

# Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms

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The ophiuroid skeleton continues to develop well beyond metamorphosis and small juveniles often lack many of the characters used to identify adult specimens. The ecological role of postmetamorphic stages is largely unknown mainly due to difficulties with their identification. Accurate descriptions of postlarvae and their development are therefore necessary to match them to their adult conspecifics. However, juveniles are known for less than 2% of the about 2000 extant species of ophiuroids. Consequently, the taxonomic value of juvenile characters is still poorly understood. In this study, the postlarval ontogeny of the non-brooding *Ophioscolex glacialis*, *Ophioscolex purpureus*, *Ophiolimna bairdi*, *Ophiopleura borealis*, *Ophiura robusta*, *Amphiura chiajei*, *Ophiopus arcticus*, *Histampica duplicata*, *Ophiothrix fragilis*, *Ophiocomina nigra*, and the brooding *Ophiomitrella clavigera*, *Ophiacantha anomala* and *Amphiura borealis* are described for the first time. The first complete description of the development of *Amphiura filiformis* is provided, for which previously only the development of the oral skeleton had been described. Previous descriptions of postlarvae of *Ophiura ophiura*, *Ophiura albida* and *Asteronyx loveni* are supplemented. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 143, 543–576.

ADDITIONAL KEYWORDS: growth series – morphology – ontogenesis – postlarvae – SEM – taxonomy.

## INTRODUCTION

The first studies on ophiuroid postmetamorphic ontogeny were made over a century ago, but progress since has been slow. Ludwig (1881, 1898, 1899) described the development of the main skeletal elements of the early ophiuroid juvenile (postlarva) and the order in which these elements are formed. His work was supplemented by that of Clark (1914). Owing to difficulties with the identification of juvenile stages, early studies focused on brooding species, particularly the small brooding *Amphipholis squamata* (Delle Chiaje, 1828), which has a wide circumtropical distribution and bears young almost all year round (Ludwig, 1881; Fewkes, 1887; Fell, 1946). However, only about 55 species of ophiuroids have been reported as brooding (Hendler, 1975), which is less than 3% of the known approximately 2000 species (Hendler *et al.*, 1995), although the reproductive mode of many species is

unknown and additional species may be recognized as brooding. Indeed, larval types are known for little over 1% of all ophiuroids, although at least 48 ophiopluteus species are known that have not been assigned to an adult (Hendler, 1975).

Postlarvae have been described for fewer than 30 non-brooding species or about 1.5% of all ophiuroids, the majority of them from the North Atlantic (Mortensen, 1912; Schoener, 1967, 1969; Stancyk, 1973; Hendler, 1978; Muus, 1981; Bartsch, 1985; Webb & Tyler, 1985; Turner & Miller, 1988; Sumida *et al.*, 1998). Surprisingly, even for the most common and well-studied species, only limited descriptions of early postmetamorphic development exist. Mortensen (1920) studied the larval development of *Amphiura filiformis* (O.F. Müller, 1776), a common, predominantly shallow-water species of the north-eastern Atlantic (Paterson, 1985), but he did not describe the postlarva, except for a brief reference to 'the very characteristic structure of the disc plates'. Muus (1981), in her study on juvenile growth, included drawings of the dorsal aspect of newly settled *A. filiformis* and *Amphiura*

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*chiajei* Forbes, 1843, again with a short reference to differences in the structure of the disc plates as a diagnostic character in combination with the shape of the terminal arm plate, but no information on the later morphogenesis of the skeleton was provided. Hendler (1988) studied the morphogenesis of the oral structures in *A. filiformis*, including a brief description of the scalation of the dorsal disc but without pictures. Sköld, Josefson & Loo (2001) presented images of *A. filiformis* postlarvae from newly settled specimens to individuals with four arm segments (including the terminal plate), but the authors admitted being uncertain about their identification, which emphasizes the need for a complete description. *Amphiura filiformis* is often found sympatric with *A. chiajei* and accurate descriptions of all growth stages of both species are therefore desirable. Fenaux (1963) provided a description of the larval development of *A. chiajei*, including the formation of the primary and terminal plates at the end of metamorphosis, but no description of the postlarval stages of *A. chiajei* is available. Another otherwise well-known, common species of European seas is *Ophiothrix fragilis* (Abildgaard, in O.F. Müller, 1789). The young of this species are known to settle on adult conspecifics and they can be found crawling in great numbers on the disc and arms of adults (Broom, 1975; my pers. observ.). The larval development of *O. fragilis* was studied in detail almost a century ago (MacBride, 1907), but apart from a brief comment in Mortensen (1927), characterizing the young *O. fragilis* as having a large, naked and shining central disc plate, no details on the postlarval development of this species have been published.

