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Postlarval development in shallow and deep-sea ophiuroids (Echinodermata: Ophiuroidea) of the NE Atlantic Ocean

PAULO Y. G. SUMIDA AND PAUL A. TYLER*

School of Ocean and Earth Science, Southampton Oceanography Centre, University of Southampton, European Way, Southampton SO14 3ZH

JOHN D. GAGE

Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, P.O.Box 3 Oban, Argyll PA34 4AD

ARNE NØRREVANG

Kaldbak Marine Biological Laboratory, FR-180 Kaldbak, Faroe Islands

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The postlarval phase is an essential period in the life history of marine invertebrates; vulnerable to high mortality, it ultimately influences the distribution and abundance of adult populations. In the deep NE Atlantic, a large number of postlarval ophiuroids have been found during certain times of the year, but their identification is difficult. The present work describes the ontogenesis of 12 post-metamorphic shallow-water or deep-sea ophiuroids from samples collected during the Biofar and Rockall Trough Programmes in the NE Atlantic Ocean. Analysis of the postlarval development reveals that species can be identified from a very early post-metamorphic phase using particular morphological characters. The ontogeny of homologous structures reveals similarities within related groups. However, at the same time, these structures give rise to different adult structures in different taxa. Data on the postlarval development of *Ophiura affinis* suggest that this species is more closely related to the genus *Ophiocten* and a change in generic status is proposed.

ADDITIONAL KEY WORDS:—postlarvae – morphology – growth series – SEM – ontogenesis.

* Correspondence to Professor P. A. Tyler. E-mail: pat8@soc.soton.ac.uk

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CONTENTS

INTRODUCTION

Studies on the postlarval development of ophiuroids are not abundant in the literature. In the 19th century and during the first half of the present one, few works depicted the morphology (Lyman, 1882) and growth (Ludwig, 1899; Clark, 1914; Campbell, 1922) of early juvenile stages. In addition, accurate identification of such species is difficult owing to the lack of detail in many illustrations.

Recently, shallow water species have been described (Stancyk, 1973; Turner, 1974; Hendler, 1978; Turner & Dearborn, 1979; Muus, 1981; Turner & Miller, 1988), and the use of scanning electron microscopy has helped to provide detailed morphological descriptions of early post-metamorphic stages (Webb & Tyler, 1985; Hendler, 1988). In the deep sea, few postlarvae have been described in detail (Gage & Tyler, 1981a; Tyler & Fenaux, 1994; Tyler *et al.*, 1995). Schoener (1967, 1969) figured, as line drawings, the growth stages of juvenile ophiuroids and traced back from the identified adults the respective postlarvae of each particular species. Schoener demonstrated that congeneric species could be identified from the very early stages of growth (but see Mortensen, 1920).

The lack of important taxonomic characters in the postlarvae makes identification of specimens collected in benthic samples difficult; as a result, they are largely ignored in benthic ecology studies (Turner & Miller, 1988). In the deep sea, postlarval ophiuroids have been collected in large quantities at certain times of the year, representing a significant proportion of the total population (Tyler & Gage, 1980; Gage & Tyler, 1981a). Gage (1994) noted that postlarval bivalves are not significant in terms of biomass, but that they dominate populations numerically. The same is true for brittlestars (Flach & Heip, 1996). In view of this problem, it is important to be able to recognize the different species of postlarvae when adults live sympatrically in benthic communities.

For this purpose, good descriptions of postlarval ophiuroids are desired in order to assign each individual to its species. In addition, such descriptions help in phylogenetic determination (Hendler, 1988) and assessment of growth rates during early stages of development. Gage & Tyler (1982a) showed that growth strategies can be different in different deep-sea ophiuroid species. The early stages of growth are particularly important as they reveal different survival strategies among species. Rapid early growth may be a strategy for predator avoidance whereas a slow growth rate may be determined by energy availability. The knowledge of postlarvae would also help in brittlestar settlement and recruitment studies (Gage & Tyler, 1981b, 1982b). Moreover, before assuming an adult life-style, the postlarvae must spend some time in the meiobenthic environment, where they might be an important component. All these factors should affect the rates of mortality and survivorship and, consequently, the maintenance of the deep-sea brittlestar populations. In this paper we describe the early post-metamorphic development of 12 species of ophiuroids from the shallow and deep NE Atlantic Ocean. The species were chosen based on the relative abundance of different growth stages and individuals. *Ophiura sarsi*, *O. ljungmani* and *Amphilepis ingolfiana* had already been previously described (Schoener, 1967, 1969). However, the line drawings presented in those papers do not allow accurate identification and their development is redescribed in the present paper. The early growth stages of *Ophiura albida* (<1 mm disk diameter) are also described, complementing the work done by Webb & Tyler (1985), who described the development of specimens larger than 1 mm in disk diameter. The aim is to produce, primarily, good descriptions of the ontogenetic development of the early growth stages of these species, showing the general aspect as well as particular characteristics of the metamorphosed ophiuroid. It is also intended to investigate possible phylogenetic affinities using the morphological characters of the postlarvae.

MATERIAL AND METHODS

Deep-sea ophiuroid postlarvae were sorted out from samples of two research programmes: Biofar (Investigations on the Marine Benthic Fauna of the Faroe Islands), organized by the Nordic Council of Marine Biology and the long-term SAMS (Scottish Association for Marine Science, former SMBA) programme in the Rockall Trough (NE Atlantic Ocean) (Gage *et al.*, 1980).

During the Biofar programme, between 1986 and 1990, a large number of ophiuroid species was collected from over 700 stations on the Faroe Shelf and Slope, Faroe Bank and Faroe-Shetland Channel (Emson *et al.*, 1994). Some of these stations yielded a large number of ophiuroid postlarvae, which are described in the present work. Of the 13 species of postlarva found, 10 are described as the other three species did not yield enough numbers to allow good descriptions. Specimens were collected at depths between 77 and 1319m, using either a modified Rothlisberg & Pearse epibenthic sampler (Brattegard & Fosså, 1991) or a detritus sledge (Table 1). For more information on Biofar stations, see Nørrevang *et al.* (1994).

Materials from the Rockall Trough programme were collected at depths of 1000–3000m using a Woods Hole-pattern epibenthic sledge. Only two species of postlarva, out of a total of six, are described in the present paper (Table 2). Again, the other species were either in poor condition or could not be identified.

Samples from both programmes were fixed in seawater formalin and transferred to 70% isopropanol for long-term storage. Postlarvae were picked out from the

TABLE 1. Station coordinates, depth, sampling gear and species of postlarvae used from the Biofar Programme. RP = Modified Rothlisberg & Pearse epibenthic sampler; DS = detritus sledge

Biofar ST	Date	Lat (N)	Long (W)	Depth (m)	Gear	Ophiuroid postlarvae
10	17.07.87	62 31	05 02	430	RP	*Ophiura sarsi*, *Ophiocten gracilis*
19	18.07.87	62 12	04 25	276	DS	*Ophiacantha bidentata*, *O. abyssicola*
27	18.07.87	61 54	05 03	225	RP	*Ophiacantha abyssicola*
29	18.07.87	61 49	05 25	170	RP	*Ophiura affinis*, *O. sarsi*, *Ophiocten gracilis*, *Ophiopholis aculeata*
32	18.07.87	61 41	05 47	354	RP	*Ophiura sarsi*
51	19.07.87	61 24	06 10	235	RP	*Ophiopholis aculeata*, *Ophiocten gracilis*, *Ophiura sarsi*, *Ophiacantha abyssicola*
56	20.07.87	61 54	06 28	77	RP	*Ophiura carnea*, *Ophiura albida*
65	20.07.87	61 35	08 05	322	DS	*Ophiura sarsi*, *O. carnea*, *Ophiocten gracilis*
73	21.07.87	61 14	08 29	185	RP	*Ophiura affinis*
100	24.07.87	61 34	06 17	283	RP	*Ophiura sarsi*, *Ophiocten gracilis*, *Ophiopholis aculeata*, *Ophiacantha bidentata*, *O. abyssicola*
132	05.05.88	61 30	07 41	225	DS	*Ophiacantha abyssicola*
137	05.05.88	61 02	07 11	542	RP	*Ophiacantha bidentata*
381	27.05.89	62 12	03 59	402	DS	*Ophiura sarsi*, *Ophiocten gracilis*, *Ophiopholis aculeata*, *Ophiacantha bidentata*, *O. abyssicola*
496	24.07.89	60 33	09 35	515	DS	*Ophiomyces grandis*, *Ophiura carnea*
601	11.04.90	61 56	05 58	140	DS	*Ophiura albida*
694	12.05.90	60 57	10 59	624	RP	*Ophiura sarsi*, *Ophiomyces grandis*
696	13.05.90	61 35	10 46	1319	RP	*Ophiactis abyssicola*
726	29.09.90	60 39	06 54	400	DS	*Ophiopholis aculeata*
737	01.10.90	62 04	10 22	850	DS	*Ophiactis abyssicola*

TABLE 2. Station co-ordinates, depth and postlarvae used from the Rockall Trough Programme. All samples were collected with a WHOI-pattern epibenthic sledge (ES)

Station	Date	Lat (N)	Long (W)	Depth (m)	Ophiuroid postlarvae
ES12	03.07.73	56 49	10 15	2076	*Ophiura ljungmani*
ES18	22.09.73	56 44	09 20	1392	*O. ljungmani*
ES34	10.05.75	56 36	11 30	2515	*Amphilepis ingolfiana*
ES99	09.07.76	60 00	10 35	1160	*Ophiura ljungmani*
ES112	25.10.76	55 12	15 50	1900	*O. ljungmani*
ES197	19.08.81	57 21	10 29	2200	*O. ljungmani*, *Amphilepis ingolfiana*
ES244	25.07.83	57 23	10 20	2150	*Amphilepis ingolfiana*
ES283	15.04.85	54 39	12 15	2946	*Amphilepis ingolfiana*
ES401	10.09.90	54 40	12 16	2900	*A. ingolfiana*
ES402	11.09.90	54 40	12 16	2905	*A. ingolfiana*
ES446	08.03.93	54 42	12 18	2846	*Ophiura ljungmani*

samples under stereomicroscope and arranged in ontogenetic series. Subsequently they were air-dried and mounted on stubs using a double-sided adhesive tape and examined under a low-vacuum scanning electron microscope (SEM) (JEOL JSM-5300LV). This equipment does not require the specimens to be gold-coated. The disk diameter was measured using the SEM scalebar.

Twelve different postlarval ophiuroids are described in the present work: *Ophiacantha abyssicola*, *O. bidentata*, *Ophiomyces grandis*, *Ophiura sarsi*, *O. carnea*, *O. ljungmani*, *O. albida*, *Ophiocten affinis* (comb. nov.), *O. gracilis*, *Amphilepis ingolfiana*, *Ophiactis abyssicola*

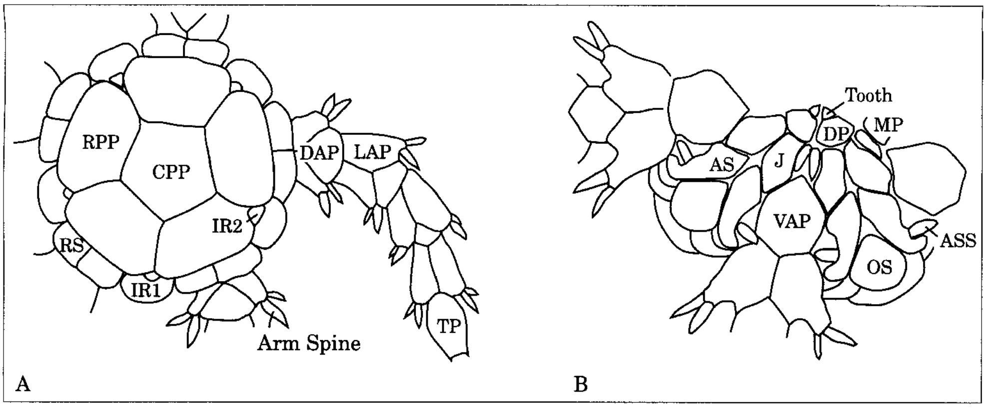


Figure 1. Main structures found in the early postlarvae. A, dorsal view; B, ventral view. AS = adoral shield; ASS = adoral shield spine; CPP = central primary plate; DAP = dorsal arm plate; DP = dental plate; IR1 and 2 = interradial plates 1 and 2; J = jaw; LAP = lateral arm plate; MP = mouth papilla; OS = oral shield; RPP = radial primary plate; RS = radial shield; TP = terminal plate; VAP = ventral arm plate.

and *Ophiopholis aculeata.* The structures in the early postlarvae are shown in Figure 1.

