

Ophiuroid Skeleton Ontogeny Reveals Homologies Among Skeletal Plates of Adults: A Study of *Amphiura filiformis*, *Amphiura stimpsonii* and *Ophiophragmus filograneus* (Echinodermata)

GORDON HENDLER

Natural History Museum, 900 Exposition Boulevard, Los Angeles, California 90007

Abstract. The characteristic oral papillae of the Family Amphiuridae are shown to have conservative patterns of ontogenesis, even among congeners with differing modes of reproduction such as *Amphiura stimpsonii*, a brooder, and *A. filiformis* which has free-living juveniles. Homologous oral papillae can be identified by tracing the distinctive ontogenetic transformations of individual skeletal elements. This method shows that the oral papillae of adults are not serially homologous, and that homologies cannot necessarily be inferred from the relative positions of papillae in any particular ontogenetic stage. For example, the most proximal oral papilla develops like a tooth on the dental plate and later moves to the proximal oral plate; a distal papilla grows as a spine on the adoral shield and moves to the distal oral plate. Based on the development of the oral papillae of *Amphiura*, *Amphiopus*, and *Ophiophragmus* species, it appears that post-larval ontogenesis of the amphiurids can be more reliable than larval morphology as an indicator of phylogenetic affinity. However, there are striking differences in postlarval skeletal ontogenesis among congeners, such as in formation of the adoral shield spines and primary plates of the disc, which may be related to modes of reproduction and postlarval biology. It can take over a year for adult oral armature to develop in free-living amphiurid juveniles, and the process occurs before hatching in brooded young. Specializations in the oral armature of postlarvae are probably critical to their survival.

Introduction

The relationship between ontogenetic patterns and phylogenetic history has been a matter of debate for two

centuries (Mayr, 1982). Putative cases of “recapitulation” (*sensu* Alberch *et al.*, 1979) attributed to shared pathways of development are at variance with instances where ontogenesis departs from an explicit recapitulation of ancestral characters (Alberch, 1985). These contradictory observations are “matters of current discussion” (Mayr, 1982: 476).

The larval development of echinoderms provides numerous examples of departures from recapitulation (see Fell, 1948; Strathmann, 1974) such as through “ceno-genesis” (*sensu* Gould, 1977)—the introduction of adaptations that are expressed only during early developmental stages. Yet, systematists continue to use ontogenetic patterns as indicators of systematic relationships in extant and fossil echinoderms (for example, see McNamara, 1986).

The larvae and embryos of closely related ophiuroids can be strikingly different; some inconsistencies between larval morphologies and adult classification are thought to result from adaptations to the larval (or embryonic) environment (Fell, 1948, 1967). Therefore, one might ask whether the ontogenetic features of postlarvae can be more reliable indicators of systematic relationships than the features of larvae. To answer that question, I compared growth series of congeners with dissimilar modes of reproduction: *Amphiura filiformis* (O. F. Müller, 1776) with pelagic ophiopluteus larvae and *A. stimpsonii* Lütken, 1859, with brooded embryos (early developmental stages described in Mortensen, 1920, 1921). Can comparisons of growth series also be used to distinguish homologous structures in closely related taxa by tracing their postlarval ontogenesis? To answer that question the ontogenesis of the oral papillae in representatives of the four major groups (*sensu* Clark, 1970) of Amphiuridae

Table I

The sequence of development of oral papillae in ophiuroid species representative of major groups of Amphiuroidae

	Stage 1					Stage 2					Stage 3					Stage 5					Stage 6					Stage 9				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
<i>A. stimpsonii</i>	+					+	+				+	+				+	+				+	+				+	+			
<i>A. filiformis</i>	+					+	+				+	+				+	+				+	+				+	+			+
<i>O. filigraneus</i>	+					+	+				+	+				+	o				+	o	+	+		+	o	+	+	
<i>O. scabriuscula</i>	+					+	+				+	+				+	o				+	o	+	+		+	o	+	+	
<i>A. squamata</i>	+					+	+				+	+				+	o				+	o	+	+		+	o	+	+	
<i>A. abditus</i>	+					+	+				+	+				+	+				+	+	+	+		+	+	+	+	
<i>A. macilentus</i>	+					+	+				+	+				+	+				+	+	+	+		+	+	+	+	

Amphiura-group: *Amphiura stimpsonii*, *A. filiformis* *Amphiodia*-group: *Ophiophragmus filigraneus*, *Ophiocnida scabriuscula*; *Amphipholis*-group: *Amphipholis squamata*; *Amphioplus*-group: *Amphioplus abditus*, *A. macilentus*. Ontogenetic stages are identical to stages in Table I. Oral papillae are listed in their order of attachment from the tip to the base of the jaw: A, infradental papillae; B, buccal scales; C, oral plate papillae; D, adoral shield spines; E, accessory papillae. Oral papillae present are denoted "+"; resorbed oral papillae denoted "o."

are analyzed. The oral papillae are small ossicles (squamous, papilliform, or spiniform) attached to the edges of the plates around the ophiuroid mouth, and they are the most critical characters employed in the taxonomy of the Amphiuroidae (Clark, 1970). The species compared are *Amphiura stimpsonii* and *A. filiformis* [*Amphiura*-group], *Ophiophragmus filigraneus* Lyman, 1875 and *Ophiocnida scabriuscula* (Lütken, 1859) [*Amphiodia*-group], *Amphipholis squamata* (Delle Chiaje, 1828) [*Amphipholis*-group], and *Amphioplus abditus* Verrill, 1871 and *Amphioplus macilentus* Verrill, 1882 [*Amphioplus*-group] (Hendler, 1978; this report). I also assess the value of homologous oral papillae as ophiuroid systematic characters.