Attempts to identify juvenile ophiuroids using keys based on adult characters encounter difficulties because these characters usually develop well beyond metamorphosis (Ludwig, 1881, 1899). Keys including juvenile characters are not available and illustrations are either lacking in many of the early studies or not detailed enough to allow accurate identifications. Only recently, with the use of scanning electron microscopy, have a number of accurate descriptions been produced (Webb & Tyler, 1985; Hendler, 1988; Sumida *et al.*, 1998). Juvenile characters of ophiuroids are important for the understanding of adaptations to the lifestyle of the small stages, which is most likely different from the adult lifestyle. As part of the benthic meiofauna the smallest postlarvae are likely to be subjected to different environmental conditions, different food sources and a higher predation pressure than larger individuals. However, as pointed out by Sumida *et al.* (1998), little is known about the ecology of most ophiuroid species on the postlarval stage, which can be attributed at least in part to the difficulties with identification.

Clark (1911: 3) pointed out that 'one of the principal reasons why the ophiurans are such a difficult group to classify is found in our ignorance of their growth changes'. In light of the small number of known postlarvae, this statement still holds true. Phylogenetic affiliations cannot be understood without including all life stages. Juvenile characters that have been shown to have taxonomic value include the form of the primary disc plates, the plate fenestrations and stereom structure, the shape of the terminal arm plate and other arm characteristics (Webb & Tyler, 1985). Hendler (1988) reviewed homologies among skeletal structures and found some characters such as oral papillae to be more reliable for interpreting phylogenetic relationships than others such as the presence or absence of a primary rosette in the scalation of the dorsal disc in small juveniles. However, the systematic value of most features in juvenile morphology is still poorly understood, because most postlarvae are unknown.

The purpose of this study is to provide accurate descriptions of previously unknown juvenile stages of ophiuroids for both ecological studies and phylogenetic analyses. Ontogenetic series of 14 species are presented for the first time in this paper, among them three viviparous species. Descriptions of postlarvae of *Ophiura albida* Forbes and *Ophiura ophiura* (L., 1758) are supplemented. The development of *Asterozox loveni* Müller & Troschel, 1842 has been described in great detail by Mortensen (1912), but its postlarvae have since been confused with several different species. A redescription therefore seems warranted.

## MATERIAL AND METHODS

The material studied originates from bottom samples and thus includes only juveniles that had already settled on the ocean bottom. Samples were initially preserved in formalin and later transferred to 80% ethanol. Most of the animals presented originate from Icelandic waters, collected by the BIOIce (Benthic Invertebrates of Iceland) programme at depths of between 17 and 3006 m. Additional material of *A. filiformis*, *A. chiajei*, *O. fragilis* and *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1789), collected in the North Sea at the Swedish west coast off Kristineberg Marine Station (KMS) and Tjärnö Marine Biological Laboratory (TMBL) at depths of between 8 and 25 m, was also included in this study. Juveniles were identified by tracing characters backwards through growth series from adults to the smallest individuals, a method successfully employed in previous studies (Schoener, 1967, 1969; Webb & Tyler, 1985; Sumida *et al.*, 1998).

All species were identified in alcohol using a dissecting microscope. Even in species with relatively thick skin, all skeletal elements and their stereom structure

are clearly visible, because the skin is transparent in small stages, only gradually thickening and becoming opaque during development. This decrease in skin transparency correlates with the development of adult characters, which can be used when the stereom structure is no longer visible.