RESULTS

Postlarval development

Subclass Ophiuridea Gray, 1840
Order Ophiurida Müller & Troschel, 1840
Suborder Ophiurina Müller & Troschel, 1840
Family Ophiacanthidae Perrier, 1891
Subfamily Ophiacanthinae Paterson *et al.*, 1982

Ophiacantha abyssicola G.O. Sars, 1871

Postlarvae of this species were found in the samples from Biofar. The earliest postlarva found measured 0.4mm disk diameter (dd) and possessed 5 arm segments. The dorsal part of the disk is formed by the central primary plate (CPP), the 5 radial primary plates (RPP), the radial shields (RS), the first interradial plate (IR1) and the k-plate (k). The CPP is strongly pentagonal, with the borders filled with several small fenestrations and a solid edge. The central part of the plate is almost imperforate, bearing few small fenestrations. Each corner of the plate has a big trifid spine pointing outwards in a total of five spines, which are sometimes missing owing to losses during the sample acquisition. When missing, the places where these spines were attached can be recognized by the larger fenestrations present on the plate (Fig. 2A). The main stem of these spines is fenestrated and branches into three

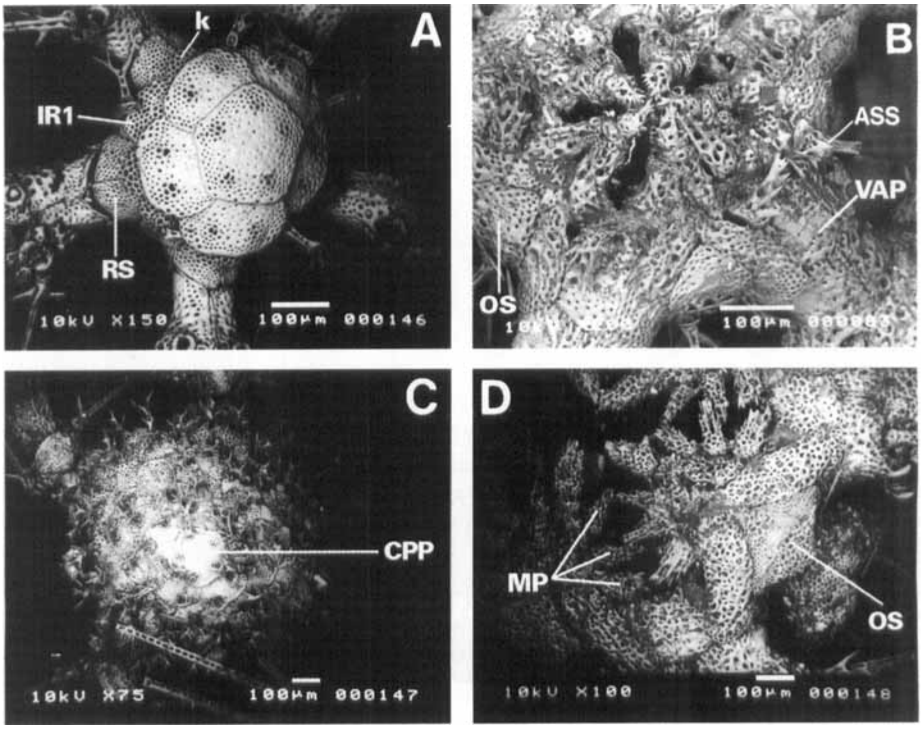


Figure 2. *Ophiacantha abyssicola* postlarval development. A, dorsal view of a 0.4mm dd postlarva showing the primary plates, radial shields (RS), k-plates (k) and the 1st interradial plates (IR1); B, ventral structure of a 0.4mm dd postlarva, with the oral shield (OS) and adoral shield spines (ASS); C, 0.9mm dd postlarva. Note the pentagonal central primary plate (CPP) in the centre of the disk; D, 2.0mm dd postlarva (ventral), with the presence of three spine-like mouth papillae (MP) (the distal-most being the former ASS) and the well-developed oral shield (OS). See Figure 1 for further details.

and each of these ramifies again into two. The RPPs have the same fenestration pattern, but only two spines are present. The RSs are broader than long and overlap the proximal arms. Besides the former plates, an IR1 is present, possessing one single spine. As an individual grows, each dorsal plate added to the disk bears just one spine. The spines also begin to erode probably owing to the animal's activity. The k-plate, together with the IR1, bears large rounded fenestrations. No spines are present on the k-plates or the RSs (Fig. 2A). The arm segments are large, bearing three spines on the proximal segments and two on the distal ones. The spines of the proximal segments are large, with large spinelets, and those of the distal ones are smaller with spinelets distributed along their edges. The lateral arm plates (LAP) are contiguous dorsally throughout their length, leaving the rounded dorsal arm plates (DAPs) on their distal-most portion. The terminal plate (TP) is bulb-shaped with several fenestrations.

At 0.9mm dd the CPP is still recognizable by the number of spines present on it and its pentagonal shape, but it is difficult to recognize the other primary plates (Fig. 2C). The number of dorsal plates increases with size and they are hardly distinguishable, with a precise description of the dorsal plates almost impossible. On the ventral side, the oral armature is well formed with strong and spinose teeth. No mouth papillae (MP) are present yet and the dental plate (DP) is small, and broader than long. The

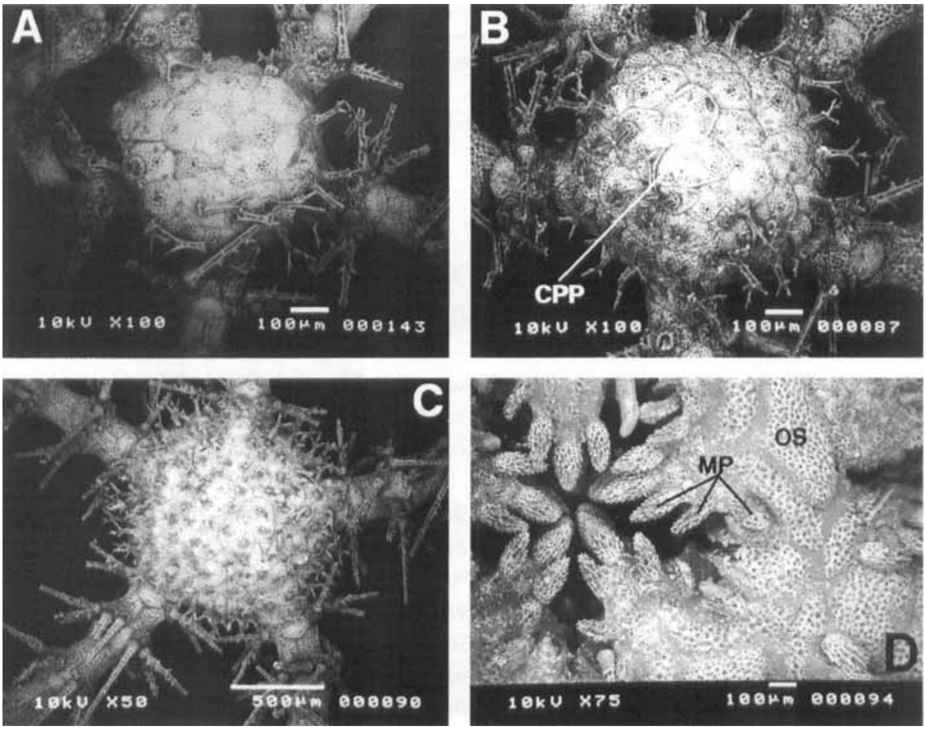


Figure 3. *Ophiacantha bidentata* postlarval development. A, 0.5 mm dd postlarva (dorsal). Note the arrangement of the dorsal plates; B, dorsal view of a 0.8 mm dd postlarva, with the central primary plate (CPP); C, 1.2 mm dd postlarva (dorsal); D, ventral view of a 3.0 mm dd postlarva showing the well-developed oral shields (OS) and the mouth papillae (MP).

adoral shield spines (ASS) are strong and spinose. The first ventral arm plate (VAP) is bell-shaped with a convex distal end. This plate is almost solid, bearing only few fenestrations on the lateral parts. The 2nd tentacle pore (TPo) is well-concealed by the ASS in the smallest postlarvae examined (Fig. 2B). At a disk diameter of 0.66 mm the 1st MP is present as a spine-like structure at the distal part of the jaw, near the base of the DP. Reaching 2.0 mm dd three large MP are present and a groove is present on the oral shield (OS), indicating the identity of this species (Fig. 2D).

Ophiacantha bidentata (Retzius, 1805)

Individuals at 0.5 mm dd were collected in Biofar samples, being very similar to *O. abyssicola*. However, a careful examination of the dorsal plates of *O. bidentata* reveals significant differences in the shape of the plates. In this species the primary plates are not easily recognized, but a CPP elongated and irregular in shape can be seen, bearing two spines similar to those described earlier for *O. abyssicola*. The dorsal plates have scattered tiny fenestrations and larger ones on the areas below the spines. The dorsal plates are all irregular in shape and most bear just one spine. The RSs are similar to those described for *O. abyssicola*. The arms possess several segments (> 4) with large spines, bearing large spinelets (Fig. 3A). At 0.8 mm dd, the irregular CPP (bearing 2 spines) is still visible (Fig. 3B) and can be used to distinguish this species from *O. abyssicola*, which bears a pentagonal CPP with 5 spines (Fig. 3C).

The early ventral development is very similar to that of *O. abyssicola*. However, they are easily distinguished when the animal attains a larger size, by the shape of the oral shields (OS), which in *O. bidentata* are broader than long and no groove is present (Fig. 3D).

Subfamily Ophiohelinae

Ophiomyces grandis Lyman, 1878

The smaller specimen of *O. grandis* shows a sac-like disk formed by several scales, some of which bear large smooth spines. The scales of the central part of the disk are largest, becoming smaller toward the edges (Fig. 4A). The teeth are bulb-shaped with a pointed end mounted on a large dental plate (DP). Several mouth papillae (MP) are present, all of which have an elongated shape. Two infradental papillae (IP) lie on the DP, three MP on each edge of the jaw and three supplementary papillae on its innermost part and finally one larger papilla is present on the adoral shields. The 2nd tentacle pore (TPo) opens close to the oral slit (Fig. 4B).

One long tentacle scale (TS) is present on each TPo of the arms (Fig. 4C) when the individual attained a larger size. The distal-most MP has now a wide flattened end. The oral shields (OS) appear as a somewhat diamond-shaped plate (Fig. 4D). Further development involves growth and broadening of the papillae and spines (Fig. 4E).

Infraorder Chilophiurina Matsumoto, 1915
Family Ophiuridae Lyman, 1865
Subfamily Ophiurinae Lyman, 1865

Ophiura sarsi Lütken, 1858

The smallest individuals examined were about 0.37 mm dd (Fig. 5A), bearing only the CPP, the five RPPs on the dorsal side and the TP of the arms. The first arm segment is only visible ventrally (Fig. 5B). The CPP has a pentagonal shape and its fenestrations are round, numerous and large throughout the plate and edges. Almost the same pattern is found in the RPP, but here the borders have slightly smaller fenestrations (Fig. 5A). The TPs are relatively large, with the distal part possessing three large spines, being regularly fenestrated throughout its length (Fig. 5A). A large adoral shield spine (ASS) is present, which is visible dorsally in the smallest forms, as it is directed radially. It is stout and bears many small spinelets (Fig. 5B). A protuberance can be seen in one of the oral shields (OS), which distinguishes the madreporite (M) from the remaining OSs.

At the size of 0.45 mm dd, the postlarva has two arm segments and few changes have occurred. The central part of the CPP has large round fenestrations, becoming smaller towards the borders and larger again at the edge of the plate. The first arm segment bears two spines and the second, one. They are small and conical in shape (Fig. 5C).

At 1.0 mm dd the first and second interradial plates (IR1 and 2) are present and the radial shields (RS) appear as a squared structure on the borders of the disk where the arm is inserted. The RSs begin to appear when the postlarva reaches