Further, one might ask whether differences in morphology between homologous structures are related to their function in various ontogenetic stages. Therefore, the adaptational significance of oral papillae are considered and the reliability of juvenile morphology as an indicator of developmental mode and substrate specificity are evaluated thus augmenting reports by Turner (1974), Hendler (1975), and Muus (1981). Information on the taxonomic features, functional morphology, and natural history of ophiuroid juvenile stages critical to an understanding of development and evolution can also be directly applicable to studies of ophiuroid reproductive biology, distributions, and population dynamics (Gage and Tyler, 1982; Hendler and Littman, 1986).

Materials and Methods

The 13 individuals of *Amphiura filiformis* examined using scanning electron microscopy (SEM) were collected from the Oresund, Denmark (Muus, 1981). Adult and free-living juvenile *A. stimpsonii* were collected from the Belize Barrier Reef (Hendler and Littman, 1986), and over 40 SEM preparations were made of embryos

dissected from the bursae of brooding females. The eight juvenile specimens of *Ophiophragmus filigraneus* from Tampa Bay, Florida, examined using SEM were originally collected and studied by Turner (1974). Adult *O. filigraneus* were collected by the author from the Indian River, off Fort Pierce, Florida. The restricted numbers of specimens examined preclude a precise delimitation of the range of body size at each developmental stage. This does not affect the validity of the sequences of stages that are reported, but it confounds comparisons between the developmental stage and body size or age of different species.

SEM samples of *O. filigraneus* were air-dried alcohol preserved specimens that were mounted on stubs using Bakelite glue and sputter coated with carbon and gold-palladium. Since the edges of many skeletal plates were obscured by integument in these preparations, soft tissue was removed from specimens of *Amphiura filiformis* and *A. stimpsonii* using a plasma-asher ("Plasmod" with pyrex chamber, March Instruments, Concord, California). Air-dried ophiuroids, held in glass containers, were ashed for 1-3.5 h before mounting them on SEM stubs. They were removed from the asher periodically to insure that the treatment did not detach skeletal elements.

Terminology and abbreviations

Two to five oral papillae are attached to each edge of an amphiuroid jaw. Proceeding proximally from the tip of the jaw each oral papilla is specified by a different name as follows: infradental papilla, buccal scale, oral plate papilla, adoral shield spine, and accessory papilla. Terminology used is based on accepted names of structures in adult ophiuroids (Hendler, 1978). However "buccal scale" is used rather than "oral tentacle scale" (*sensu* Clark, 1970) for reasons previously explained (Hendler, 1978). "Oral plate papilla," used here, replaces

Table II

The body sizes of *Amphiuridae* at different ontogenetic stages

Stage	<i>Amphiura stimpsonii</i>		<i>Amphiura filiformis</i>		<i>Ophiophragmus filigraneus</i>		<i>Amphioplus abditus</i>		Ontogenetic transformation
	AS	dd	AS	dd	AS	dd	AS	dd	
1	t	0.4	?	#	?	#	55 h	larva	B appears.
2	t	0.4	t	0.3	1	0.5	t	0.3	D appears.
3	7	0.5	9	0.7	14	1.4	5	0.7	A appears.
4	7	0.5	25	0.8	14	1.4	9	0.9	D points proximally.
5	*****		*****		55	2.4	*****		B resorbed.
6	*****		*****		55	2.4	17	1.1	C appears.
7	19	1.2	25	0.8	55	2.4	17	1.1	D migrates to distal oral plate.
8	19	1.2	?	3.2	55	2.4	21	1.3	Positive allometric growth of oral plate, adoral shield, oral shield; movement of ventral arm plate.
9	*****		*****		?	?	>30	1.6	E appears.

Symbols: AS, number of arm segments; dd, disk diameter in mm; t, terminal arm plate; ?, data not available; *****, specified ontogenetic transformation omitted in the species; A, infradental papillae; B, buccal scales; C, oral plate papillae; D, adoral shield spines; E, accessory papillae; #, smallest specimens examined are Stage 2 with B- and D-papillae.

the potentially misleading designation "third oral papilla" (Hendler, 1978). The size of ophiuroids is expressed as the diameter of the disk ("dd") and the number of arm segments ("AS"). Arm segment number is counted from the first arm segment under the disk to the distalmost segment of the arm, excluding the terminal plate at the arm tip. In this report dd is the primary indicator of body size. Although the number of AS varies among individuals of any dd, only the maximum number of AS are presented for any given dd.

Results

Special features of each species are discussed below, and the major ontogenetic changes of the oral skeleton of *Amphiura stimpsonii*, *A. filiformis*, and *Ophiophragmus filigraneus* are illustrated in Figures 2–4 and summarized in Table I. The size (dd and AS) of different developmental stages of the three species, and of *Amphioplus abditus*, are compared in Table II.

Amphiura stimpsonii Lütken

In the youngest individual examined the rudimentary skeletal elements form a fragile crust near the surface of the large yolk mass (Fig. 1A). During development, the disk diameter and number of arm segments increase and the yolk mass is overgrown and hidden by the disk. The largest brooded embryos found were 0.7 mm dd with 10 AS. Young may be released at a smaller size (some free-living juveniles are only 0.6 mm dd with 8 AS) but most

small, free-living juveniles were 0.8 mm dd with 10 AS. The largest adult specimen examined with SEM (4.04 mm dd) had arms broken at 63 segments beyond the disk.

The earliest stage examined was 0.42 mm dd, with arms composed of only a terminal plate (Figs. 1A, 2A; Tables I, II). The oral frame consists of adoral shields, and of paired jaw plates that bear a dental plate and tooth. The rudiments of two oral papillae, the buccal scale and adoral shield spine, are inconspicuous; the adoral shield spine was found in only one of three specimens at this stage. A buccal scale is present in all specimens, and presumably develops before the adoral shield spine (Tables I, II).