After identification, individuals of different sizes were selected for scanning electron microscopy (SEM). The integument was removed as far as possible, without disintegrating the skeleton, by submerging the specimens in solutions of 1 : 1 water and household bleach (NaOCl) for 5–20 s. Bleaching time increased with the size of the animal and it also differed between species. After bleaching, the animals were air-dried and mounted on aluminium stubs using non-permanent spray glue. Small specimens were mounted wet and left to dry on the glue. When necessary, an animal was removed from the stub by dissolving the glue in butyl acetate, and remounted with new glue to scan the opposite side of the individual. The samples were scanned using a Hitachi FE-SEM 4300.

The term 'postlarva' is not well defined and is here used from a morphological point of view for young animals after completion of metamorphosis until the development of adult characters. However, the transition from postlarva to adult is fluent as many species continue to grow well beyond the point where they can be considered identifiable by adult characters. In addition, the term 'juvenile' has been used interchangeably with 'postlarva' in the literature for newly metamorphosed animals to sizes of at least 2 mm disc diameter (Webb & Tyler, 1985). From a physiological point of view, sexually immature but morphologically well-developed individuals should probably be treated as juveniles rather than adults, although the term 'postlarva' seems no longer appropriate. Disc diameter (dd) has been measured from the edge of an inter-radius across the dorsal disc surface to the edge of the opposite radius (distal edge of the radial shields where present), using the magnification given by the SEM or in larger animals using a dissecting microscope and micrometer. The ophiuroid disc always incorporates the modified first arm segment, which proximally joins with its vertebra to the jaw, externally represented by the first ventral plate and the adoral shields. Excluding this specialized segment, the number of arm segments is counted from the first 'true' segment, containing a regular vertebra and lateral plates, to the distalmost segment before the terminal plate. The term primary rosette refers to the central primary plate and the five radial primary plates on the dorsal disc. The terminology and abbreviations used follow Sumida *et al.* (1998) to facilitate parallel usage of both papers. Mouth papillae are numbered following Sumida *et al.* (1998), which means the buccal scale is the first mouth papilla and the one forming

proximal to it is labelled as second mouth papilla, while the adoral shield spine is excluded from the series of mouth papillae. This is in contrast to Hendler (1988), who suggested that the adoral shield spine should be counted as second mouth papilla, because it appears second to the buccal scale and gradually moves closer to the series of mouth papillae during development often becoming indistinguishable from them in the adult. If that suggestion was followed the papilla developing proximal to the buccal scale would be the third mouth papilla. The classification follows Smith, Paterson & Lafay (1995).

#### ABBREVIATIONS

|     |  |
|-----|--|
| AS  | adoral shield  |
| ASS | adoral shield spine  |
| BS  | buccal scale   |
| CPP | central primary plate  |
| DAP | dorsal arm plate   |
| DP  | dental plate   |
| IP  | infradental papillae   |
| IR  | inter-radial plate   |
| J   | jaw  |
| k   | k-plate, wedge-shaped plate separating a pair of radial shields (from the German word <i>Keil</i> meaning wedge; Ludwig, 1899) |
| LAP | lateral arm plate  |
| M   | madreporite  |
| MP  | mouth papilla  |
| OS  | oral shield  |
| RPP | radial primary plate   |
| RS  | radial shield  |
| SIR | secondary inter-radial plate   |
| TP  | terminal plate   |
| Tpo | tentacle pore  |
| TS  | tentacle scale   |
| VAP | ventral arm plate  |

#### RESULTS

CLASS OPHIUROIDEA GRAY, 1840  
 ORDER EURYALIDA LAMARCK, 1816  
 FAMILY ASTERONYCHIDAE MÜLLER &  
 TROSCHEL, 1840

*ASTERONYX LOVENI* MÜLLER & TROSCHEL, 1842  
 (FIG. 1A–Q)

*Ophiuraster patersoni* Litvinova, 1998  
*Ophiomyxa serpentaria* – Stöhr, 2004 (postlarvae only)  
 The habitus of the smallest postlarvae with a relatively large disc and short, not clearly offset arms is more similar to Asteroidea than Ophiuroidea. Among North Atlantic ophiuroid postlarvae this is a unique shape. The smallest individuals measure 1.8 mm dd, with two arm segments, which is the largest for any species known so far, but slightly smaller than those

presented by Mortensen (1912). The postlarvae are characterized by large, slightly raised primary plates, a thick skin, evident particularly on the naked areas of the dorsal interradius, and large plates bordering the disc margin (Fig. 1A). The TP is bulbous, ending in three short thorns and oval RSs are present (Fig. 1B). The DP bears a rugose, triangular tooth and on each lateral edge a low, wide, rugose MP. The oral plates of adjacent jaws are connected by transparent skin (Fig. 1C). Growth is allometric, with arm length increasing faster than disc size.