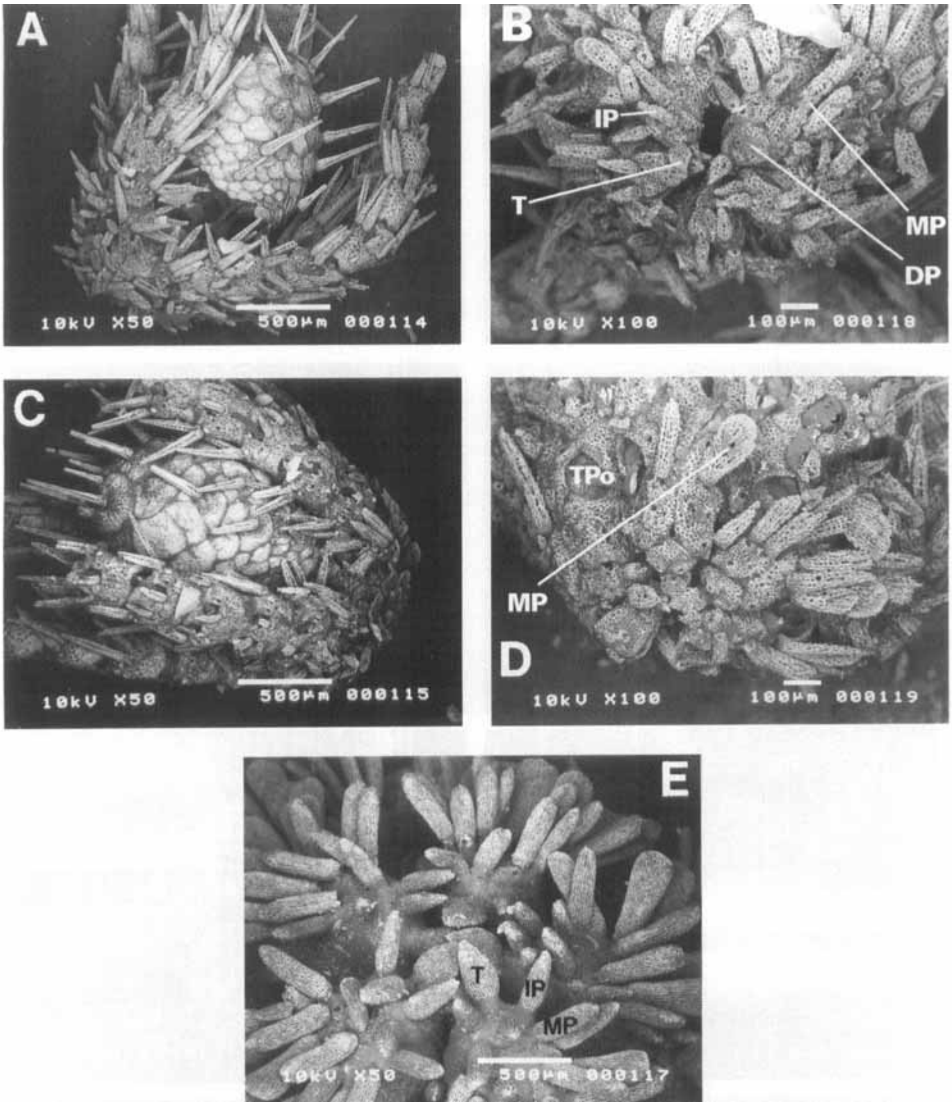
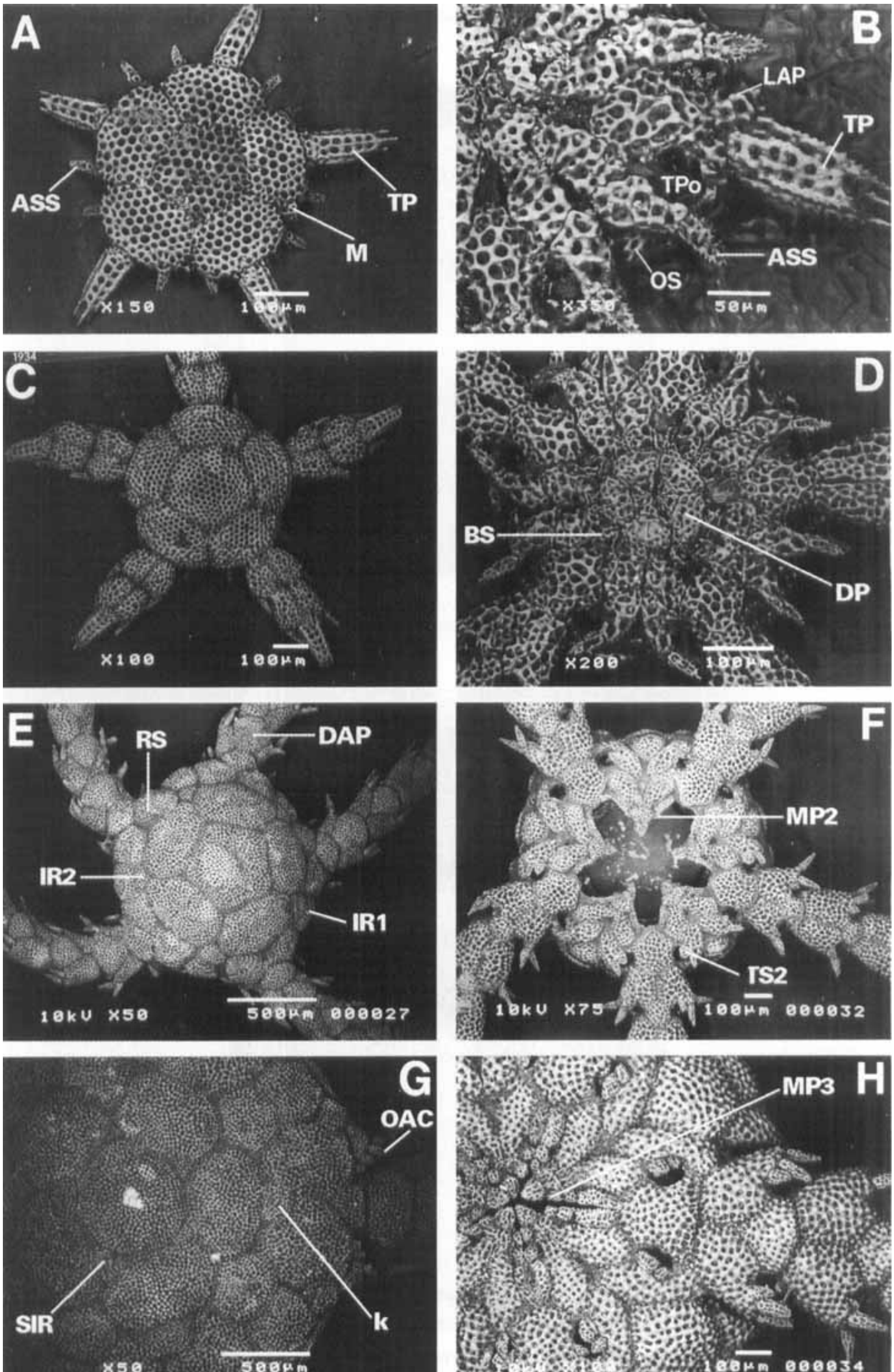


Figure 4. Some stages of the post-metamorphic development of *Ophiomyces grandis*. A and C, lateral view; B, D and E, ventral view. T = tooth; IP = infradental papilla; MP = mouth papilla; TPo = tentacle pore; DP = dental plate.

between 0.70 and 0.80 mm dd, but they are very small and difficult to observe. The postlarva has already developed several arm joints and the first ventral arm plate (VAP) assumed a pentagonal aspect, with a slightly convex distal edge. The ASSs are not visible dorsally. The first two dorsal arm plates (DAP) are broad and fan-shaped and contiguous, whereas the subsequent DAPs are smaller and non-contiguous (Fig. 5E). Three spines are present on the proximal arm joints and two on the distal ones.

At 2.7 mm dd the k-plates (k) were added to the dorsal side, as well as secondary plates among the CPP and RPPs. The outer arm comb (OAC) is well formed on


A
ASS
TP
M
X150
100μm
B
LAP
TP
TPo
ASS
OS
50μm
C
X100
100μm
D
BS
DP
X200
E
RS
DAP
IR2
IR1
10kV X50
500μm 000027
F
MP2
TS2
10kV X75
100μm 000032
G
OAC
SIR
k
X50
500μm
MP3
H
100μm 000034

the genital plate and the DAP can be seen intruding between them into the disk (Fig. 5G). The secondary interradial plates (SIR) are also seen.

Reaching 3.8 mm in dd, the arm combs resemble those of the adult, with the comb extending into the disk, as well as the first DAP, which is inserted between the distal end of paired RSs. The RSs are 'hexagonal' in shape, with a continuous mid-line suture. Intermediate interradial plates are present on the dorsal side.

At 0.37 mm dd, on the oral side, the tooth has a triangular shape with a pointed apex and some accessory spinelets on the borders. The dental plate is large and fenestrated mounted on somewhat rectangular oral plates. Each pair of the oral plates is connected by an interdigitation on the proximal side and no mouth papilla is present at this size. The adoral shields are longer than broad, bearing a spine that is about two thirds its size. The 1st ventral arm plate (VAP) is regularly fenestrated and diamond-shaped, with a small notch resulting from the presence of the 2nd tentacle pore (TPo). The first appearance of the lateral arm plates (LAP) can be seen on the proximal side of the terminal plates. No tentacle scales are present at this stage (Fig. 5B). Also visible in this stage are the oral shields (OS), present on the interradial portion, between the distal corners of the adoral shields, as slightly oval, fenestrated plates (Fig. 5B). The presence of OSs in the earliest postlarva agree with the results of several authors, who reported the appearance of this plate during the metamorphosis of the larva (Fewkes, 1887; Fell, 1941; Hendler, 1978).

The dental plate (DP) has increased in size and a small buccal scale (BS) is visible at 0.45 mm dd on the proximal outer part of the jaw, occupying its entire length (Fig. 5D). This is the first mouth papilla to appear in this species, arising as a small scale on the proximal portion of the oral plate when the animal is around 0.39 mm in dd.

At 1.0 mm dd, the 2nd mouth papilla (MP2) is present on the proximal side of the oral plate and the 2nd tentacle scale (TS) of the 2nd tentacle pore (TPo) is a broad process placed next to the adoral shield spine (ASS) (which forms the 1st TS). The remaining TPo of the arms bear one TS each (Fig. 5F).

Reaching 1.5 mm dd, the genital slits become conspicuous on each side of the arm base, the distal edge of the 1st VAP is straight and a 3rd TS is added to the 2nd TPo, opposite to the other two. The ASS assumes a form of a scale covering, partially, the 2nd TPo. The 3rd mouth papilla (MP3) has also appeared on each side of the dental plate and the tooth is a stronger structure (Fig. 5H).

At 3.8 mm dd, the three MPs are well developed, with the third being somewhat elongated, about half the size of the tooth. The 1st VAP is almost triangular in shape and the 2nd TPo is elongated, with 6 scales in total on its edges. The oral shields are broad and teardrop-shaped, with a constriction on the proximal third.

Figure 5. *Ophiura sarsi* postlarval development. A, 0.37 mm dd postlarva showing the primary plates, terminal plates (TP), adoral shield spines (ASS) and madreporite (M); B, ventral view of a 0.37 mm dd postlarva showing the mouth structure, the 1st ventral arm plate (VAP) and the first appearance of the lateral arm plates (LAP). Note the oral shields on the interradial area (OS). TPo = tentacle pore; C, 0.45 mm dd postlarva (dorsal); D, postlarva at 0.45 mm dd (ventral). Note the appearance of the 1st mouth papilla (the buccal scale – BS) and the massive dental plates (DP); E, 1.0 mm dd postlarva (dorsal) showing the radial shields (RS) and the interradial plates 1 and 2 (IR1 and IR2). DAP = dorsal arm plate; F, ventral view of a postlarva at 1.0 mm dd showing the 2nd mouth papilla (MP2) and the 2nd tentacle scale of the 2nd tube pore; G, 2.7 mm dd postlarva showing the k-plates (k), the secondary interradial plates (SIR) and the outer arm combs (OAC); H, 1.5 mm dd postlarva with the ventral side presenting the 3rd mouth papilla (MP3).

Ophiura carnea Lütken, 1858

The smallest postlarvae found in the Biofar samples are around 0.6 mm dd. At this stage, the postlarva has a pentagonal CPP and five RPPs. Also present are the RSs and the IR1s. A dorsal view reveals the presence of the adoral shield spines (ASS) (Fig. 6A). The fenestration pattern in this species is characteristic, the central part of the CPP bears regularly-spaced medium-sized circular fenestrations, while the borders have small and more numerous round holes (Fig. 6A). The ASSs in *O. carnea* are quite smooth and delicate (Fig. 6B), differing from the stout and spinose spines of *O. sarsi* (Fig. 5B).

At 1.2 mm dd, the IR1s and RSs are much larger in size and the IR2 is already present. The RSs are almost square in shape (Fig. 6C). The relative size of the CPP is much smaller in this species at this stage than that of *O. sarsi*.

When the animal reaches 1.8 mm dd, the interradial plates are well developed, the RSs begin to elongate and the k-plate (k) is present, but small (Fig. 6E). The outer arm combs (OAC) are visible on the genital plates (Fig. 6E). At 2.9 mm dd the animal has the adult characteristics. The outer and inner combs grow towards the interior of the disk and the dorsal arm plate intrudes into the disk with an elongated shape. The k-plate attained a large size, being broad triangular in shape. Adjacent to the k-plate are intermediate interradial plates (IIR). Secondary interradial plates (SIR) can be seen among the primary plates (Fig. 6G).

On the ventral side, the individual at 0.6 mm dd bears a fully developed mouth papilla (= buccal scale), which is present on the oral plate throughout the oral slit. Its outer part possesses small spinelets on the border. The tooth is triangular in shape, spinulose, bearing large fenestrations. The dental plate is large and trapezoidal (Fig. 6B). The ASS is a quite long and slender process with squared fenestrations and pointed radially. The 1st VAP is arrow-shaped with a slight notch on each of its distal lateral sides, where the 2nd tentacle pores are inserted. A very small OS can be seen among the distal part of the adoral shields and the IR1 (Fig. 6B).

Reaching 1.3 mm dd, the OSs have a teardrop shape and the ASSs change to form small scale-like structures, the tentacle scales of the 2nd tentacle pores. At this stage the genital slits are clearly visible. The small 2nd mouth papilla (MP) lies on the proximal part of the first one (Fig. 6D). The 3rd MP is present when the individual is 1.8 mm dd. At this stage, the tentacle pore begins to elongate, possessing 2 tentacle scales on each side (Fig. 6F).

Finally, at 2.9 mm dd the oral frame is well formed with large teeth and a 4th MP. The second tentacle pore is very elongated with four tentacle scales on each

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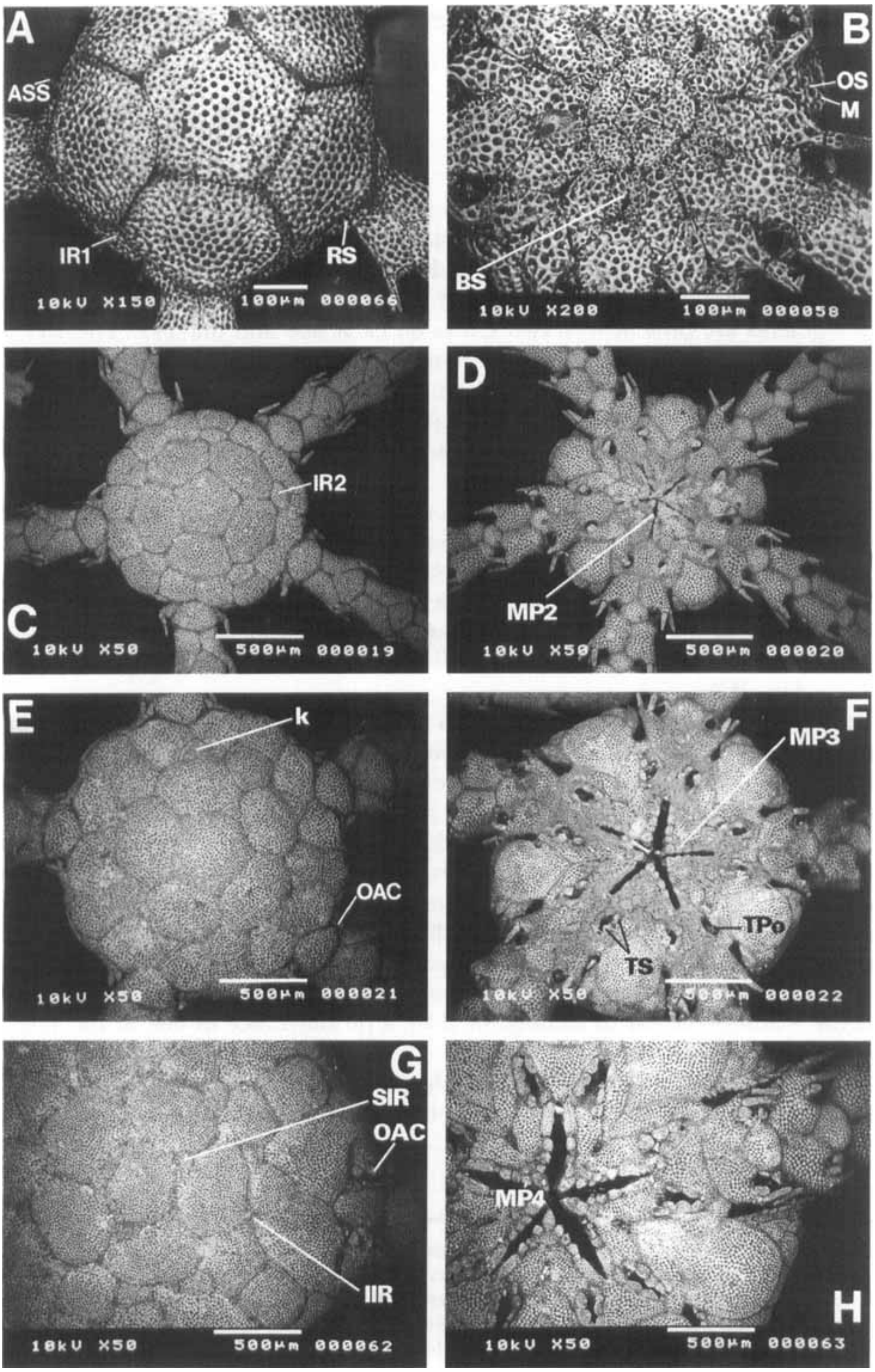
Figure 6. *Ophiura carnea* postlarval development. A, dorsal view of a 0.6 mm dd postlarva, showing the primary plates, the first appearance of the radial shields (RS) and the 1st interradial plate (IR1). Note also the arm spines and the adoral shield spine (ASS); B, ventral view of a 0.6 mm dd postlarva with a well-developed buccal scale (BS). Note the small oral shield (OS) with the madreporite (M) and the mouth structure; C, 1.2 mm dd postlarval (dorsal). See interradial plate 2 (IR2); D, 1.3 mm dd postlarva (ventral), with the presence of the 2nd mouth papilla (MP2); E, 1.8 mm dd postlarva showing the outer arm combs (OAC) and the k-plates (k); F, postlarva at 1.8 mm dd; the 3rd mouth papilla (MP3) has appeared and additional tentacle scales (TS) are present on the second tube pore (TP_0), which is now more elongated; G, 2.9 mm dd postlarva presenting the well-developed outer and inner arm combs, the secondary interradial plates (SIR) and intermediate interradial plates (IIR); H, ventral view of a 2.9 mm dd postlarva with a well-developed oral frame and the presence of the 4th mouth papilla (MP4). See Figure 1 for further details.


