 13.9-, 16.8-, 20.2-mm-dd specimens. Scale bars: F–J=1.0 mm; K=1.5 mm.

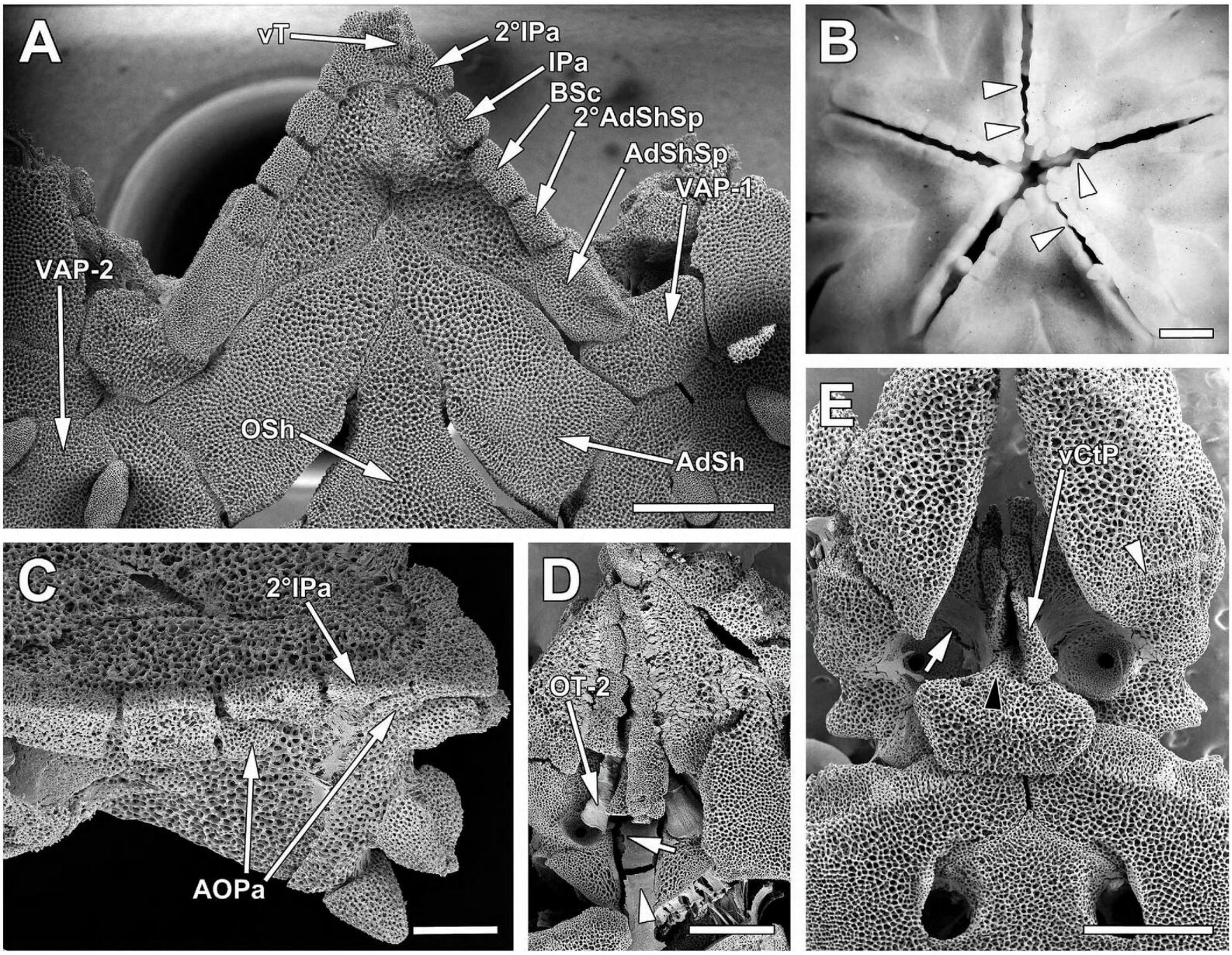

**Figure 3** *Ophiomusa lymani* (Thomson, 1873). **A,** ventral view of jaw. **B,** ventral view of the oral region of an alcoholic specimen; arrowheads mark several points at which OPas *s.l.* on opposing jaws dovetail with one another. **C,** adradial view of apex of the jaw, showing the insertion of AOPas between larger OPas *s.l.* **D,** dorsal view of dissected jaw; arrowhead marks radial nerve cord and arrow is directed toward severed connection between the nerve and OT-2. **E,** ventral view of two adjacent jaws; arrow marks presumptive neural groove beside the ventral tentacle basin; black arrowhead marks the proximal lobe of VAP-1; to the left of the arrowhead there is a foramen directed toward the vCtP; white arrowhead marks suture line between the proximal and distal elements of the OP. A, C–E: SEM micrographs; LACM E.1995-203.1; 18.4-, 20.7-mm-dd specimens. B: Stereomicroscope image of specimen prior to dissection; 20.7-mm-dd specimen. Scale bars: A=1.5 mm; B=1.0 mm; C=0.5 mm; D, E=1.0 mm.

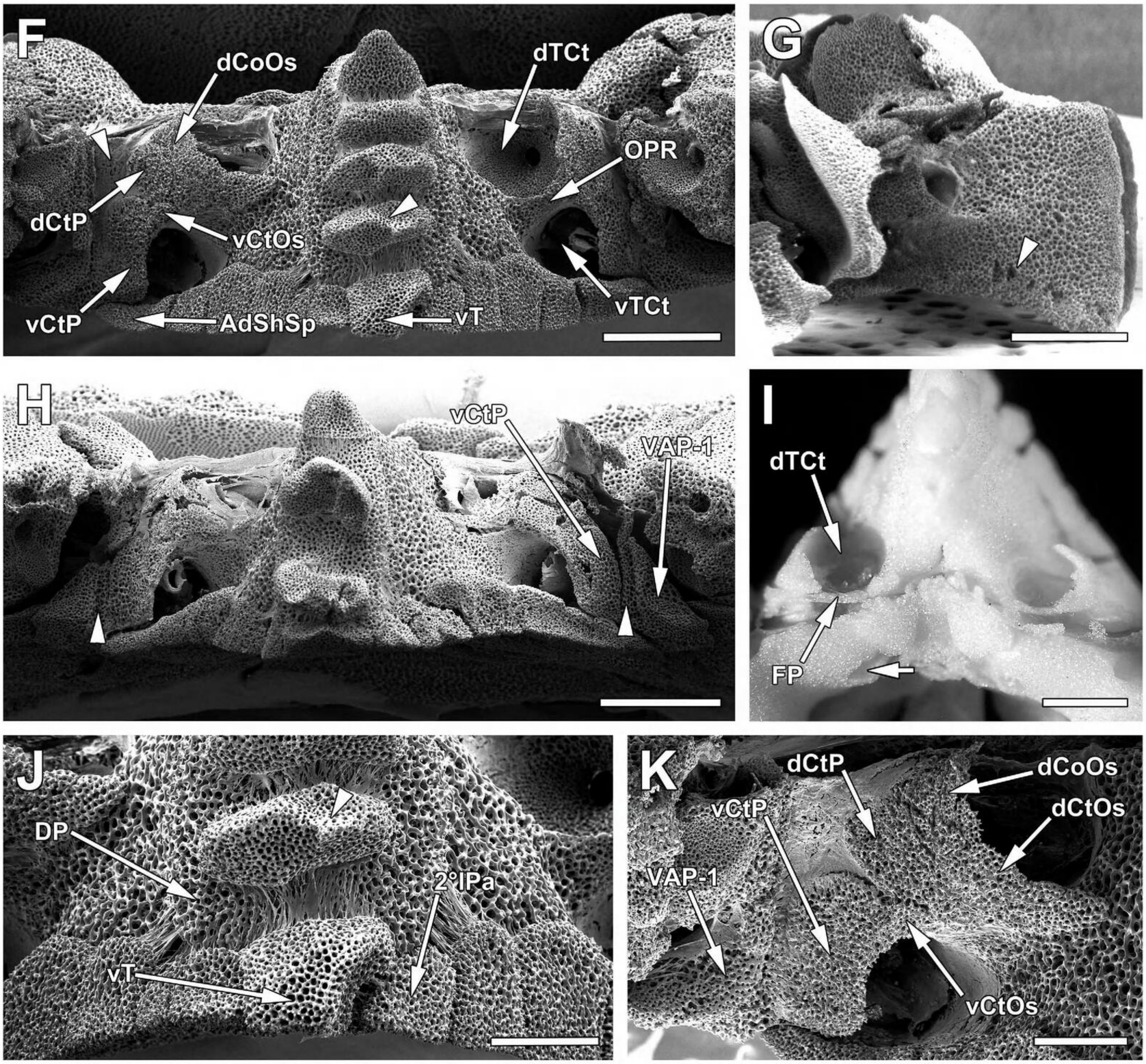

**Figure 3 cont.** *Ophiomusa lymani* (Thomson, 1873). **F,** proximal view of jaw; arrowhead indicates a facet on the tooth. **G,** oblique adradial view of jaw; arrowhead indicates one of the small fossae associated with OPas *s.l.* **H,** proximal view of jaw; arrowheads mark a groove beside the proximal, medial ridge of VAP-1, into which a vCtP inserts. **I,** dorsal view of jaw; arrow indicates the abradial water ring foramen. **J,** proximal view of ventral apex of jaw; arrowhead indicates facet on the tooth. **K,** adradial view of jaw showing dorsal and ventral TCts. F–H, J, K: SEM micrographs; LACM E.1995-203.1; 18.4-, 20.7-mm-dd specimens. I: Stereomicroscope image of a specimen undergoing dissection; 20.7-mm-dd specimen. Scale bars: F–I=1.0 mm; J, K=0.5 mm.

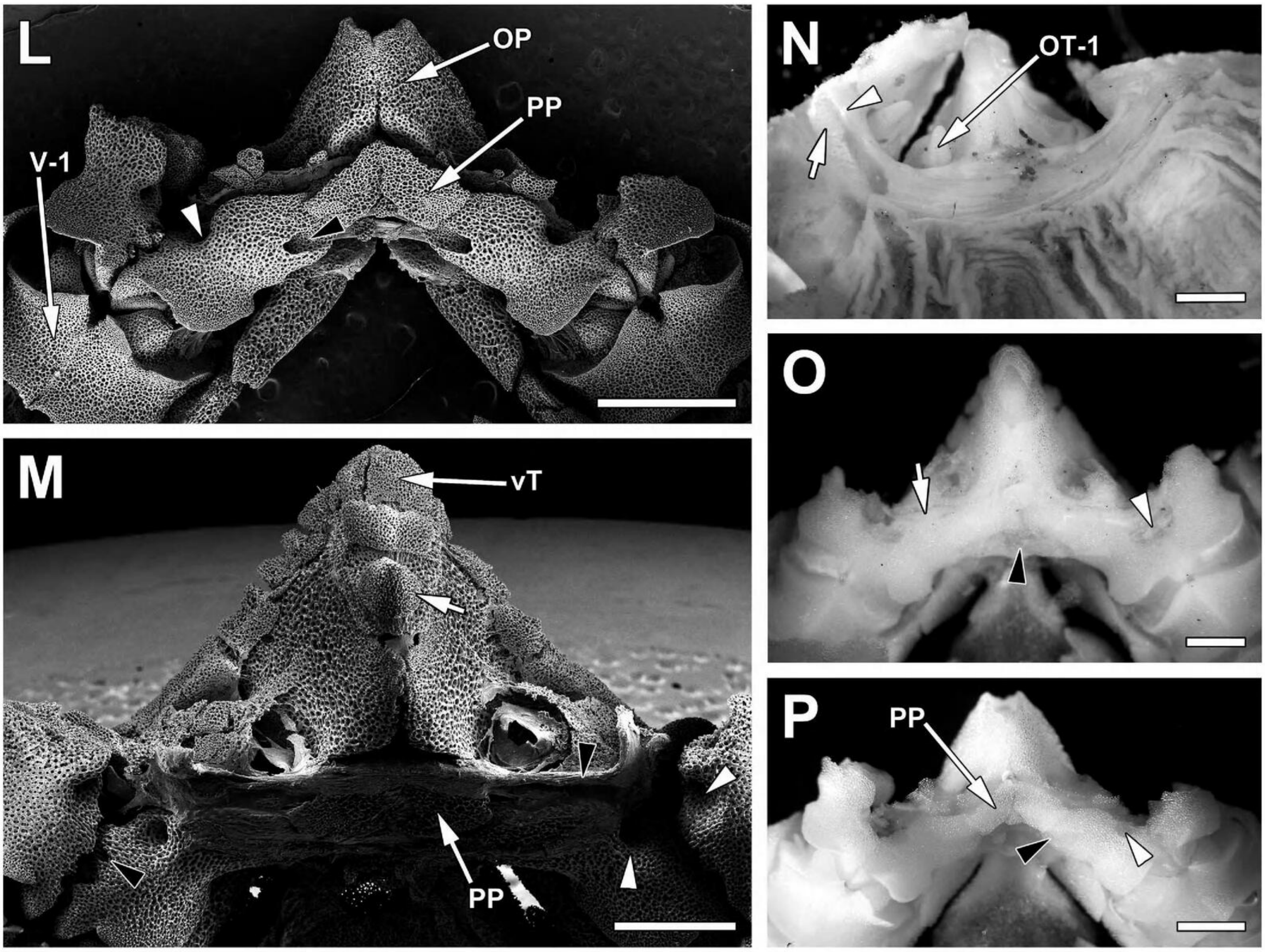

**Figure 3 cont.** *Ophiomusa lymani* (Wyville-Thomson, 1873). **L,** dorsal view of dissected jaw; white and black arrowheads mark adradial and abradial water ring foramina, respectively. **M,** oblique dorsal view of jaw; arrow marks tapered, dorsalmost tooth; black arrowhead on the left marks an ArtS of the OP; black arrowhead on the right indicates circumoral esophageal ligament, white arrowheads mark adradial water ring foramina of adjacent jaws. **N, O,** and **P** show sequential stages in the removal of integument from the dorsal surface of a dissected jaw. **N,** arrowhead indicates esophageal tissue, arrow indicates circumoral esophageal ligament. **O,** arrow marks the radial nerve cord, white arrowhead marks the water ring between adradial foramina of adjacent jaws, black arrowheadmarks water ring between abradial water ring foramina of a jaw. **P,** white and black arrowheads mark adradial and abradial water ring foramina, respectively. L, M: SEM micrographs; LACM E.1995-203.1; 18.3-mm-dd specimen; N–P: Stereomicroscope images of two specimens undergoing dissection; 18.4-, 20.7-mm-dd specimens. Scale bars: L=1.5 mm; M–P=1.0 mm.

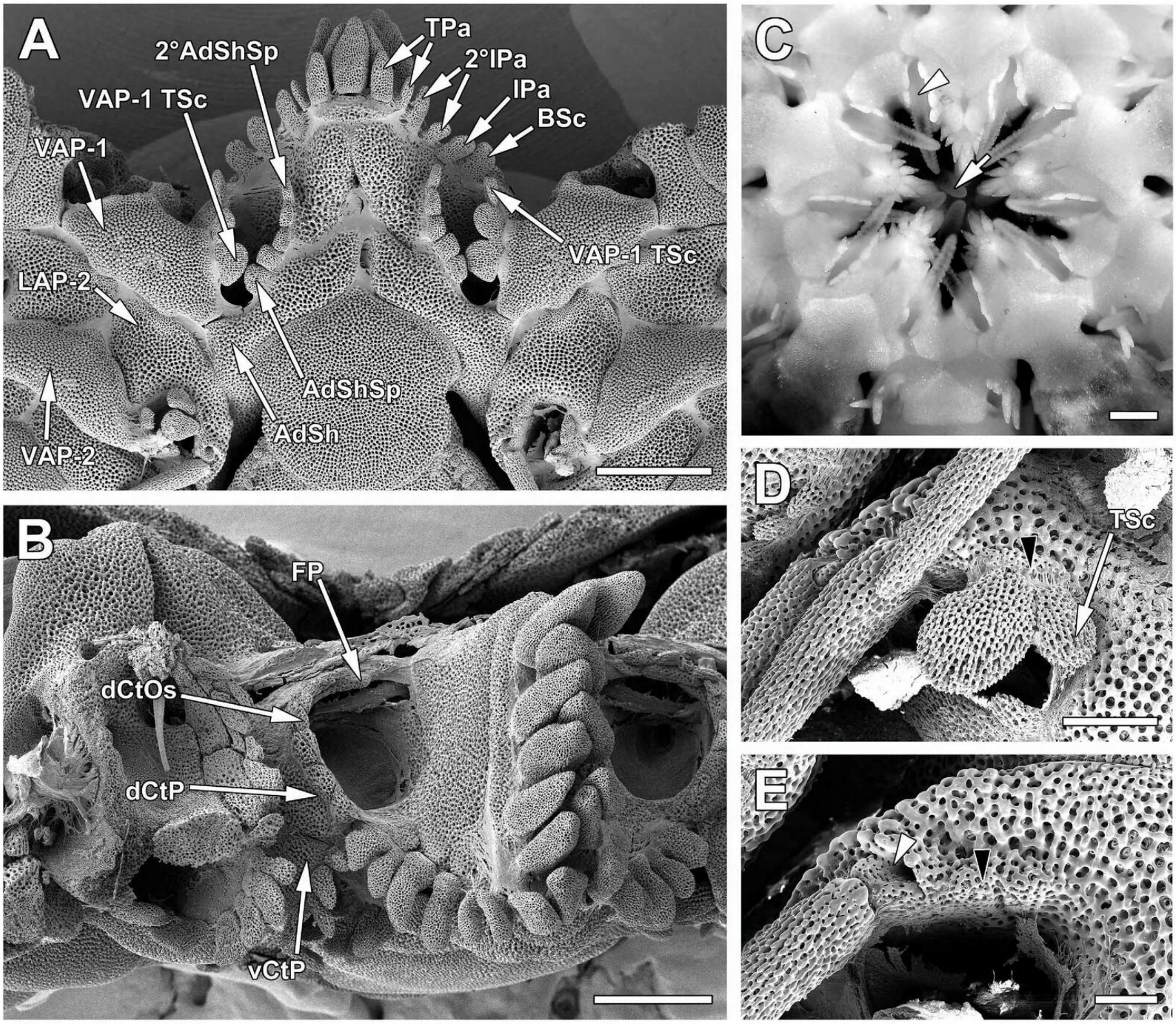

**Figure 4** *Ophiura sarsii* Lütken, 1855 (**A, B, D, E**), and *Ophiura luetkenii* (Lyman, 1860) (**C**). **A,** ventral view of jaw. **B,** proximal view of jaw. **C,** ventral view of the oral region of a living individual of *O. luetkenii*; arrowhead indicates OT-2, arrow indicates OT-1. The protrusion of OT-2 through the vTCt and proximal OSl demonstrates the continuity of the latter two structures. **D,** detail of tentacle scales on a basal arm segment; black arrowhead marks the ArtS of TScs on the LAP. **E,** detail of tentacle scale and arm spine articulation on a basal arm segment; white arrowhead marks the muscle fossa in the ArtS of an ASp on the LAP; black arrowhead marks the ArtS of a TSc, which appears to lack neural foramina or muscular fossae. A, B, D, E: SEM micrographs; LACM E.1971-361.35; 13.4-, 13.9-, 20.0-mm-dd specimens. C: Stereomicroscope image of a living *O. luetkenii*; 15.4 mm dd; Santa Monica Bay, California. Scale bars: A–C=1.0 mm; D=250 µm; E=150 µm.

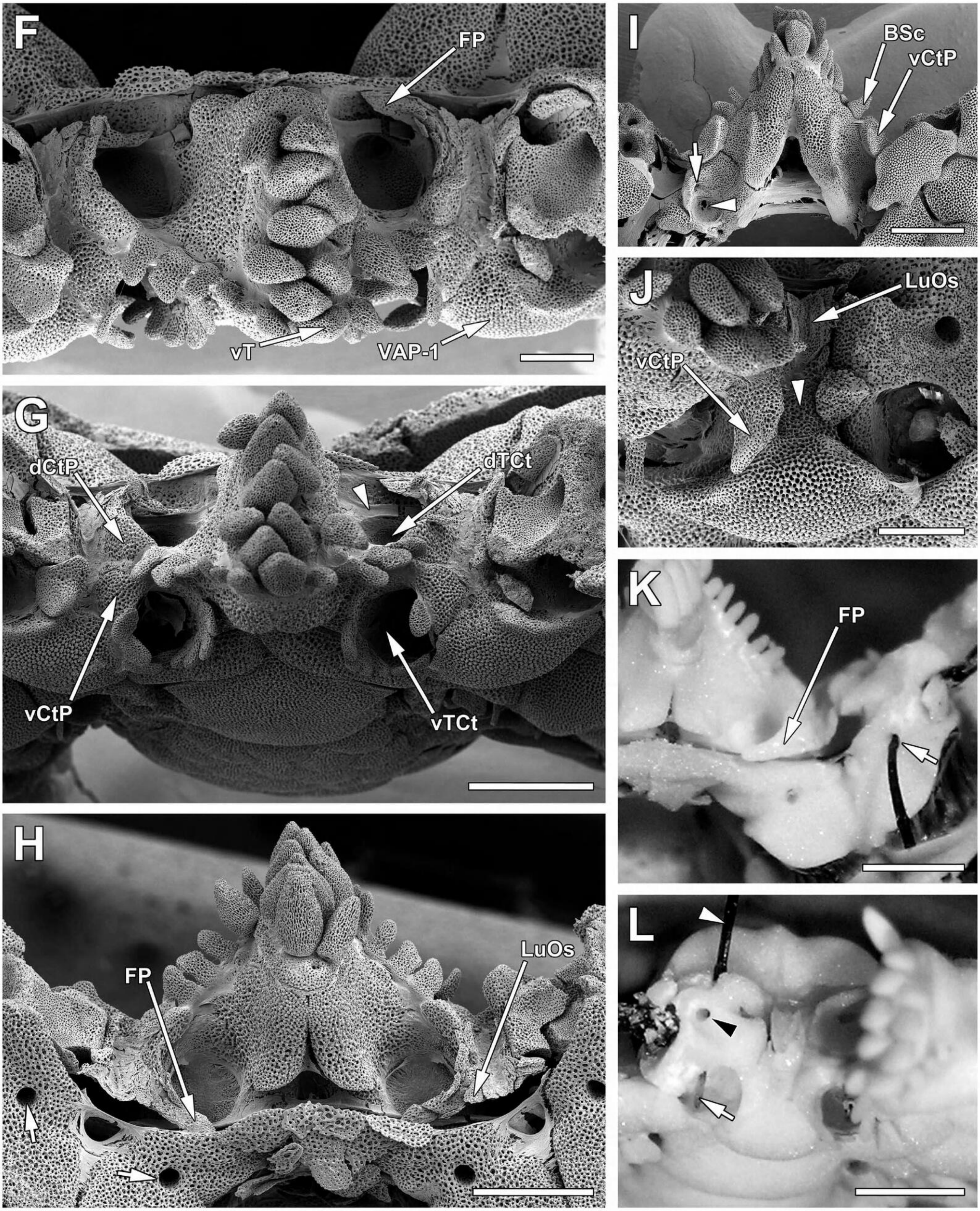

**Figure 4 cont.** *Ophiura sarsii* Lütken, 1855. **F,** proximal view of jaw; the labeled FP is broken. **G,** oblique proximal view of jaw, showing apertures of the ventral and dorsal TCts; arrowhead indicates circumoral nerve ring, and a PP is above the arrowhead. **H,** dorsal view of jaw, arrows mark the single water ring foramen in each OP.

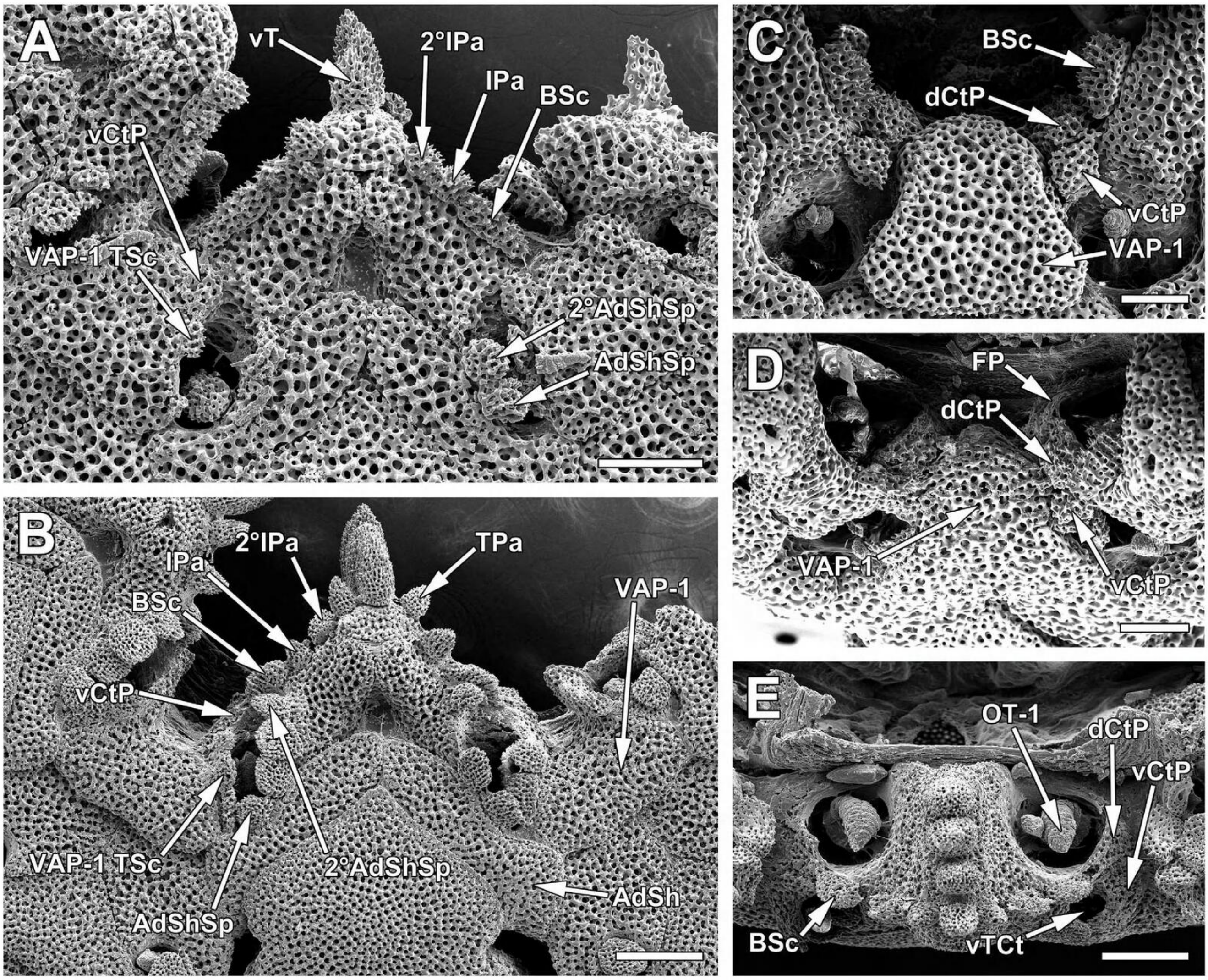

**Figure 5** *Ophiura luetkenii* (Lyman, 1860). Skeletal ontogenesis. **A,** ventral view of jaw, 2.4-mm-dd juvenile. **B,** ventral view of jaw, 4.3-mm-dd juvenile. **C, D,** ventral and oblique views of the distal edge of the OSl, 2.6-mm-dd juvenile; showing VAP-1 and contiguous ossicles. **E,** proximal view of jaw, 4.3-mm-dd juvenile. A–E: SEM micrographs; A, LACM E.2000-246.1; B, LACM E.2013-89.1; C–D, LACM E.1991-252.1; E, LACM E.2013-89.1. Scale bars: A=150 µm; B=250 µm; C=100 µm; D=90 µm; E=250 µm.