At 2.5 mm dd, the TP is hollow and inflated with a wide distal opening (Fig. 1I). Narrow RSs are present in addition to the primaries (Fig. 1D), and the LAP bears two hook-shaped arm spines (Fig. 1F). The large marginal plates have been interpreted as LAP of the first arm segment, which move to the ventral side of the disc during development and form the ASS (Mortensen, 1912; Stöhr, 2004; Fig. 1E). The vertebrae seem to have an hour-glass-shaped articulation, but their undeveloped condition makes them difficult to interpret (Fig. 1G, H).

At 3.2 mm dd, long bar-like RSs are visible beneath the thick skin, overlaid by several round overlapping plates on their proximal half (Fig. 1J). In the centre of the disc, fragments of the primary plates with irregular edges are barely visible, perforated by large fenestrations. There are no DAPs and the LAPs bear two hook-shaped spines. The TP is bulbous, hollow and composed of several plates (Fig. 1L). The jaw bears a rugose apical tooth and 2–3 smaller rugose MP to either side (Fig. 1K). There is no ASS and the M is the only OS. The VAP is pentagonal with straight lateral and distal edges and proximal angle; the following plates are widely separated by the LAPs. Short bursal slits are present below the raised oral frame, next to the first arm segment. The ventral disc is naked, covered with thick skin. The vertebrae show an hour-glass-shaped articulation (Fig. 1P, Q).

At 4 mm dd, the proximal ends of the RSs are overlaid by numerous plates and the primary plates have disappeared completely (Fig. 1M). The LAP bears four hooks, the ventral ones with two teeth and the dorsalmost spine with only a terminal tooth (Fig. 1O). The TP tapers to a narrow end with a small opening. There are still three small, widely spaced MP and the deeper teeth are larger and more block-like than the first tooth (Fig. 1N). At this size, the animals can be identified using keys based on adult characters.

*Remarks:* The small postlarvae of *Asteronyx loveni* have been described as *Ophiuraster patersoni* by Litvinova (1998), but Stöhr (2004) showed that *O. patersoni* is a postlarva. Unfortunately, the growth series was then mistakenly associated with *Ophiomyxa serpen-*

*taria*. There are striking similarities between small *A. loveni* and *O. serpentaria* such as the thick skin, the serrated mouth papillae, the absence of dorsal arm plates and the hook-shaped arm spines (on the distal arm in adult *O. serpentaria*). Recently obtained clearly identifiable larger juveniles of *A. loveni* suggested that the postlarvae previously presented as *O. serpentaria* are actually younger individuals of *A. loveni*, which changes the synonymy of *O. patersoni* once again. Mortensen's (1912) description supports this conclusion.