A
ASS
IR1
RS
10kV X150 100μm 000066
B
OS
M
BS
10kV X200 100μm 000058
C
IR2
10kV X50 500μm 000019
D
MP2
10kV X50 500μm 000020
E
k
OAC
10kV X50 500μm 000021
F
MP3
TPo
TS
000022
G
SIR
OAC
IIR
10kV X50 500μm 000062
H
MP4
10kV X50 500μm 000063

side, almost inside the oral slit. The outer arm comb is clearly visible on the genital plate and the oral shields are more elongated (Fig. 6H).

Ophiura ljungmani (Lyman, 1878)

At 0.52 mm dd, the dorsal side bears a pentagonal CPP and 5 RPPs; these have large fenestrations in the centre and smaller ones near the borders (Fig. 7A). Some fenestrations are irregular in shape and some are round. The disk is slightly pentagonal with a notch on the outer part of the junction between the RPPs. Three arm segments are present with two spines on each side and the TPs. The TPs are large and strong, with rows of fenestrations running along their length (Fig. 7A).

At 0.6 mm dd, only the primary plates are present, but larger in size and with larger fenestrations on the centre of the plate and smaller ones at the edges. The notch between the RPPs is less pronounced. The arm spines are relatively small and slender, bearing very small spinelets.

At 1.0 mm dd, the IR1 can be seen from above, as well as a slight signal of the radial shields on the sides of the arm, alongside the disk edge. The stereom structure of the plates remains the same, although the plates are bigger in size (Fig. 7E).

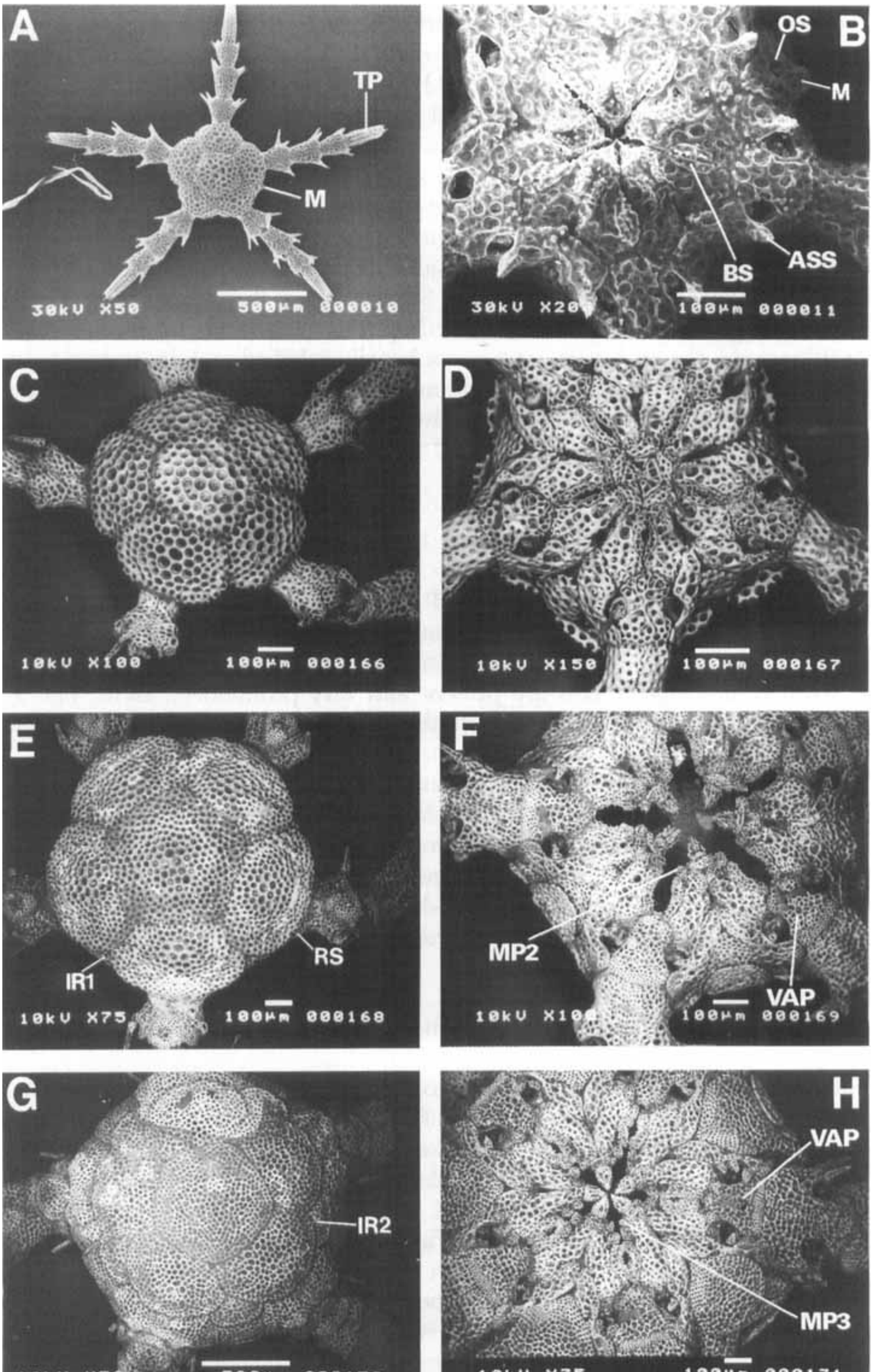
Individuals of 1.5 mm dd have well-developed primary plates: the IR1 and 2 plates and radial shields. The dorsal arm plates are bell-shaped, with the 1st being broader than the subsequent ones. The shape of the CPP is more rounded on the corners (Fig. 7G).

At 2.7 mm dd, the CPP assumes an almost circular outline and secondary interradial scales are present on the point of contact of the CPP and RPPs. The radial shields are longer, and a relatively large k-plate is present between the proximal portions of the RSs, separating almost half of their mid-line suture.

Ventrally, the early 0.52 mm dd postlarva is very similar to the other *Ophiura* species described above. The tooth is broadly triangular and pointed, with some small spinelets; the dental plate is a large, fenestrated structure, with a v-shaped distal edge. A large and block-like mouth papilla is present (= buccal scale). The adoral shield spine is small and stubby, bearing some small spinelets along its edge. The first VAP is pointed proximally and convex distally. The oral shields are present and the madreporite (M) is distinguished by a protuberance in one of the sides of the plate (Fig. 7B).

At 0.6 mm dd, the first VAP changes shape, having a straight distal portion and a notch on each side, related to the presence of the second tentacle pore (Fig. 7D).

Figure 7. Postlarval development of *Ophiura ljungmani*. A, dorsal view of a 0.4 mm dd postlarva. Note the shape and fenestration pattern of the primary plates, the strong terminal plates (TP) and the madreporite (M); B, ventral structure of a postlarva at 0.4 mm dd; note the elongated buccal scale (BS). Only one oral shield (OS) is present on the interradial area with the madreporite; C, 0.6 mm dd postlarva (dorsal) showing the large fenestrations in the centre of the primary plates; D, 0.6 mm dd (ventral); all the oral shields are present at this stage; E, 1.0 mm dd postlarva (dorsal) showing the first sign of the radial shields (RS) and the interradial plate 1 (IR1); F, ventral view of a 1.0 mm dd postlarva; the 2nd mouth papilla (MP2) is present. Note the fenestration pattern of the 1st ventral arm plate (VAP); G, dorsal view of a 1.5 mm dd postlarva; H, 1.5 mm dd postlarva (ventral). The first appearance of the 3rd mouth papilla (MP3) is noted at this stage. See Figure 1 for further details.


A
TP
M
30kV X50
500µm 000010
B
OS
M
BS
ASS
30kV X20
100µm 000011
C
10kV X100
100µm 000166
D
10kV X150
100µm 000167
E
RS
IR1
10kV X75
100µm 000168
F
MP2
VAP
10kV X10
100µm 000169
G
IR2
10kV X50
500µm 000170
H
VAP
MP3
10kV X75
100µm 000171

The mouth structure at 1.0 mm dd presents a much stronger and spinulose tooth; the 2nd mouth papilla (MP2), which is a small, scale-like structure, is located at the proximal end of the 1st mouth papilla (MP). The 1st VAP distal portion is much wider with numerous, regularly distributed small fenestrations, whereas the proximal three quarters presents larger fenestrations, arranged in a more complex stereom structure. The ASS forms the 1st tentacle scale of the 2nd tentacle pore (TPo), and both oral shields and IR1 are visible ventrally (Fig. 7F).

Reaching 1.5 mm dd, a 3rd MP is formed, which is slightly smaller than the 2nd MP and also scale-like, located on the sides of the dental plate. The 1st VAP is almost triangular and the 2nd TPo bear 3 scales along their outer edge. The oral shields are large, resembling a broad teardrop (Fig. 7H).

At 2.7 mm dd, the oral structure is more heavily calcified and the second tentacle pore is enlarged and is almost inside the mouth, bearing an additional scale on the inner edge. The 1st VAP has a convex distal edge pointed in the middle. The oral shield is broader with a pointed proximal and rounded distal portion.

Ophiura albida (Forbes, 1839)

At 0.6 mm dd, the specimen has 5 RPP and a pentagonal CPP, with a complex stereom structure; apparently, the original plate bears round, medium-sized fenestrations in the centre and smaller ones at the borders. Alongside the edge of the disk, strongly rectangular RSs are present and very pronounced IR1s. The arms are quite broad and strong (4 joints), with the dorsal arm plates (DAP) much broader than long. Two arm spines are present on each arm joint. The terminal plates (TP) are somewhat bulb-shaped with several fenestrations (Fig. 8A).

Ventrally, at 0.8 mm dd, a broad triangular tooth is inserted on a large, rhomboidal dental plate. Only one large, block-like mouth papilla (= buccal scale) is present on the side of the oral plates. The 1st VAP is pentagonal in shape and on its lateral parts a tentacle pore is present, with one stubby adoral shield spine (ASS) placed as a tentacle scale. The oral shield (OS) is well developed, resembling a teardrop (Fig. 8B).

Ophiocten affinis (Lütken, 1858) **comb. nov.**

Individuals with a dd of 0.68 mm were obtained from the Biofar samples. On the dorsal surface the CPP is pentagonal and five RPPs are present at 0.8 mm dd. The RSs are much broader than long and between paired RSs the IR1 and 2 are clearly seen. Among the primary plates a small plate, the secondary interradial plate (SIR), is present. The arms are well developed, bearing two medium-sized spines. The spines are smoother in smaller animals (Fig. 9B) and become slightly thicker in the larger ones (Fig. 9A). The first dorsal arm plate (DAP) is broad and short, and the subsequent plates are longer and fan-shaped (Fig. 9A).

At 1.3 mm dd, several secondary scales (ss) surround the primary plates, but these are still very conspicuous. The RSs are larger and the k-plate (k) is present on the suture line between paired RSs. The intermediate interradial plate lies between k-plate and the RS. The DAPs are now contiguous and elongated, with the exception of the first plate, which is much smaller than the subsequent ones. The arm combs start to appear on each side of the arm as a small spine on the outer edge of the RSs (Fig. 9C).