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**I,** ventral view of jaw with superficial plates removed; arrowhead marks water canal foramen in the tentacle basin of OT-2; arrow indicates a possible neural foramen in the OP, through which a branch of the radial nerve cord may innervate OT-2. **J,** proximal view of VAP-1 within the OSl; arrowhead marks the proximal lobe of VAP-1 between the OPRs of adjacent jaws. **K,** dorsal view of jaw; arrow marks entry of an eyelash that is inserted in a water ring foramen in the distal element of an OP. **L,** proximal view of the same jaw shown in K; white arrowhead indicates eyelash inserted in water ring foramen; black arrowhead indicates water canal of OT-1, through which the eyelash is visible; white arrow marks tip of the eyelash, which has passed through the water canal of OT-2 and entered the vTCt. F–J: SEM micrographs; LACM E.1971-361.35; 13.4-, 13.9-mm-dd specimens. K, L: Stereomicroscope images of jaw from which tissue and superficial ossicles were removed; 13.4-mm-dd specimen. Scale bars: F=0.5 mm; G–I=1.0 mm; J=0.5 mm; K, L=1.0 mm.

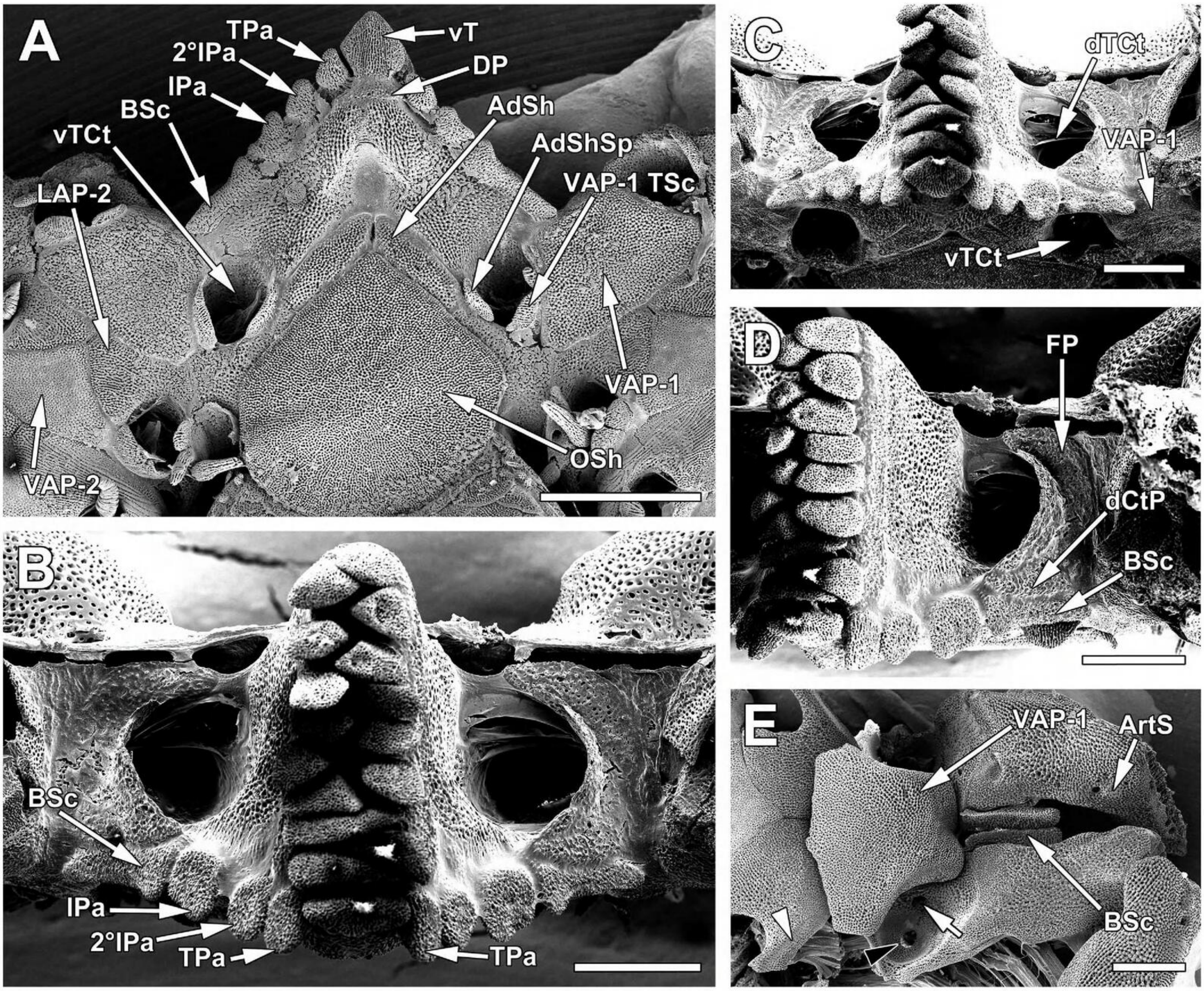

**Figure 6** *Ophiocten sericeum* (Forbes, 1852). **A,** ventral view of jaw. **B,** proximal view of jaw. **C,** oblique proximal view of jaw, showing orifices of vTCts. **D,** oblique view of jaw. **E,** ventral view of jaw with superficial plates removed; white arrowhead marks beveled articulation surface on the edge of LAP-2; black arrowhead marks the water canal foramen in the tentacle basin of OT-2; arrow indicates presumptive neural foramen; note that VAP-1 was inadvertently displaced from its normal position on the OP. A–E: SEM micrographs; LACM 1972-256.17; 13.6-, 12.6-mm-dd specimens. Scale bars: A=1.0 mm; B–E=0.5 mm.

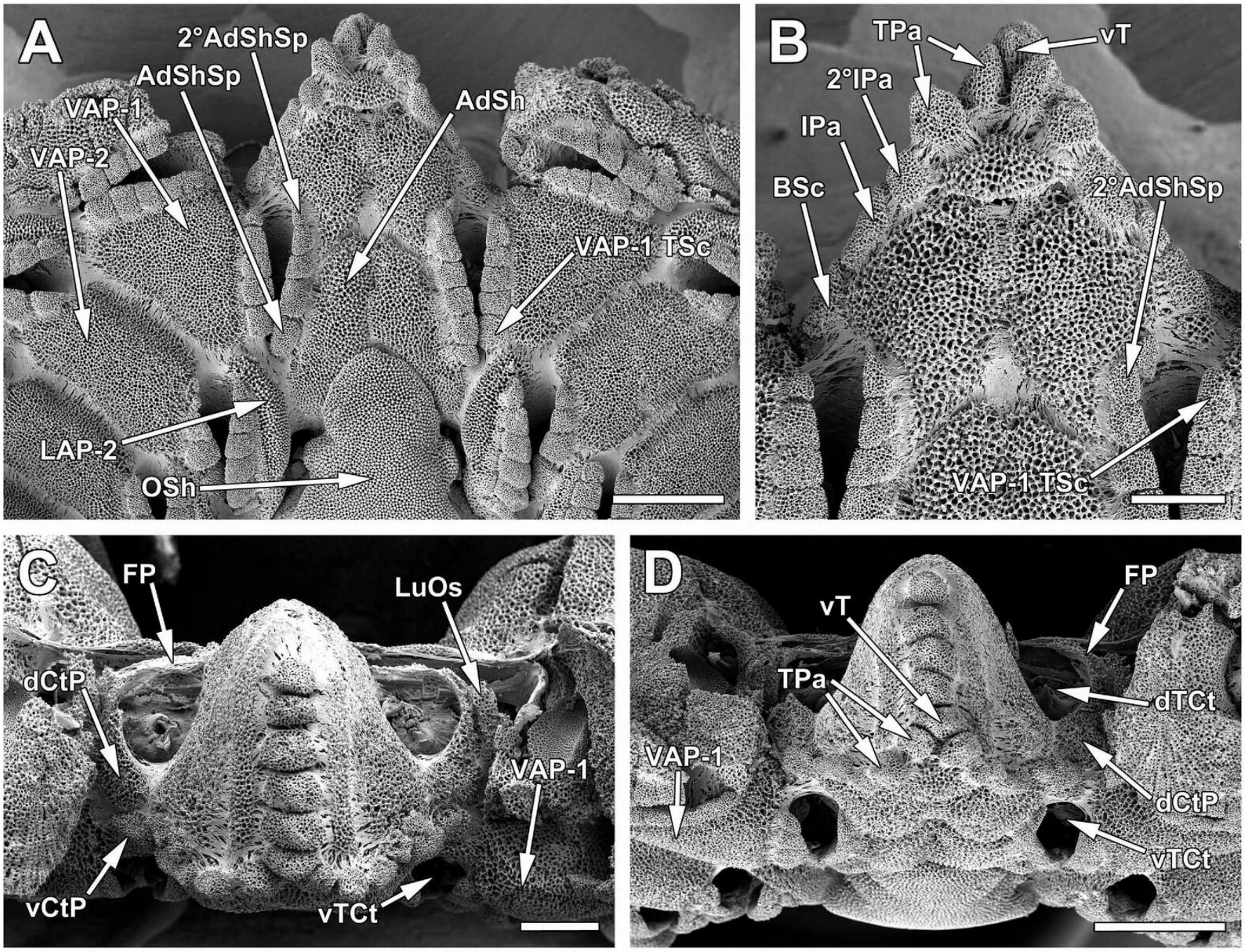

**Figure 7** *Stegophiura nodosa* (Lütken, 1855). **A,** ventral view of jaw. **B,** detail of the jaw apex. **C,** proximal view of jaw; note that vCtP does not obstruct the proximal OSl. **D,** oblique proximal view of jaw, showing orifices of the dTCts and vTCts, which are dorsal to the smaller, proximal tube foot pores. A–D: SEM micrographs; LACM 1962-239.4; 12.5-mm-dd specimen. Scale bars: A=1.0 mm; B, C=0.5 mm; D=1.0 mm.

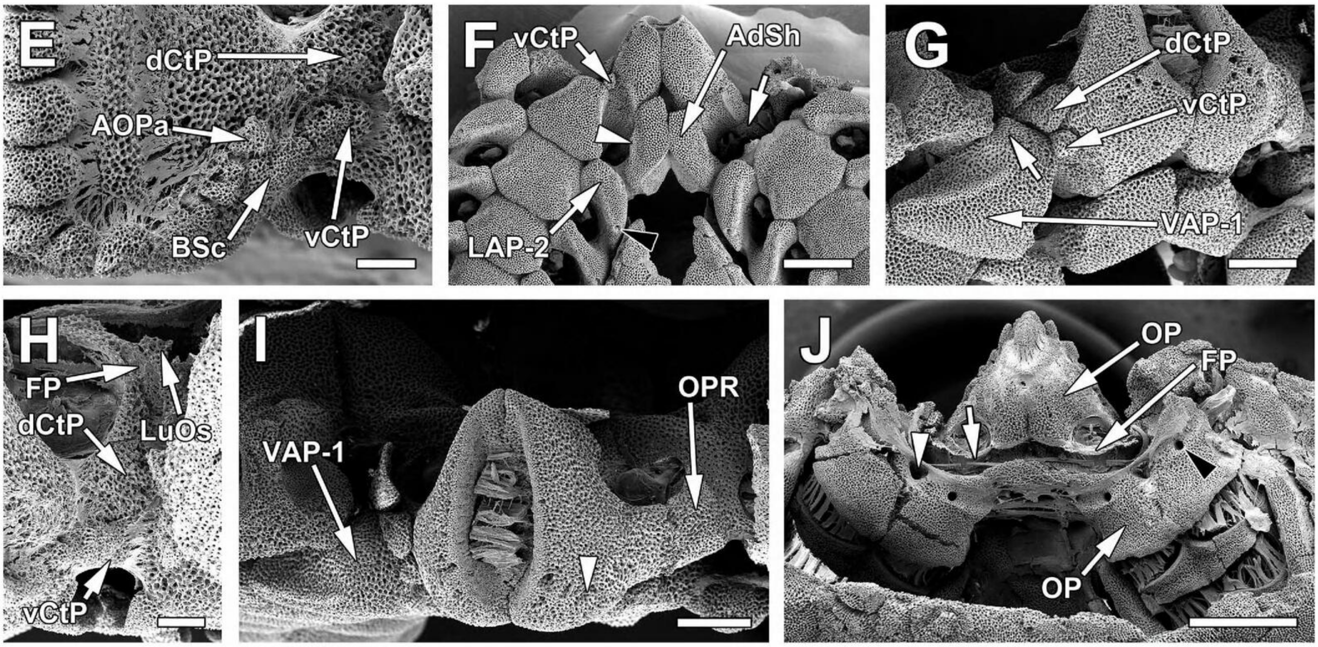

**Figure 7 cont.** *Stegophiura nodosa* (Lütken, 1855). **E,** detail of adradial surface of jaw. **F,** ventral view of jaw with superficial plates removed, revealing the rudimentary vCtP; white arrowhead marks ArtS of AdShSp and 2°AdShSps on the AdSh; white arrow marks the presumptive neural groove associated with the tentacle basin of OT-2; black arrowhead marks a foramen associated with the arm spine on LAP-2. **G,** ventral surface of jaw with superficial plates removed; arrow marks curved dorsal projection on the stout proximal edge of VAP-1. **H,** adradial view of jaw, showing dorsal and ventral TCts and CtPs. **I,** oblique proximal view of jaw with superficial ossicles removed; arrowhead marks fossa associated with proximal OPas *s.l.* **J,** dorsal view of jaw; arrow indicates nerve ring within a groove on the OP; black arrowhead marks the single water ring foramen in an OP; white arrowhead marks the channel accommodating the radial water canal. E–J: SEM micrographs; LACM 1962-239.4; 12.5-mm-dd specimen. Scale bars: E=250 µm; F=1.0 mm; G=0.5 mm; H=250 µm; I=0.5 mm; J=1.0 mm.

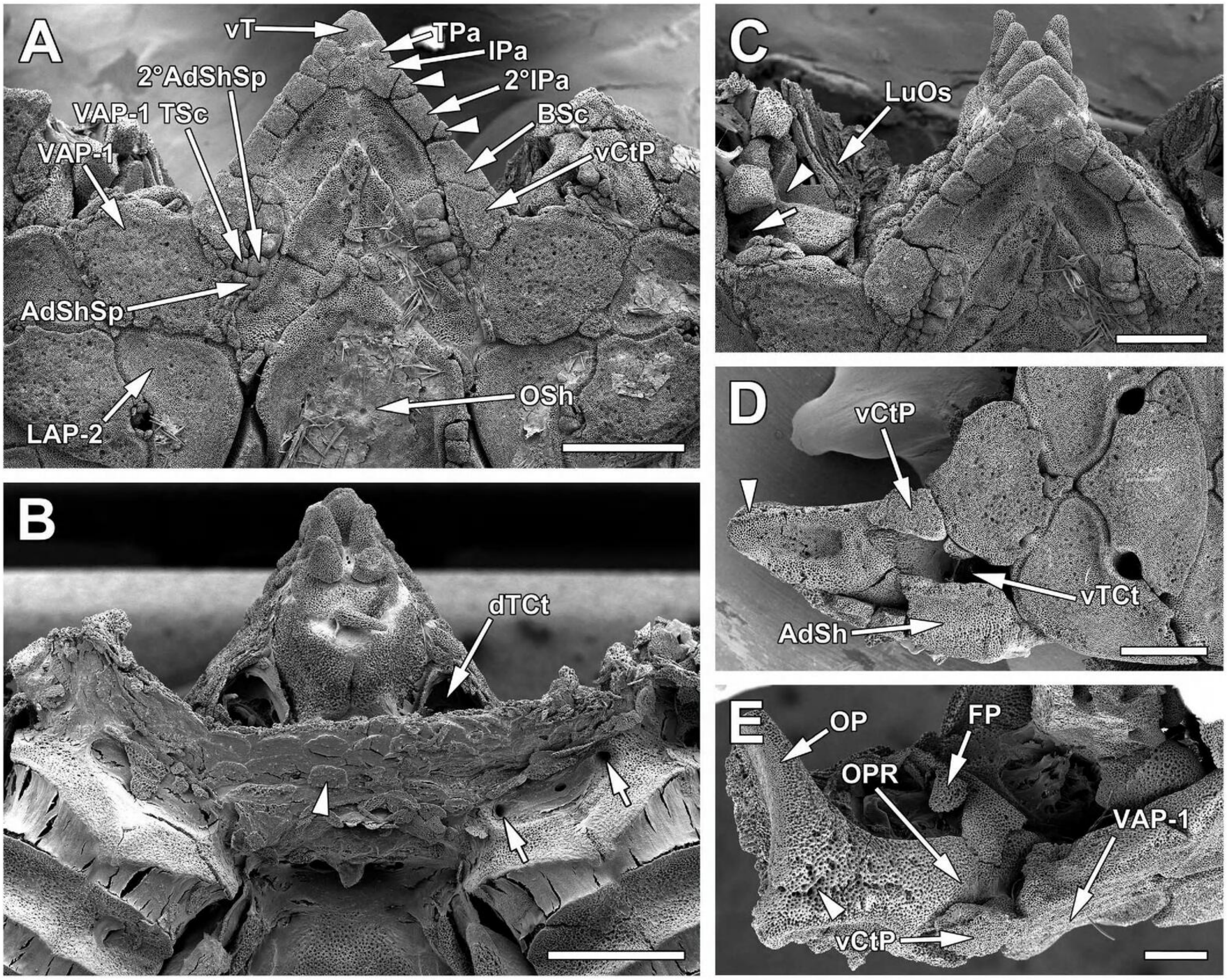

**Figure 8** *Ophioplinthus gelida* (Koehler, 1901). **A,** ventral view of jaw; unlabeled arrowheads mark AOPas. **B,** dorsal view of jaw; an arrowhead indicates one of numerous ossicles embedded in the circumoral esophageal ligament; arrows mark single water ring foramina in two adjacent OPs, and the opening between these foramina accommodates the radial water canal. **C,** oblique ventral view of jaw; arrow indicates the tentacle basin of OT-2; arrowhead marks the tentacle basin of OT-1. **D,** ventral view of partial jaw with superficial ossicles removed; arrowhead marks ArtS of an IPa, which is composed of sparsely perforate stereom. **E,** adradial view of jaw with superficial ossicles removed; arrowhead indicates fossae and ArtS associated with OPas *s.l.* on the OPR. A–E: SEM micrographs; LACM 1982-139.3; 17.8-mm-dd specimen. Scale bars: A, B=1.5 mm; C, D=1.0 mm; E=0.5 mm.

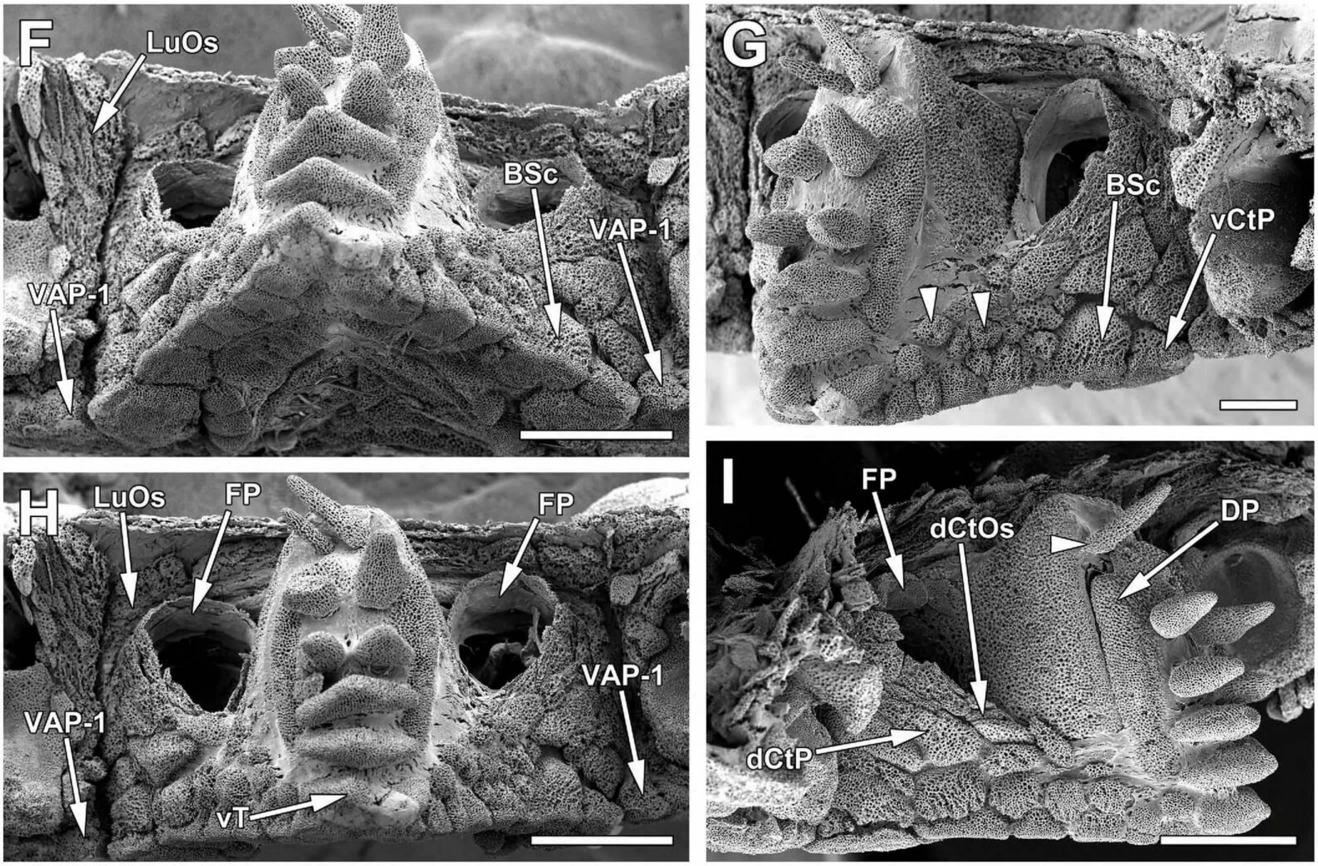

**Figure 8 cont.** *Ophioplinthus gelida* (Koehler, 1901). **F,** oblique proximal view of jaw; orifices of vTCts are concealed. **G,** adradial view of jaw; arrowheads mark AOPas. **H,** proximal view of jaw. **I,** adradial view of jaw; arrowhead indicates a spiniform dorsal tooth that is borne on the OP, rather than on the DP. F–I: SEM micrographs; LACM 1982-139.3; 17.8-mm-dd specimen. Scale bars: F=1.0 mm; G=0.5 mm; H, I=1.0 mm.

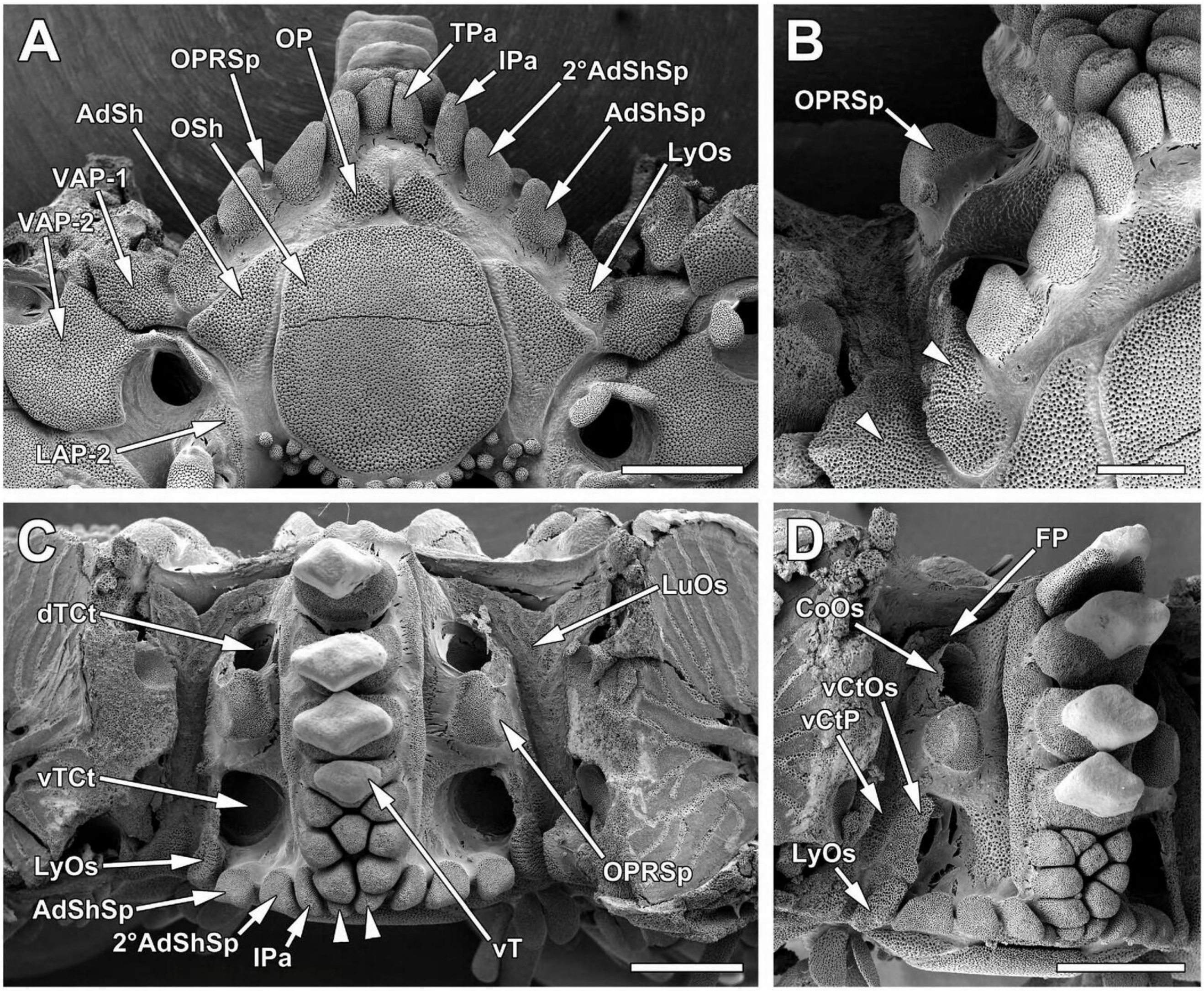

**Figure 9** *Ophiocoma echinata* (Lamarck, 1816a). **A,** ventral view of jaw. **B,** detail of jaw, ventral view; arrowheads directed to microscopic ridges on VAP-1 and LyOs, which may support tracts of ciliated epithelium. **C,** proximal view of jaw; arrowheads indicate a pair of small, relatively newly formed TPas on the ventral edge of the DP; note chevron pattern of LuOss covering the PG. **D,** oblique proximal view of jaw. A–D: SEM micrographs; LACM E.1980-196.2; 16.1-, 16.3-mm-dd specimens. Scale bars: A=1.0 mm; B=0.5 mm; C, D=1.0 mm.