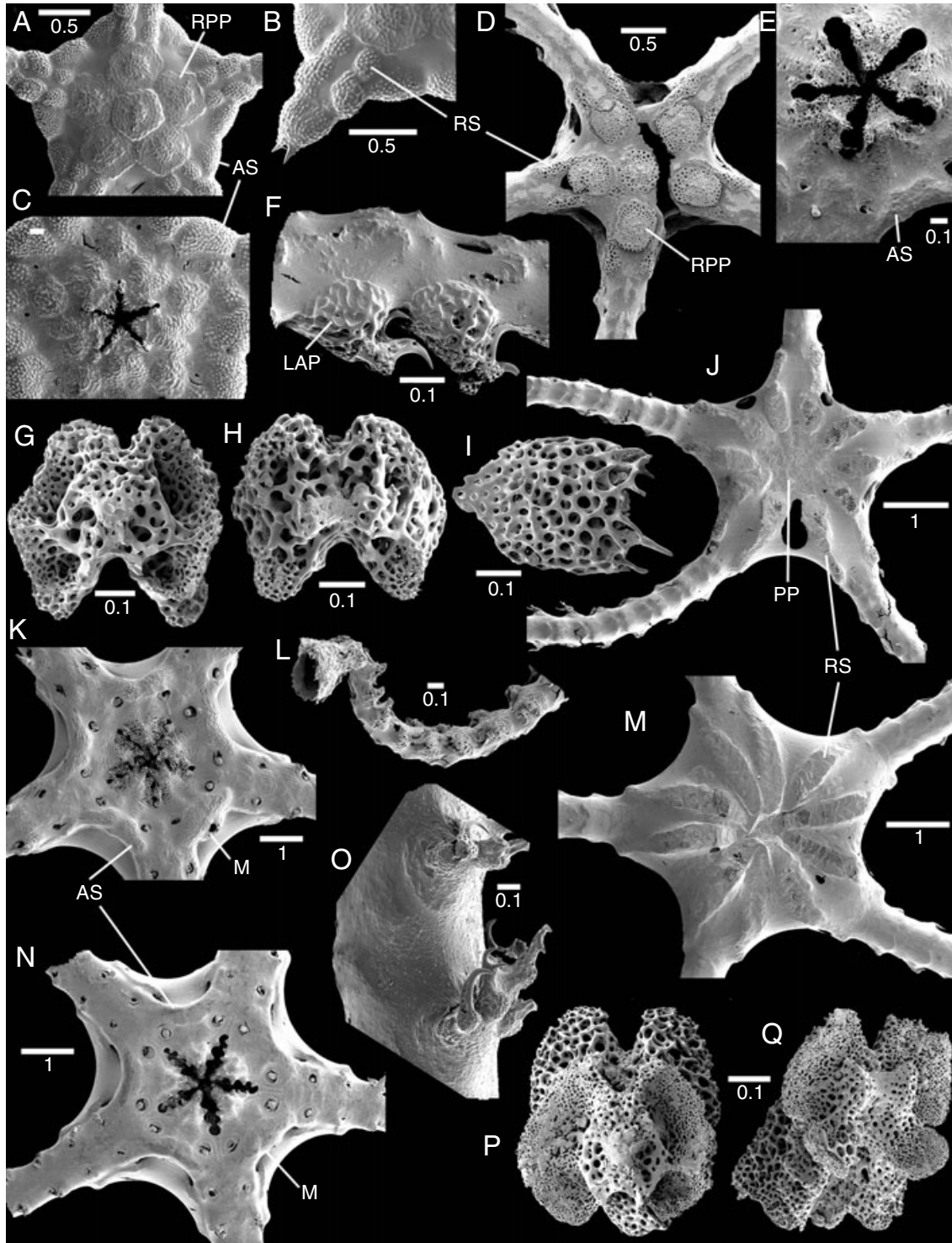
The large 'marginal plates' of the small postlarvae were interpreted as ASSs by Stöhr (2004), which concurs with Mortensen (1912). They lie next to the first 'true' arm segment, enclosing the LAP of that segment. RSs are present in the smallest individuals on top of the LAP of the first arm segment (Fig. 1A), which is unusual for such a young stage. However, these animals may not represent the earliest postlarva and examination of metamorphosing larvae is required.

Postlarvae of *A. loveni* are unmistakable among the species presented here. They have their closest affinities with *Ophiuraster belyaevi* Litvinova, 1998 from the Kerguelen Islands, which is probably the young of another species of *Asteronyx*.