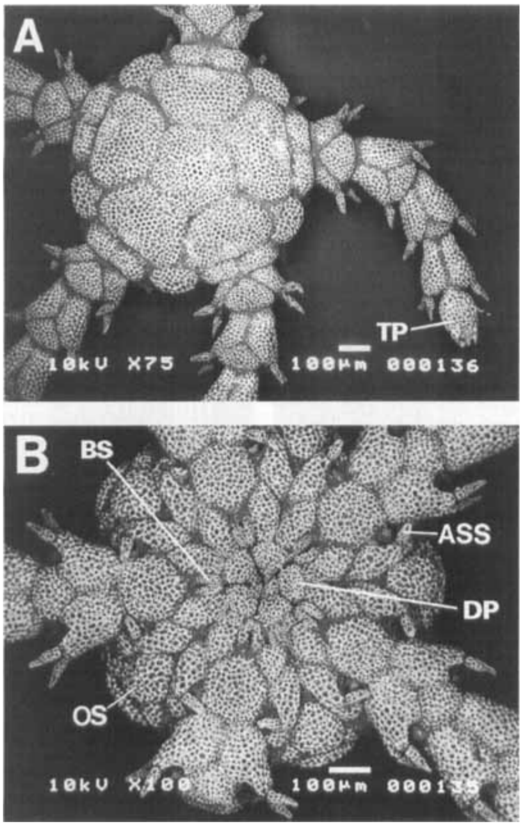


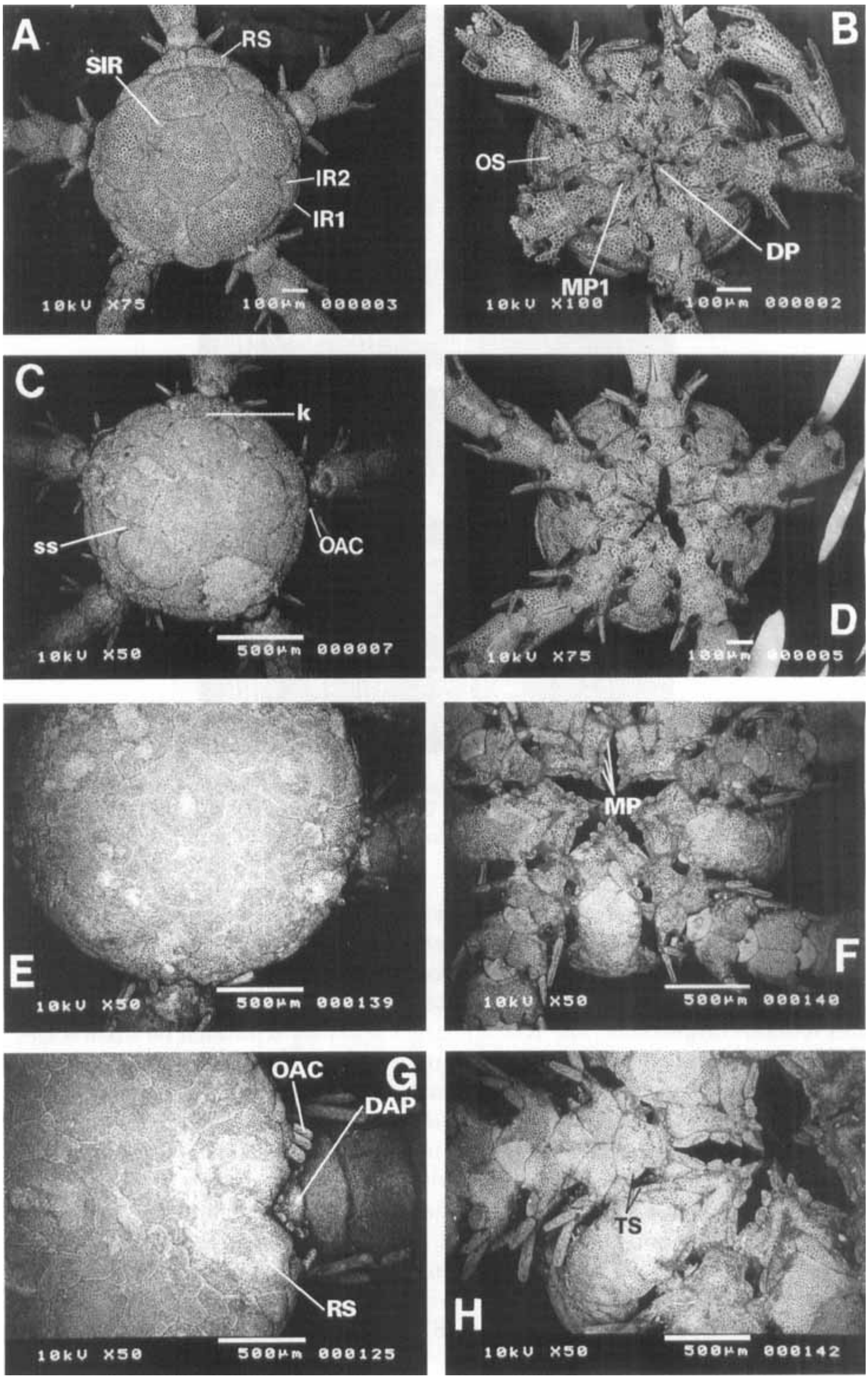
Figure 8. Early stages of the postlarval development of *Ophiura albida*. A, dorsal view of a 0.8 mm dd postlarva showing the bulb-shaped terminal plates (TP); B, ventral view of a 0.8 mm dd individual; note the large dental plate (DP) and the presence of the buccal scale (BS). See Figure 1 for further details.

Reaching 2.0 mm dd, all the plates on the dorsal side are surrounded by small scales. The disk is circular in shape and only a very slight notch is present on the disk borders over the arm bases. The arm combs are more developed (Fig. 9E).

At 3.0 mm dd, a larger number of secondary scales are present, although the primary plates remain conspicuous. The RSs are larger and fully separated by small scales. A well-pronounced notch in the disk edge is now present over the arm bases. The outer comb is well developed, bearing small, blunt spines. The first DAP is small, possessing small spinelets arranged in a row (V-shaped) forming the inner comb. The remaining DAPs are broader than long, with the distal border convex and a rounded ridge running along the arm axis on the mid-line of the plate (Fig. 9G).

On the ventral side at 0.68 mm dd, the teeth are triangular, thin and pointed. The dental plate is somewhat ellipsoidal. On the jaw, only a single, long mouth papilla (=buccal scale) is present, covering the entire length of the oral gap. The adoral shields are longer than broad, bearing a relatively small spine beside the 2nd tentacle pore (TPo). The oral shields (OS) are large triangular structures. The 1st VAP is a broad arrow-shaped plate with a straight distal end. The arm spines are relatively large and slender, nearly two thirds the size of the arm joint (Fig. 9B).

At 1.0 mm dd, the 2nd mouth papilla (MP) is present and the first sign of the apppearance of the 3rd MP is noticed (Fig. 9D). The 1st VAP, although with the


A
SIR
RS
IR2
IR1
10kV X75 100µm 000003
B
OS
DP
MP1
10kV X100 100µm 000002
C
k
ss
OAC
10kV X50 500µm 000007
D
10kV X75 100µm 000005
E
10kV X50 500µm 000139
MP
F
10kV X50 500µm 000140
OAC
G
DAP
RS
10kV X50 500µm 000125
TS
H
10kV X50 500µm 000142

same shape, now has two distinct fenestration patterns; the distal portion bears small, regularly distributed fenestrations, whereas in the rest of the plate the fenestrations are larger and irregularly distributed. The adoral shield spine starts to change in form to a scale-like structure. The bursal slit is well developed at that stage (Fig. 9D).

At 2.0 mm dd, all three MPs are well formed and the OSs assume the elongated shape found in the adult. The 1st VAP is almost rectangular in shape and the tentacle pores bear one scale (Fig. 9F). At 3.0 mm dd, the outer scale of the 2nd TPo is elongated and an additional scale is present on the inner edge. The 2nd TPo remains outside the mouth slit, next to the 1st VAP (Fig. 9H).

Ophiocten gracilis (G.O. Sars, 1871)

This is a common species in the Northeast Atlantic (Paterson *et al.*, 1982). In the Biofar material the smallest postlarvae found measured 0.48 mm dd. *O. gracilis* appears to settle on the sediment with a relatively high number of arm segments (~5) and even specimens found in the plankton bear more than one arm joint (pers. observ.).

On the dorsal side, specimens at 0.65 mm dd have five broad RPPs and a very large pentagonal CPP; the latter has a solid edge bearing tiny fenestrations, and the central part has irregularly distributed small fenestrations, becoming larger towards the borders. The RPPs have a similar border, but the central fenestrations are larger throughout the plate. The IR1 is present but not visible dorsally. The RSs are very small. The arms bear two large spines on each segment. The dorsal arm plates (DAP) are bell-shaped and the arm joints elongated, with the exception of the first, which is shorter (Fig. 10A).

At 1.2 mm dd, the IR1 and IR2 are well developed and the RSs are rectangular in shape. The k-plate (k) is present between the RSs. Among the primary plates a small secondary interradial plate (SIR) is present. The arm spines are longer and 3 in number on the proximal segments. The 1st DAP is short and broad and the remaining plates are very elongated. The outer arm combs (OAC) first appear as a spine on the borders of the RSs (Fig. 10C).

Reaching 1.5 mm dd, the arm combs are more fully developed, the k-plate is larger, almost separating the adjacent RSs. The IR3 starts to appear and intermediate interradial plates are present between the interradial plates and RSs (Fig. 10E).

Figure 9. Postlarval development of *Ophiocten affinis* **comb. nov.** A, dorsal view of a 0.8 mm dd postlarva showing the primary plates, the interradial plates (IR1 and 2) and the radial shields (RS). Note also the secondary interradial plates (SIR); B, ventral view of a 0.68 mm dd postlarva showing the ellipsoid dental plate (DP) and 1st mouth papilla (MP1). The oral shields (OS) are also present; C, 1.3 mm dd postlarva (dorsal) showing the secondary scales (ss) surrounding the primary plates. Note the k-plate (k) and the first sign of the outer arm combs (OAC); D, 1.0 mm dd (ventral); E, 2.0 mm dd postlarva (dorsal). Note the slight notch in the disk over the bases of the arms; F, 2.0 mm dd postlarva (ventral) presenting three mouth papillae (MP); G, 3.0 mm dd postlarva showing the fully-developed arm combs on the genital plates and on the 1st dorsal arm plates (DAP); H, ventral structure of a 3.0 mm dd postlarva. Note the 2nd tentacle pore and its scales (TS). See Figure 1 for further details.

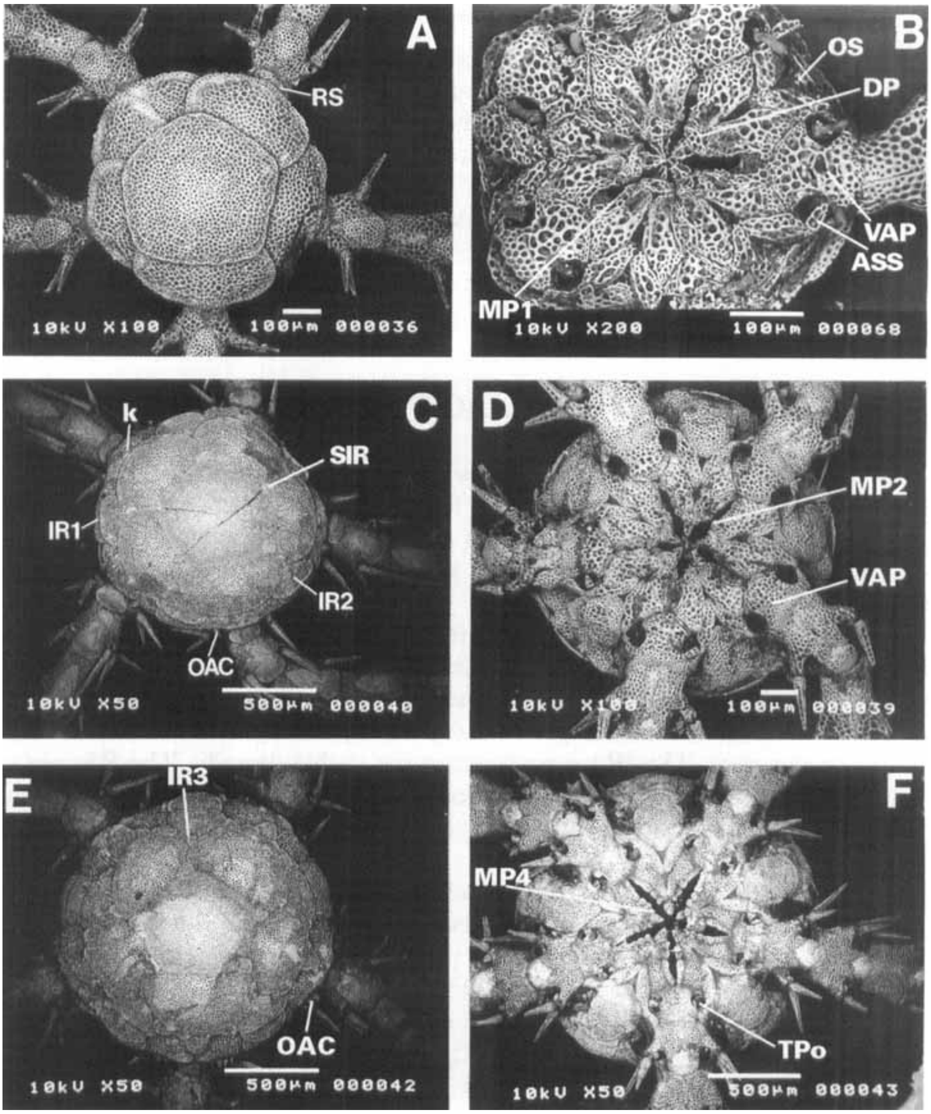


Figure 10. Post-metamorphic development of *Ophiocten gracilis*. A, dorsal view of a 0.65 mm dd postlarva showing the primary plates and well-developed arms. Note a slight sign of the radial shields (RS); B, ventral structure of a 0.48 mm dd postlarva showing the ellipsoid dental plate (DP) and the 1st mouth papilla (MP1). Note also the small oral shield (OS); C, 1.2 mm dd postlarva, with the interradial plates 1 and 2 (IR1 and 2) and the secondary interradial plates (SIR). The first appearance of the arm combs (OAC) is noticed, as well as the k-plate (k); D, 0.45 mm dd postlarva (ventral), with the presence of the 2nd mouth papilla (MP2). Note the fenestration pattern of the 1st ventral arm plate (VAP); E, 1.5 mm dd postlarva showing the larger outer arm combs and the 3rd interradial plate (IR3); F, 1.6 mm dd postlarva showing the ventral structure. Note the presence of the 4th mouth papilla (MP4) and the 2nd tentacle pore (TPo). See Figure 1 for further details.