The final oral papilla to develop is the infradental. A rudiment of the infradental papilla occurred at the tip of the jaw in a specimen 0.46 mm dd with 7 AS. Initially, the infradental papilla lies in an indentation on the dental plate, not on the jaw plate itself (Fig. 2B). The dental and oral plates are relatively larger than in the previous stage; they have grown ventral to the lowest tooth (out of the plane of Fig. 2C). At this stage and in newly hatched specimens approximately 0.7 to 0.9 mm dd with at least 10 AS, allometric growth transforms the oral frame. As a result of the enlargement of the oral shield and growth and divergence of the adoral shields, the adoral shield spine moves to a more proximal, adradial position on the adoral shield and it projects over the pore of the second buccal papilla rather than over the periphery of the disk (compare the orientation of the adoral shield spine [d] in Figs. 1A, 2A, C).

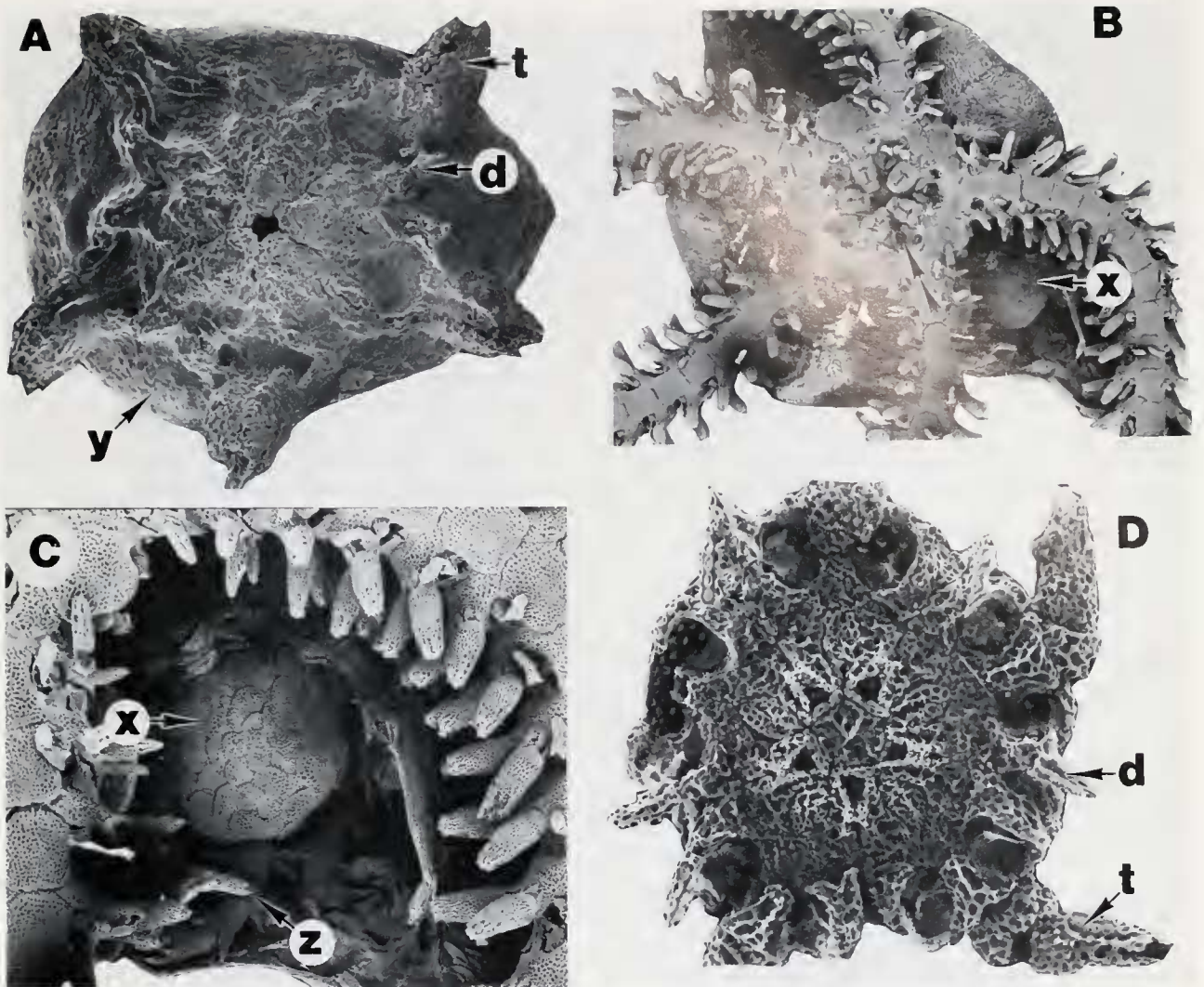


Figure 1. (A) *Amphiura stimpsonii*: early (Stage 2) unshatched embryo 0.42 mm dd showing large yolk mass and protruding terminal arm plate and small adoral shield spine. Specimen not plasma-ashed to remove integument. (B, C) *Amphiura stimpsonii*: ventral interradial body wall removed to show advanced brooded embryo in the bursa. Note gaps between jaws of adult (double arrowhead in B) and lack of primary rosette on disk of embryos (in C). (D) *Amphiura filiformis*: newly settled (Stage 2) juvenile 0.33 mm dd, with relatively large adoral shield spine. Plasma-ashed specimen. Abbreviations: d, adoral shield spine; t, terminal arm plate; x, disk of embryo; y, yolk mass; z, arm of embryo.

In a specimen 1.2 mm dd with 19 AS (Fig. 2D) the adoral shield spine moves from the adoral shield to the “distal oral plate” (*sensu* Hendler, 1978) that is, distal to a suture line (visible in Fig. 2C) that bisects the jaw. This remarkable transition is a consequence of marked allometric growth of the oral and adoral shields in specimens 0.86 to 3.76 mm dd (and probably of the oral plate muscle-attachment surfaces as shown for *Amphioplus abditus* in Hendler, 1978: Fig. 6). Due to differential growth rates of these jaw elements, the first ventral arm plates move from a superficial to an internal position on the disk, and the proximal end of the plate sinks into the oral gap (not shown in Fig. 2, but see Hendler, 1978: Fig. 5).