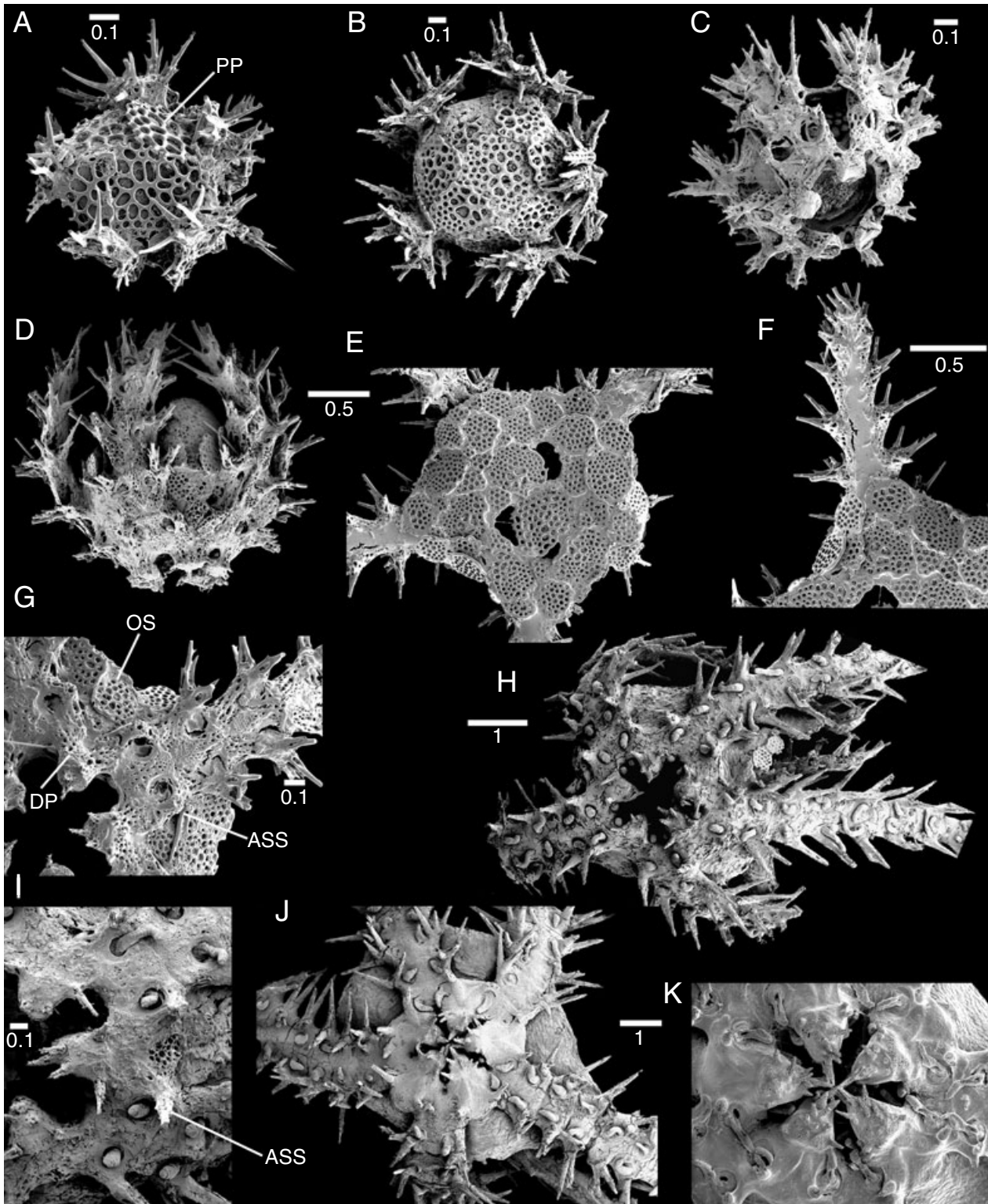
ORDER OPHIURIDA MÜLLER & TROSCHEL, 1840  
 FAMILY OPHIOMYXIDAE LJUNGMAN, 1867  
*OPHIOSCOLEX GLACIALIS* MÜLLER & TROSCHEL, 1842  
 (FIG. 2A–I)

The animals are covered with thick skin, transparent in small stages, obscuring the plates in the larger individuals. The smallest postlarva found has a dd of 0.5 mm, with a round, convex disc, and the short arms consisting of two segments are vertically erect above the disc (Fig. 2A). The dorsal part of the disc consists of five plates of different sizes and shapes. The plates overlap at the edges and meet in the centre, while the CPP appears to be lacking. The plate stereom is perforated by large oval fenestrations, which extend to the plate edge, giving it a jagged appearance. The TP of the arms bears 3–5 long, simple terminal spines. Each of the two arm segments bears two large arm spines on either side with several secondary teeth and a broader base. The jaw appears to end in the DP; no tooth is visible.

At 0.9 mm dd, a CPP can be recognized, surrounded by a circle of seven similar, round RPPs. The plate fenestrations are smaller than before, larger in the central part of the plates, and smaller on the margins (Fig. 2B). There are still only two multipointed, fenestrated spines to each side of an arm segment. The jaw is short, lacking oral papillae (Fig. 2C). The ASS is similar to the following arm spines.