The ventral side of individuals at 0.48 mm dd is well developed and all ventral ossicles have large fenestrations. The teeth are pointed, triangular with small spinelets on each side. The dental plate is ellipsoidal, very similar to that of *Ophiocten affinis*.

A large mouth papilla covers the whole length of the outer part of the oral plate. The 1st VAP is arrow-shaped, but its proximal edge is strongly convex and its distal edge slightly convex; on each side a deep notch leaves a way for the second tentacle pore. The adoral shield spine (ASS) is small with large fenestrations, placed next to the 2nd tentacle pores (TPo). The oral shield (OS) is a small plate among the adoral shields and IR1. The IR1 is larger, but not yet seen on the dorsal part (Fig. 10B).

At 0.9mm dd, the 2nd mouth papilla (MP) is present on the proximal side of the 1st MP. The ASS lies by the edge of the 2nd TPo forming a tentacle scale (Fig. 10D). The OSs are larger and the distal borders of the 1st VAP become straight with very small and regularly distributed fenestrations, differing from the remainder of the plate, which has larger and irregularly distributed fenestrations. The arm spines are large, with small spinelets distributed along their edge (Fig. 10D).

At 1.6mm dd, the teeth are more heavily calcified, the 3rd MP is present as another small scale-like ossicle. The 1st VAP now is almost rectangular in shape. Two tentacle scales are present on the 2nd TPo and only one on the others (Fig. 10F).

Infraorder Gnathophiurina Matsumoto, 1915
Superfamily Amphilepididae Matsumoto, 1915

Amphilepis ingolfiana Mortensen, 1933

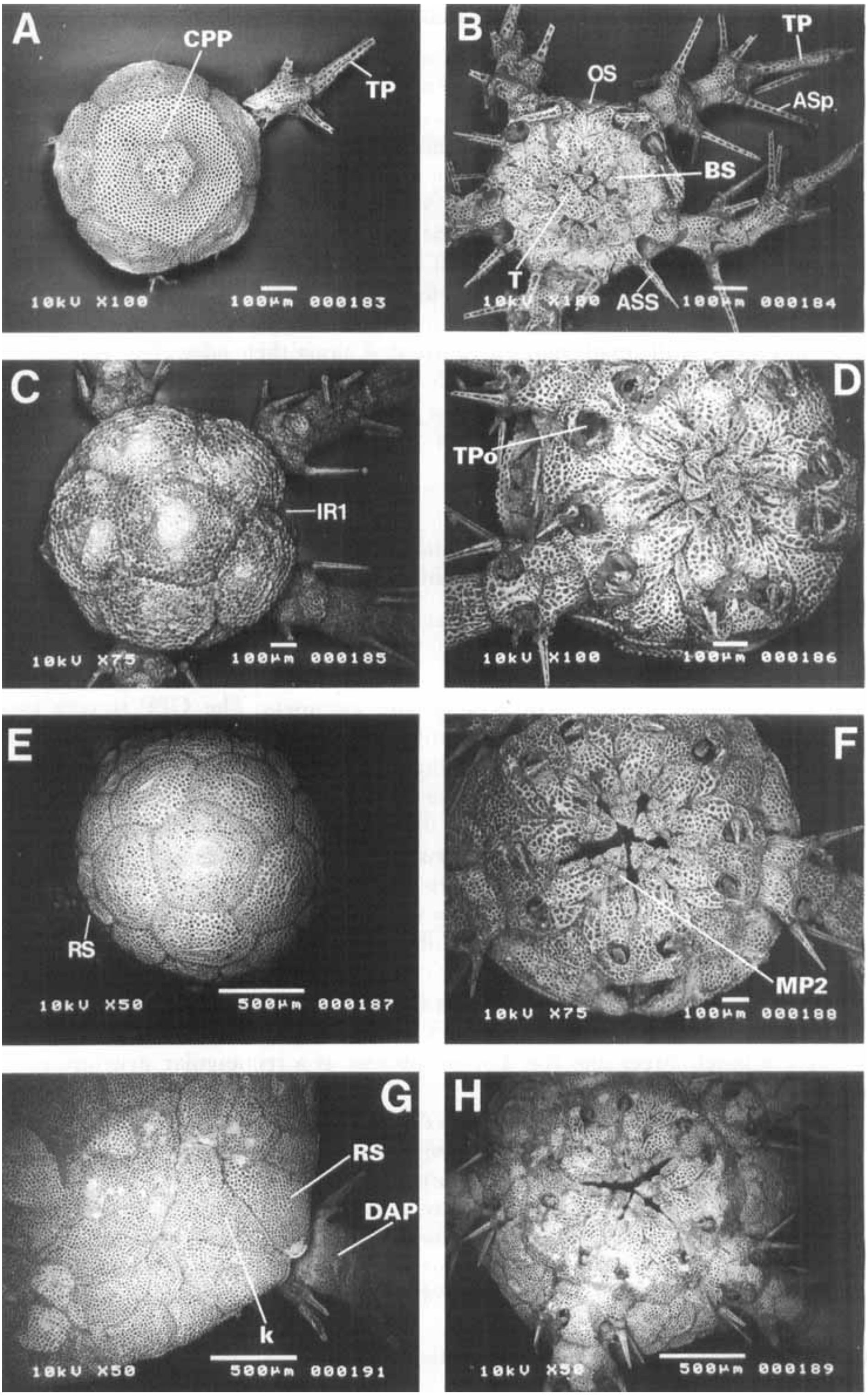
The smallest postlarva measured 0.6 mm dd and its shape is readily recognized. Only the primary plates are present in this specimen. The CPP is very large, occupying almost the entire dorsal side and its central part is raised. The fenestrations are medium-sized and evenly distributed throughout the plate. The RPPs are broader than long and the stereom structure of their central parts is slightly denser. Specimens with 1 or 2 arm segments are present at this size; the arm spines are very long and slender, with rectangular fenestrations running along their length. The terminal plate (TP) is thin and larger than the arm segments (Fig. 11A).

At 1.0 mm dd, the IR1s are visible on the interradial area and the elevation on the CPP almost disappears. However, all six primary plates have a more solid stereom structure on their central parts. The dorsal arm plates (DAP) are fan-shaped and the arm spines are the same size as the arm segments, with the exception of the first (Fig. 11C). At 1.5mm dd, the RPPs bear a kind of scar almost in the centre. The IR1 is much larger and the RSs are present as a rectangular structure on the edge of the disk (Fig. 11E).

When the animal has attained 2.0mm dd, the IR2 has already appeared, as well as the k-plate (k), which stands between the proximal parts of the paired RSs. Intermediate interradial scales are also present.

Finally, at 3.5mm dd, more scales are added to the dorsal side and the RSs (triangular in shape now) are almost fully divided by the, now long, triangular k-plate, with the exception of the distal part. The first DAP is square and the spines look relatively much smaller than when observed in the early postlarva (Fig. 11G).

On the ventral side, specimens at 0.6mm dd present a very large flat tooth, broadly triangular in shape, bearing relatively large fenestrations. This kind of tooth was not found in any of the ophiuroid postlarvae examined previously. The dental plate is very thin and bar-shaped. A large block-like papilla (=buccal scale) is present covering the whole of the oral slit. The adoral shield spines (ASS) are very


A
CPP
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100µm 000184
C
IR1
10kV X75
100µm 000185
D
TPo
10kV X100
100µm 000186
E
RS
10kV X50
500µm 000187
F
MP2
10kV X75
100µm 000188
G
RS
DAP
k
10kV X50
500µm 000191
H
10kV X50
500µm 000189

large and slender, about one quarter the size of the disk. The 1st VAP is long with a large notch on the lateral sides and convex on both the proximal and distal side. The oral shields (OS) are barely visible on the interradial area (Fig. 11B).

At 1.0mm dd, the dental plate is thicker, the oral shield is triangular in shape and the ASS stands next to the 2nd tentacle pore (TPo). The first VAP is now bell-shaped (Fig. 11D).

A second mouth papilla (MP2) is present at 1.5mm dd as a small scale-like process on the proximal side of the jaw. The tooth is much stronger and the dental plate larger. The oral shield developed into a fan-shaped structure (Fig. 11F). In the subsequent development, the enlargement of the disk and a slight increase in size of the MP2 takes place (Fig. 11H).

Superfamily Gnathophiuridea Matsumoto, 1915
Family Ophiactidae Matsumoto, 1915
Ophiactis abyssicola (M. Sars, 1861)

Postlarvae measuring 0.4mm dd possess primary plates, three arm segments and terminal plates (TP). The fenestration pattern consists of large holes of varying size and shape (from a circular to elipsoidal shape) spread throughout the plate, with the fenestrations tending to be smaller at the borders. Each arm segment possesses two arm spines and the TP is fenestrated and bulb-shaped (Fig. 12A).

Specimens at 0.5 mm dd possess a distinctive dorsal structure with respect to the fenestration pattern. The pentagonal CPP bears large fenestrations in the central part and smaller ones on the borders. A second layer is present over the central portion of the CPP, showing bridges that divide the holes into two or three parts. The same pattern is seen on the 5 RPPs. The RSs are small plates on each side of the arm, alongside the edge of the disk. The IR1 is visible on the interradial part of the animal, between the far corners of the adjacent RPPs (Fig. 12C).

At 1mm dd both IR1 and IR2 are conspicuous on the disk, the RSs are much larger and the k-plate (k) is present (Fig. 12E). At this stage (1.4mm dd) additional scales have been added to the dorsal plates, the intermediate interradial plate between the k-plate and IR2, and the secondary interradial plate (SIR) among the primary plates. The arm spines are much larger in size (Fig. 12G). Some specimens at 1.4mm dd have spines on the dorsal side of the disk surface, which are short and conical, distributed on the corners of the plates (Fig. 12I).

At 1.8mm dd many more plates are present, mainly on the interradial region and around the RSs, which are well developed and begin to be separated by the k-plate (Fig. 12K).

Figure 11. Post-metamorphic development of *Amphilepis ingolfiana*. A, dorsal view of a 0.6mm dd individual. Note the raised central portion of the central primary plate (CPP) and the large terminal plates (TP); B, postlarva at 0.6mm dd (ventral). Note the buccal scales (BS) and the large teeth (T), adoral shield spines (ASS) and arm spines (ASp); C, 1.0mm dd postlarva (dorsal), with the 1st interradial plate (IR1); D, 1.0mm dd postlarva (ventral); E, 1.5mm dd postlarva (dorsal); F, 1.5mm dd individual (ventral) showing the 2nd mouth papilla (MP2); G, detail of the proximal arm segments, radial shields (RS) and k-plate (k) of a 3.5mm dd individual; H, ventral structure of a 3.5mm dd postlarva. See Figure 1 for further details.

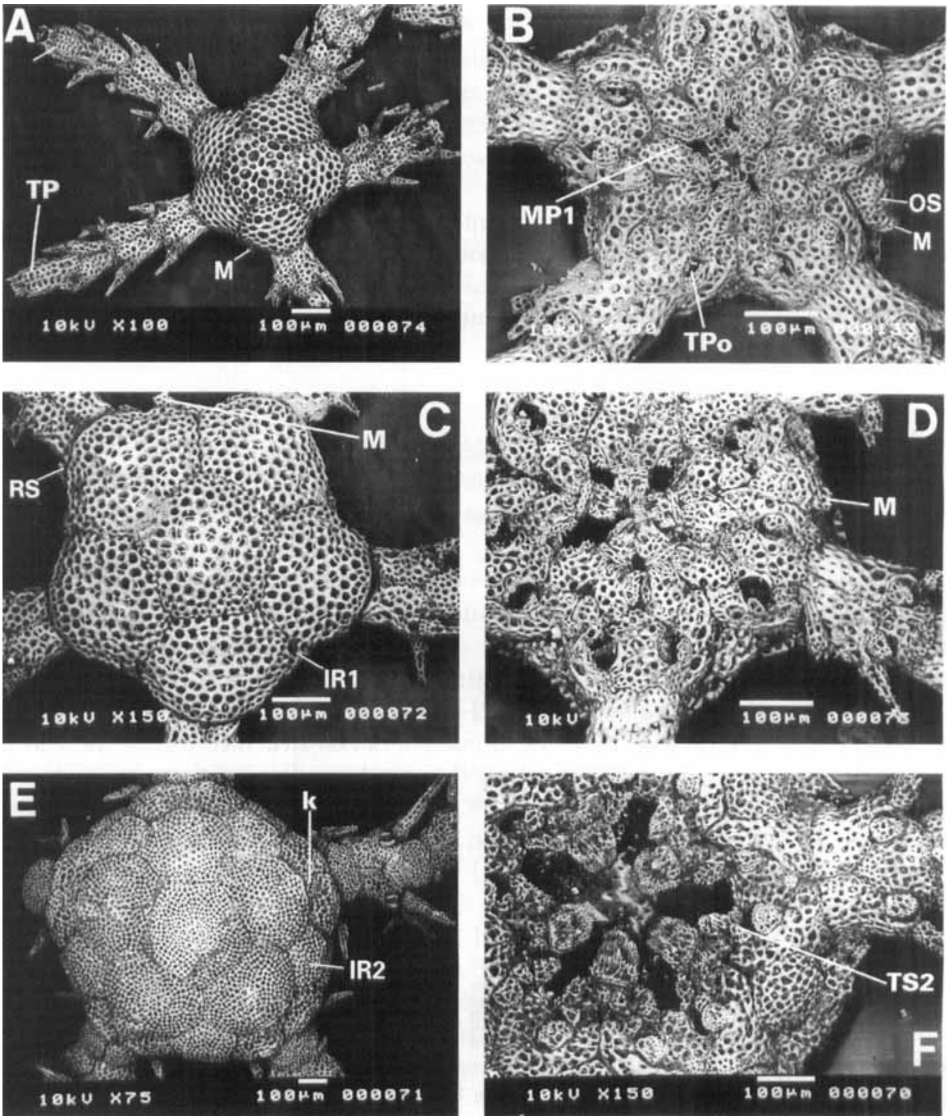

Figure 12. Postlarval development of *Ophiactis abyssicola* (A–L). A, 0.4 mm dd postlarva with three arm segments. Note the fenestration pattern of the primary plates, the terminal plates of the arms (TP) and the madreporite (M); B, ventral view of a 0.4 mm dd postlarva showing the 1st mouth papilla (MP1) and the oral shield (OS) with the madreporite. See also the tentacle scale of the 2nd tentacle pore (TPo); C, 0.5 mm dd postlarva (dorsal) showing the 'bridges' formed in the central fenestrations of the primary plates. Note also the appearance of the 1st interradial plates (IR1) and radial shields (RS); D, 0.5 mm dd postlarva (ventral); E, Dorsal view of a 1.0 mm dd postlarva with the 2nd interradial plates (IR2) and the k-plates (k); F, 0.9 mm dd postlarva (ventral) with a second tentacle scale (TS2) on the 2nd tube pore.