As ontogenesis proceeds, the adoral shield spines show negative allometric growth. The infradental papillae change from a spinelike to a blocklike shape, and move from the dental plate to the tips of the oral plates by the time individuals reach 1.2 mm dd with 19 AS (Fig. 2D). In early stages the oral slits are tightly sealed by the series of teeth and oral papillae (infradental papillae and operculiform buccal scales) that are attached to the ventral edge of the jaw. As *Amphiura* grows, the surface of the jaw bulges ventrally, leaving the buccal scale attached deep within the oral slit. By the time the individual is 2.2 mm dd with 37 AS, enlargement of the proximal end of the scale transforms the buccal scale to a spine-shaped

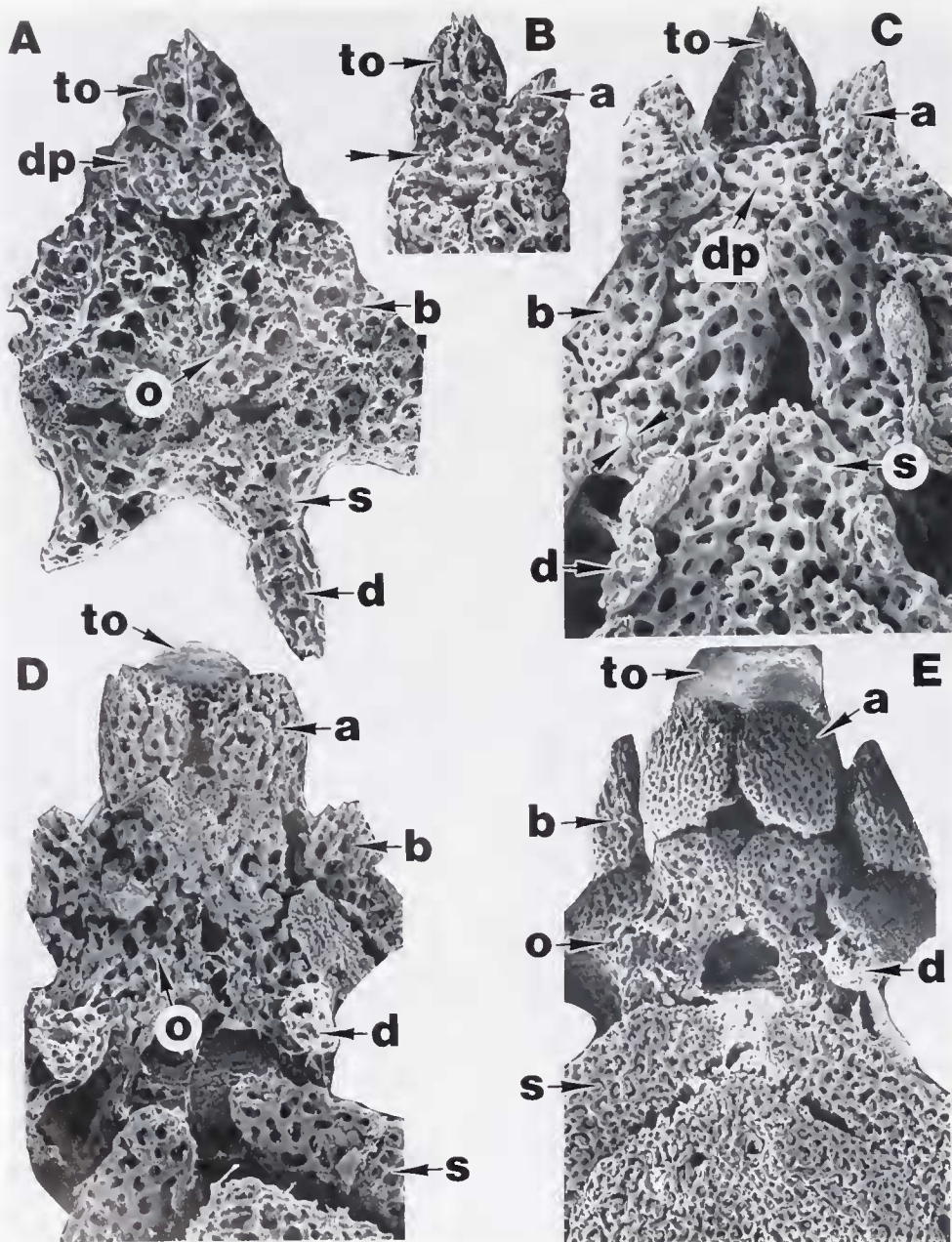


Figure 2. *Amphiura stimpsonii*: growth stages of jaw and oral papillae. Stages numbered according to Table 1. (A) Stage 2 (brooded); 0.51 mm dd, 4 AS. (B) Stage 4 (brooded); 0.9 mm dd, 10 AS; detail of jaw apex, double arrowhead indicates indentation on dental plate at attachment site for (missing) infradental papilla. (C) Stage 4 (free-living); 0.8 mm dd, 10 AS; opposing arrowheads indicate suture between proximal and distal oral plates of the jaw (*sensu* Hendler, 1978). (D) Stages 7-8; 1.2 mm dd, 19 AS; opposing arrowheads indicate suture between proximal and distal oral plates of the jaw (*sensu* Hendler, 1978). (E) Adult; 3.76 mm dd. Abbreviations: a, infradental papilla; b, buccal scale; d, adoral shield spine; dp, dental plate; o, oral plate; s, adoral shield; to, tooth.

oral papilla. In the adult (Fig. 2E), a gap separates the buccal scale from the first ventral arm plate and the oral region (initially sealed by the contiguous oral papillae) is incised by five large oral slits (Fig. 1B).

Throughout development the dorsal surface of the disk has an irregular arrangement of small scales (Fig.