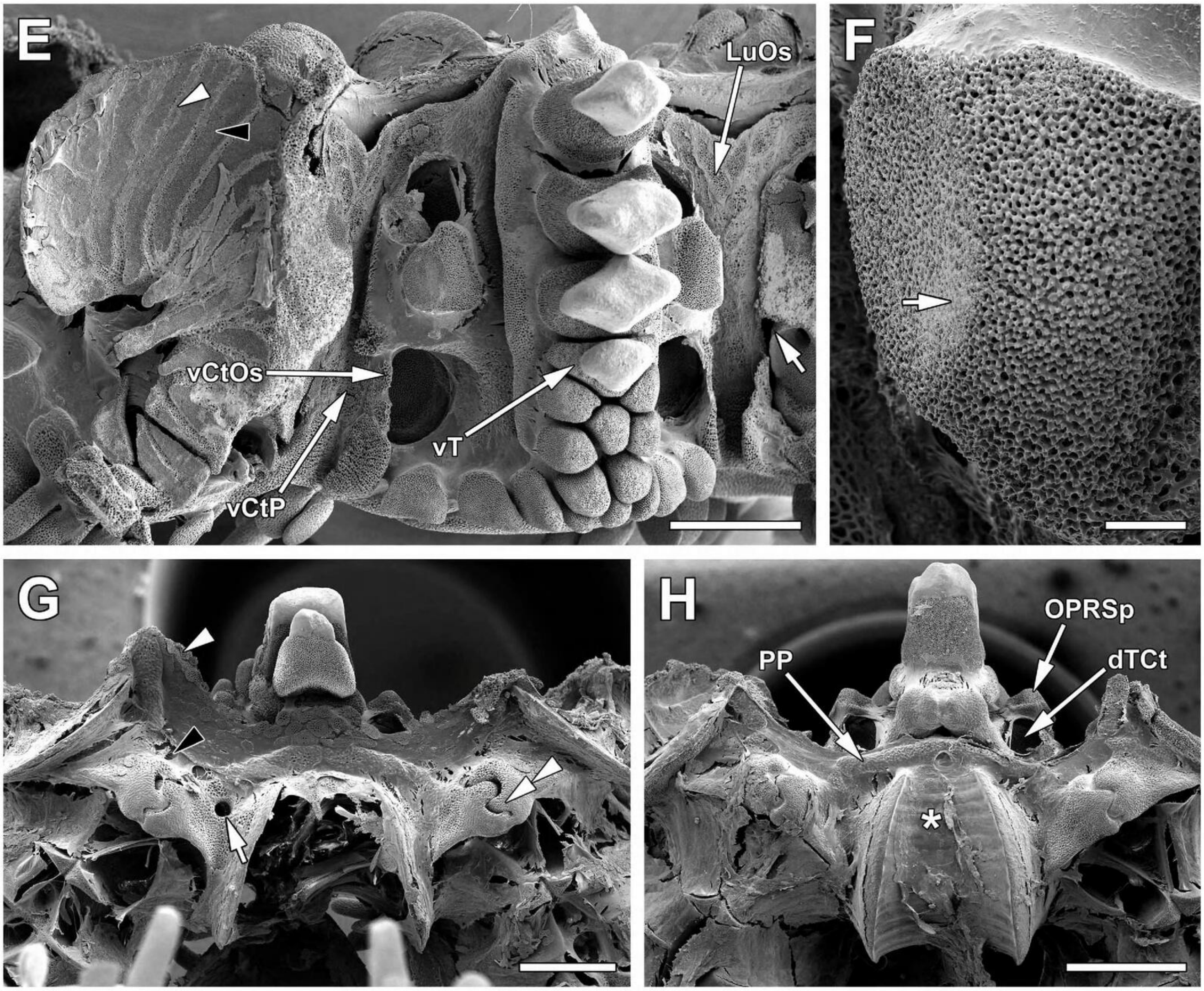

**Figure 9 cont.** *Ophiocoma echinata* (Lamarck, 1816a). **E,** adradial view of jaw; the abradial muscle fossa of the OP presents alternating bands of stereom on which connective tissue (white arrowhead) and muscle (black arrowhead) are connected; white arrow indicates a possible neural channel associated with OT-2; a small, tubercle-shaped vCtOs that protrudes from the ventral edge of the OPR is directly above the labeled vCtOs. **F,** detail of OPRSp; arrow marks abraded stereom that may be evidence of occlusal wear. **G,** dorsal view of jaw; black arrowhead marks groove occupied by the water ring; white arrow indicates a single water ring foramen in an OP; double white arrowheads indicate interdigitating ridges on adradial articular areas of adjacent OPs; close examination of the OPRSp to the right of the dorsalmost tooth reveals a slender gap between this ossicle and the OP. **H,** dorsal view of jaw; asterisk marks bands of abradial musculature between jaws. A slender gap between the OPRSp and OP is detectable in the dTCt to the right. E–H: SEM micrographs; LACM E.1980-196.2; 16.1-, 16.3-mm-dd specimens. Scale bars: E=1.0 mm; F=100 µm; G=1.0 mm; H=1.5 mm dd.

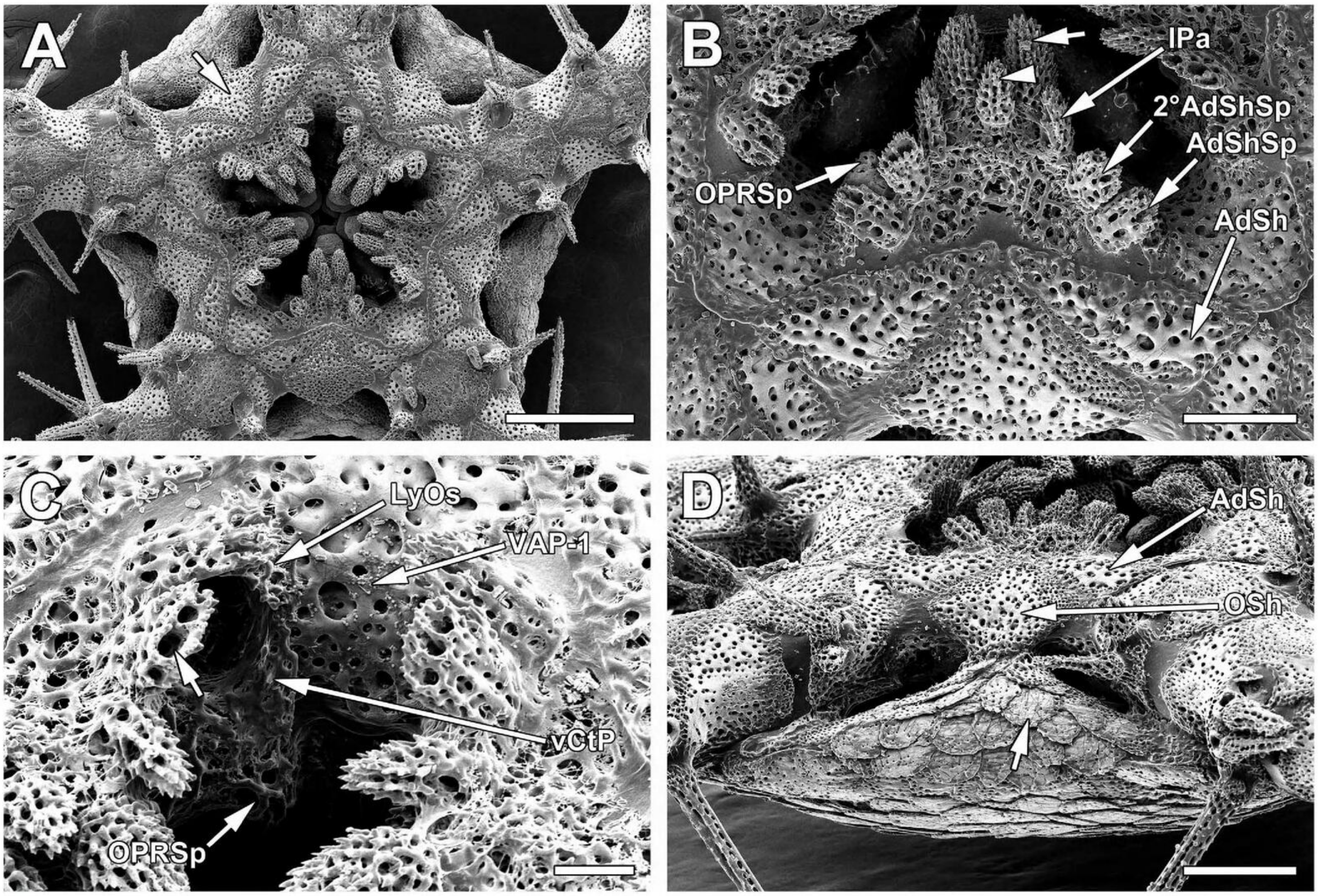

**Figure 10** *Ophiocoma wendtii* Müller and Troschel, 1842. Skeletal ontogenesis. **A,** ventral view of disk; arrow indicates the jaw shown in B. **B,** ventral view of jaw; arrow indicates the first-formed pair of TPas; arrowhead marks a newly formed medial TPa. **C,** oblique view of the distal edge of the OSl and the vTCt; arrow indicates enlarged pores in the AdShSp, which may enclose mucous glands. **D,** oblique view of ventral interradius; arrow marks a scale composed of minutely perforated stereom. A–D: SEM micrographs; LACM E.1983-130.3; 1.96-mm-dd specimen. Scale bars: A=0.5 mm; B=150 µm; C=50 µm; D=250 µm.

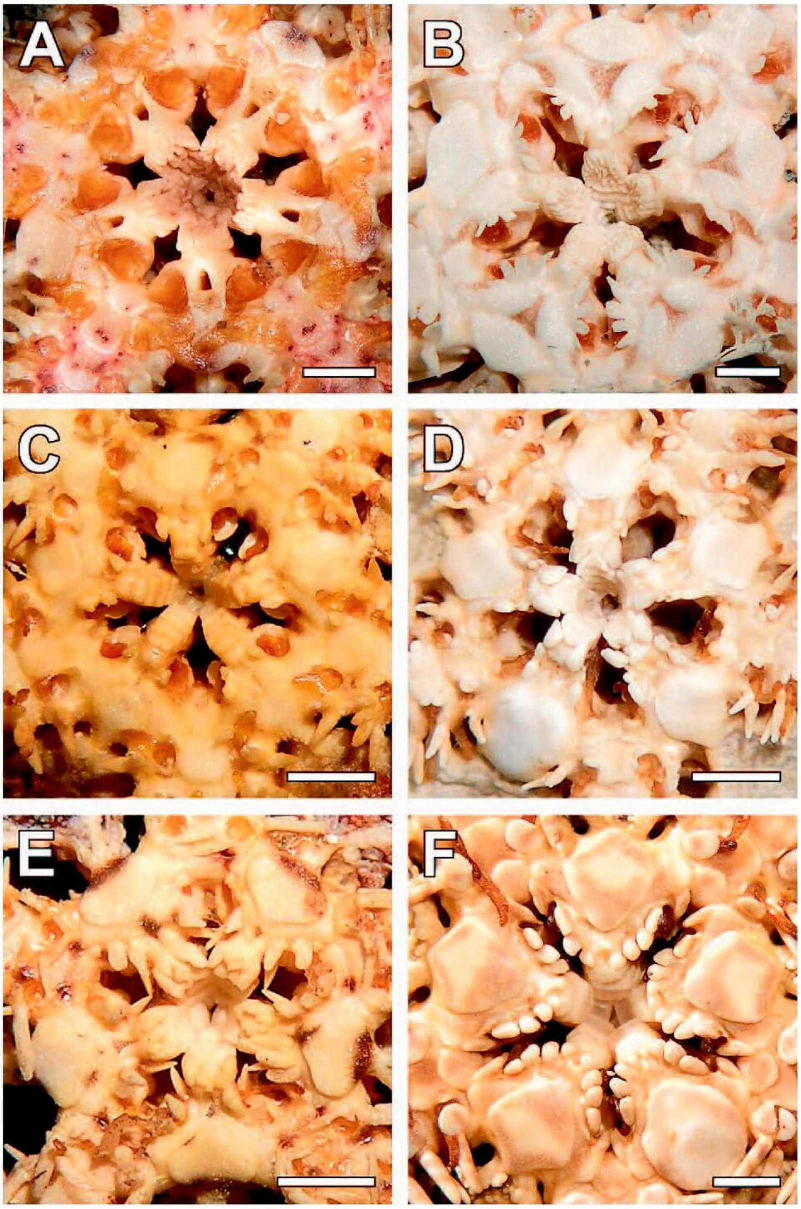

**Figure 11** Buccal funnels of representative species of the families of Amphilepidida and Ophiacanthida. **A,** *Ophiothrix spiculata* Le Conte, 1851, (Ophiotrichidae: Amphilepidida), LACM 1939-117.14, 9.9 mm dd. **B,** *Ophiopholis longispina* H.L. Clark, 1911, (Ophiopholidae: Amphilepidida), LACM E.1964-297.1, 11.5 mm dd. **C,** *Ophiactis quinqueradia* Ljungman, 1872, (Ophiactidae: Amphilepidida), LACM 1939-213.10, 9.7 mm dd. **D,** *Amphioplus abditus* (Verrill, 1871), (Amphiuridae: Amphilepidida), LACM E.1970-363.2, 10.4 mm dd. **E,** *Ophiopsila californica* A.H. Clark, 1921, (Ophiopsilidae: Amphilepidida), LACM E.1949-72.5, 7.8 mm dd. **F,** *Ophionereis porrecta* Lyman, 1860, (Ophionereididae: Amphilepidida), LACM E.1957-302.1, 13.2 mm dd. Scale bars: A–F=1.0 mm.

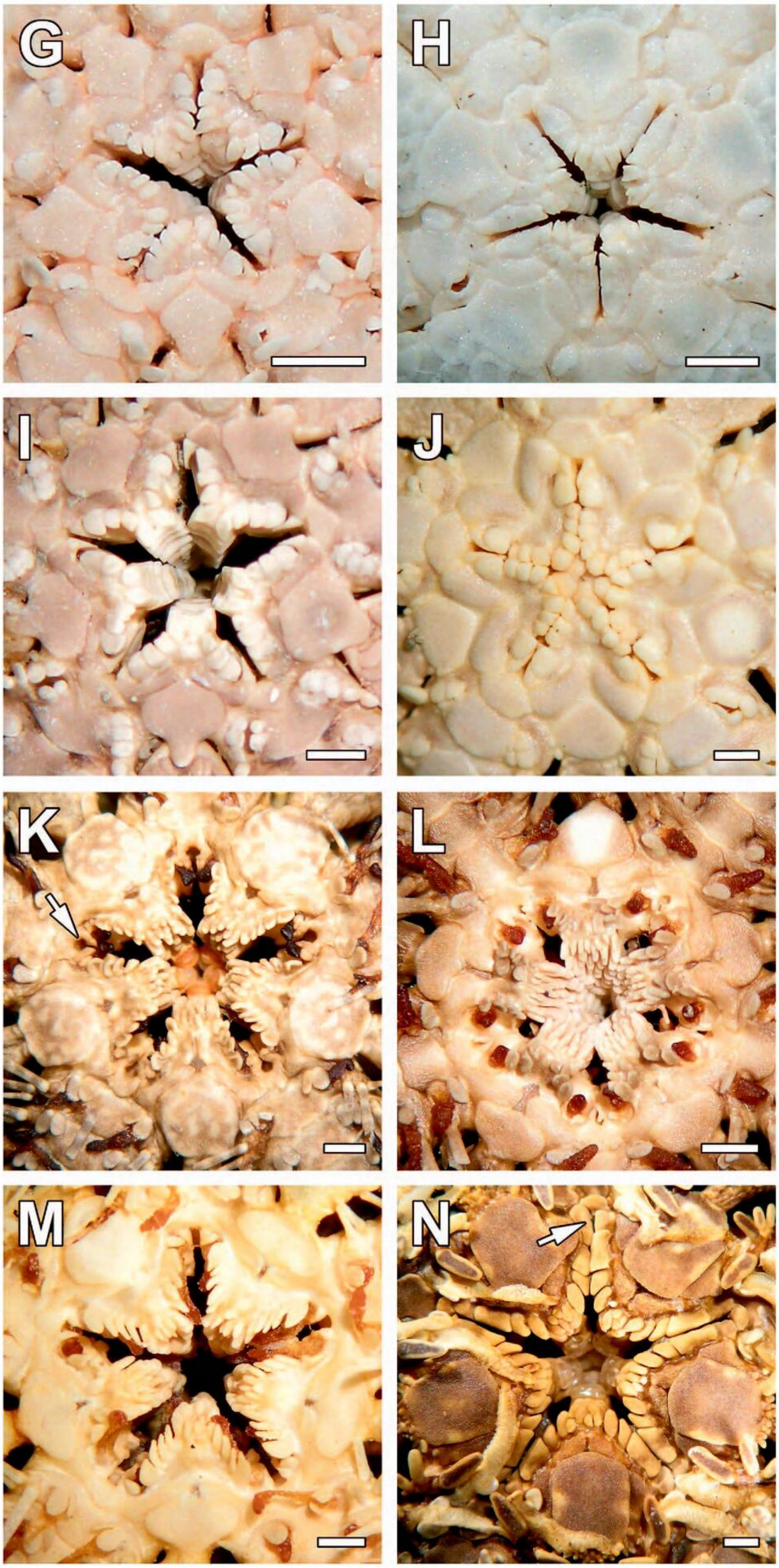

**Figure 11 cont.** Buccal funnels of representative species of the families of Amphilepidida and Ophiacanthida. **G,** *Ophiozonella oedilepis* (Murakami, 1942), (Ophiolepididae: Amphilepidida), LACM 78-227.2, 7.7 mm dd. **H,** *Ophiozonella longispina* H.L. Clark, 1908, (Hemieuryalidae: Amphilepidida), LACM 74-207.3, 8.7 mm dd. **I,** *Ophioplocus januarii* (Lütken, 1856), (Hemieuryalidae: Amphilepidida), LACM 87-290.1, 14.4 mm dd. **J,** *Ophioplocus esmarki* Lyman, 1874, (Hemieuryalidae: Amphilepidida), LACM E.1954-14.16, 8.7 mm dd; note that a buccal funnel is lacking in this species, in contrast with *O. januarii*. **K,** *Clarkcoma pulchra* (H.L. Clark, 1928), (Clarkcomidae: Ophiacanthida), LACM E.1972-450.1, 19.0 mm dd; arrowhead indicates the ventral opening of a channel between the CtPs. **L,** *Ophiopteris papillosa* (Lyman, 1875), (Ophiopteridae: Ophiacanthida), LACM E.1960-313.3, 14.7 mm dd. **M,** *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789), (Ophiotomidae: Ophiacanthida), LACM E.887, 21.2 mm dd. **N,** *Ophiocoma echinata* (Lamarck, 1816a), (Ophiocomidae: Ophiacanthida), LACM E.1939-217.10, 22.9 mm dd; arrow indicates LyOss that cover the ventral opening of a channel between the CtPs; note the lustrous, translucence of the dorsal teeth that are capped with imperforate stereom. Scale bars: G–N=1.0 mm.

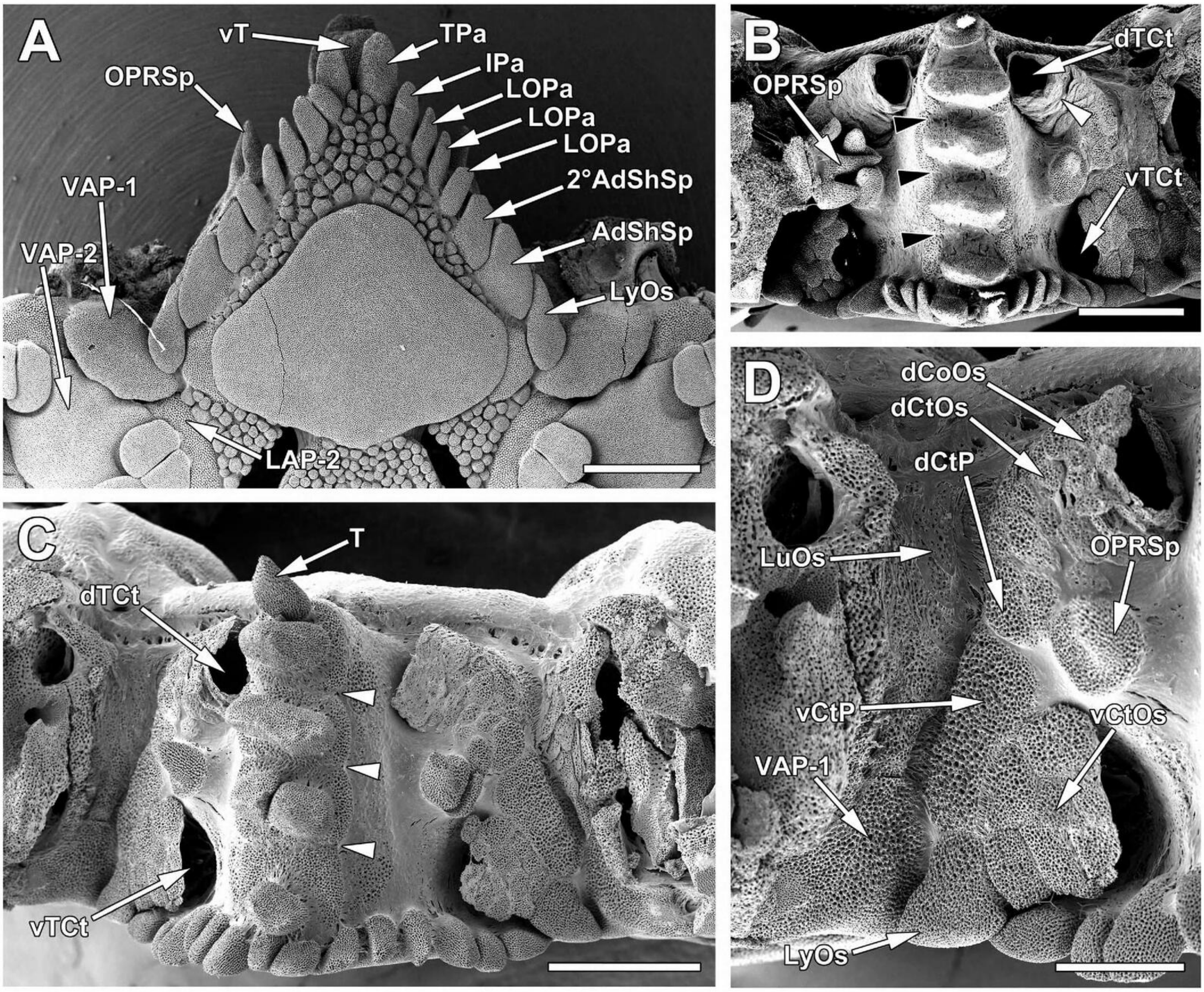

**Figure 12** *Ophioderma rubicunda* Lütken, 1856. **A,** ventral view of jaw. **B,** proximal view of jaw; arrowhead indicates imbricate CoOss of the dTCt; note interdigitation of opposing OPRSps. **C,** oblique proximal view of jaw; arrowheads indicate seams between four elements of the DP. **D,** adradial detail of OP, showing dorsal and ventral TCts. A–D: SEM micrographs; LACM E.1985-461.2; 15.0-, 15.1-mm-dd specimens. Scale bars: A-C=1.0 mm; D=0.5 mm.

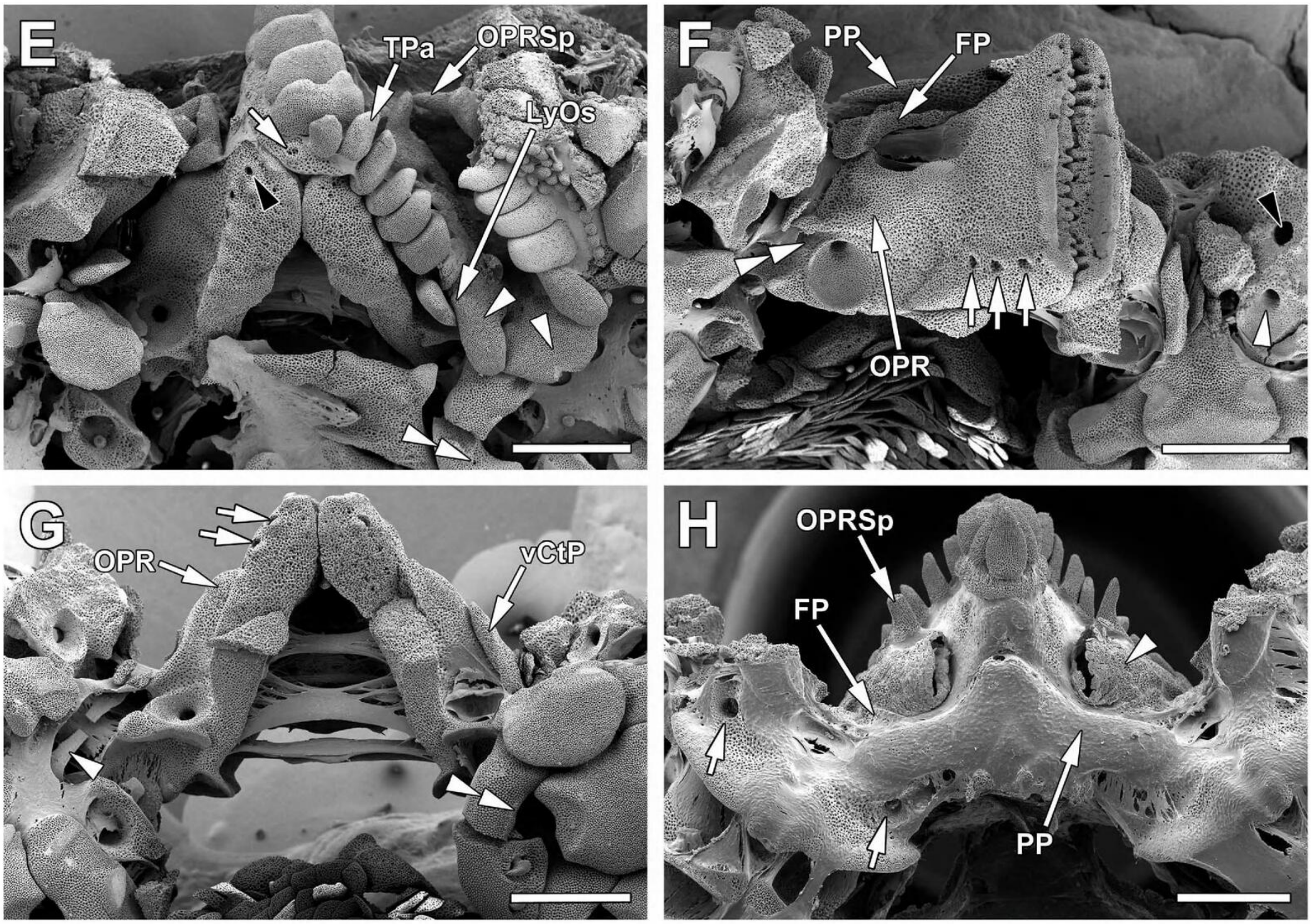

**Figure 12 cont.** *Ophioderma rubicunda* Lütken, 1856. **E,** ventral view of jaw, with superficial ossicles removed; arrow indicates central fossa of the ArtS of a TPa; black arrowhead marks fossa and ArtSs associated with proximal OPas *s.l.*; white arrowheads are directed toward microscopic striations on VAP-1 and LyOs, which may support tracts of ciliated epithelium; double arrowheads mark a possible neural foramen beside the ArtS of a TSc on LAP-2. **F,** adradial view of jaw with superficial ossicles removed; arrows mark fossae and ArtSs of proximal OPas *s.l.* on the OP; water vascular channels to OT-1 and OT-2 are marked by black and white arrowheads, respectively. **G,** ventral view of jaw with superficial ossicles removed; arrows mark fossae and ArtSs associated with proximal OPas *s.l.* on the OP; arrowhead marks the radial nerve cord; double arrowheads mark ArtS of TScs on LAP-2. **H,** dorsal view of jaw; arrows indicates the single water ring foramina on two adjacent jaws; arrowhead marks imbricate CoOss of the dTCt. E: SEM micrographs, LACM E.2003-58.1; 18.2-mm-dd specimen; F–H: LACM E.1985-461.2; 15.0-mm-dd specimen. Scale bars: E–H=1.0 mm.