Ventrally, the earliest postlarva at 0.4 mm dd bears a large, spinulose tooth with large fenestrations. The dental plate is rectangular and one large, block-like papilla (= buccal scale) is present. The 1st VAP is arrow-shaped, narrowing laterally where the 2nd tentacle pore (TPo) is inserted. The 2nd TPo bears one broad scale, as do

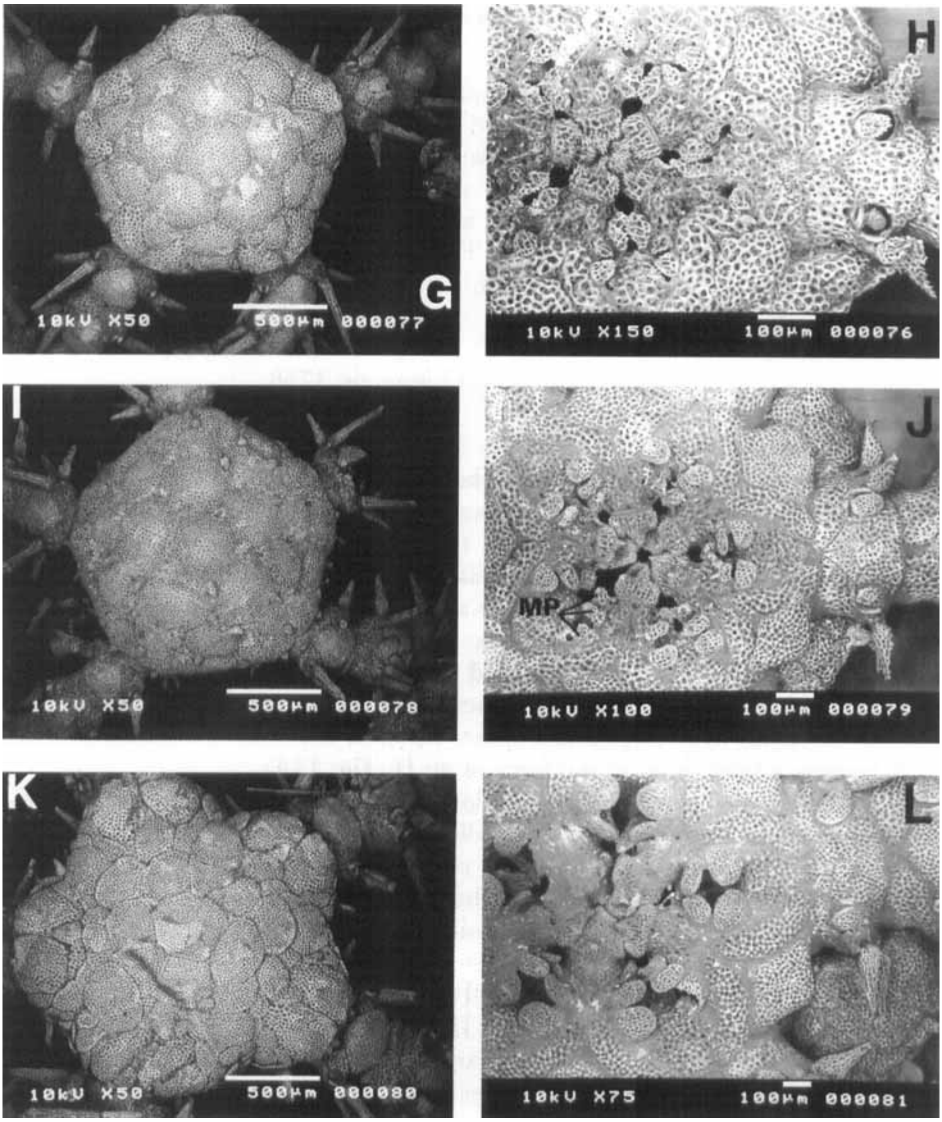

Figure 12—*contd.* G, 1.4 mm dd postlarva (dorsal). Note that no dorsal spine is present in this individual (compare with fig. 12I); H, 1.1 mm dd postlarva (ventral); I, 1.4 mm dd postlarva (dorsal) showing dorsal spines; J, 1.4 mm dd postlarva (ventral). Note the mouth papillae (MP); K, 1.8 mm dd postlarva (dorsal); L, ventral view of a 2.6 mm dd postlarva.

the remaining tentacle pores. The oral shield (OS) is present on each interradius and is relatively large. The madreporite (M) is clearly visible and is distinguished by a protuberance (Fig. 12B).

At 0.5 mm dd, not many changes occur from the former stage, only the teeth are more spinulose and crown-shaped (Fig. 12D). At 0.9 mm dd, the strong spinulose inferior teeth are more conspicuous. The 1st mouth papilla (MP) is a prominent structure and the 2nd TPo is almost inside the oral slit, with its 1st tentacle scale covering it almost entirely. A second smaller scale can be seen next to the 1st tentacle scale of the 2nd TPo. The 1st VAP has changed in form and now has a straight proximal and a pointed distal line. The OSs are rounded in shape (Fig. 12F). The 2nd TPo gets closer to the mouth as the animal grows (Fig. 12H), being completely inside the mouth (Fig. 12J) at 1.4 mm dd. During this process the 1st MP change in form, from a large scale-like process to a blunted finger-like structure, which is located deeper into the mouth slit (see Figs. 12 D, F, J and L). The 1st and 2nd TPo scales enlarge considerably in size as they migrate towards the mouth, forming the 2nd and 3rd MP (Fig. 12 D, F, J and L). The OSs take a lozenge shape and the teeth become characteristically heart-shaped (Fig. 12L).

Ophiopholis aculeata Linnaeus, 1758

The smallest individual found in the Biofar samples is 0.3mm dd and is the smallest ophiuroid postlarva obtained. The specimen presented the primary rosette and 3 arm segments. The CPP is pentagonal, solid with almost no fenestrations, but with some smaller ones scattered on the borders of the plate and a trifid spine on each corner. The 5 RPPs have similar structures, but with just one spine on each of the far corners, between the two adjacent RPPs, and one on the mid-distal edge, right on the mid-line suture of the LAPs. It is worth noting that the dorsal spines on this species seem to be inserted not on a single plate but on the mid-line suture between two or more of the plates, with each half inserted on each plate. The arm segments bear 2 spinulose spines on each side and the dorsal arm plates (DAP) possess a bifid spine in the form of an H (Fig. 13A).

At 0.6mm dd, a deposition of a secondary layer of carbonate changes the stereom structure of the plate, forming some medium-sized fenestrations except in the very centre of the primary plates. The IR1 is present and bears 3 spines distributed evenly on the outer edge. On the arm, the 1st DAP has 4 spines on the distal edge and the adoral shields are much larger and spinous. Between the arm and the disk lie the paired RSs which are small and rectangular, with 2 spines (Fig. 13B).

Reaching 1.0mm dd, the RSs and IR1s are much larger and the plates are increasingly surrounded by spines. The IR2 appears on the interradial area (Fig. 13C). As the animal grows, spines appear on the borders of the dorsal plates and also on the DAPs (Fig. 13D) and the spines of the DAPs become scale-like, bordering the distal and lateral edges of these plates (Fig. 13E).

On the ventral side, specimens at 0.7mm dd show strong crown-shaped teeth and spinulose inferior teeth. The dental plate is very wide, short and imperforated. No mouth papillae are present and the oral gap is strongly rounded. The 1st VAP is somewhat bell-shaped with the proximal side shorter and straight. The oral shield (OS) is lozenge-shaped and the madreporite (M) can be recognized. Very small

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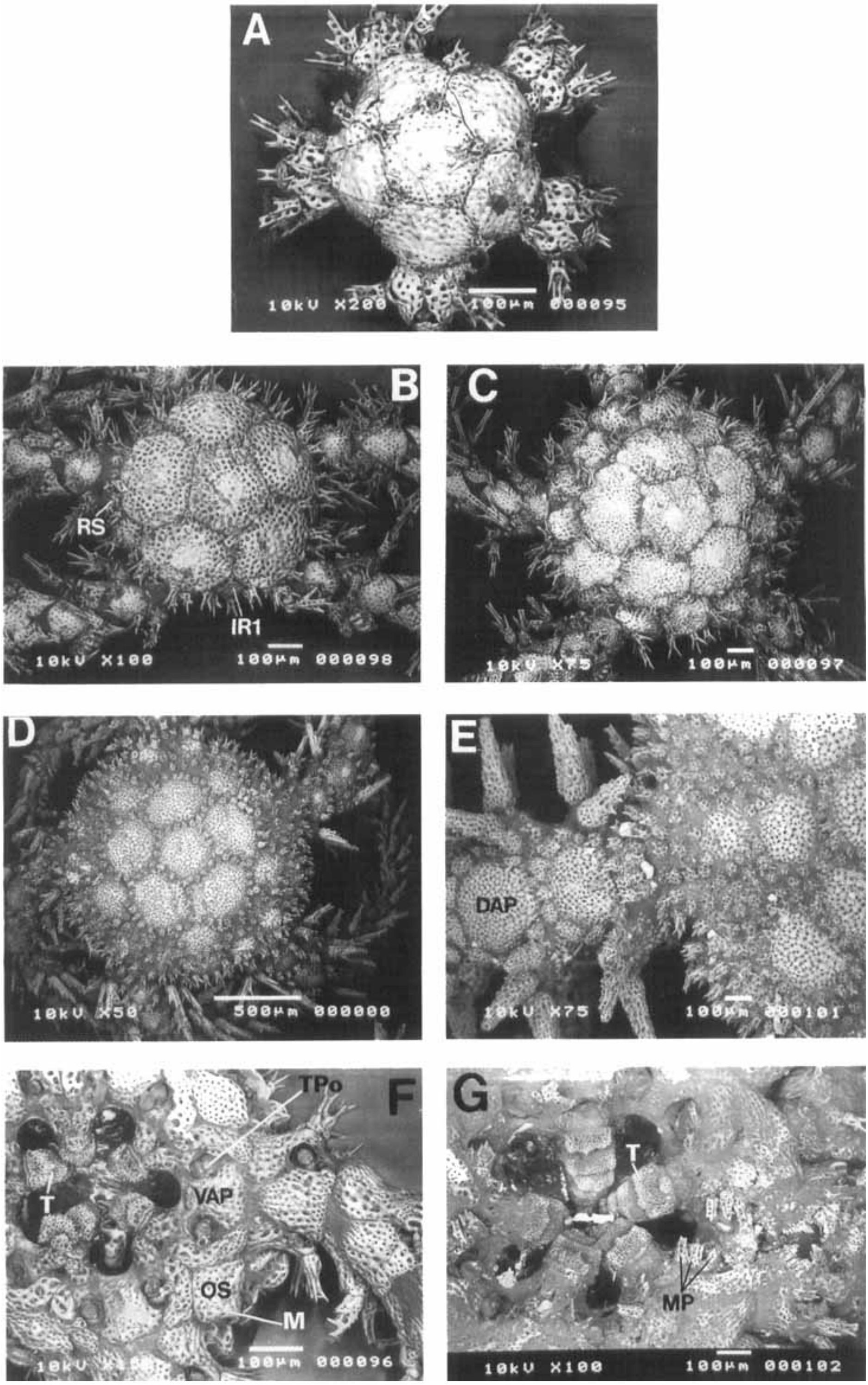
Figure 13. *Ophiopholis aculeata* postlarval development. A, dorsal view of a 0.3mm dd postlarva; B, 0.6mm dd individual (dorsal) with the 1st interradial plates (IR1) and the radial shields (RS); C, 1.0mm dd postlarva (dorsal); D, 1.5mm dd individual (dorsal). Note the arrangement of the disk spines; E, detail of the proximal arm segments and disk edge of a 3.0mm dd postlarva; F, ventral view of a postlarva at 0.7mm dd individual showing the teeth (T), the 2nd tentacle pore (TPo) and the oral shields (OS) with the madreporite (M); G, 2.0mm dd postlarva (ventral). Note the strong teeth and the mouth papillae (MP).


A
10kV X200
100μm 000095
B
RS
IR1
10kV X100
100μm 000098
C
10kV X75
100μm 000097
D
10kV X50
500μm 000000
E
DAP
10kV X75
100μm 000101
F
TPo
T
VAP
OS
M
100μm 000096
G
T
MP
10kV X100
100μm 000102

fenestrations are present on the ventral surface (Fig. 13F). At 2.0mm dd 3 spine-like MP are present (Fig. 13G).

DISCUSSION

General comments

One of the primary aims of the present study has been the accurate description of postlarval ophiuroids. These can be collected in large numbers in certain deep-sea areas at certain times of the year and many times they are put aside owing to the lack of expertise to match them to the respective adult. Most taxonomic keys are based on adult characters, which are not conspicuous or, more frequently, not well developed in the postlarvae. Thus, different features must be found in order to identify such organisms.