1C). However, a distinct rosette with a central and five radial primary plates that is characteristic of many ophiuroids was never seen in *A. stimpsonii*. Five pairs of radial shields were found in a specimen 1.20 mm dd with 19 AS (also in a specimen with 15 AS, dd not measured). In individuals about 1.18 mm dd with 20 AS, the dorsal

scales near the edge of the disk are markedly smaller than scales near the center, an indication that new scales originate at the periphery.

Amphiura filiformis (O. F. Müller)

The smallest juvenile, 0.30 mm dd, has arms with only a terminal plate; its oral frame resembles that of *Amphiura stimpsonii* of similar size. It already has two oral papillae, the buccal scales and adoral shield spines, that project beyond the periphery of the disc (Figs. 1D, 3A). The adoral shield spines are relatively larger than those in *A. stimpsonii* (Figs. 2A, 3A).

A. filiformis may have more arm segments than *A. stimpsonii* of approximately the same dd (Tables I, II). Oral skeleton ontogenesis progresses through the same sequence of stages as in *A. stimpsonii*. The infradental papillae, the third oral papillae to develop, form on the edge of the dental plate, become block-shaped, and eventually attach to the tip of the oral plate. The adoral shield spine migrates from the distal to the proximal end of the adoral shield, and then to the oral plate, growing to a relatively larger size than in *A. stimpsonii*. As *A. filiformis* grows, the enlargement of the jaws leaves the buccal scale attached deep in the oral slit. The buccal scale develops a sharp process at the proximal end, but the distal end (in contrast with the scale in *A. stimpsonii*) remains in contact with the first ventral arm plate. *Amphiura filiformis* develops a distal oral papilla ("accessory papilla" *sensu* Hendler, 1978) that is not found in *A. stimpsonii*. This papilla (not illustrated in Fig. 3) forms at the juncture of the adoral shield and first ventral arm plate as shown, for example, in Madsen (1970: Fig. 13).

The dorsal surface of the disk of newly settled *A. filiformis* has one central and five radial primary plates (Muus, 1981: Fig. 7), and radial shields are present in a specimen as small as 0.46 mm dd with 3 AS. The radial shields and primary plates are separated by a series of smaller disc scales in a specimen 0.84 mm dd with 25 AS; they are visible in large specimens and widely separated by numerous small disc scales of nearly uniform size.

Ophiophragmus filigraneus (Lyman)

The smallest individuals studied, 0.50 mm dd with 1 AS, have buccal scales and adoral shield spines. A specimen 1.4 mm dd with 14 AS resembles *A. stimpsonii* at 0.9 to 1.2 mm dd with 10 to 20 AS. It has three oral papillae: the infradentals are spinelike, buccal scales are superficial, and adoral shield spines are still attached to the adoral shield. Two ontogenetic developments in *O. filigraneus* radically depart from the pattern in *Amphiura* species. First, in specimens larger than 2.4 mm dd, all the buccal scales are resorbed (one exceptional specimen 2.5 mm dd with >35 AS still has buccal scales on one jaw).

Second, a structure (the "oral plate papilla") which does not correspond to any of the oral papillae in *Amphiura* species arises between the base of the adoral shield and the infradental papilla (Fig. 4C, D; Tables I, II). Interestingly, another member of the *Amphiodia*-group, *Ophiocnida scabriuscula* resorbs the buccal scale—probably at the same growth stage that resorption occurs in *O. filigraneus* (Tables I, II). A specimen 2.2 mm dd, with 61 AS, has vestiges of the buccal scales; adult individuals entirely lack the buccal scale (Hendler, unpub. obs.).

The adoral shield spine of *Ophiophragmus*, like that in *Amphiura*, migrates to the oral plate (Fig. 4B, C; Tables I, II). In large individuals the infradental papilla becomes blocklike, and the oral plate papilla and adoral shield spine become blunt and flattened. The oral papillae form a continuous series along the side of the jaw, but they do not seal the space between adjacent jaws.

The dorsal disc scales develop similarly in *O. filigraneus* and *A. filiformis*. The smallest *O. filigraneus* have a rosette of six primary plates, an individual 0.6 mm dd with 3 AS has radial shields, and the primary plates and radial shields are separated by small disc scales in an individual 1.4 mm dd with 14 AS. A fence of spines on the periphery of the disk, a distinctive character of *Ophiophragmus* species, is present in the 1.4 mm dd specimen and all the scales in the ventral interradii bear rough, pointed processes. These scales are smaller than but similar to the scales comprising the fence. In larger specimens, the fence spines increase in size and number, but large, smooth scales dominate the ventral interradii and surround a patch of rough scales. Thomas (1963) showed that adults and juvenile *Ophiophragmus cubanus* (H. L. Clark, 1917) were once treated as two species because of a similar contrast in the disc spination of large and small specimens.

Discussion

Conservative patterns of ontogenesis in amphiuroids

Various amphiuroid species have brooded embryos, yolk larvae with abbreviated development, or ophioplutei with different numbers of larval arms (Hendler, 1975). Considering the diversity in mode of development and the potential for modification of the developmental program, amphiuroids would seem an unlikely group to examine for ontogenetic clues to systematic relationships. Interestingly, the patterns of oral papilla development shown in this study indicate that ontogenesis in postlarvae may be a reliable indicator of systematic relationships.