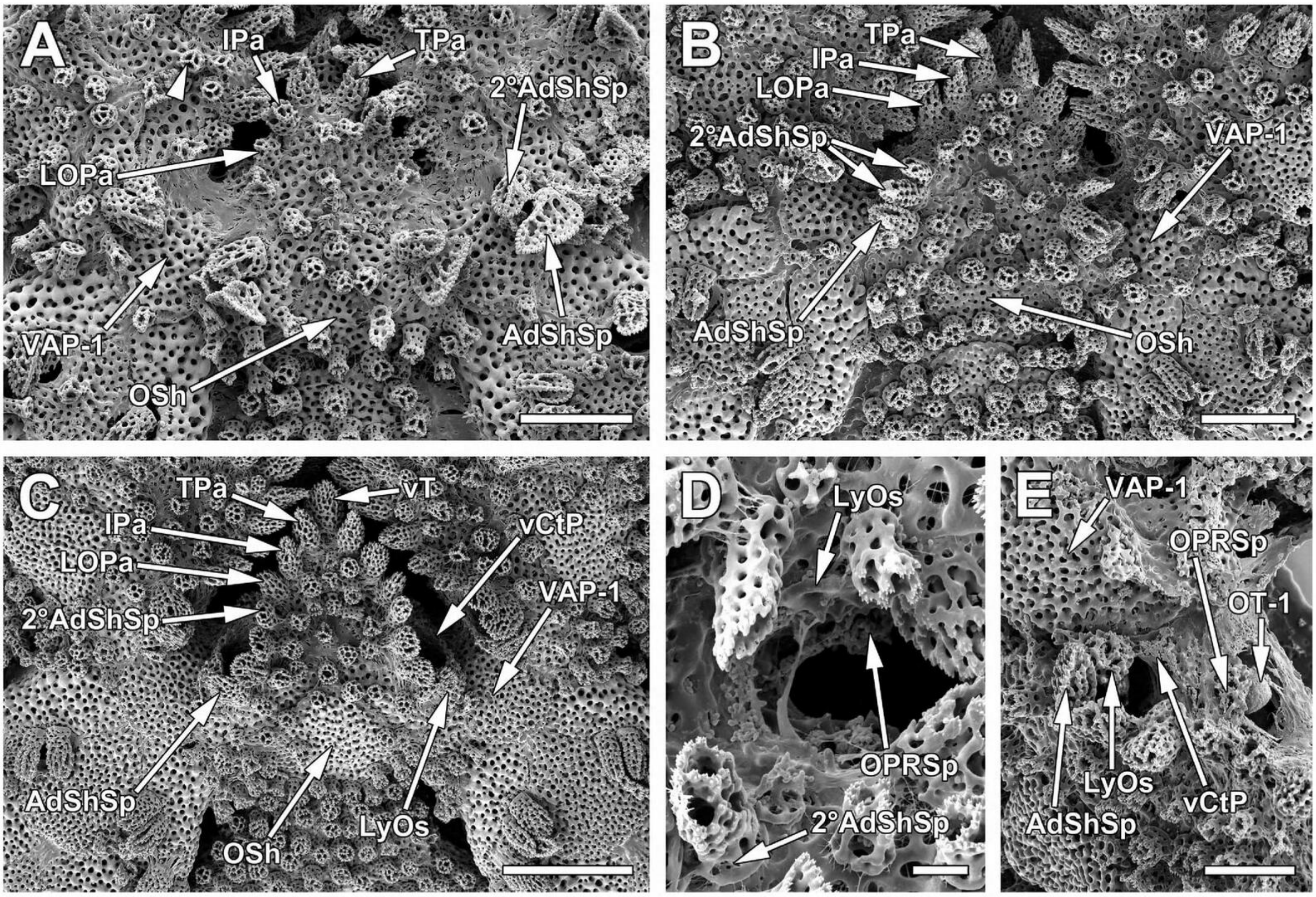

**Figure 13** *Ophioderma rubicunda* Lütken, 1856. Skeletal ontogenesis. **A–E:** ventral view of jaw; SEM micrographs. **A,** 1.3-mm-dd juvenile; LACM E.1981-225.2; arrowhead marks a triradiate granule. **B,** 1.7-mm-dd juvenile ; LACM E.1981-221.2. **C,** 2.2-mm-dd juvenile ; LACM E.1983-132.5. **D,** 1.7-mm-dd juvenile; LACM E.1981-221.2; detail of distal OSl. **E,** 2.1-mm-dd juvenile; LACM E.1981-221.3; detail of adradial view of jaw. Scale bars: A, B=150 μm; C=250 μm; D=25 μm; E=100 μm.

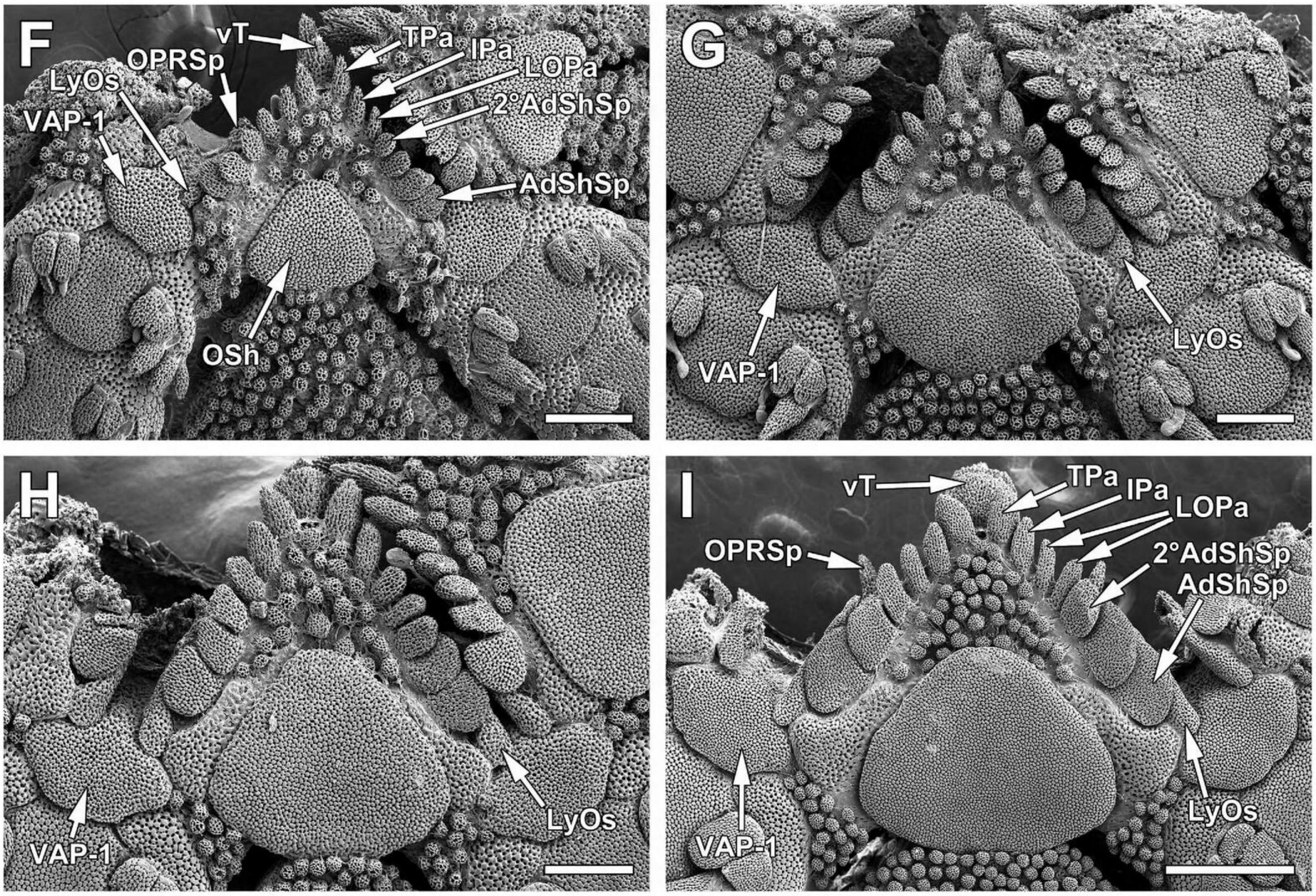

**Figure 13 cont.** *Ophioderma rubicunda* Lütken, 1856. Skeletal ontogenesis. **F–I:** ventral view of jaw; SEM micrographs. **F,** 2.9-mm-dd juvenile; LACM E.1980-197.1. **G,** 3.9-mm-dd juvenile; LACM E.1986-528.1. **H,** 4.0-mm-dd juvenile; LACM E.1981-288.1. **I,** 6.2-mm-dd juvenile; LACM E.1981-287.1. Scale bars: F, G, H=250 μm; I=0.5 mm.

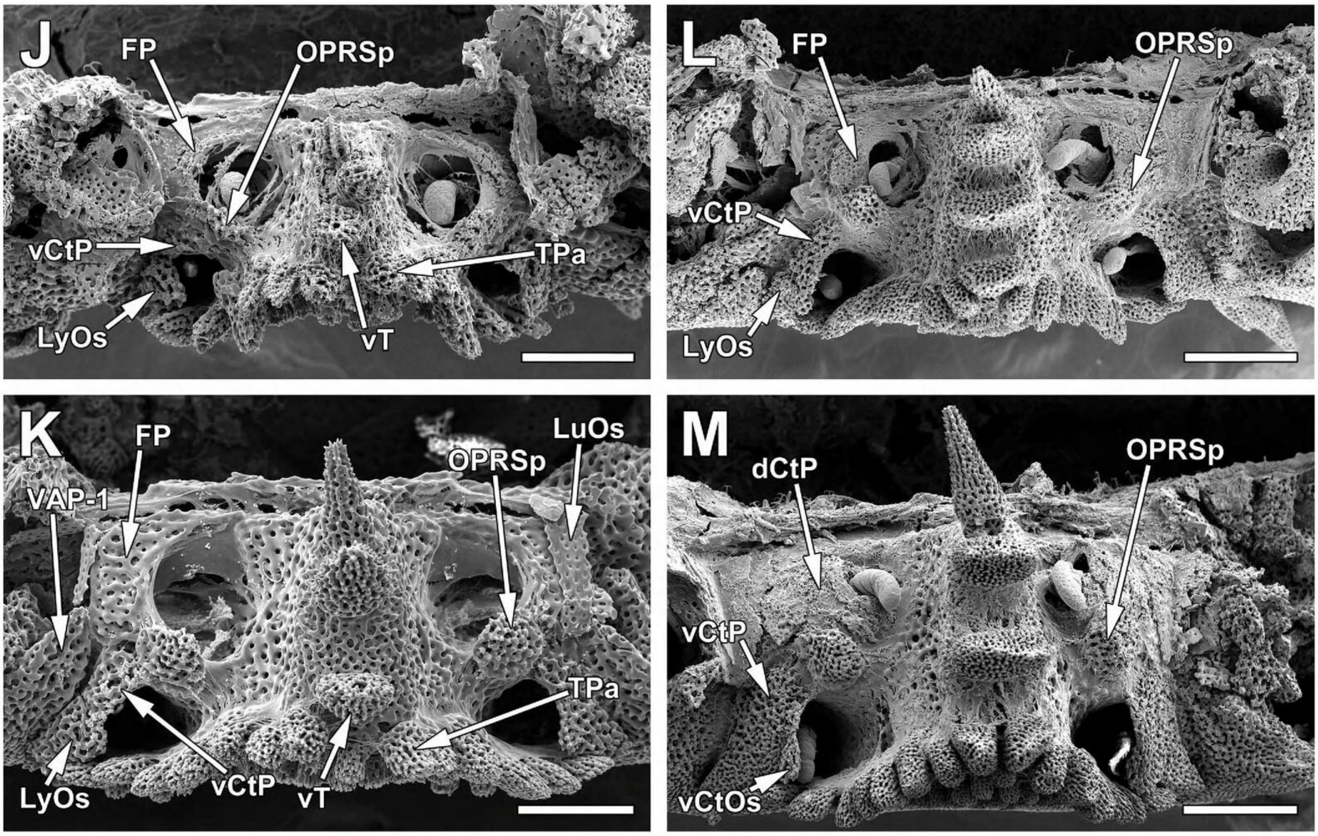

**Figure 13 cont.** *Ophioderma rubicunda* Lütken, 1856. Skeletal ontogenesis. **J-M:** proximal view of jaw; SEM micrographs. **J,** 2.1-mm-dd juvenile ; LACM E.1981-221.3. **K,** 2.9-mm-dd juvenile; LACM E.1980-197.1. **L,** 3.9-mm-dd juvenile; LACM E.1986-528.1. **M,** 4.0-mm-dd juvenile; LACM E.1981-288.1. Scale bars: J, K=150 μm; L, M=250 μm.

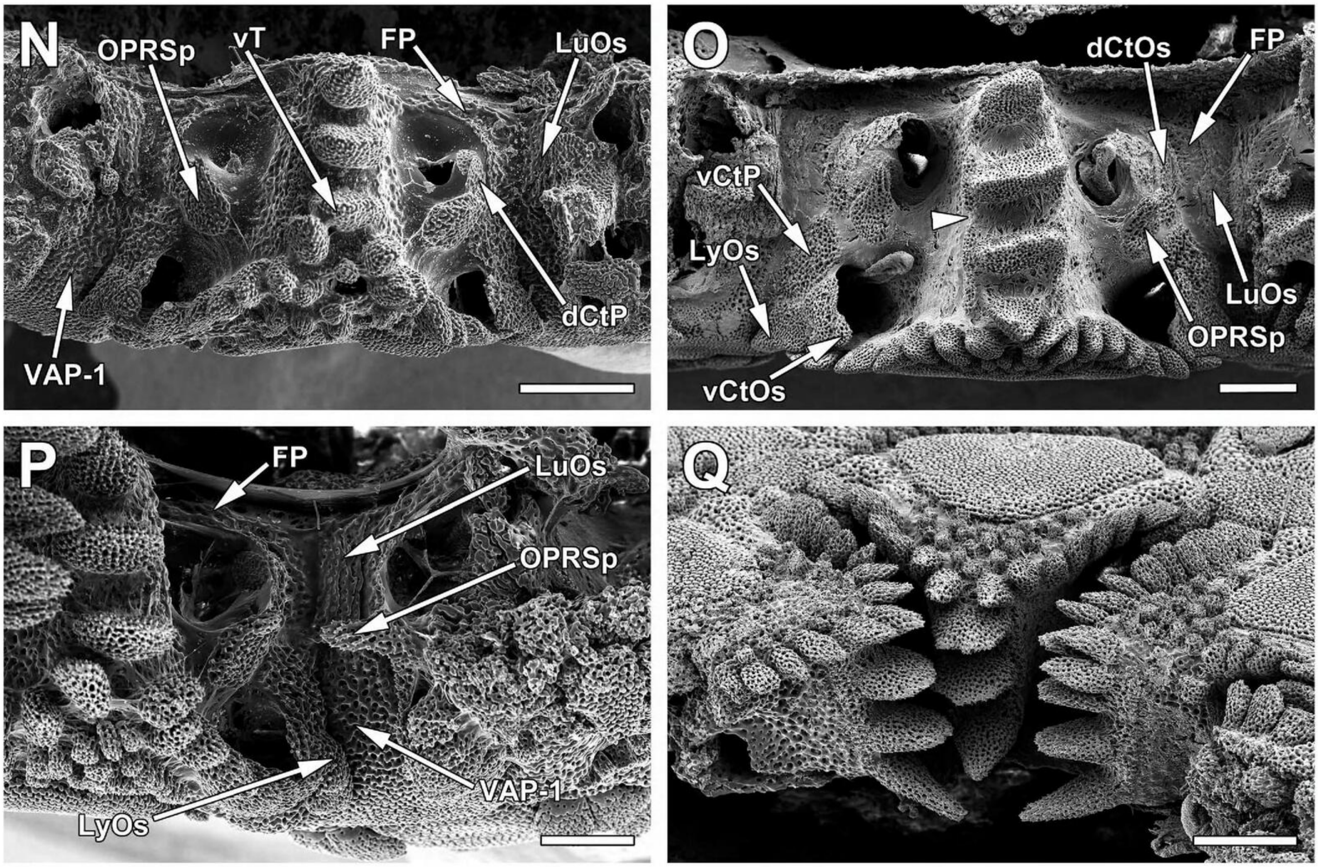

**Figure 13 cont.** *Ophioderma rubicunda* Lütken, 1856. Skeletal ontogenesis. **N–Q:** proximal view of jaw; SEM micrographs. **N,** 4.6-mm-dd juvenile; LACM E.1981-289.1. **O,** 6.2-mm-dd juvenile ; LACM E.1981-287.1. **P,** 4.6-mm-dd juvenile ; LACM E.1981-289.1. **Q,** 3.9-mm-dd juvenile; LACM E.1986-528.1; note that teeth on adjacent jaws differ in number and intermesh with one another. Scale bars: L–O=250 µm; P=150 µm; Q=250 µm.

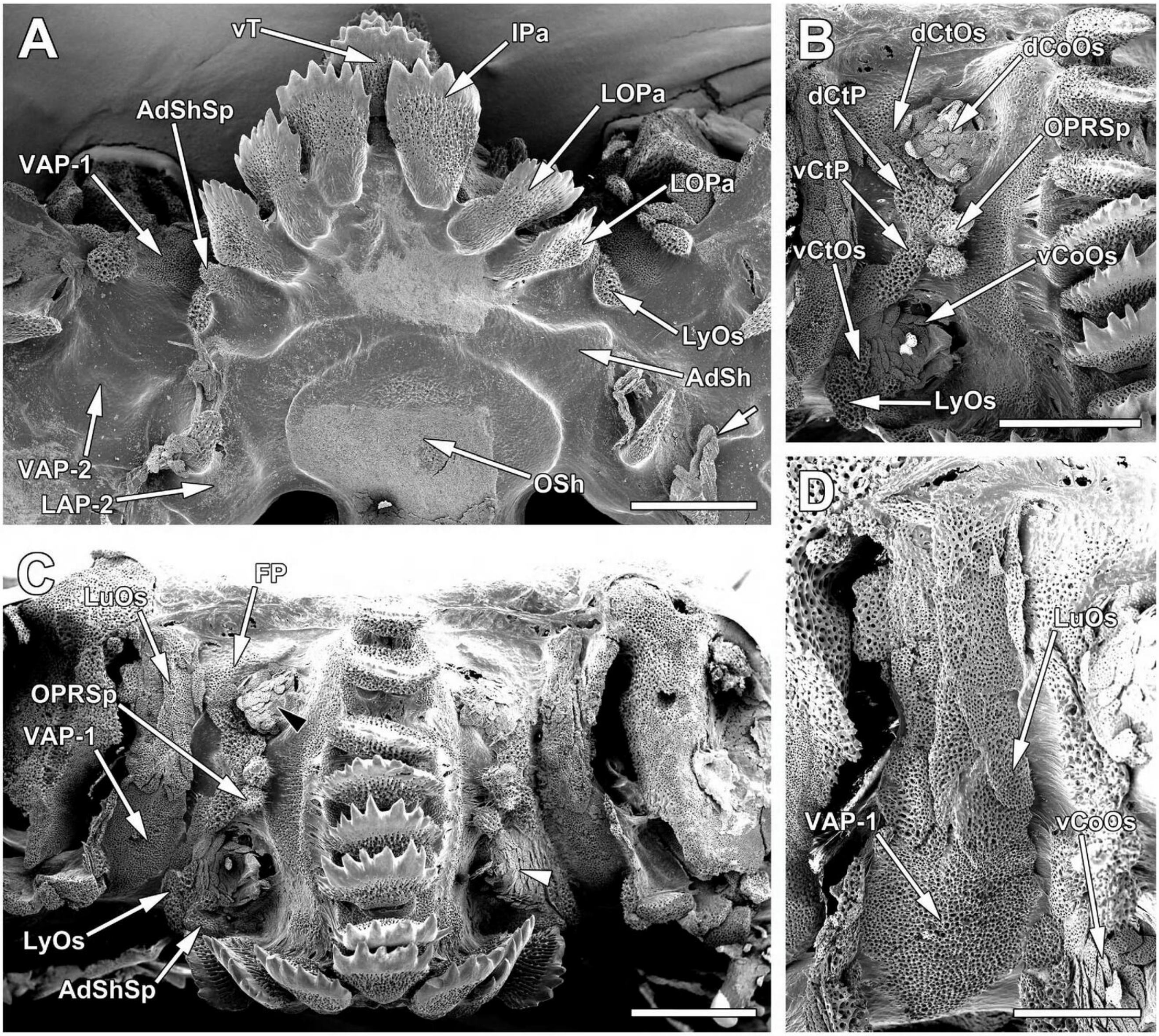

**Figure 14** *Ophiomyxa flaccida* (Say, 1825). **A,** ventral view of jaw; arrow indicates several "sheath plates" associated with a tube foot of the second AS. **B,** adradial view of jaw, showing dorsal and ventral TCts. **C,** proximal view of jaw; black arrowhead and white arrowhead indicate collars of imbricate CoScs incorporated in the dorsal and ventral TCts, respectively. **D,** detail of perradial region between adjacent jaws; note that LuOs overlap the proximal edge of VAP-1. A–D: SEM micrographs; LACM E.1997-101.15; 20.1-mm-dd specimen. Scale bars: A–C=1.0 mm; D=0.5 mm.

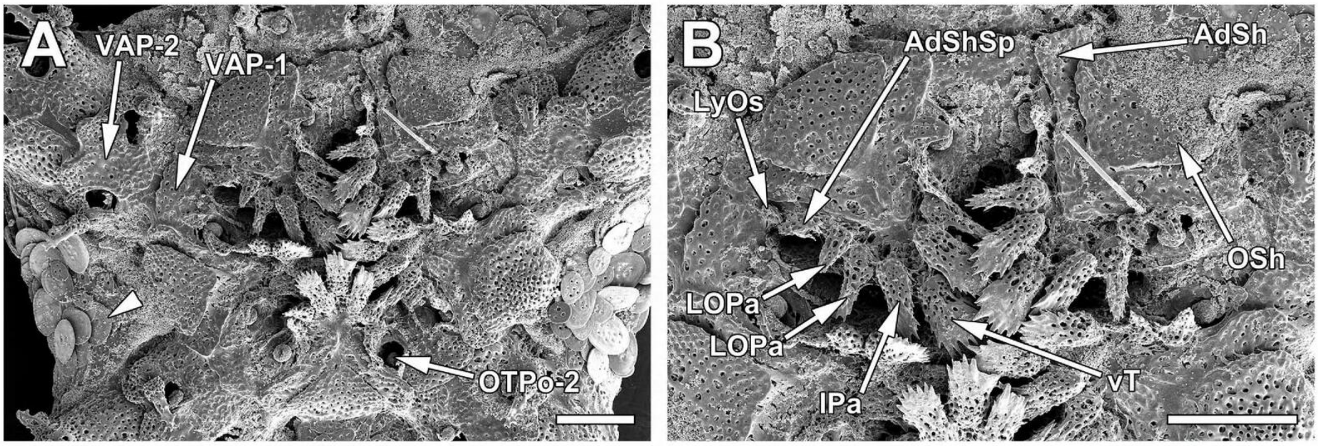

**Figure 15** *Ophiomyxa flaccida* (Say, 1825). Skeletal ontogenesis. **A,** ventral view of disk; arrowhead marks a squamous interradial scale that is composed of minutely perforated stereom. **B,** ventral view of jaws. A–B: SEM micrographs; LACM E.1981-231.3; 2.1-mm-dd specimen. Scale bars: A, B=250 µm.

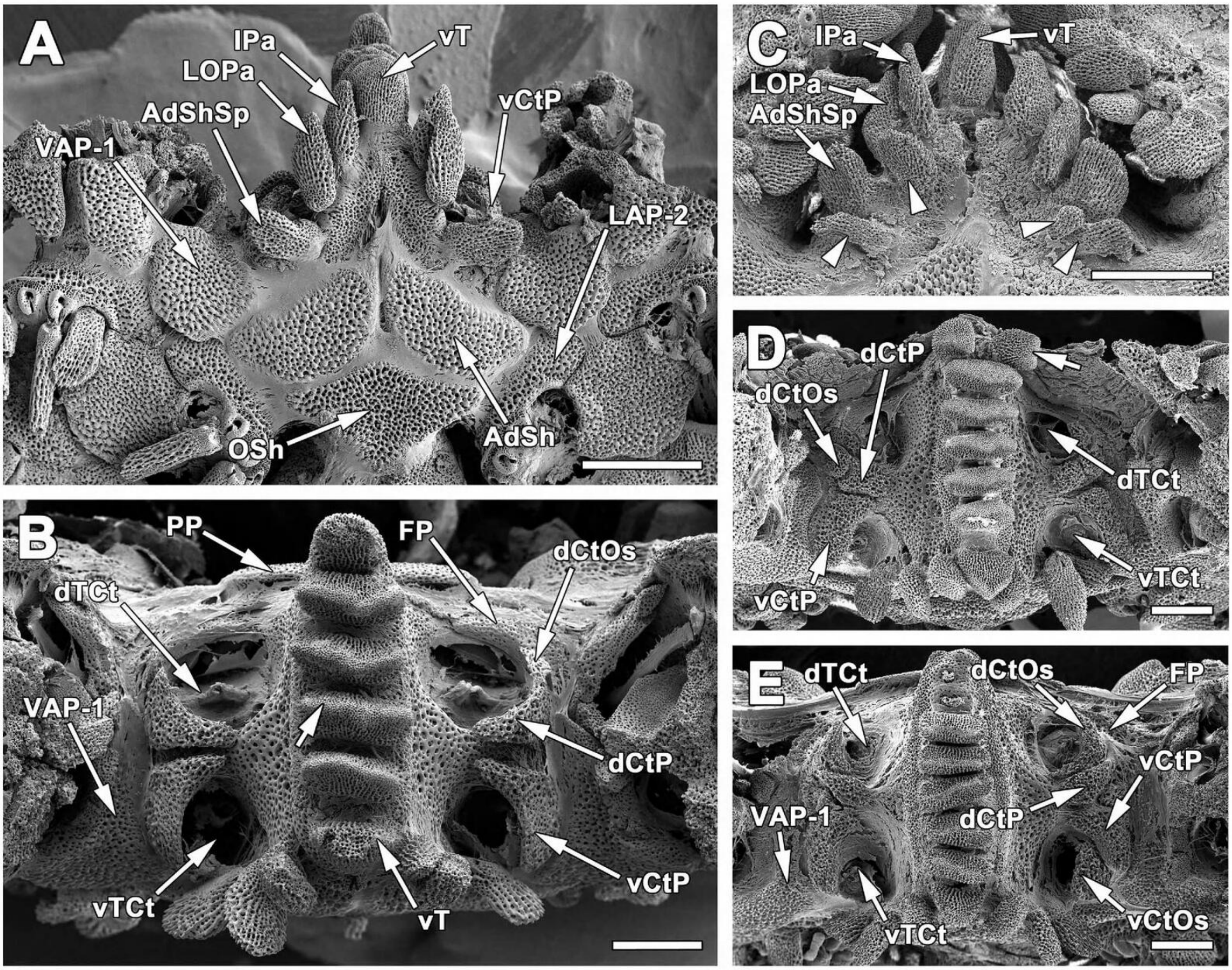

**Figure 16** *Ophiacantha bidentata* (Bruzelius, 1805). **A,** ventral view of jaw. **B,** proximal view of jaw; arrow indicates dense, reinforced stereom on the proximal edge of a tooth. **C,** ventral view of jaw; supernumerary papillae indicated by arrowheads. **D,** proximal view of jaw; arrow indicates an anomalous pair of dorsalmost teeth. **E,** proximal view of jaw; exposed dental ArtSs are noticeable on the dorsal end of the DP. A–E: SEM micrographs; LACM 1978-263.1; 11.7-, 14.7-mm-dd specimens. Scale bars: A, C=1.0 mm; B=0.5 mm; C=1.0 mm; D, E=0.5 mm.