The study of morphological characteristics of early post-metamorphic stages revealed that the primary plates are very important specific features. The relative size of the central primary plate and its fenestration pattern and size are decisive in distinguishing congeneric species (see Taxonomic discussion, below). Some of the arm characteristics, as the size and shape of the adoral shield spines, dorsal arm plates and arm spines and the size, shape and fenestration pattern of the terminal plates can also be very useful (see *Ophiura albida*). Other important characters include the dental plate, teeth, mouth papillae and first ventral arm plate, but these appear to be more conservative within genera. However, the dental plate and the first ventral arm plate showed a certain degree of variation within the genus *Ophiura*. This variation may be important in grouping closely related congeneric species.

Despite the fact that Mortensen (1920) could not recognize the postlarvae of two species of *Amphiura*, other authors detected that some congeneric species were distinguishable from a very early post-metamorphic stage (Schoener, 1967, 1969; Muus, 1981; Webb & Tyler, 1985). The present data show that more species may be added to this list and evidence suggests all the species studied here have a distinct and recognizable postlarva.

Taxonomic discussion

Genus *Ophiacantha*

The mouth structures of *O. abyssicola* and *O. bidentata* are very similar in the smaller individuals. The shape and arrangement of the dorsal plates are very useful in the distinction of both species. *O. abyssicola* bears a pentagonal central primary plate (CPP) with five spines distributed on the corners of the plate, whereas *O. bidentata* possesses a irregular CPP (bean-shaped) with only two spines. As specimens get larger the dorsal structure becomes unclear and at this stage the oral shield (on the ventral side) is used for identification. In *O. abyssicola* the oral shield presents a groove in the median region of the plate, while in *O. bidentata* this structure is wide and plain, with no groove present.

Genus *Ophiura*

Postlarvae of *O. sarsi* and *O. carnea* are very similar under light microscopy. However, early stages of *O. carnea* can be distinguished under SEM by the fenestration pattern of the primary plates, with fenestrations which are small in the centre of the plate and much smaller on the edges. The central primary plate is smaller relative to the disk diameter and the adoral shield spines are slender and smooth, as opposed to the stubby and rough spines of *O. sarsi.*

The relative size of the central primary plate in *O. carnea* distinguishes it from *O. ljungmani*; the latter also has much larger fenestrations in the central parts of the primary plates, more elongated terminal plates, a somewhat ellipsoidal dental plate (as opposed to romboidal). A further distinguishing feature is the fenestration pattern and shape of the first ventral arm plate (in larger specimens, >1 mm dd). These characters and the relatively larger central primary plate also distinguish this species from *O. albida.*

O. albida differs largely owing to the the presence of a bulb-shaped terminal plate and the different stereom structure of the primary plates. The dorsal arm plates are also much wider than long in this species.

Genus *Ophiocten*

O. gracilis is easily distinguished from all examined *Ophiura* species by the presence of a very large central primary plate, with a characteristic fenestration pattern composed of small fenestrations in the centre of the plate which become larger towards the edges and then very small again at the very edge. The arm spines are much larger and the dorsal arm plates are more elongated.

Postlarvae of *O. affinis* can be distinguished from the former species of Ophiurinae by the different fenestration structure of the primary plates, the early appearance of the secondary interradial plate and by the presence of secondary scales surrounding the primary plates in individuals larger than 1 mm dd.

The systematic position of Ophiura affinis

The relationship between *Ophiura* and *Ophiocten* has been questioned by several authors (Mortensen, 1927, 1933, 1936; Clark & Courtman-Stock, 1976), owing mainly to the characteristics exhibited by the species *O. affinis*, which is, apparently, intermediate between both genera. Paterson *et al.* (1982) discuss such characters and, despite the fact that *O. affinis* possesses only one major characteristic in common with *Ophiura* (a well-developed notch on the disc margin above the arm bases), still consider the species as belonging to that genus. The characteristics found in *O. affinis* and species of *Ophiocten*, when adult, include the emergence of the second oral tentacle pore outside the mouth, the shape of ventral arm plates and the tentacle pore and scales of the proximal arm segments. The only intermediate feature found in *O. affinis* is the arm combs, which show an intermediate feature between both genera, which together with the notch over the arm bases, form the main characters that place *O. affinis* in the genus *Ophiura.* Yet Paterson *et al.* (1982) argue that the status of *O. affinis* needs to be checked after a revision is carried out for the genus *Ophiura.*

The well-developed notch over the arm bases and the arm combs considered typical of *Ophiura* is subject to a great deal of variation within this genus and even within the species *O. affinis.* In his description of this species, Mortensen (1927) describes the notch present over the arm as a small structure, containing only two small dorsal plates, whereas Paterson *et al.* (1982) point out a well-developed notch.

TABLE 3. Comparison of the main postlarval characters of *Ophiocten gracilis*, *Ophiura affinis* and *Ophiura sarsi*. VAP = Ventral Arm Plate

Characters	*Ophiocten gracilis*	*Ophiura affinis*	*Ophiura sarsi*
Teeth	long and slender	long and slender	broad triangle
Dental plate	ellipsoid	ellipsoid	rhomboid
1st VAP shape	convex proximally straight distally	convex proximally straight distally	pointed proximally convex distally
1st VAP fenestration pattern	large fenestrations throughout the plate, but the distal part with small and regularly distributed fenestration	large fenestrations throughout the plate, but the distal part with small and regularly distributed fenestration	fenestrations with the same size and distributed evenly throughout the plate
General shape of the disc and arms	disc with a sharp edge, with the arms not appearing to issue from the dorsal side of the disc	disc with a sharp edge, with the arms not appearing to issue from the dorsal side of the disc	margins of the disc not sharp arms appearing to issue from the dorsal side of the disc

Within the genus *Ophiura*, the notch can be well developed in species such as *O. carnea*, *O. sarsi* and *O. ljungmani*, or non-existent as in *O. clemens*, *O. nitida* and *O. violainae* (see Paterson, 1985). The same degree of variation is found for the arm combs, which can assume several shapes and dispositions. In the genus *Ophiocten*, there is, generally, no marked notch over the arm bases, but the same variation in the arm combs does occur. Mortensen (1927) points out that in *Ophiocten* ". . . usually a continuous comb of papillae across the base of the arms" is present. However, variation exists within the genus and some species show the arm combs continuous over the arm bases as in *Ophiocten sericeum* and *O. centobi* (Paterson *et al.*, 1982); arm combs confined to each side of the arms, as in *O. gracilis* (Paterson *et al.*, 1982) and *O. bisquamatum* (Mortensen, 1936); or arm combs reduced or absent as in *O. hastatum* (Paterson *et al.*, 1982). The characters observed in *Ophiura affinis* fall certainly within the range of variation found in both genera. Paterson *et al.* (1982) show the disposition of the arm combs in *Ophiocten abyssicolum* and argue that "the form of the papillae on the dorsal arm plates may suggest an affinity with *Ophiura affinis*". The range of variation in the shape and disposition of the arm combs is probably a good indicator of specific affinities, but not consistent enough to describe different genera within the Ophiurinae. Characters such as the emergence of the second tentacle pore and number of scales around this pore appear to be reliable distinguishing features between *Ophiura* and *Ophiocten*.

The study of homologous structures in the postlarvae of *Ophiura affinis* and *Ophiocten gracilis* showed that the similarity with *Ophiocten* is greater when comparing the early states of some important features. Characters such as the shape of the disk, tooth, dental plate and first ventral arm plate appear to be conservative within both genera. Comparing these characters with those found in *Ophiura sarsi* (Table 3), we found conspicuous differences, particularly in the shape of the dental plate. In *Ophiura sarsi* it is a large and robust rhomboidal plate, whereas in *Ophiocten gracilis* and *Ophiura affinis* it is ellipsoidal and more delicate. The tooth is also clearly different, with that of *Ophiura sarsi* being broader at the base. The characteristics referred to *O. sarsi* seem to agree with those of other postlarvae of *Ophiura* species, e.g. *O. carnea* (present work), *O. ophiura* and *O. albida* (Webb & Tyler, 1985). *O. ljungmani* presents an intermediate dental plate morphology.

The first ventral arm plates in *Ophiura affinis* and *Ophiocten gracilis* are also very similar (as is the distal part of the 1st VAP in *O. ljungmani*), as well as the general shape of the disk, mainly on the margins over the arm bases. In *Ophiura sarsi*, this part is continuous with the dorsal side of the disc and in *Ophiura affinis* and *Ophiocten gracilis* it is clearly detached. Mortensen (1927) points out that feature as distinctive of *Ophiocten*, where ". . . the notch above the arms is feeble and the arms thus not having the appearance of issuing from the dorsal side". Ursin (1960) found it very easy to distinguish small specimens of *O. affinis* from those of *O. albida*, but could not discern *O. ophiura* (= *O. texturata*) from *O. albida* and suggested that juveniles of both species were probably similar. In fact, small individuals of *Ophiura* are quite alike and difficult to recognize and the observations made by Ursin (1960) reinforces the proposal that *Ophiura affinis* does not belong to the genus *Ophiura*. Koehler (1897) described small individuals of *O. affinis* as a new species of *Ophiocten* (*O. scutatum*). Furthermore, the adult features in common with the *Ophiura* described above are, therefore, considered within the range of variation found among congeners of *Ophiocten*. We propose that the postlarval characteristics described above and the adult features known for the species are sufficient to consider *Ophiura affinis* as belonging to the genus *Ophiocten*.

Phylogenetic considerations

The ontogenesis of homologous structures in the ophiuroid postlarvae can be useful when defining systematic and phylogenetic relationships among taxonomic groups (Hendler, 1988).

The development of the mouth papillae differed among the different genera studied. In *Ophiura* and *Ophiocten* the first mouth papilla (= buccal scale) is block-like, appearing on the distal part of the jaw in larger specimens. Additional mouth papillae are added in an unidirectional sequence, from distal to proximal along the jaw. The same pattern of development is observed for *Ophiura ophiura* (Webb & Tyler, 1985) and probably for *O. scomba* (pers. obs.). The mouth papilla in these species appears to be serially homologous. However, the fourth mouth papilla (and maybe the third) appears to originate from the dental plate, in which case it 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. The general development of the oral frame within the family Ophiuridae seems to differ between different genera. Schoener (1967, 1969) presented the oral frames of five different genera of deep-sea species and they look very different from the *Ophiura*/*Ophiocten* examined. Unfortunately, Schoener did not show the development of the mouth papillae in detail and provided no descriptions.

The mouth papillae in both *Ophiacantha abyssicola* and *Ophiactis abyssicola* are not serially homologous. In *Ophiacantha abyssicola*, the first mouth papilla is formed by the adoral shield spine, which is serially homologous with the arm spines (see Hendler, 1988), whereas the second mouth papilla is formed on the jaw (not shown in the present paper).

In *Ophiactis abyssicola*, the first mouth papilla is probably the adoral shield spine and the second is the buccal scale. The development of the buccal scale in this species (and in *Ophiactis balli*, pers. observ.) is similar to that of some amphiurids. Hendler (1988) shows that in the *Amphiura* and *Amphioplus* groups the buccal scale are not resorbed as in the *Amphiodia* and *Amphipholis* groups. The buccal scale in those groups suffers an enlargement of the proximal end in a similar fashion to that of *Ophiactis abyssicola*. In *O. abyssicola*, the buccal scale develops further to form an elongated mouth papilla placed deep inside the mouth.

The appearance of the secondary interradial plates in the Ophiuridae is also interesting. In some species like *O. ljungmani* (Schoener, 1967; present work), *O. scomba* (pers. observ.), *O. ophiura* (Webb & Tyler, 1985), *Ophiocten affinis* and *O. gracilis*, these plates appear earlier during ontogenesis (<1.5mm dd). Later appearance occurs in *Ophiura sarsi*, *O. carnea* and *O. albida* (Webb & Tyler, 1985) (>2.5mm dd).

Development of the oral frame in *Ophiocten* species appears to stop at an early stage, similar to early ontogenetic stages in *Ophiura*. Could this represent a paedomorphic feature in the evolution of the genus *Ophiocten*? How much these events reflect phylogenetic affinities among the groups is not yet known, but these characters could be useful data to test phylogenetic schemes of the Ophiuroidea, such as that of Smith *et al.* (1995). Nevertheless, more data should be gathered on the early development of ophiuroids in order to test such phylogenies.

Ecological considerations

Gage (1994) emphasizes that recruitment and age structure in deep-sea populations are important in understanding processes structuring highly diverse communities found in sediments and for the knowledge of rates of colonization to predict recovery times from perturbations (see also Gage, 1991). The early phases in the development of juveniles are of great importance since such organisms are subject to high rates of mortality (Gage, 1984; Tyler *et al.*, 1991). Competition for resources can also be significant.

Recently, Medeiros-Bergen (1996) related different types of tooth with micro- and macrophagous feeding habits in adult ophiuroids. The mouth structure of congeneric postlarvae is very similar and conservative within the group. This suggests that congeneric species could compete for the same kinds of food (some specimens were observed to consume large food items, such as entire forams) and space, generating intra- and interspecific competition. In habitats containing several congeneric species, settlement, recruitment and growth rates should be fundamental in structuring those communities, controlling the relative abundance and distribution of adult populations. Fast growth rates can be very important in avoiding predation by larger organisms. Tyler *et al.* (1993) report that juveniles of the deep-sea urchin *Hemiaster expergitus* are heavily preyed on by the seastar *Bathybiaster vexillifer*. Gage & Tyler (1982c) point out that the deep-sea ophiuroid *Ophiomusium lymani* grows rapidly to a larger size during the early post-metamorphic stages, probably to avoid predation. Postlarvae of *Ophiocten gracilis* also grow very fast and start gametogenesis very early during development (Sumida *et al.*, in prep.). As the animals grow larger, they probably become less susceptible to predators after attaining a certain size. Gage (1984) points out that postlarvae and juveniles initially grow quickly, but are subjected to high mortality through predation and resource competition.

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