Species representing the major groups of Amphiuroidae (*sensu* Clark, 1970), including taxa with different reproductive modes, all have related sequences of oral papilla development (Tables I, II). For example, the buccal scales and adoral shield spines develop before the infra-

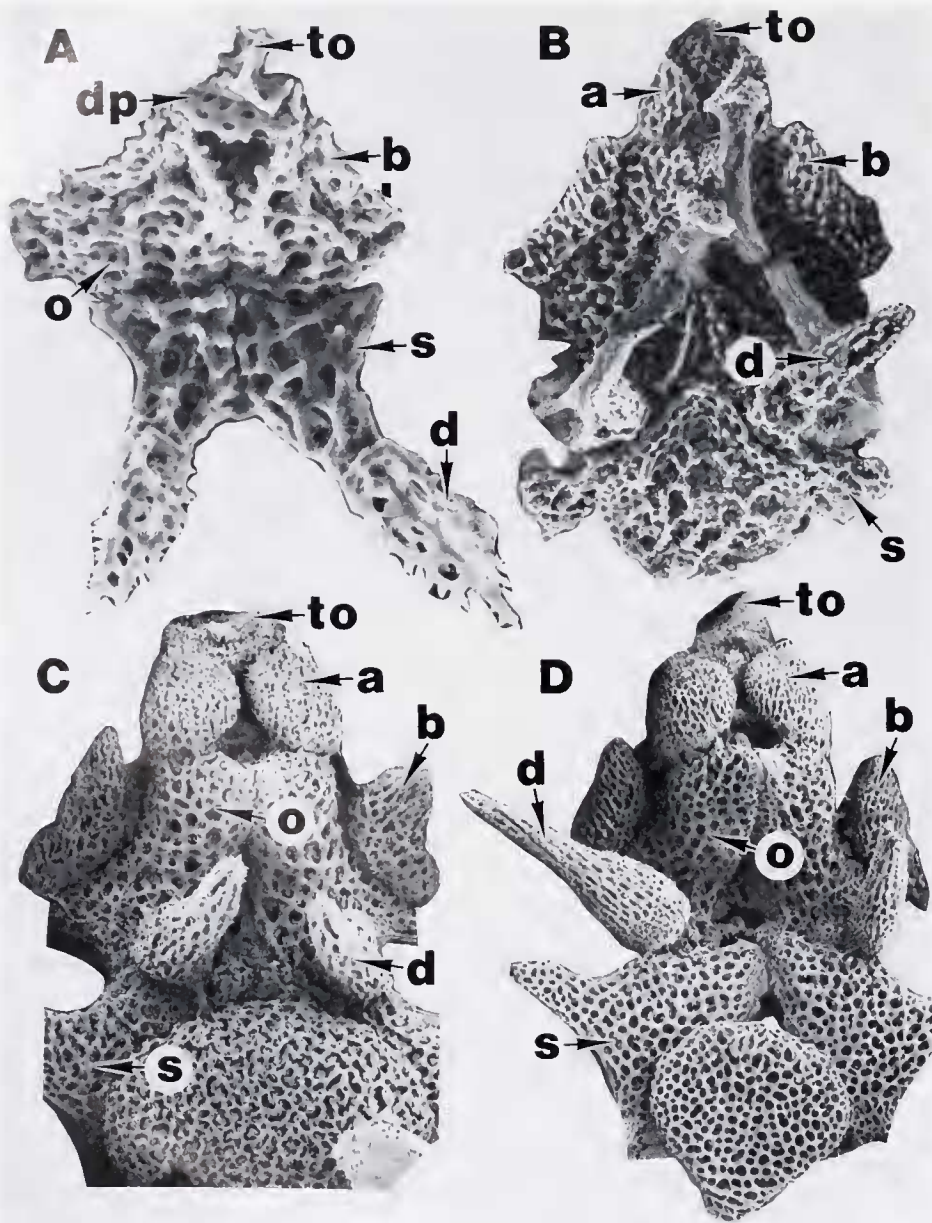


Figure 3. *Amphiura filiformis*: growth stages of jaw and oral papillae. Stages numbered according to Table I. Abbreviations as in Figure 2. (A) Stage 2; 0.33 mm dd, terminal arm plate. (B) Stage 4; 0.86 mm dd, 25 AS. (C) Stages 7–8; 3.20 mm dd. (D) Adult; 4.62 mm dd, >125 AS.

dental papillae in *A. filiformis* and *A. stimpsonii*. Late larval stages of *A. filiformis* have not yet been studied to determine whether the buccal scale appears before the adoral shield spine, as it does in *A. stimpsonii*. In both *Amphiura* species, the rudiments of infradental papillae originate on the dental plate and transfer to the tips of the oral plates; the buccal scales move from the superficial distal edge of the adoral shield to the oral plate. The intrageneric similarity in oral papilla ontogenesis of these two *Amphiura* species is paralleled by *Amphiopus macilentus* and *A. abditus*, congeners with nearly identical

patterns of oral papilla ontogeny (Hendler, 1978; unpub. obs.; see Table I, this report). Similarities in the sequence of formation, origin, and morphological development of structures in related species provide a basis for determination of homologies of skeletal elements using standard morphological criteria of homology (Wiley, 1981).

Homologies of amphiurid oral papillae

Two aspects of the ontogenesis of *A. filiformis*, *A. stimpsonii*, and *O. filigraneus* indicate that amphiurid