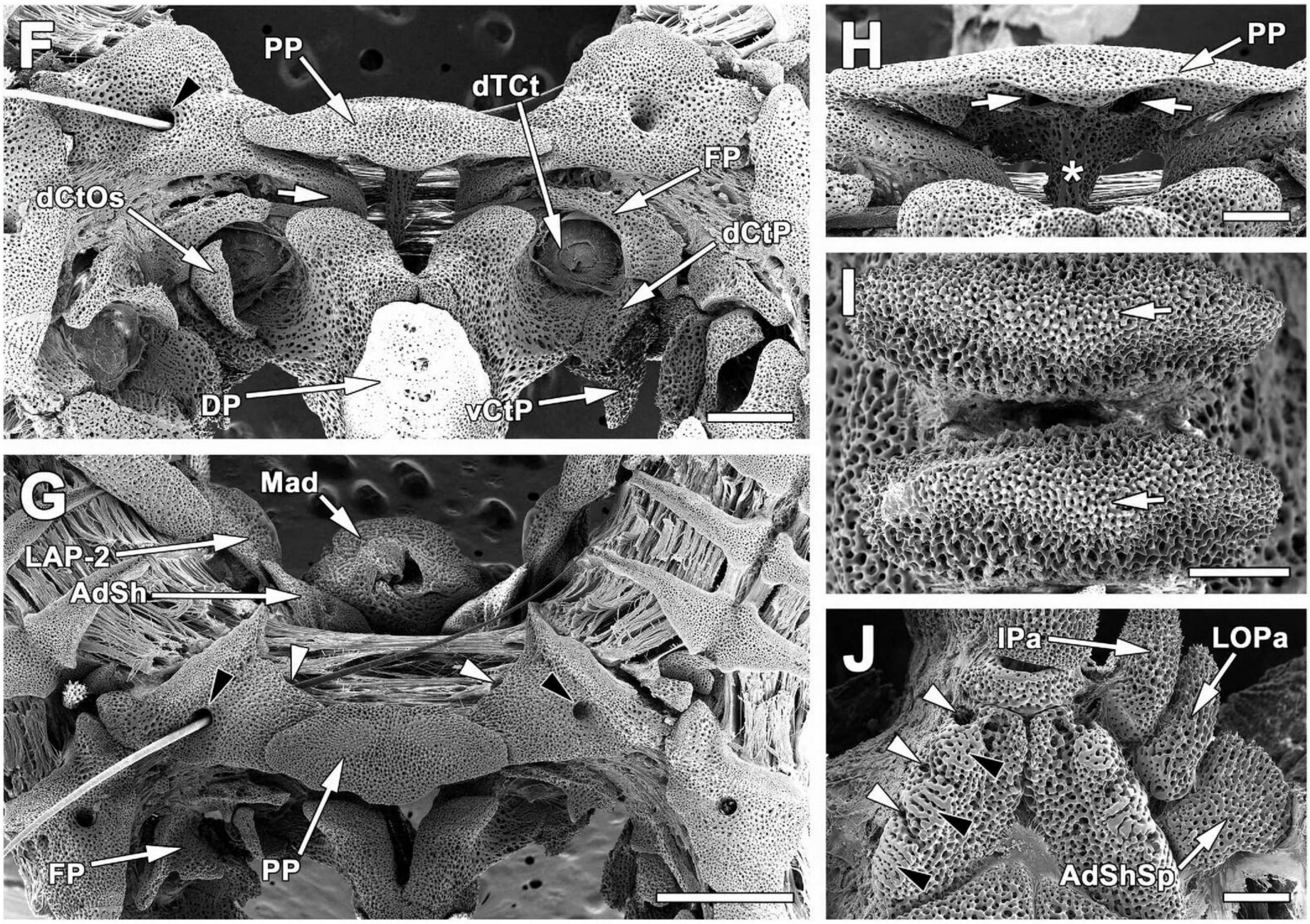

**Figure 16 cont.** *Ophiacantha bidentata* (Bruzelius, 1805). **F,** oblique dorsal view of jaw showing the pedunculate PP; white arrow indicates neural groove in dorsal surface of OP; note that projections of the FP are aligned with this groove and with the route of the nerve ring; black arrowhead indicates an adradial water ring foramen that is penetrated by an eyelash. **G,** dorsal view of jaw; white arrowheads indicate abradial water ring foramina, and black arrowheads indicate adradial water ring foramina; an eyelash penetrates the adradial foramen on the left side of the jaw and exits the abradial foramen of the OP; note the orifice and cavity on the dorsal side of the madreporite at the site where the stone canal joins the madreporic ampulla. **H,** detail of the PP; asterisk indicates the peduncle of the PP; opposing arrows indicate openings of a conduit on the ventral edge of the PP, which may be associated with the nerve ring. **I,** detail of teeth; arrows mark dense stereom with minute pores on the proximal edge of the tooth. **J,** detail of the apex of the jaw; black arrowheads mark ArtSs of OPas *s.l.*, which are composed of sparsely perforate stereom; white arrowheads indicate fossae beside the ArtSs. F–J: SEM micrographs; LACM 1978-263.1; 13.7-, 14.7-mm-dd specimens. Scale bars: F=0.5 mm; G=1.0 mm; H=250 µm; I=150 µm; J=250 µm.

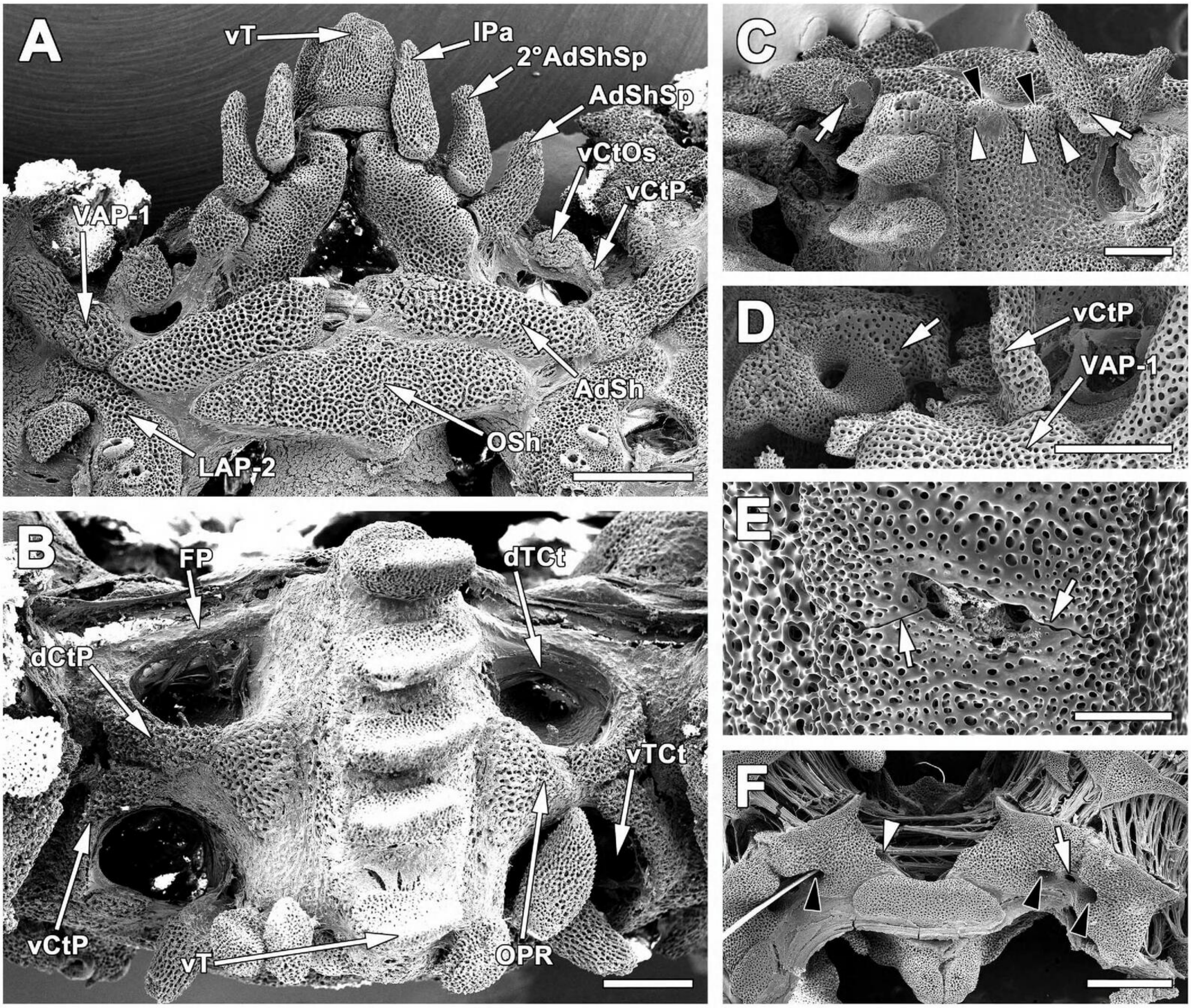

**Figure 17** *Ophiophthalmus normani* Lyman, 1879. **A,** ventral view of jaw. **B,** proximal view of jaw. **C,** adradial view of the ventral edge of a jaw; black arrowheads mark ArtSs of the OPas *s.l.*, which are composed of sparsely perforate stereom; white arrowheads indicate fossae beside the ArtSs; white arrows indicate fossae that are immediately distal to the ArtS on the OPas *s.l.*; a hairline fissure is visible near the ventral end of the DP. **D,** detail of the vTCt; white arrow indicates a notch beside the tentacle basin, which may hold a radial nerve cord branch that innervates OT-2. **E,** detail of the DP; white arrows indicates a hairline fissure separating a pair of dental foramina. **F,** dorsal view of jaw; white arrow marks the dorsal foramen of the radial water canal; white arrowhead indicates an abradial water ring foramen, and black arrowheads indicate adradial water ring foramina; an eyelash penetrates the adradial foramen, exits the abradial foramen of the OP of the jaw, and extends to the abradial foramen on the adjacent OP. A–F: SEM micrographs; LACM 1965-139.2; 14.5-, 14.7-, 15.0-, 16.3-, 16.4-, 17.0-mm-dd specimens. Scale bars: A=1.0 mm; B–D=0.5 mm; E=250 μm; F=1.0 mm.

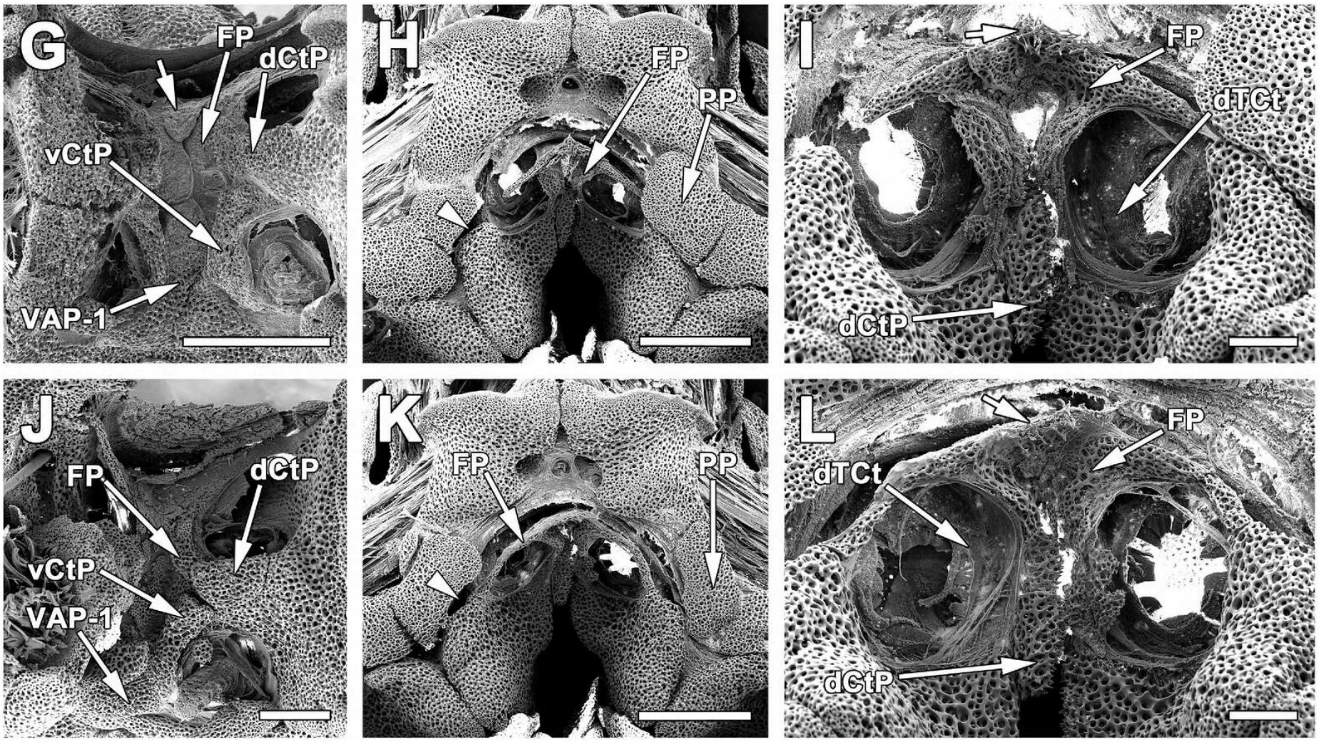

**Figure 17 cont.** *Ophiophthalmus normani* Lyman, 1879. **G–L** details of the perradial gap and associated FPs, showing the relationship between the FPs, PPs, and circumoral nerve ring. **G,** proximal perradial view between two jaws; white arrow indicates the perradial ossicle linking two adjacent FPs; note that the dorsal lobe of VAP-1 covers the ventral portion of the PG. **H,** dorsal view; white arrowhead marks neural groove in OP, which is exposed below a fractured PP. **I,** proximal detail of image H; white arrow indicates spinose, perradial ossicle connecting adradial arms of adjacent FPs. **J,** proximal perradial view between two jaws; note that at upper right an eyelash penetrates a fractured OP; the vertical channel below the eyelash held a branch of the water ring connected to the OT basins; note small vCtOs beside the vCtP. **K,** dorsal view; white arrowhead marks neural groove in OP, which is below the PP; note that arms of FPs follow the circular path of the nerve ring. **L,** oblique detail of image K; note that a slender supplementary ossicle joins the abradial arm of the FP to a protuberance on the OP; white arrow indicates perradial, spinose ossicle connecting the two adjacent FPs. G–L: SEM micrographs; LACM 1965-139.2; 16.4-, 17.0-, 17.2-mm-dd specimens. Scale bars: G, H=1.0 mm; I=250 µm; J=0.5 mm; K=1.0 mm; L=250 µm.

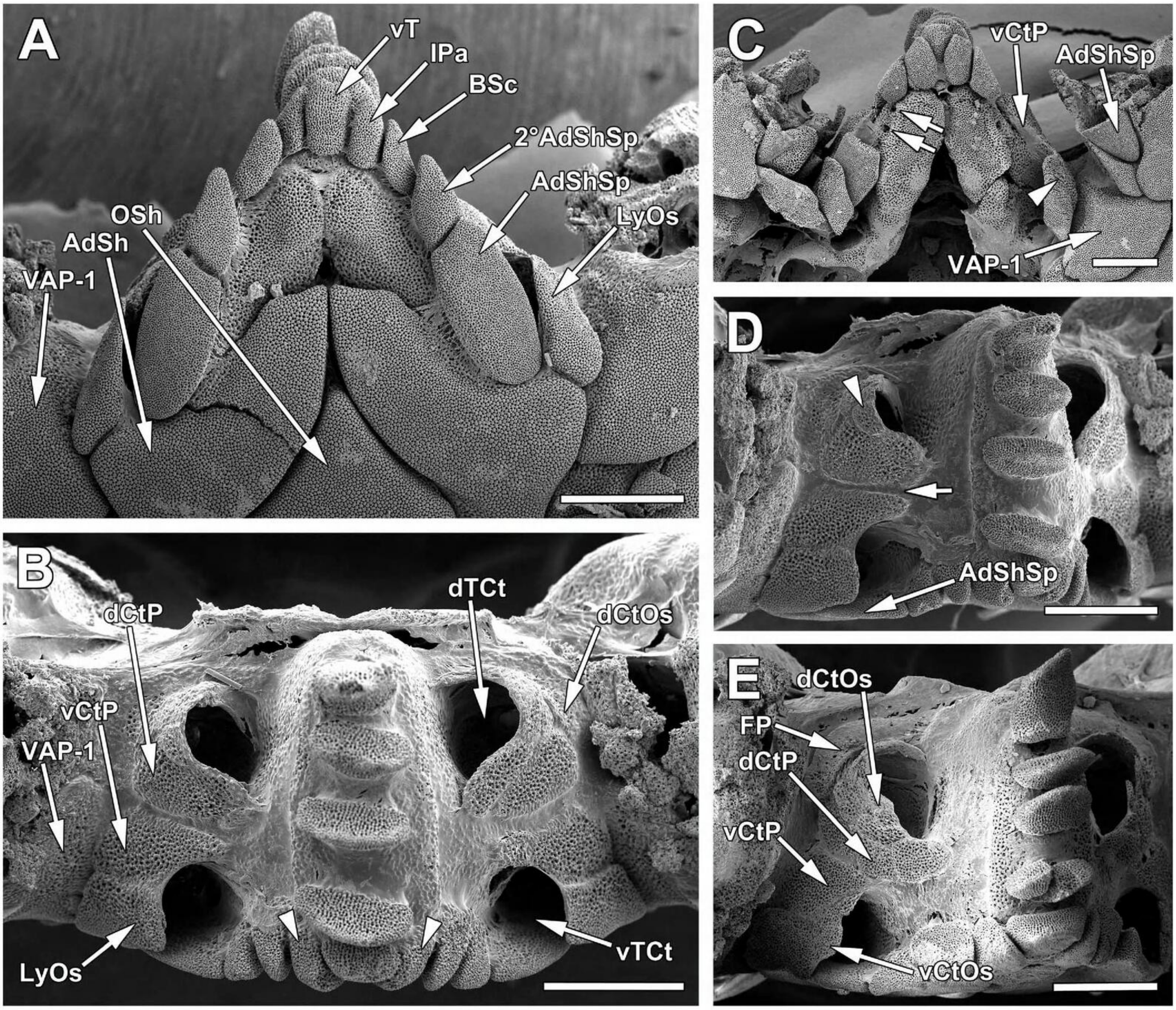

**Figure 18** *Ophiolepis impressa* Lütken, 1859. **A,** ventral view of jaw. **B,** proximal view of jaw; arrowheads mark a pair of IPas that overlap the vT. **C,** ventral view of jaw with superficial ossicles removed; arrows mark fossae and ArtSs composed of sparsely perforate stereom, which are associated with proximal IPas *s.l.* on the OP; arrowhead is directed toward microscopic striations on LyOs, which may be associated with tracts of ciliated epithelium. **D,** adradial view of jaw; arrow marks OPR; arrowhead indicates collar of dTCt, which is composed of imbricate CtOss. **E,** adradial view of jaw with a dTCt that is composed of more CtOss than the structure in D. A–E: SEM micrographs; LACM E.1980-196.1; 12.5-, 13.8-, 14.1-mm-dd specimens. Scale bars: A–E=0.5 mm.

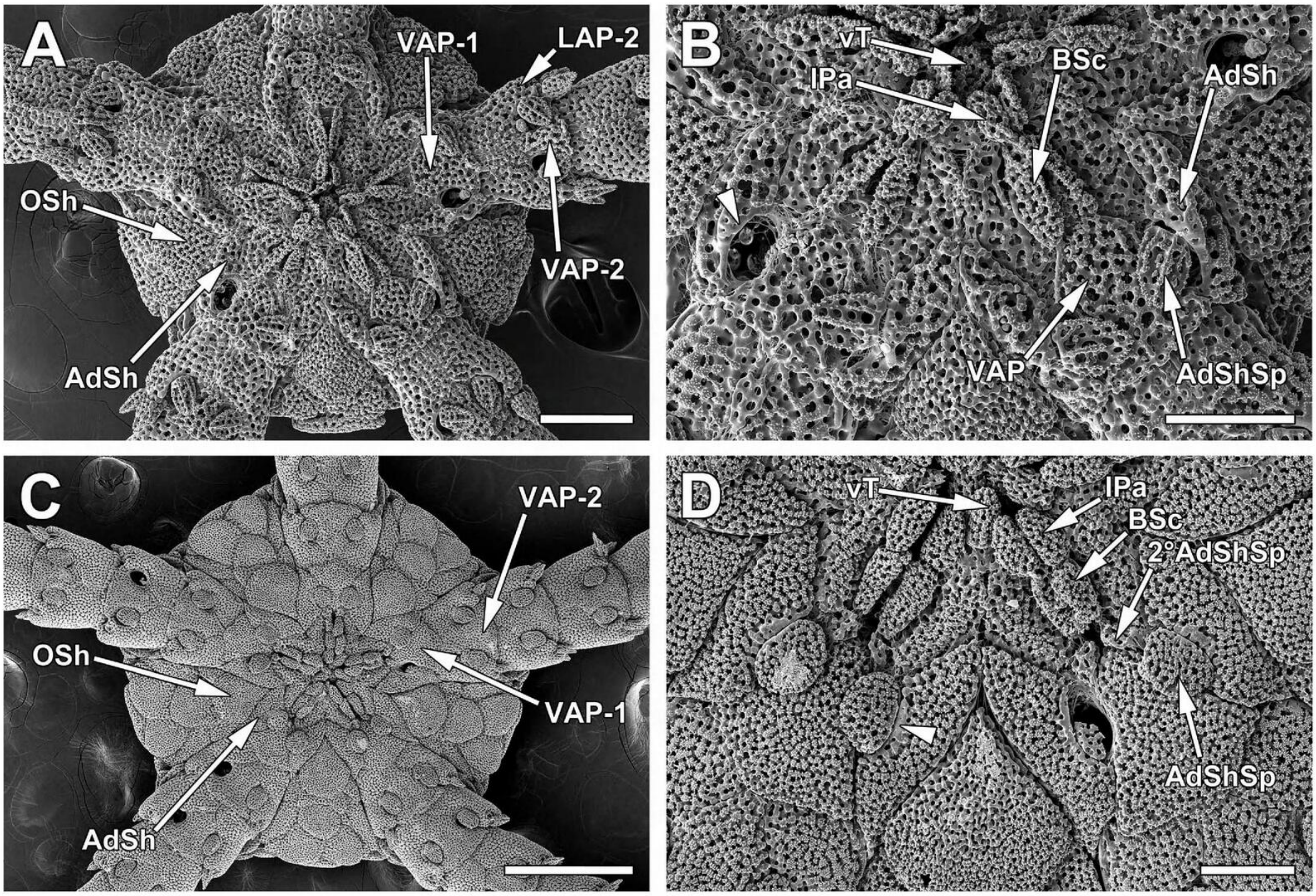

**Figure 19** *Ophiolepis paucispina* (Say, 1825). Skeletal ontogenesis. **A,** ventral view of disk and jaw; **B,** detail of disk; arrow marks ArtS of AdShSp on the AdSh; 0.7-mm-dd juvenile. **C,** ventral view of disk and jaw; **D,** detail of disk; arrow marks ArtS of AdShSp on the AdSh; 1.50-mm-dd juvenile. A–D: SEM micrographs, LACM E.1981-230.2. Scale bars: A=150 µm; B=100 µm; C=0.5 mm; D=100 µm.

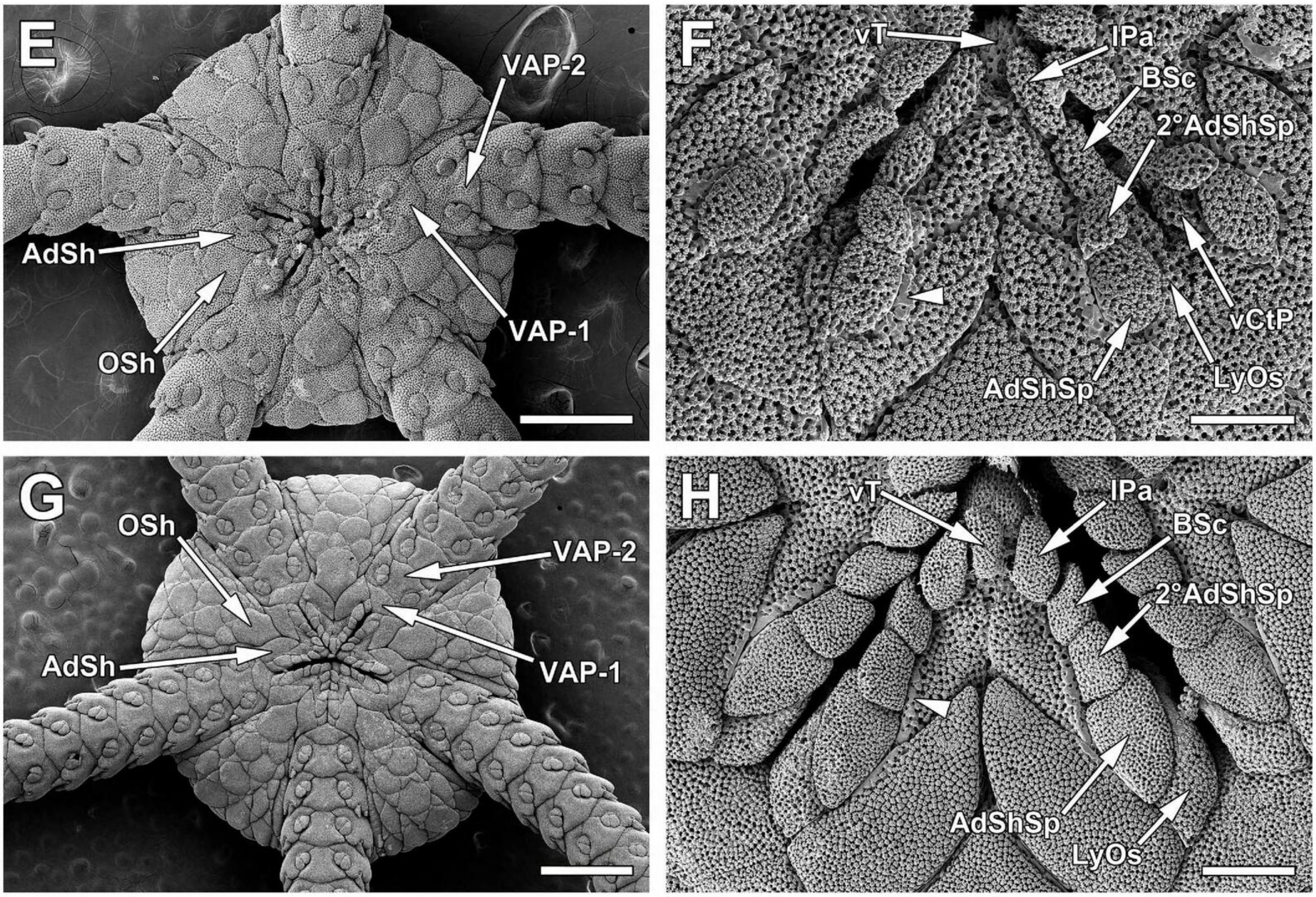

**Figure 19 cont.** *Ophiolepis paucispina* (Say, 1825). Skeletal ontogenesis. **E,** ventral view of disk and jaw; **F,** detail of disk; arrow marks ArtS of AdShSp on the AdSh; 1.72-mm-dd juvenile. **G,** ventral view of disk and jaw; **H,** arrow marks ArtS of AdShSp on the OP; 4.4-mm-dd juvenile. E–H: SEM micrographs; LACM E.1981-230.2. Scale bars: E=0.5 mm; F=100 μm; G=1.0 mm; H=150 μm.

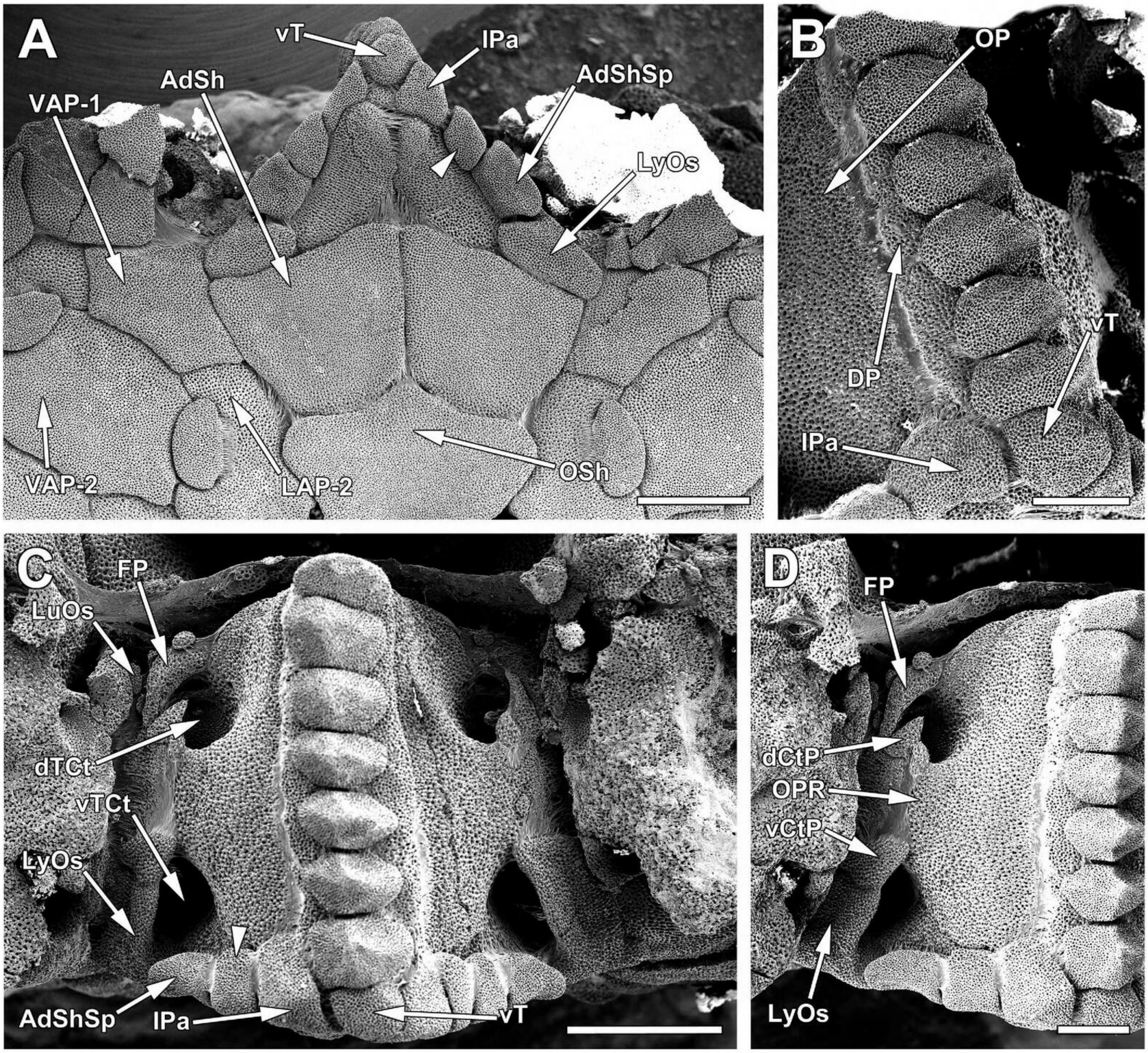

**Figure 20** *Sigsbeia murrhina* Lyman, 1878. **A,** ventral view of disk; arrowhead marks an OPa *s.l.* with indeterminate homology. **B,** detail of proximal edge of jaw. **C,** proximal view of jaw; arrowhead marks an OPa *s.l.* with indeterminate homology. **D,** adradial view of jaw. A–D: SEM micrographs; LACM E.1989-459.1; 14.5-mm-dd specimen. Scale bars: A=1.0 mm; B=0.5 mm; C=1.0 mm; D=0.5 mm.

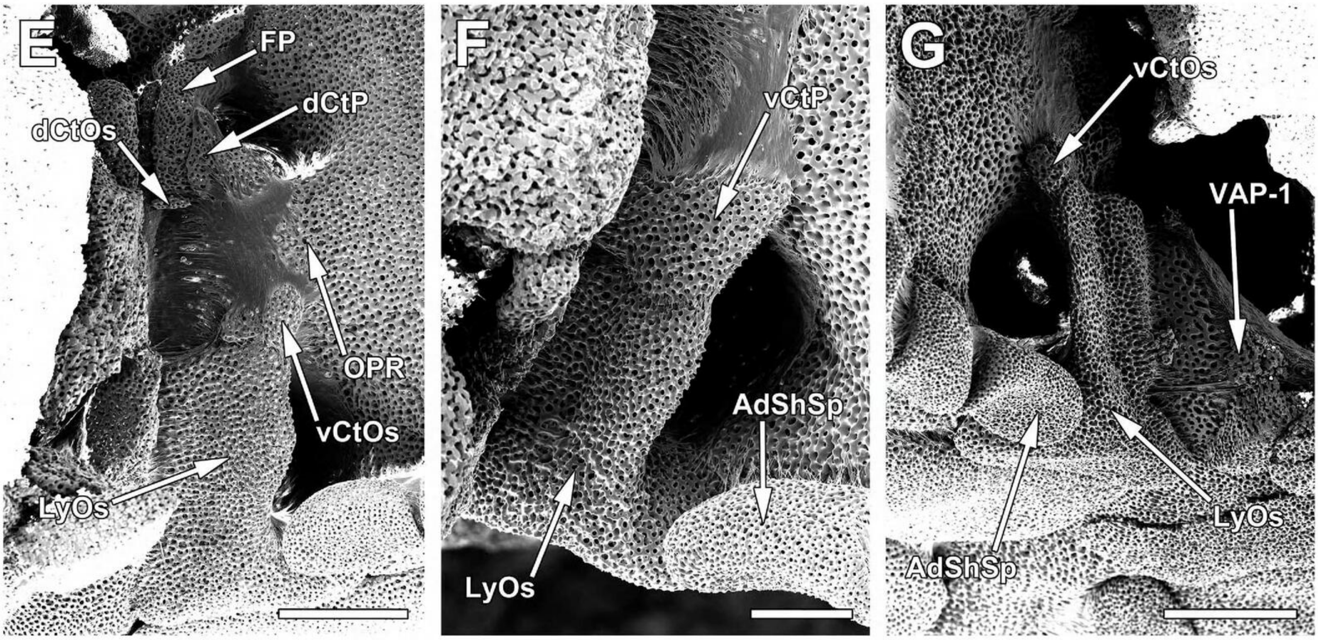

**Figure 20 cont.** *Sigsbeia murrhina* Lyman, 1878. **E, F, G,** details of the adradial portion of several jaws that exhibit variations in the morphology of their dorsal and ventral TCts. E–G: SEM micrographs; LACM E.1989-459.1; 14.5-mm-dd specimen. Scale bars: E=0.5 mm; F=250 μm; G=0.5 mm.

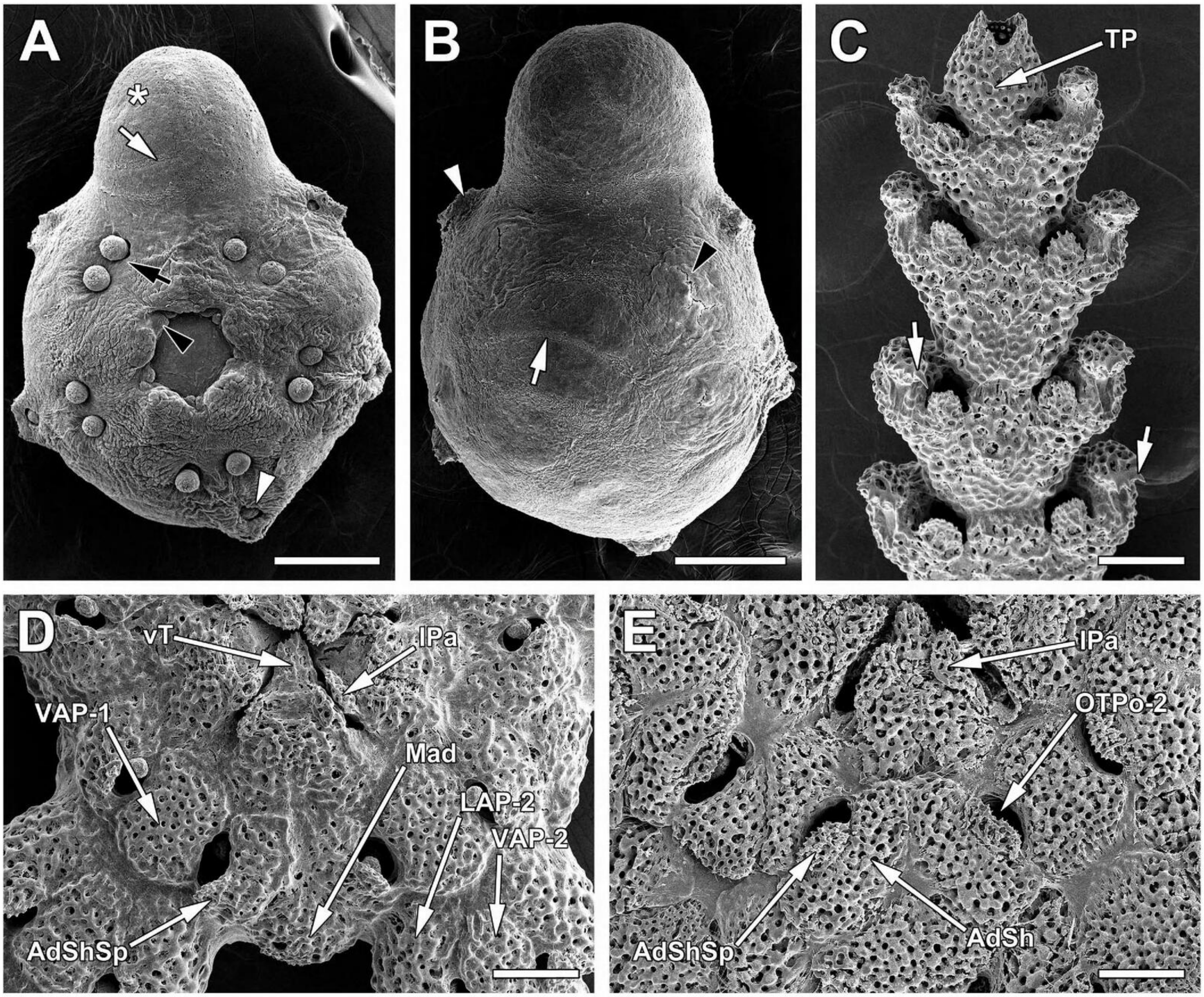

**Figure 21** *Sigsbeia conifera* Koehler, 1914. Skeletal ontogenesis. **A,** brooded embryo, ventral view; asterisk marks preoral lobe; white arrow indicates presumptive trace of ciliary band; white arrowhead marks terminal tube foot emerging from TP; black arrowhead and arrow mark OT-1 and OT-2, respectively. **B,** brooded embryo, dorsal view; white arrowhead marks TP; black arrowhead indicates radial primary plate, which appears to have a central protrusion; arrow indicates trace of presumptive ciliary band overlying the central primary plate. **C,** ventral view of a brooded individual, showing detail of an arm tip; arrows mark ventrally directed spinules on arm spines, which may enable the free-living juvenile to grip the host; 0.7-mm-dd (7 ASs) juvenile. **D,** ventral view of a brooded individual, showing jaw and ventral interradius; 0.7-mm-dd juvenile. **E,** ventral view of jaw of free-living individual; 1.2-mm-dd juvenile. A–E: SEM micrographs; LACM E.1986-95.1. Scale bars: A, B=150 µm; C–E=100 µm.

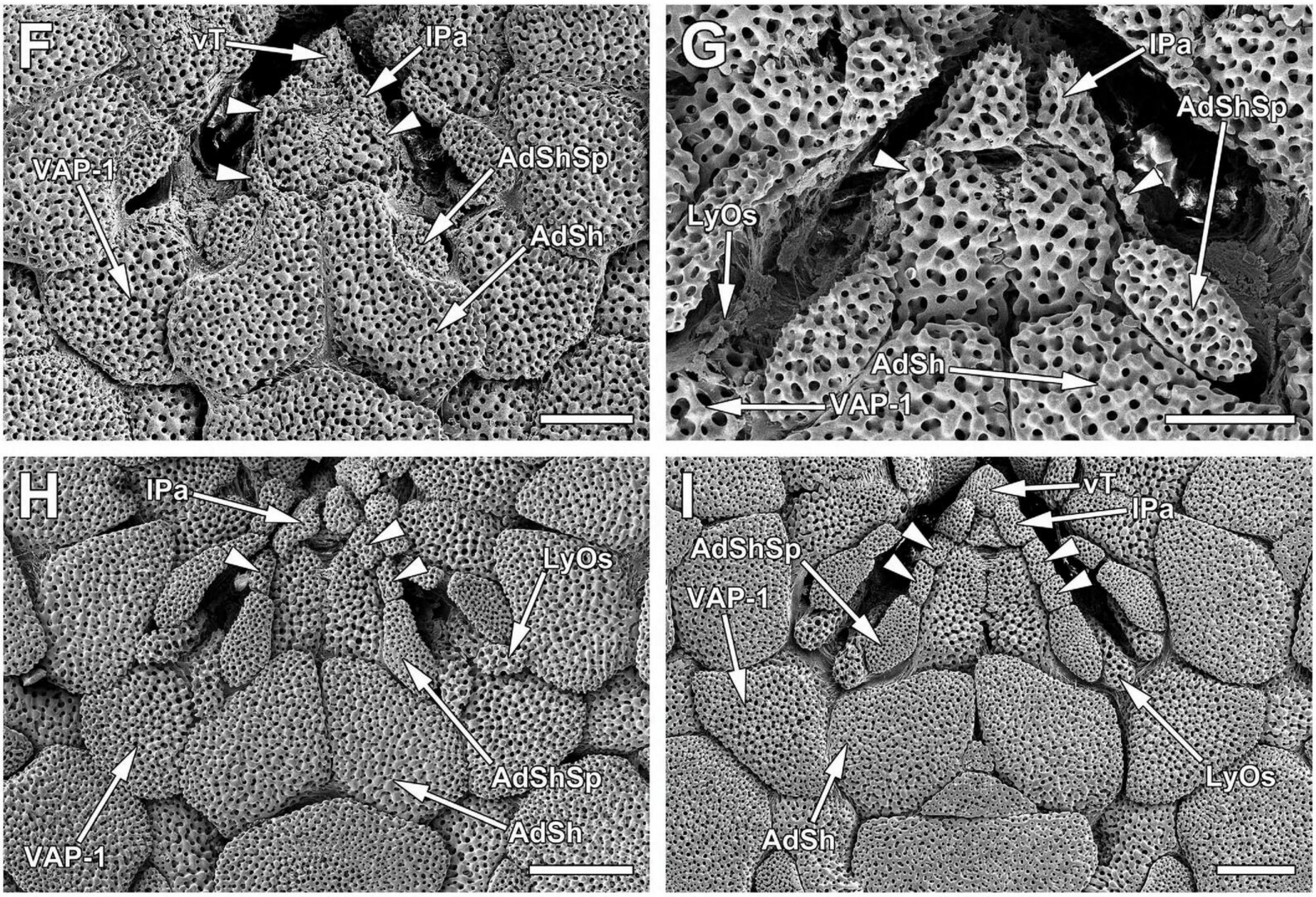

**Figure 21 cont.** *Sigsbeia conifera* Koehler, 1914. Skeletal ontogenesis. **F–I** ventral view of jaws of free-living individuals. **F,** 2.1-mm-dd juvenile; arrowheads mark several ossicles with indeterminate homologies, one abuts an IPa, another abuts an AdShSp, and the third is distal to an IPa; note that the numbers and sizes of these ossicles vary, even on one jaw. **G,** 2.3-mm-dd juvenile; arrowheads mark two ossicles with indeterminate homologies, one abuts an IPa, and another is between an IPa and an AdShSp; another minute, unmarked ossicle abuts an AdShSp on the left side of the jaw; note that a small ossicle that is presumed to be the rudiment of LyOs is within the OSl beside VAP-1. **H,** 3.5-mm-dd juvenile; arrowheads mark three ossicles with indeterminate homologies. **I,** 4.6-mm-dd adult; arrowheads mark ossicles with indeterminate homologies, which are symmetrically arranged in this individual; note the difference in stereom structure between the OPas *s.l.* and LyOss. F–I: SEM micrographs; LACM E.1986-95.1. Scale bars: F=150 µm; G=100 µm; H, I=250 µm.

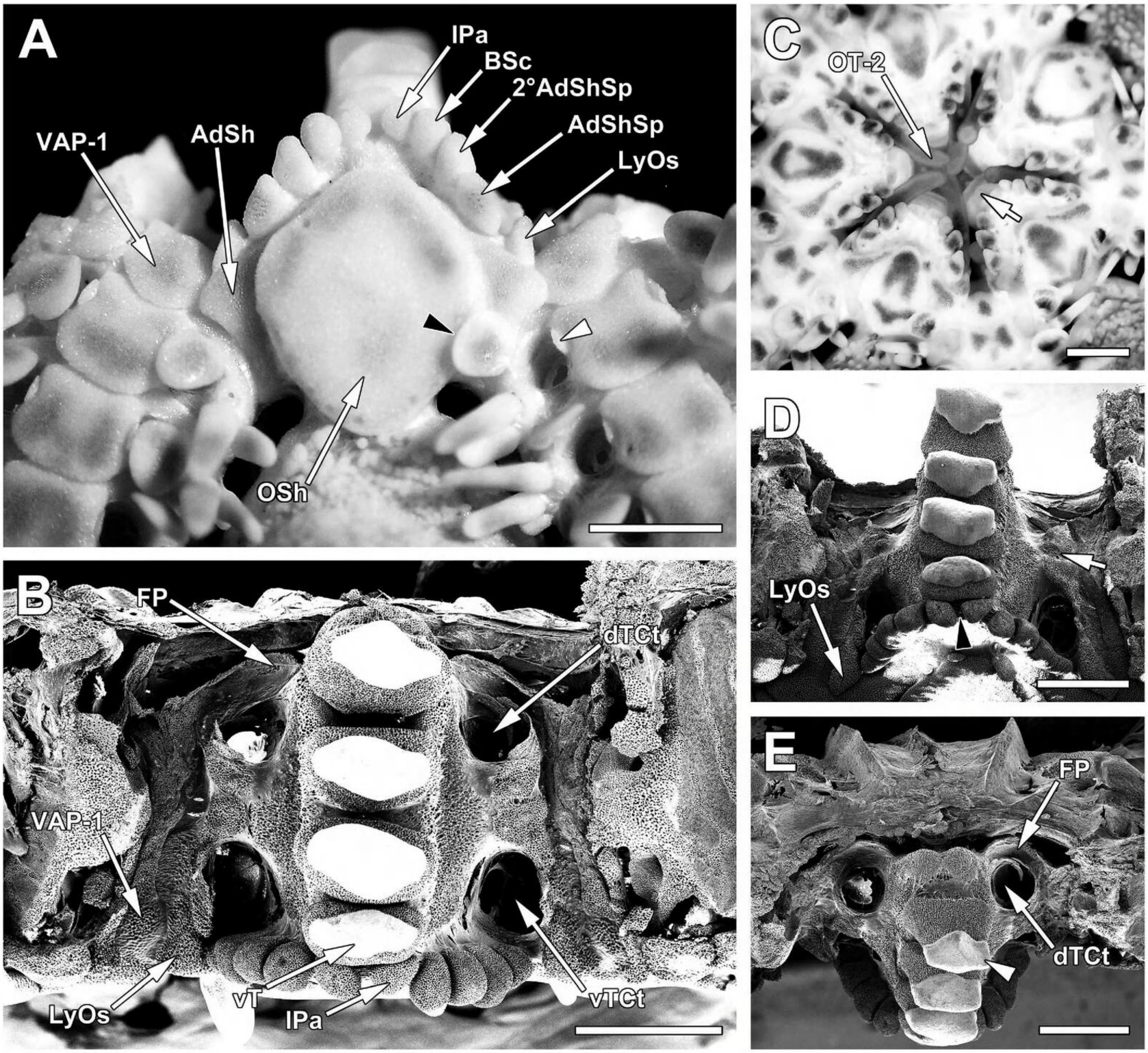

**Figure 22** *Ophionereis porrecta* Lyman, 1860. **A,** ventral view of jaw; black and white arrowheads mark TScs on a LAP-2 and VAP-2, respectively; note that VAP-1 lacks a corresponding TSc. **B,** proximal view of jaw. **C,** disk of living individual, ventral view; arrow indicates increasing length of ascending teeth within the buccal funnel. **D,** oblique proximal view of jaw; black arrowhead indicates attachment of IPas to the ventral edge of the DP. **E,** oblique dorsal view of jaw; arrowhead marks cap of imperforate stereom on the dorsalmost tooth. B, D–E: SEM micrographs; LACM E.2005-77.1; 12.7-mm-dd specimen; A: Stereomicroscope images of uncoated dissected jaw, 16.9-mm-dd specimen; C: Stereomicroscope image of living individual; 13.3-mm-dd specimen; Maliko Bay, Maui, Hawaii. Scale bars: A–-E=1.0 mm.

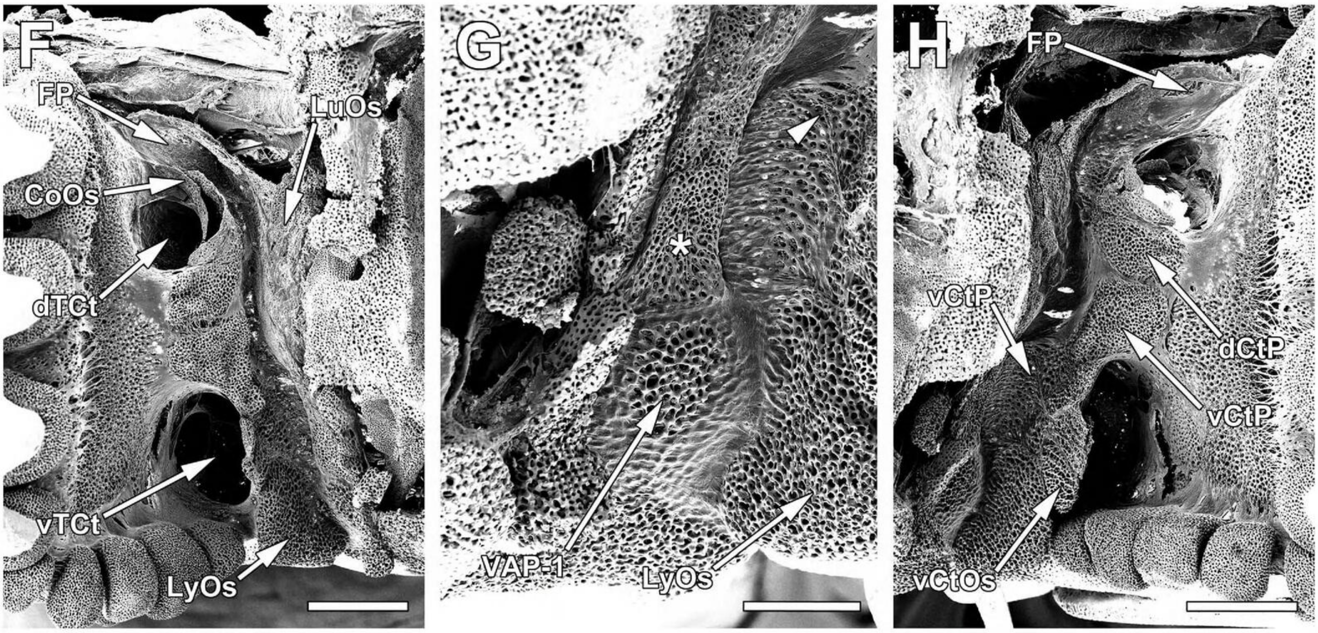

**Figure 22 cont.** *Ophionereis porrecta* Lyman, 1860. **F,** oblique proximal view of jaw, showing column of imbricate LuOss that form a chevron pattern in the PG and overlap the FPs. **G,** oblique view of ventral perradial armature; asterisk indicates large, campanulate LuOs overlapping the truncate VAP-1; white arrowhead marks a seam between the upper and lower vCtPs. **H,** oblique proximal view of jaw showing the twisted, bilobate upper vCtP and the elliptical, lower vCtP; note the panel of CtOss at the proximal edge of the vCtPs. F–H: SEM micrographs; LACM E.2005-77.1; 12.7 mm dd. Scale bars: F=0.5 mm; G=250 µm; H=0.5 mm.