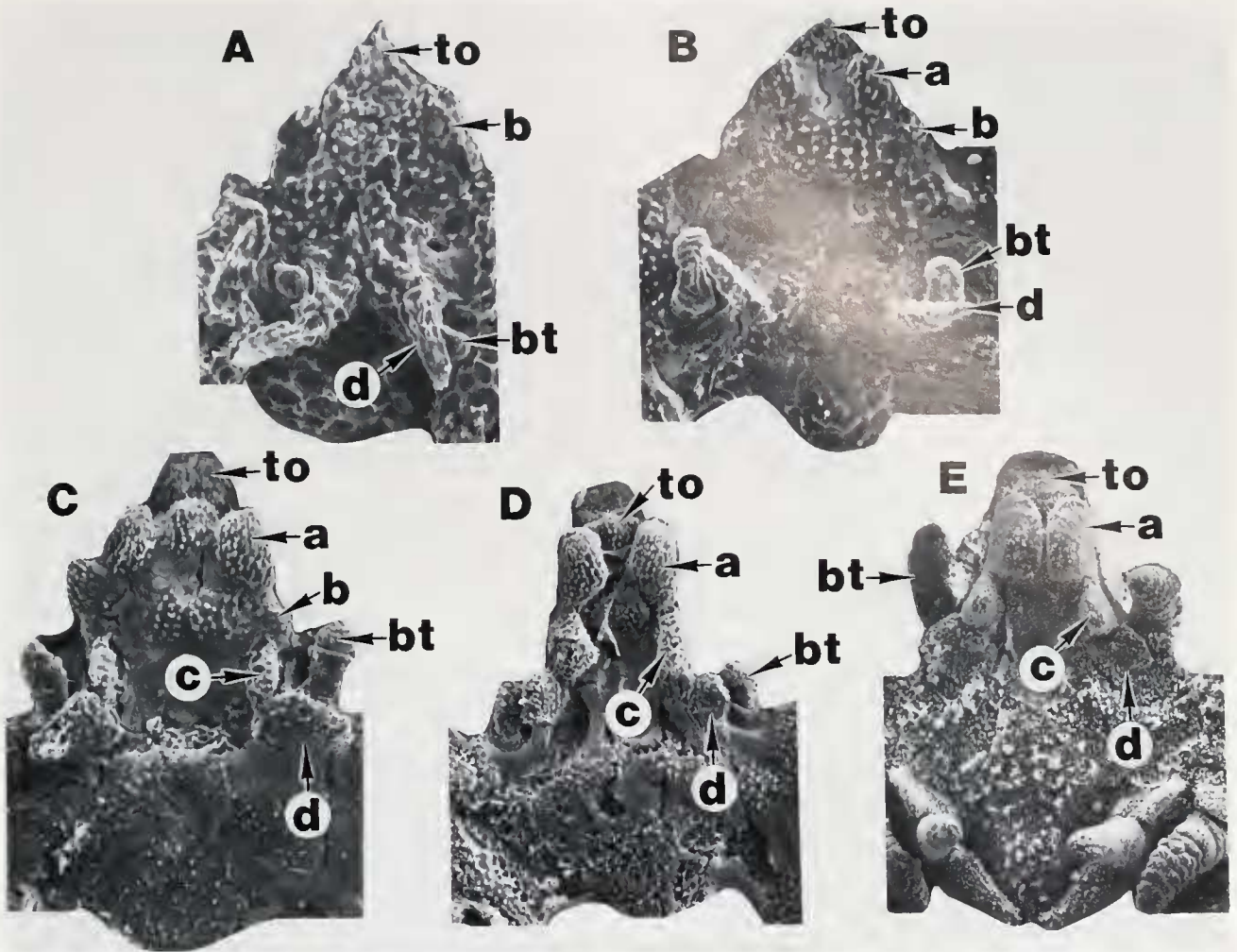


Figure 4. *Ophiophragmus filigraneus*: growth stages of jaw and oral papillae. Stages numbered according to Figure 1; abbreviations as in Figure 2. The buccal tentacles (bt) are intact, and the oral plates and adoral shields are covered with integument because samples were not plasma-ashed to remove soft tissue. (A) Stage 2; 0.5 mm dd, 2 AS. (B) Stage 4; 1.4 mm dd, 14 AS. (C) Stages 5–8 initialized; 2.5 mm dd, >35 AS. (D) Stages 5–8 complete; 2.7 mm dd, >87 AS. (E) Adult; 6.9 mm dd, 319 AS.

oral papillae are not all derived from identical structures—that they are not serially homologous (*sensu* Roth, 1984). First, the oral papillae do not develop in a unidirectional sequence, such as proximal to distal along the jaw. Second, the anlage of each papilla is associated with a different skeletal plate. For example, as skeletal elements the adoral shields are regarded as homologues of the lateral arm plate, therefore the adoral shield spine (an oral papilla) is serially homologous with the arm spines that are attached to lateral arm plates of each arm segment (Hendler, 1978). In contrast, the association of the infradental papilla with the dental plate indicates that as a skeletal element it is homologous with dental papillae or teeth.

Specific oral papillae of different taxa are provisionally regarded as homologous if they originate at the same site

and develop, or are resorbed, in the same chronological sequence. For example, in the taxa studied the buccal scale, adoral shield spine, infradental, oral plate papilla, and accessory papilla appear in sequence and each papilla forms at a characteristic site (Tables I, II). Thus, the buccal scales of all amphiurids are presumably homologous as oral papillae, the adoral shield spines of all amphiurids are presumably homologous as oral papillae, and so on.

Amphiurids lacking an “oral tentacle scale” (*sensu* Clark, 1970) resorb the buccal scale during ontogenesis; those with the “oral tentacle scale” retain the buccal scale. As previously predicted (Hendler, 1978), *Amphiura*-group and *Amphioplus*-group species retain the buccal scale, but *Amphipholis*-group and *Amphiodia*-group species resorb the buccal scale during ontogenesis (Table

1). It follows that the three oral papillae of *Amphiura stimpsonii* are not all homologous with those of *Amphipholis squamata* (compare the oral papillae of both species at stage 9 in Table I). In both taxa the infradental papillae are homologous, and the papillae derived from adoral shield spines are homologous. The middle papilla of *Amphiura* is derived from a buccal scale, but the buccal scale is resorbed in *Amphipholis* and its middle oral papilla (the oral plate papilla) arises late in ontogenesis and has no homologue in *Amphiura*. Furthermore, the four pairs of oral papillae in *Amphiura filiformis* are not all homologous with the first four pairs in *Amphioplus abditus* (Tables I, II). The four papillae in *Amphiura* (proximal to distal) are the infradental, buccal scale, adoral shield spine, and accessory papilla; the oral plate papilla (the third papilla in *Amphioplus* and *Ophiophragmus*) does not develop in *Amphiura* species.