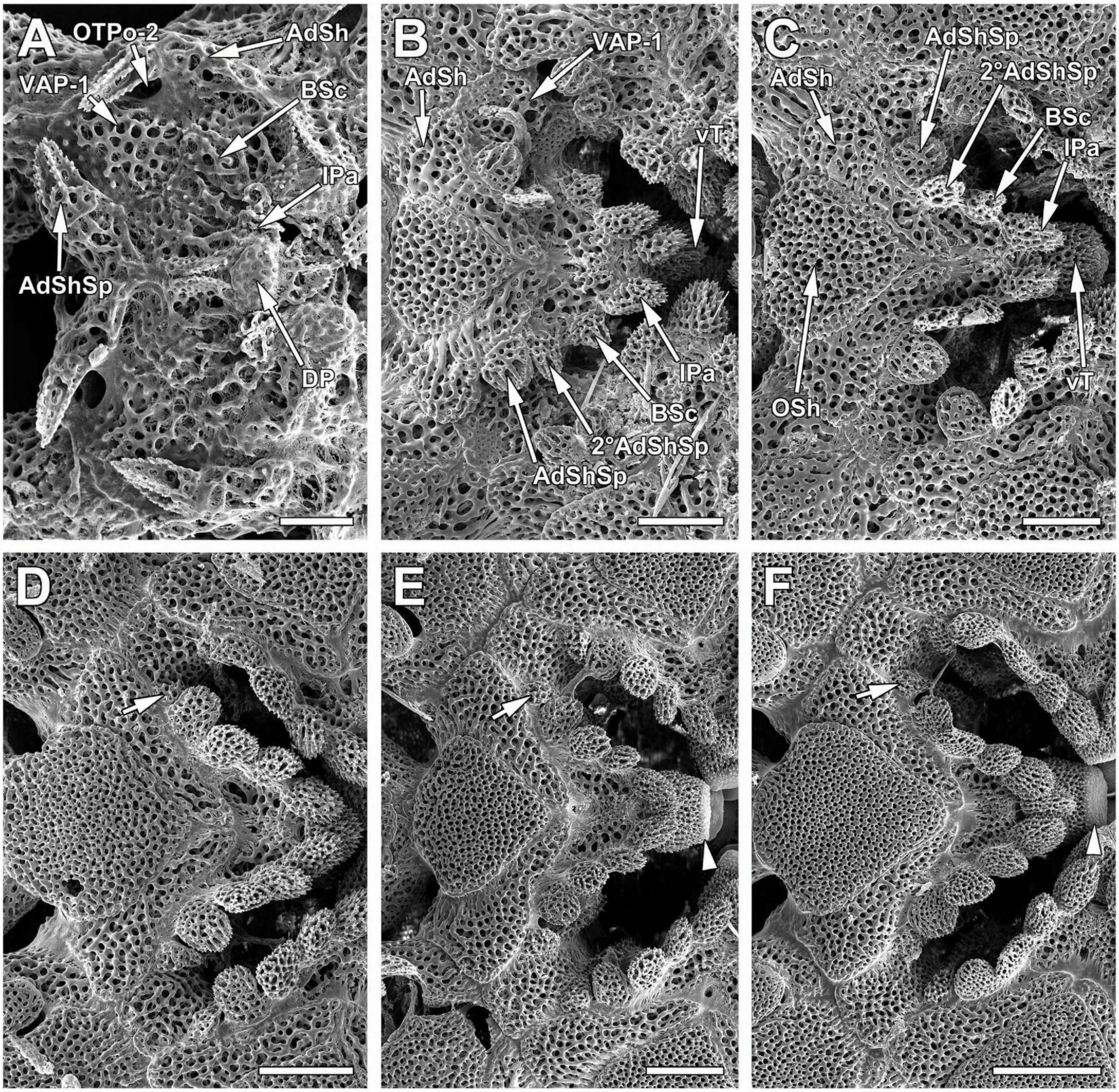

**Figure 23** *Ophionereis olivacea* H.L. Clark, 1901. Skeletal ontogenesis. Ventral view of the jaws of a brooded juvenile (**A**) and free-living juveniles (**B–F**). **A,** 0.4mm-dd juvenile. **B,** 1.1-mm-dd specimen. **C,** 1.5–mm-dd juvenile. **D,** 2.0–mm-dd juvenile; note that arrow marks rudiment of LyOs in this and the succeeding micrographs. **E,** 2.2-mm-dd juvenile; arrowhead indicates thin cap of imperforate stereom. **F,** 3.5-mm-dd juvenile; arrowhead indicates thick cap of imperforate stereom. A–F: SEM micrographs; LACM 89-329.7. Scale bars: A–C=100 µm; D, E=150 µm; F=250 µm.

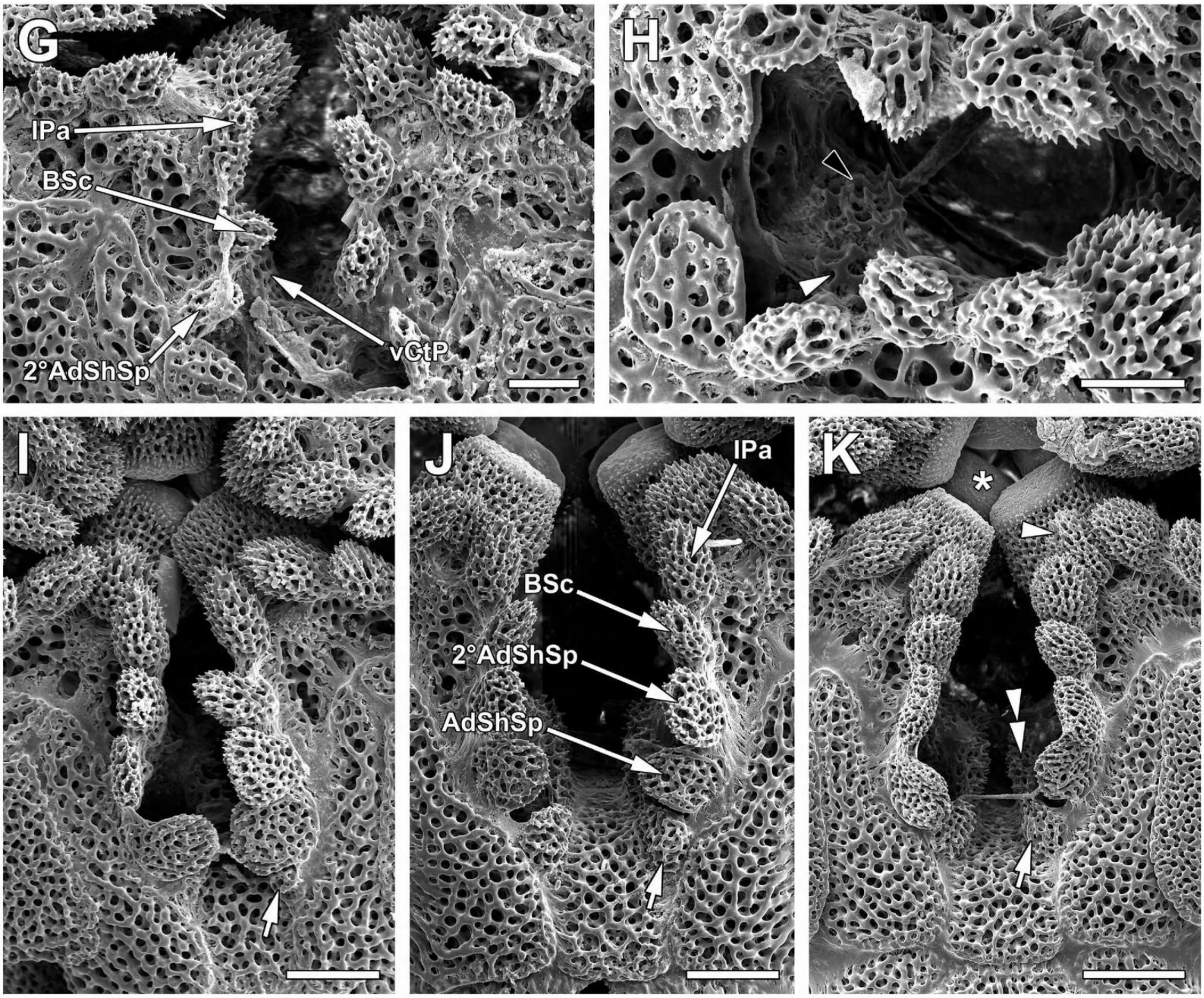

**Figure 23 cont.** *Ophionereis olivacea* H.L. Clark, 1901. Skeletal ontogenesis. Ventral view of jaws of free-living juveniles. **G,** 1.1-mm-dd juvenile; detail of OSl showing vCtP above VAP-1. **H,** 1.5-mm-dd juvenile; detail of OSl; black arrowhead marks vCtP; white arrowhead marks rudiment of LyOs between vCtP and VAP-1. **I,** 2.0–mm-dd juvenile; note that teeth intermesh. **J,** 2.2-mm-dd juvenile. **K,** 3.5-mm-dd juvenile; asterisk indicates thick cap of imperforate stereom on tooth; note that opposing teeth intermesh; arrowhead marks newly developing tooth above IPas; double arrowhead marks vCtP that is dorsal to LyOs. G–K: SEM micrographs; LACM 89-329.7. Scale bars: G, H=50 μm; I, J=100 μm; K=150 μm.

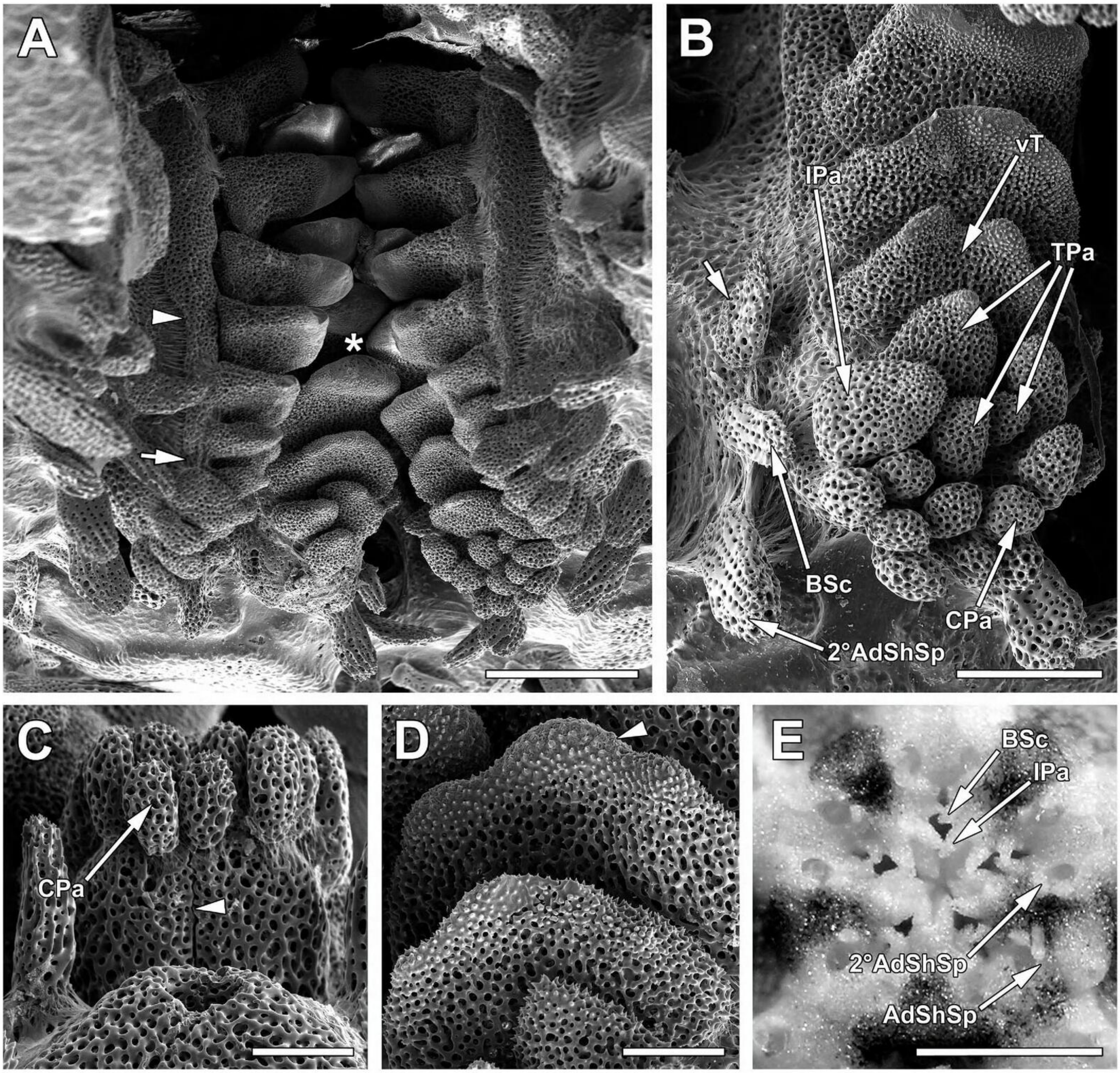

**Figure 24** *Ophiopsila riisei* Lütken, 1859 (**A–D**), and *Ophiopsila californica* A.H. Clark , 1921 (**E**). **A,** oblique view of buccal cavity showing four jaws; asterisk indicates intermeshed teeth closing the buccal funnel; arrowhead marks a seam between DP and OP; arrow indicates tapering ventral edge of DP; note that the IPa, which is below the arrow, articulates on the OP. **B,** detail of apex of jaw, proximal view; arrow marks spiniform ossicle that has an indeterminate homology, which articulates below the OPR. **C,** detail of apex of jaw, ventral view; arrowhead marks articulation between conjoined OPs; note that CPas are attached to OP. **D,** detail of teeth, oblique ventral view; arrow marks thin layer of imperforate stereom at edge of tooth. **E,** ventral view of disk of juvenile *O. californica*; note that VAP-1 inclines upward in the OSl, abutting the OPR. A–D: SEM micrographs of *O. riisei*; LACM E.2005-78.1; 7.3-mm-dd specimen. E: Stereomicroscope image of juvenile *O. californica*; LACM 96-42.1; 1.7-mm-dd specimen. Scale bars: A=0.5 mm; B=250 μm; C=150 μm; D=100 μm; E=1.0 mm.

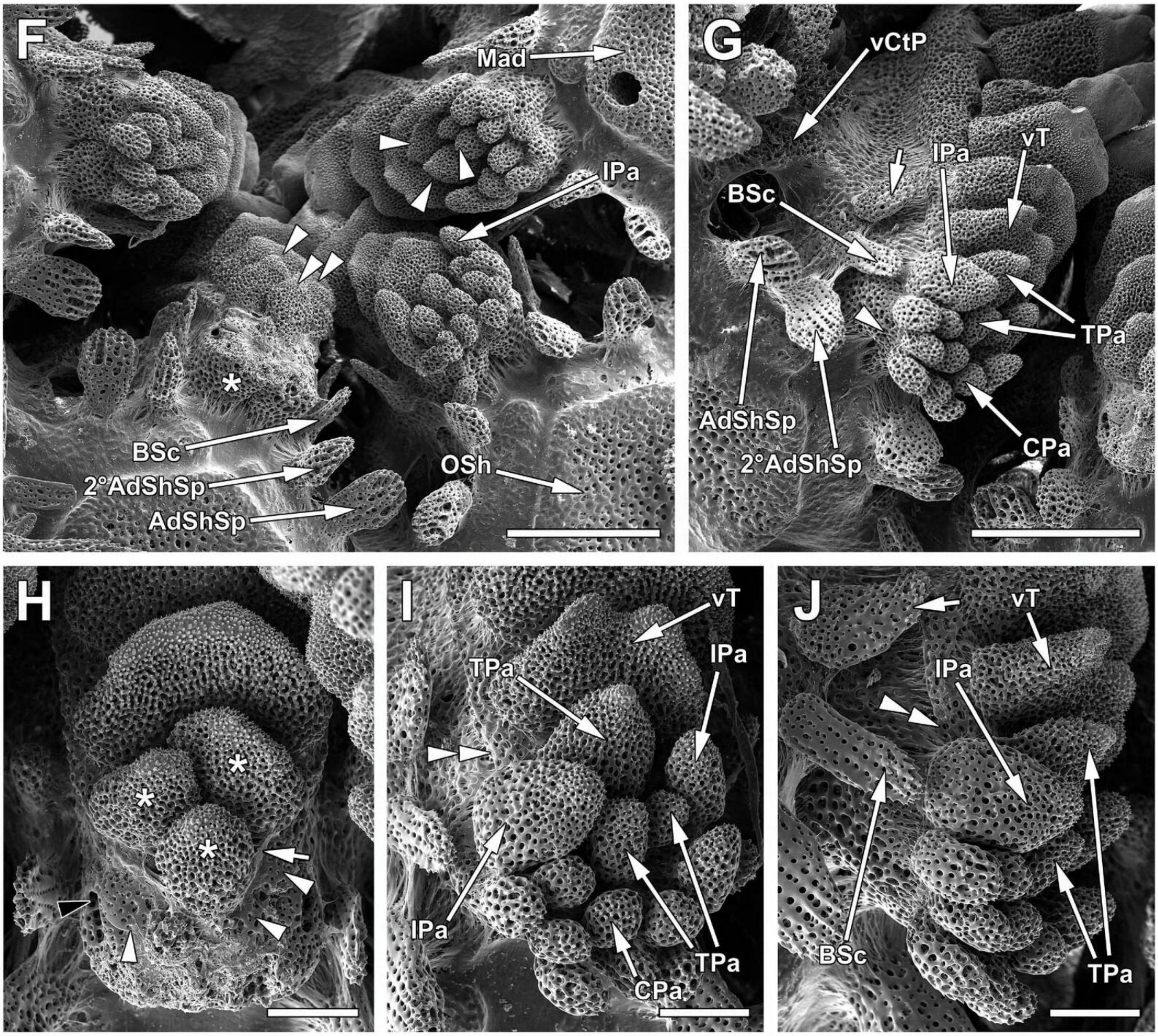

**Figure 24 cont.** *Ophiopsila riisei* Lütken, 1859. **F,** ventral view of four jaws; asterisk marks crest on apex of a jaw; note that the crest protrudes farther ventrally than the DP; arrowheads mark three TPas on each of two jaws. **G,** adradial view of jaw apex; arrowhead marks crest of jaw; arrow marks indeterminate spiniform ossicle above BSc. **H,** proximal view of jaw apex from which CPas were removed; note that TPas, indicated by asterisks, are borne on ventral edge of the DP; arrow indicates narrow extremity of DP; arrowheads mark sparsely perforate sterom on the crest of the oral plate on which CPas were borne; black arrowhead marks a fossa at the articulation site of the IPa. **I,** apex of jaw, proximal view; double arrowheads mark narrowing of DP and constriction of the OP beside the TPas. **J,** apex of jaw, adradial view; double arrowheads mark narrowing of DP and constriction of the OP beside the TPas; arrow marks spiniform ossicle with indeterminate homology. F–J: SEM micrographs of *O. riisei*; LACM E.2005-78.1; 7.3-mm-dd. Scale bars: F, G=0.5 mm; H–J=150 μm.

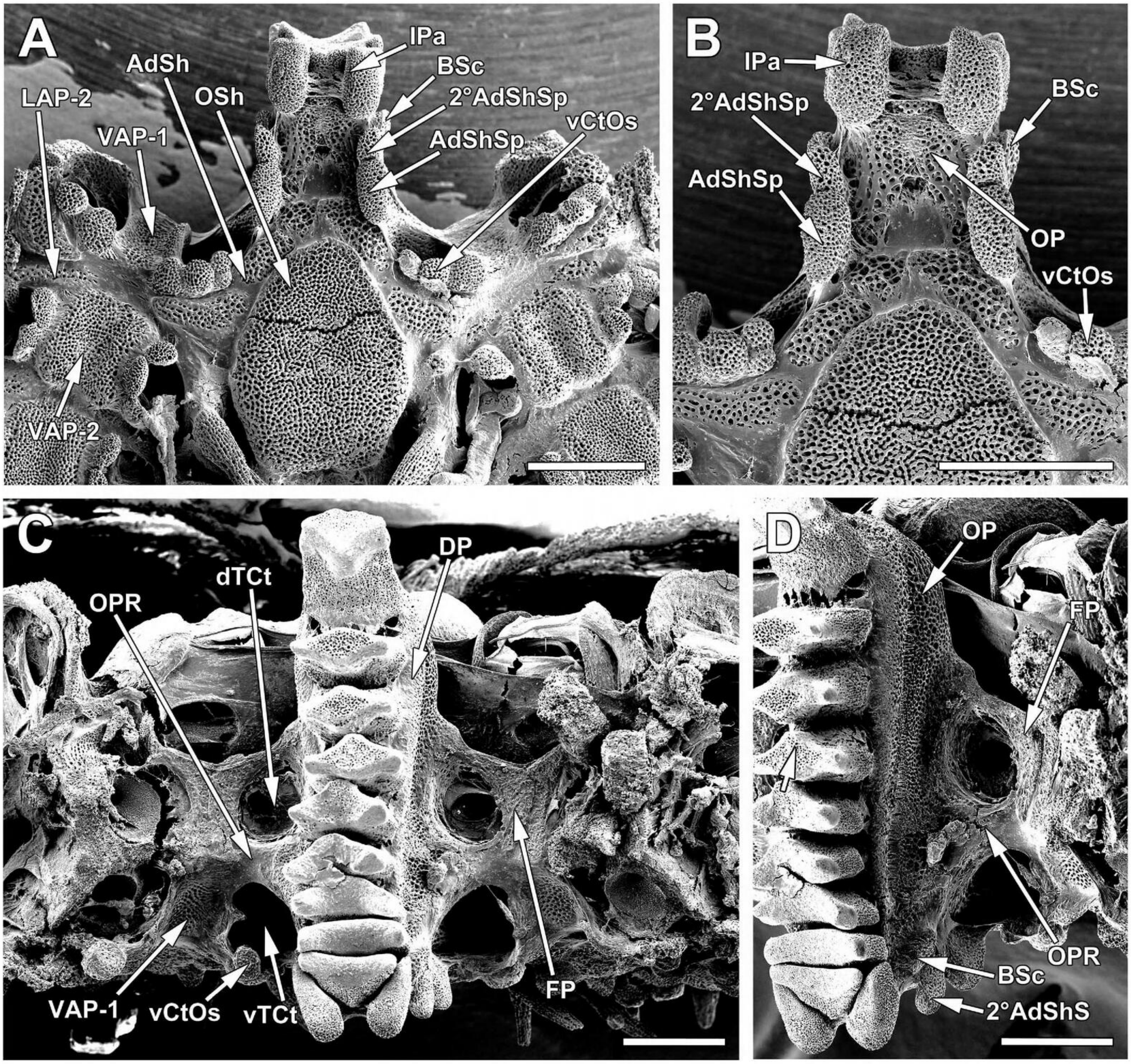

**Figure 25** *Amphioplus abditus* (Verrill, 1871). **A,** ventral view of jaw. **B,** apex of jaw; note that AdShSp and 2°AdShSp conform to one another in shape. **C,** proximal view of jaw; note that adjacent FPs overlap one another. **D,** adradial view of jaw; arrow indicates dorsally directed, medial cusp that is composed of discontinuous imperforate stereom. A–D: SEM micrographs; LACM E.1970-363.1; 10.1-mm-dd, 10.6-mm-dd specimens. Scale bars: A–D=0.5 mm.

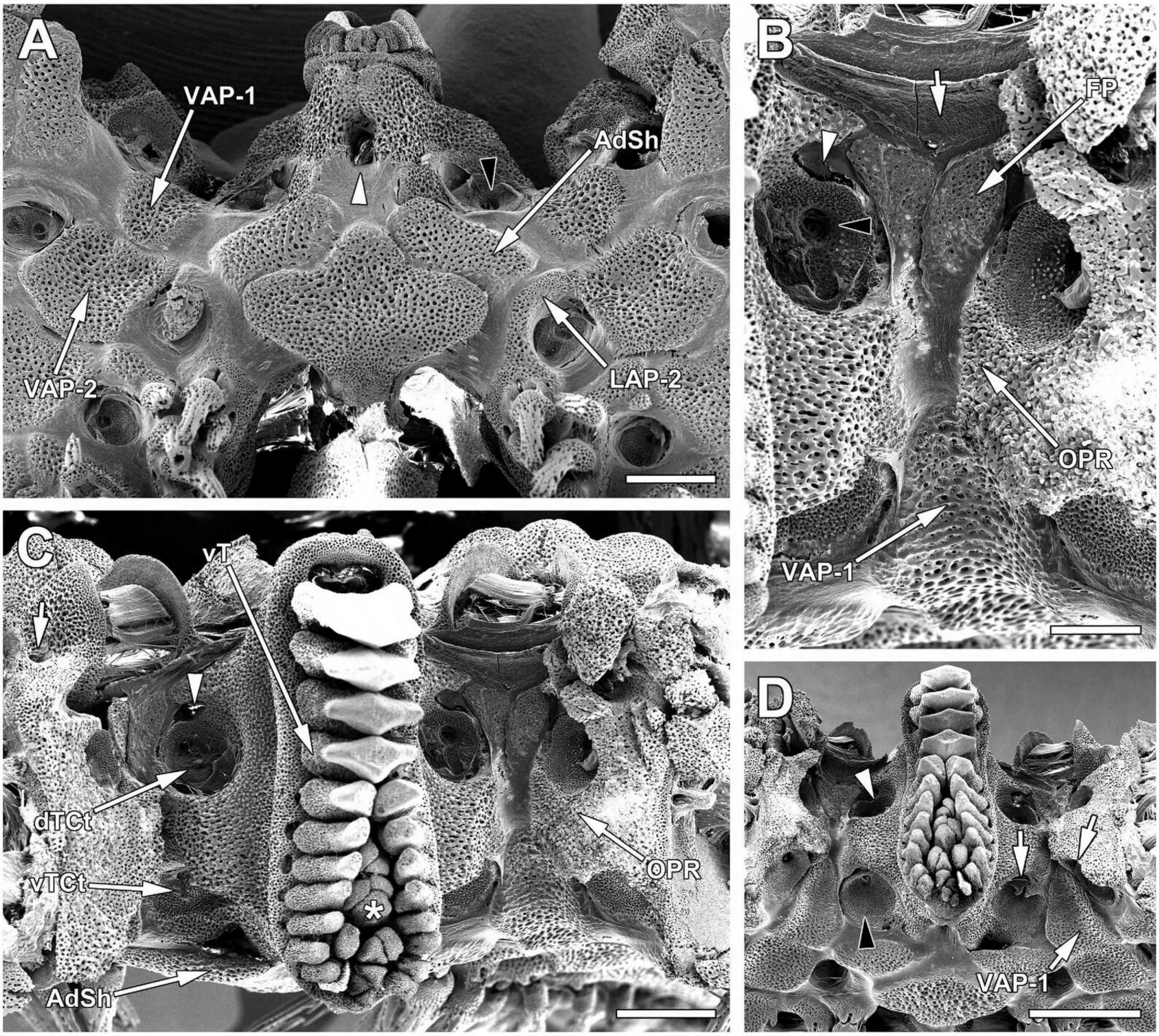

**Figure 26** *Ophiothrix spiculata* Le Conte, 1851. **A,** ventral view of jaw; white arrowhead indicates medial fossa between conjoined OPs; black arrowhead indicates tentacle basin of OT-2. **B,** detail of perradial region between adjacent jaws; white arrowhead marks a gap between the FP and OP, which may admit a branch of the circumoral nerve ring innervating OT-1; black arrowhead marks foramen of water canal in the tentacle basin of OT-1; arrow marks the circumoral esophageal ligament. **C,** proximal view of jaw; arrowhead marks presumptive neural gap; arrow indicates the solitary water ring foramen in an OP; asterisk indicates a medial column of abbreviated TPas flanked by columns of larger TPas; note the foramen of a large dental muscle behind the detached dorsalmost tooth. **D,** oblique proximal view of jaw; white arrowhead marks the presumptive neural gap in the dTCt; black arrowhead marks tentacle basin in the vTCt; arrows indicate presumptive neural channels that penetrate the OPs and terminate beside the tentacle basin of OT-2; nerve innervating OT-2 may occupy a groove on the adradial edge of the tentacle basin; note that VAP-1 bridges VAP-2 and the OPR, contacts the AdSh barely if at all, and is separated from LAP-2. A–D: SEM micrographs; LACM E.2004-1.2; 12.0-mm-dd specimen. Scale bars: A=0.5 mm; B=250 µm; C=0.5 mm; D=1.0 mm.

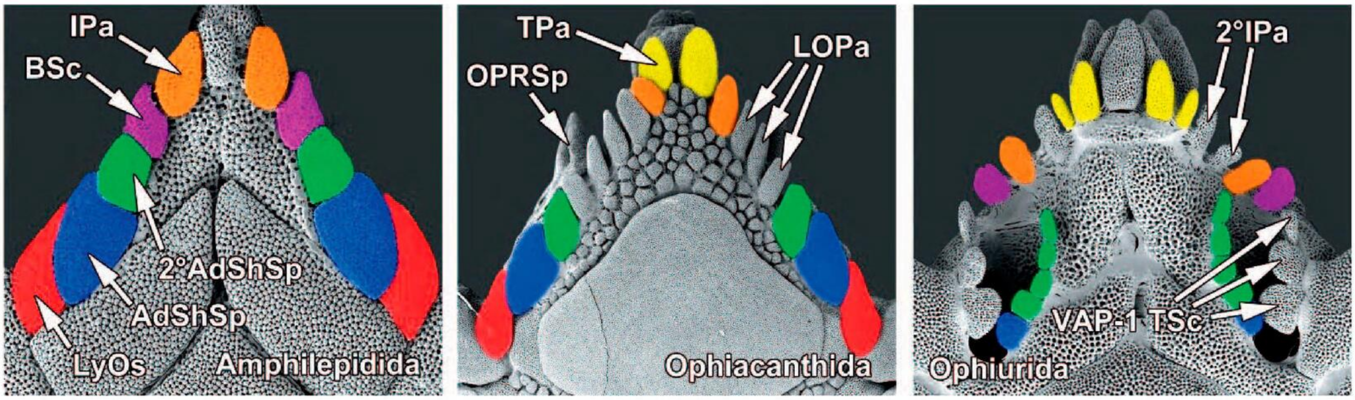

**Figure 27** Characteristic configurations of oral papillae (OPas *s.l.*) of three principal orders of Ophiuroidea: Amphilepidida (*Ophiolepis paucispina*), Ophiacanthida (*Ophioderma rubicunda*), and Ophiurida (*Ophiura sarsii*). Only the types of ossicles shared by two or more orders are color coded: IPa=orange, BSc=purple, 2°AdShSp=green, AdShSp=blue, LyOs=red. LOPas and OPRSps are limited to Ophiacanthida, and 2°IPas and VAP-1 TScs are limited to Ophiurida. The Ophiurida lack LyOss. Typically, species in a given order have a similar sequence of ossicles from proximal to distal on the jaw. However, the position of a particular type of OPa *s.l.* in a given species depends on the morphology of the ossicle on which it is borne and on the other types of OPas *s.l.* that are present.

**Table 1** Occurrence of OPas *s.l.*, PeSk ossicles, and buccal funnels among ophiuroid taxa. Presence (green) or absence (red) is indicated for each skeletal structure. Records are based on 17 exemplar species that were dissected in the present study, which represent 14 families. Information on an additional 19 families is based on a restricted number of species cited throughout the text. Ossicles were identified on the basis of their morphology and ontogenesis. Information on the occurrence of buccal funnels, TPas, and BScs in all 33 families is summarized in the three right-hand columns. Color code: green = structure present, red = structure lacking, orange = occurrence indeterminate/problematic, blue = presence/absence varies among confamilial species, white = information lacking. Names of exemplar species and other pertinent comments are footnoted below.

| Order and Family | Buccal funnel | Teeth | TPa | IPa | 2° IPa | BS | LOPa | AOPa | 2° AdShSp | AdShSp | LyOs | vCtP | vCtOs | vCoOs | VAP-1 TSc | OPRSp | dCtP | dCtOs | dCoOs | FP | LuOs | Buccal funnel | TPa | BSc |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AMPHILEPIDIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophiotrichidae [1] | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟩 | 🟥 |
| Ophiopholidae | | | | | | | | | | | | | | | | | | | | | | 🟩 | 🟩 | 🟥 |
| Ophiactidae | | | | | | | | | | | | | | | | | | | | | | 🟩 | 🟥 | 🟩 |
| Ophiothamnidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟥 | 🟩 |
| Amphiuridae [2] | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟧 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟩 |
| Amphilepididae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟥 | 🟩 |
| Ophiopsilidae | | | | | | | | | | | | | | | | | | | | | | 🟩 | 🟩 | 🟩 |
| Ophionereididae [3] | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟦 [18] | 🟥 | 🟩 |
| Amphilimnidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟥 | 🟩 |
| Hemieuryalidae [4] | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟧 | 🟥 | 🟥 | 🟧 | 🟩 | 🟩 | 🟧 | 🟧 | 🟥 | 🟥 | 🟥 | 🟧 | 🟧 | 🟥 | 🟩 | 🟩 | 🟦 [19] | 🟦 [20] | 🟦 [21] |
| Ophiolepididae [5] | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟦 [22] | 🟥 | 🟩 |
| OPHIOLEUCIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophioleucididae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| Ophiernidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| OPHIACANTHIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophiacanthidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟦 | 🟧 |
| Ophiacanthidae [6] | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | | | |
| Ophiacanthidae [7] | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟩 [23] | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | | | |
| Clarkcomidae | | | | | | | | | | | | | | | | | | | | | | 🟩 | 🟩 | |
| Ophiopteridae | | | | | | | | | | | | | | | | | | | | | | 🟩 | 🟩 | |
| Ophiotomidae | | | | | | | | | | | | | | | | | | | | | | 🟦 [24] | 🟩 | 🟥 |
| Ophiocamacidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| Ophiobyrsidae | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophiomyxidae [8] | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟦 [25] | 🟥 |
| Ophiopezidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| Ophiodermatidae [9] | 🟥 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 |
| Ophiocomidae [10] | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 |
| OPHIOSCOLECIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophioscolecidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | 🟥 |
| Ophiohelidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| OPHIURIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Ophiopyrgidae [11] | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 |
| Ophiopyrgidae [12] | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 |
| Ophiuridae [13] | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 |
| Ophiuridae [14] | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 |
| Astrophiuridae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | |
| Ophiomusaidae [15] | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟩 | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟩 | 🟩 | 🟥 | 🟥 | 🟩 | 🟩 |
| Ophiosphalmidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟩 | 🟩 |
| EURYALIDA | | | | | | | | | | | | | | | | | | | | | | | | |
| Gorgonocephalidae [16] | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟩 | 🟩 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 |
| Euryalidae | | | | | | | | | | | | | | | | | | | | | | 🟥 | 🟥 | |
| Asteronychidae [17] | 🟥 | 🟩 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟥 | 🟩 | 🟥 | 🟩 | 🟥 |

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[1] *Ophiothrix spiculata*; [2] *Amphioplus abditus*; [3] *Ophionereis porrecta*; [4] *Sigsbeia murrhina*; [5] *Ophiolepis impressa*; [6] *Ophiophthalmus normani*; [7] *Ophiacantha bidentata*; [8] *Ophiomyxa flaccida*; [9] *Ophioderma rubicunda*; [10] *Ophiocoma echinata*; [11] *Ophioplinthus gelida*; [12] *Stegophiura nodosa*; [13] *Ophiocten sericeum*; [14] *Ophiura sarsii*; [15] *Ophiomusa lymani*; [16] *Asteroporpa annulata*; [17] *Asteronyx longifissus*; [18] present in *Ophionereis* spp. but apparently lacking in *Ophiochiton ternispinus* Lyman, 1883 (Borges and Amaral, 2007:fig. 9); [19] present in *Ophioplocus januarii*, but occurrence is uncommon; [20] presence in *Ophiozonoida obscura*, which has a buccal funnel and IPas, is exceptional; [21] present in *Ophioplocus esmarki*, but appears to be lacking in *Sigsbeia conifera*; [22] presence in *Ophiozonella oedilepis* is exceptional; [23] occurrence is sporadic among individuals; [24] verified only in *Ophiocomina nigra*; [25] verified only in *Ophiarachna incrassata*.

**Table 2** Presence of tooth papillae (TPas) in orders and families of Ophiuroidea. An example of one species exhibiting TPas is listed for each family. Therefore, these records are not necessarily indicative of the presence of TPas among confamilial species.

| Order and Family | Species exhibiting tooth papilla | Catalog number/citation |
|---|---|---|
| OPHIURIDA | | |
| Ophiosphalmidae | *Ophiosphalma jolliense* (McClendon, 1909) | [LACM 41-205.2] |
| Ophiomusaidae | *Ophiomusa lymani* (Thomson, 1873) | [LACM E.1962-283.2] |
| Astrophiuridae | *Astrophiura wanikawa* Fujita and Hendler, 2001 | Fujita and Hendler, 2001:pl. 2, fig. B |
| Ophiuridae | *Ophiura sarsii* Lütken, 1855 | [LACM E.1949-308.10] |
| Ophiopyrgidae | *Stegophiura nodosa* (Lütken, 1855) | [LACM 1962-239.4] |
| OPHIOLEUCIDA | | |
| Ophiernidae | *Ophiernus adspersus* Lyman, 1883 | [LACM 78-226.1] |
| Ophioleucidae | *Ophioleuce seminudum* Koehler 1904 | [LACM E.1934-333.1] |
| OPHIOSCOLECIDA | | |
| Ophioscolecidae | *Ophioscolex glacialis* Müller and Troschel, 1842 | [LACM E.1928-4.1] |
| Ophiohelidae | *Ophiomyces multispinus* Ziesenhenne, 1940 | [LACM E.1938-73.1] |
| OPHIACANTHIDA | | |
| Ophiacanthidae | *Ophiolimna bairdi* (Lyman, 1883) | Martynov, 2010: fig. 13H, J |
| Clarkcomidae | *Clarkcoma canaliculata* (Lütken, 1869) | [LACM E.1972-450.1] |
| Ophiopteridae | *Ophiopteris papillosa* (Lyman, 1875) | [LACM E.1960-313.3] |
| Ophiotomidae | *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789) | [LACM E.887] |
| Ophiocamacidae | *Ophiocamax vitrea* Lyman, 1878b | Martynov and Litvinova, 2008: figs. 12D, 16D |
| Ophiobyrsidae | *Ophiosmilax mirabilis* Matsumoto, 1915 | Matsumoto, 1917:fig. 5b |
| Ophiomyxidae | *Ophiarachna incrassata* (Lamarck, 1816a) | [LACM 1939-293.1] |
| Ophiopezidae | *Ophiopeza spinosa* (Ljungman, 1867) | [LACM E.1958-250.1] |
| Ophiodermatidae | *Ophioderma rubicunda* Lütken, 1856 | [LACM 97-137.4] |
| Ophiocomidae | *Ophiocoma echinata* (Lamarck, 1816a) | [LACM E.1939-217.10] |
| AMPHILEPIDIDA | | |
| Hemieuryalidae | *Ophiozonoida obscura* Koehler, 1922a | [F146305] |
| Ophiopsilidae | *Ophiopsila californica* A.H. Clark, 1921 | [LACM E.1941-365.5] |
| Ophiopholidae | *Ophiopholis longispina* H.L. Clark, 1911 | [LACM E.964-297.1] |
| Ophiotrichidae | *Ophiothrix spiculata* Le Conte, 1851 | [LACM 1939-117.14] |

**Table 3** Records of the occurrence of buccal scales (BScs) among the orders and families of Ophiuroidea. Presence or absence of BScs was inferred from juvenile ophiuroids, on the basis of analyses of skeletal ontogenesis described herein and on an assessment of previous literature. Classification and designations of taxa *incertae sedis* are based on O'Hara et al., 2017:S7 and O'Hara et al., 2018. The presence of a BSc was deemed problematic or doubtful in the species that are in boldface.

| Order and Family | Buccal scale present | Buccal scale lacking | Literature citation |
|---|---|---|---|
| AMPHILEPIDIDA | | | |
| Ophiotrichidae | | *Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789) | Stöhr, 2005 |
| Ophiopholidae | | *Ophiopholis aculeata* (Linnaeus, 1867) | Sumida et al., 1998 |
| Ophiactidae | *Ophiactis resiliens* Lyman, 1879 | | Falkner and Byrne, 2006 |
| | *Ophiactis abyssicola* (M. Sars, 1861) | | Sumida et al., 1998 |
| | *Hemipholis cordifera* (Bosc, 1802) | | Turner and Miller, 1988 |
| Ophiothamnidae | *Histampica duplicata* (Lyman, 1875) | | Stöhr, 2005 |
| Amphilepididae | *Amphilepis ingolfiana* Mortensen, 1933a | | Sumida et al., 1998 |
| Amphilepidida *incertae sedis* | *Ophiopus arcticus* Ljungman, 1867 | | Stöhr, 2005 |
| Amphiuridae (*) | *Amphioplus abditus* (Verrill, 1871) | | Hendler, 1978 |
| | *Amphipholis squamata* (Delle Chiaje, 1828) | | Schultze, 1852; Ludwig, 1882 |
| | *Amphiura filiformis* (O.F. Müller, 1776) | | Hendler, 1988; Stöhr, 2005 |
| | *Amphiura constricta* Lyman, 1879 | | Falkner and Byrne, 2006 |
| | *Amphiura stimpsonii* Lütken, 1859 | | Hendler, 1988 |
| | *Ophiophragmus filograneus* (Lyman, 1875) | | Hendler, 1988 |
| | *Amphiura borealis* (G.O. Sars, 1871) | | Stöhr, 2005 |
| | *Amphiura chiajei* Forbes, 1843 | | Stöhr, 2005 |
| | *Amphiodia craterodmeta* H.L. Clark, 1911 | | Martynov et al., 2015 |
| | *Acrocnida brachiata (*Montagu, 1804) | | Webb and Tyler, 1985 |
| | *Acrocnida (=Amphiocnida)sp.* | | Mortensen, 1925b |
| | *Amphiura capensis* Ljungman, 1867 | | MacKinnon et al., 2017; (*) |
| Ophiopsilidae | *Ophiopsila riisei* Lütken, 1859 | | present study |
| Ophionereididae | *Ophionereis squamulosa* Koehler, 1914a | | Mortensen, 1921 |
| | *Ophionereis olivacea* H.L. Clark, 1900 | | present study |
| Amphilimnidae | ***Amphilimna olivacea* (Lyman, 1869)** | | present study |
| Hemieuryalidae | | ***Sigsbeia conifera* Koehler, 1914a** | present study |
| | *Ophioplocus esmarki* Lyman, 1874 | | Hendler, 2007 |
| Ophiolepididae | *Ophiozonella novaecaledoniae* Vadon, 1991 | | Vadon, 1990 |
| | *Ophiolepis paucispina* (Say, 1825) | | present study |
| OPHIACANTHIDA | | | |
| Ophiacanthidae | ***Ophiolimna bairdi* (Lyman, 1883)** | | Stöhr, 2005 |
| | | *Ophiacantha anomala* G.O. Sars, 1872 | Stöhr, 2005 |
| | | *Ophiomitrella clavigera* (Ljungman,1865) | Stöhr, 2005 |
| | | *Ophiacantha kokusai* Martynov et al., 2015 | Martynov et al., 2015 |
| | | *Ophiacantha rhachophora* H.L. Clark, 1911 | Martynov et al., 2015 |
| | | *Ophiacantha trachybactra* H.L. Clark, 1911 | Martynov et al., 2015 |
| | | *Ophiacantha abyssicola* Sars, 1872 | Sumida et al., 1998 |
| | | *Ophiacantha bidentata* (Bruzelius, 1805) | Sumida et al., 1998 |
| Ophiotomidae | | *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789) | Stöhr, 2005 |
| Ophiacanthida *incertae sedis* | ***Ophiolamina eprae* Stöhr and Segonzac, 2006** | | Stöhr and Segonzac, 2006 |
| Ophiomyxidae | | *Ophiomyxa flaccida* (Say, 1825) | present study |
| Ophiodermatide | | *Ophioderma wahlbergii* Müller and Troschel, 1842 | Landschoff and Griffiths, 2015 |
| | | *Ophioderma rubicunda* Lütken, 1856 | present study |
| Ophiocomidae | | *Ophiocoma wendtii* Müller and Troschel, 1842 | present study |
| Ophioscolecida | | | |
| Ophioscolecidae | | *Ophioscolex glacialis* Müller and Troschel, 1842 | Stöhr, 2005 |
| | | *Ophiolycus purpureus* (Düben & Koren, 1846) | Stöhr, 2005 |
| OPHIURIDA | | | |
| Ophiomusaidae | *Ophiomusium lymani* (Thomson, 1873) | | Hendler, 1998 |
| Ophiosphalmidae | *Ophiosphalma jolliense* McClendon, 1909 | | Hendler, 1998 |

**Table 3** Continued.

| Order and Family | Buccal scale present | Buccal scale lacking | Literature citation |
|---|---|---|---|
| Ophiuridae | *Ophiura albida* Forbes, 1839 | | Sumida et al., 1998; Stöhr, 2005 |
| | *Ophiura carnea* Lütken, 1858 | | Sumida et al., 1998 |
| | *Ophiura sarsii* Lütken, 1855 | | Sumida et al., 1998 |
| | *Ophiura ljungmani* (Lyman, 1878b) | | Sumida et al., 1998 |
| | *Ophiura ophiura* (Linnaeus, 1758) | | Stöhr, 2005 |
| | *Ophiura robusta* (Ayres, 1852) | | Stöhr, 2005 |
| | *Ophiura leptoctenia* H.L. Clark, 1911 | | Martynov et al., 2015 |
| | *Ophioctenella acies* Stöhr and Segonzac, 2005 | | Stöhr and Segonzac, 2005 |
| | *Ophiocten affinis* (Lütken, 1858) | | Sumida et al., 1998 |
| | *Ophiocten gracilis* (G.O. Sars, 1871) | | Sumida et al., 1998 |
| Ophiopyrigidae | *Amphiophiura sculpta* (Duncan, 1879) | | Murakami, 1941 |
| | *Ophiopleura borealis* Danielssen and Koren, 1877 | | Stöhr, 2005 |
| | *Ophioplinthus gelida* (Koehler, 1901) | | present study |
| | ***Spinophiura jolliveti* Stöhr and Segonzac, 2006** | | Stöhr and Segonzac, 2006 |
| EURYALIDA | | | |
| Asteronychidae | | *Asteronyx loveni* Müller and Troschel, 1842 | Stöhr, 2005 |
| Gorgonocephalidae | | *Gorgonocephalus arcticus* Leach, 1819 | present study |
| Ophiuroidea *incertae sedis* | Kirk's ophiuroid | | Fell, 1941 |

(*) Based on SEM micrographs, provided by Jannes Landschoff, a 0.68-mm-dd juvenile *Amphiura capensis* has an IPa, BSc, and AdShSp.

**Table 4** Occurrence of lateral oral papillae (LOPas) among Ophiocomidae, based on the species of *Breviturma* and *Ophiocoma* and on a limited sampling of *Ophiocomella*, *Ophiomastix*, and *Ophiarthrum* species. Species that are in boldface exhibit LOPas. Species-groups designations are *sensu* Devaney (1970).

| Genera, species-groups, and species | Catolog number/literature citation |
|---|---|
| *Breviturma* spp. | |
| ***Breviturma brevipes* Peters, 1851** | [LACM E.1947-54.1] |
| ***Breviturma doederleini* Loriol, 1899** | [LACM 1986-477.4] |
| ***Breviturma dentata* Müller and Troschel, 1842** | [LACM 1958-250.2] |
| ***Breviturma krohi* Stöhr et al. 2013** | Stöhr et al., 2013 |
| “Pica” species-group | |
| ***Ophiocoma pica* Müller and Troschel, 1842** | [LACM 1965-396.1] |
| ***Ophiocoma* longispina H.L. Clark, 1917** | Devaney, 1970:fig. 33 |
| *Ophiocoma pusilla* (Brock, 1888) | [LACM 1959-313.2] |
| “Scolopendrina” species-group | |
| *Ophiocoma aethiops* Lütken, 1859 | [LACM 1949-379.1] |
| *Ophiocoma anaglyptica* Ely, 1944 | [LACM 1986-482.2] |
| *Ophiocoma cynthiae* Benavides-Serrato and O’Hara, 2008 | [LACM 1958-286.1] |
| *Ophiocoma echinata* (Lamarck, 1816a) | [LACM E.1939-217.10] |
| *Ophiocoma endeani* (Endean, 1964) [=*Ophiocoma alternans*] | Endean, 1964:text-fig. 1; Rowe and Pawson 1977:349 |
| *Ophiocoma erinaceus* Müller and Troschel, 1842 | [LACM 1965-397.1] |
| *Ophiocoma macroplaca* (H.L. Clark, 1915a) | [LACM 1965-398.1] |
| *Ophiocoma occidentalis* H.L. Clark, 1938 | [LACM 1969-417.1] |
| *Ophiocoma schoenleini* Müller and Troschel, 1842 | [LACM 1947-57.2] |
| *Ophiocoma scolopendrina* Müller and Troschel, 1842 | [LACM 1998-128.1] |
| *Ophiocoma wendtii* Müller and Troschel, 1842 | [LACM E.1939-181.6] |
| “Pumila” species-group | |
| *Ophiocoma pumila* Lütken, 1856 | [LACM 55-109.2] |
| *Ophiocoma alexandri* Lyman, 1860 | [LACM 1936-14.3] |
| *Ophiocoma valenciae* Müller and Troschel, 1842 | H.L. Clark, 1915b:pl. 16, fig. 8 |
| Additional representative Ophiocomidae | |
| *Ophiocomella ophiactoides* H.L. Clark, 1901 | [LACM E.1939-210.10] |
| *Ophiocomella sexradia* (Duncan, 1887a) | [LACM 1924-6.1] |
| *Ophiomastix janualis* Lyman, 1871 | [LACM E.1948-98.1] |
| *Ophiomastix annulosa* (Lamarck, 1816a) | [LACM 89-424.1] |
| *Ophiomastix variabilis* Koehler, 1905 | [LACM 1986-482.3] |
| *Ophiomastix mixta* Lütken, 1869 | [LACM 67-292.1] |
| *Ophiomastix caryophyllata* Koehler, 1905 | [LACM 1998-129.2] |
| *Ophiarthrum elegans* Peters, 1851 | [LACM 1986-478.1] |

## NOTES ADDED IN PRESS

After this contribution was accepted for publication, I received a paper by Wilkie and Brogger (2018), which proposes that ophiuroids have two different types of jaws that are distinguished by a particular internal ossicle overlying the jaw. "Type A" jaws have an inclined peristomial plate, whereas the "type B" jaws have a horizontal peristomial plate. The authors suggest that each type of jaw has teeth, DPs, and OPs with a characteristic morphology. Remarkably, however, they did not recognize that species with 'type B' jaws possess the complex structure that was described herein as a "buccal funnel," and they did not perceive that a buccal funnel is lacking in species with "type A" jaws. They discern "type B" jaws in *Ophioplocus januarii*, a hemieuryalid, and in species of Ophiotrichidae, Ophiopholidae, Ophiactidae, Amphiuridae, and Ophiocomidae - the same taxa that, herein, were shown to have buccal funnels. Additionally, they infer that type B jaws of phylogenetically unrelated taxa of Amphilepidida and Ophiacanthida are homoplastic - the same conclusion drawn in the present study regarding the buccal funnels of these taxa. Nevertheless, the authors are unable to account for the convergent evolution of type B jaws, because they presume that there is no evidence that the function and morphology of ophiuroid jaws "are related to mastication or any other aspect of alimentation." Evidence for quite the opposite conclusion, which was marshaled in the present study, indicated that jaws function differently in macrophagous and microphagous ophiuroids, that buccal funnels, which repeatedly evolved in the guild of microphagous ophiuroids, are used to compact food, and that characteristic modifications of their teeth, DP, and OP are adaptive for processing particulate material.

The publication by Wilkie and Brogger brought to my attention a thesis by Berecoechea (2014), which contains SEM micrographs of the jaws of 12 species of ophiuroids that were not dissected in the present study. These figures depict morphological features that are not mentioned in the thesis but were described herein. They augment and corroborate my findings pertaining to skeletal ontogenesis and morphology of jaws, OPs, PPs, and the water vascular system of ophiuroids. A micrograph of a juvenile *Ophiomyxa vivipara* reinforces my results for *Ophiomyxa flaccida*, showing that the initial OPas s.l. are a tooth, IPa, LOPa, and AdShSp, and that a BSc is lacking. Figures of Ophiuridae, Ophiacanthidae, Ophiactidae, and Amphiuridae, support my contention that intermeshed teeth are a pervasive feature of ophiuroids. The micrographs indicate that there is a foramen in the ventral tentacle basin of *Ophiura* (*Ophioglypha*) *lymani* and *Ophiocten amitinum* Lyman, 1878, which corresponds to the putative neural foramen that I identified in congeneric species. The micrographs substantiate that ArtSs and fossae on the OPs are commonly associated with OPas *s.l.* Moreover, the occurrence of a fossa beside the ArtS on the OPa *s.l.* itself, shown in *Ophiacantha vivipara* Ljungman, 1871, and *Ophioplocus januarii*, complements my finding regarding *Ophiophthalmus normani*. Micrographs in the thesis show that dual water ring foramina occur in *Gorgonocephalus chilensis*, *O. amitinum*, and *Ophiochondrus stelliger* Lyman, 1879, confirming my discovery of this feature in other gorgonocephalids, ophiurids, and ophiacanthids. Similarly, an SEM micrograph in Wilkie and Brogger (2018) reveals that *Ophiacantha vivipara* has dual water ring foramina and FPs, which greatly resemble structures that were described in *Ophiacantha bidentata* in the present study.

Berecoechea, J.J. 2014. *Alimentación en Ophiuroidea (Echinodermata) de Argentina: estudios a partir del análisis de morfología y microestructura de mandíbulas y dientes. Tesis di Licenciatura.* Facultatd de Ciencias Exactas y Naturales, Universidad de Buenos Aires, vi + 66 pp.

Wilkie, I.C., and M.L. Brogger. 2018. The peristomial plates of ophiuroids (Echinodermata: Ophiuroidea) highlight an incongruence between morphology and proposed phylogenies. PLoS ONE 13(8):e0202046. doi:10.1371/journal.pone.0202046