In most cases, homologies have not been determined for the oral papillae that are important in the classification of ophiuroid families (Matsumoto, 1917). Developmental series could be used to evaluate such homologies. For that purpose, brooded embryos of representative species would likely be more readily available than growth series of free-living young. It is important that the ontogenesis of the oral papillae of brooded embryos and free-living juveniles discussed in this report are so very similar since this is an indication that homologies inferred from growth series of brooded embryos can be applied to species with free-living larvae. Thus, homologies inferred from character transformation series in brooded embryos can be used to assess the systematic affinities of species with planktonic larvae. Information on ontogenetic character transformations derived from growth series is also applicable to the identification of young individuals in ecological studies. In samples from the deep-sea, for example, where juvenile ophiuroids are disproportionately abundant, they are so morphologically different from adults that they often cannot be identified even to family or genus (Grassle and Sanders, 1973; pers. obs.).

Phylogenetic relationships suggested between taxa are strictly tentative if they are derived solely from oral papilla homologies that are based on ontogenetic patterns. Wherever possible, systematic relationships inferred from ontogenesis should be independently corroborated (see Alberch, 1985). However, ignoring the relationships suggested by ontogenesis would be "throwing out the baby with the bathwater."

Skeletal adaptations of juvenile amphiurids

The adaptive significance and variability of skeletal features such as oral papillae bear upon their usefulness for interpreting systematic and evolutionary relationships. Several observations suggest that the oral papillae,

despite their changing functional roles during ontogenesis, are consistent and reliable taxonomic characters.

At 1 year, the mean dd of *Amphiura filiformis* is 0.6 mm (range 0.4–0.8) (Muus, 1981). *Amphioplus abditus* reaches a similar size (0.4–0.8 mm dd) by 8 months (Hendler, 1978). Their oral papillae still show the juvenile arrangement of small spine-like infradentals, opercular buccal scales, and distally directed adoral shield spines. Not until 1 to 2 years after metamorphosis does the oral armature assume adult characteristics. The brooded embryos of *A. stimpsonii* hatch at about the same size and with the same oral armature as the year-old, free-living juveniles that are on the verge of transformation to adult morphology.

Although the radical changes of the oral armature which distinguish the juvenile and adult occur over a long period, the earliest post-metamorphic stages of *A. filiformis* can ingest food items large enough to fill the entire disk (Muus, 1981). The functions of all the juvenile oral structures are not yet known but surprisingly, free-living juveniles probably use the adoral shield spines for locomotion and not for feeding. The adoral shield spine in the brooded embryo of *Amphiura stimpsonii* is very small and possibly vestigial, but free-living post-larvae of *A. filiformis*, *O. filograneus*, and *Amphioplus abditus* (Figs. 1A, D, 2A, 3A, 4A this report; Hendler, 1978) have relatively much longer adoral shield spines. Until the 8 AS stage, *A. abditus* juveniles walk on the tips of their tube feet (Hendler, 1977), and the youngest stages of *A. abditus* walk on the second buccal papillae and use the adoral shield spines to support the disc during locomotion (Hendler, unpub. obs.). Unfortunately, the function of the adoral shield spine in advanced growth stages and the significance of interspecific differences in its morphology in adults have not been investigated.

Interestingly, the adoral shield spine is present in the juveniles of bottom-dwelling ophiuroids, and absent in epizoic taxa such as Asteronychidae and Ophiotrichidae (examples in Mortensen, 1912; Guille, 1964). However, juveniles of the latter taxa have large hooked arm spines, probably used for clinging and crawling, which show marked negative allometric growth. The specialized arm spines and the presence or absence of the adoral shield spine in the young may be adaptations for locomotion on the preferred substratum. Thus, there may be gross differences between the oral papillae of ophiuroid families with radically different ecological specializations. However, within a family such as the Amphiuridae the oral papillae are conservative features, even among species with different developmental modes.

Some commonly used taxonomic characters were found to be less consistent among related species. For example, a rosette consisting of one central and five radial plates is present on the disc of *A. filiformis* and absent in *A. stimpsonii*. The difference in scalation may be

related to their modes of reproduction, but the absence of a rosette is not characteristic of all brooding species. For example, viviparous *Amphipholis squamata* develops from 0.10 mm eggs (Fell, 1946), and has a primary rosette (Murakami, 1940). In contrast, *Sigsbeia conifera* Koehler, a brooding species with relatively yolky eggs, lacks a primary rosette (Hendler and Littman, 1986; Hendler, unpub. obs.). Mortensen (1936) reports brooding species with (e.g., *Ophiozonella falklandica* Mortensen) and without (e.g., *Ophiomages cristatus* Koehler) primary rosettes. I am not aware of any ophiuroid species with planktonic larvae that do not develop a primary rosette, but in some brooding forms absence of the rosette is congenital. The presence or absence of a central rosette is clearly of limited value for deducing genealogical relationships among ophiuroids. However, investigations of disk scalation might make it possible to infer the mode of reproduction from the adult morphology of extant as well as fossil ophiuroids.

Acknowledgments

I am indebted to colleagues who provided specimens used in this study: David Pawson and Maureen Downey (Smithsonian Institution), Lucienne Fenaux (Station Zoologique), John Gage (Scottish Marine Biological Association), Kirsten Muus (Marine Biological Laboratory, University of Copenhagen), and Richard Turner (Florida Institute of Technology). John Miller (Harbor Branch Oceanographic Institution) and Barbara Littman (Smithsonian Institution) assisted with field work in Florida and in Belize. The staff of the National Museum of Natural History SEM Laboratory, Smithsonian Institution, provided valuable assistance. In addition, I am grateful to David Pawson, Robert Peck, and Daniel Cohen for reading and commenting on the manuscript. This report is contribution number 230 of the Smithsonian Institution Caribbean Coral Reef Ecosystem/Investigations of Marine Shallow Water Ecosystems, and contribution number 219 of the Smithsonian Marine Station-Link Port.

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