**Figure 1.** *Asteronyx loveni* postlarval development, note the thick, partly removed, skin. A, 1.8 mm dd postlarva dorsal; B, arm of same postlarva, note the radial shields; C, same individual ventral, note the large adoral shields; D, 2.5 mm dd postlarva dorsal; E, same individual ventral; F, arm of same individual lateral; G, vertebra proximal face; H, vertebra distal face; I, bulbous terminal plate; J, 3.2 mm postlarva dorsal; K, same ventral; L, arm distal, note the wide terminal plate; M, 4 mm dd postlarva dorsal; N, same ventral; O, arm spines of same; P, 3.2 mm postlarva vertebra proximal face; Q, distal face. *Abbreviations:* AS, adoral shield; LAP, lateral arm plate; M, madreporite; PP, primary plates; RPP, radial primary plates; RS, radial shield. Scale bars in millimetres.



**Figure 2.** *Ophioscolex glacialis* postlarval development. A, 0.5 mm dd postlarva dorsal; B, 0.9 mm dd postlarva dorsal; C, 0.9 mm postlarva ventral; D–G, 1.7 mm postlarvae; D, lateral; E, dorsal, note the irregular pattern of plates; F, arm dorsal; G, ventral, a spiniform tooth and two mouth papillae have formed; H, I, 3 mm dd juvenile ventral, note the large adoral shield spine; J, K, adult ventral. *Abbreviations:* ASS, adoral shield spine; DP, dental plate; OS, oral shield; others as in Fig. 1. Scale bars in millimetres.

In the larger postlarvae, the disc has a sac-like shape, which in combination with the often upwards directed arms results in a habitus similar to that of the ophiacanthid genus *Ophiomyces*. With four arm segments and 1.7 mm dd (Fig. 2D–G), the number of dorsal disc plates has increased, but individual plates cannot be traced back to earlier stages. RSs appear to be lacking. Each LAP bears three thorny spines and the TP bears a cluster of five spines (Fig. 2F). The ventral disc is covered with smaller round plates similar to the dorsal plates. A spiniform tooth has formed, accompanied by two shorter spiniform MP on the DP (Fig. 2G). On the AS, next to the second TPo, a spine-like ASS is present, although this has fallen off on most plates, leaving the spine articulation visible (Fig. 2G).

Until the animals possess about 11–12 arm segments, the arms tend to stand vertical above the high sac-like disc. In larger animals, the disc flattens and the arms retain a more horizontal position. At 3 mm dd there are two apical papillae forming a cluster with the tooth, widely separated from the single lateral papilla to each side of the jaw; all are spiniform (Fig. 2H, I). These characters are close to the adult state, allowing identification using common keys.

In adults, the thin glassy scales are deeply embedded in the skin. There is a cluster of spiniform papillae on the DP and 1–2 MP on the distal oral plate (Fig. 2J, K). The ASS is the only spine next to a TPo, all other pores being scale-less.

*Remarks:* The postlarva of *Ophioscolex glacialis* is unusual with its *Ophiomyces*-like (Ophiacanthidae) habitus, which distinguishes it clearly from other postlarvae known so far. However, the spiniform mouth papillae and the thick skin distinguish it from *Ophiomyces*. In *Ophiomyces*, the sac-like shape of the disc has been attributed to the lack of radial shields (Paterson, 1985), which are thought to stabilize the disc. Possibly, the same is true for *O. glacialis*, because no radial shields can be distinguished among the disc plates of the postlarvae.

*OPHIOSCOLEX PURPUREUS* DÜBEN & KOREN, 1846  
(FIG. 3A–J)

A single specimen with 0.6 mm dd and five arm segments is smallest among all postlarvae found of this species. The dorsal part of the disc consists of the CPP and five RPPs, with small RSs visible beneath the RPPs on the arm bases. The OSs are visible at the disc edge, one of them with a short stump-like protrusion identifying it as the M. The plate margins bear few short, conical, serrated spines with wide round bases. Plate fenestrations are rather small and the plate margins are almost imperforate

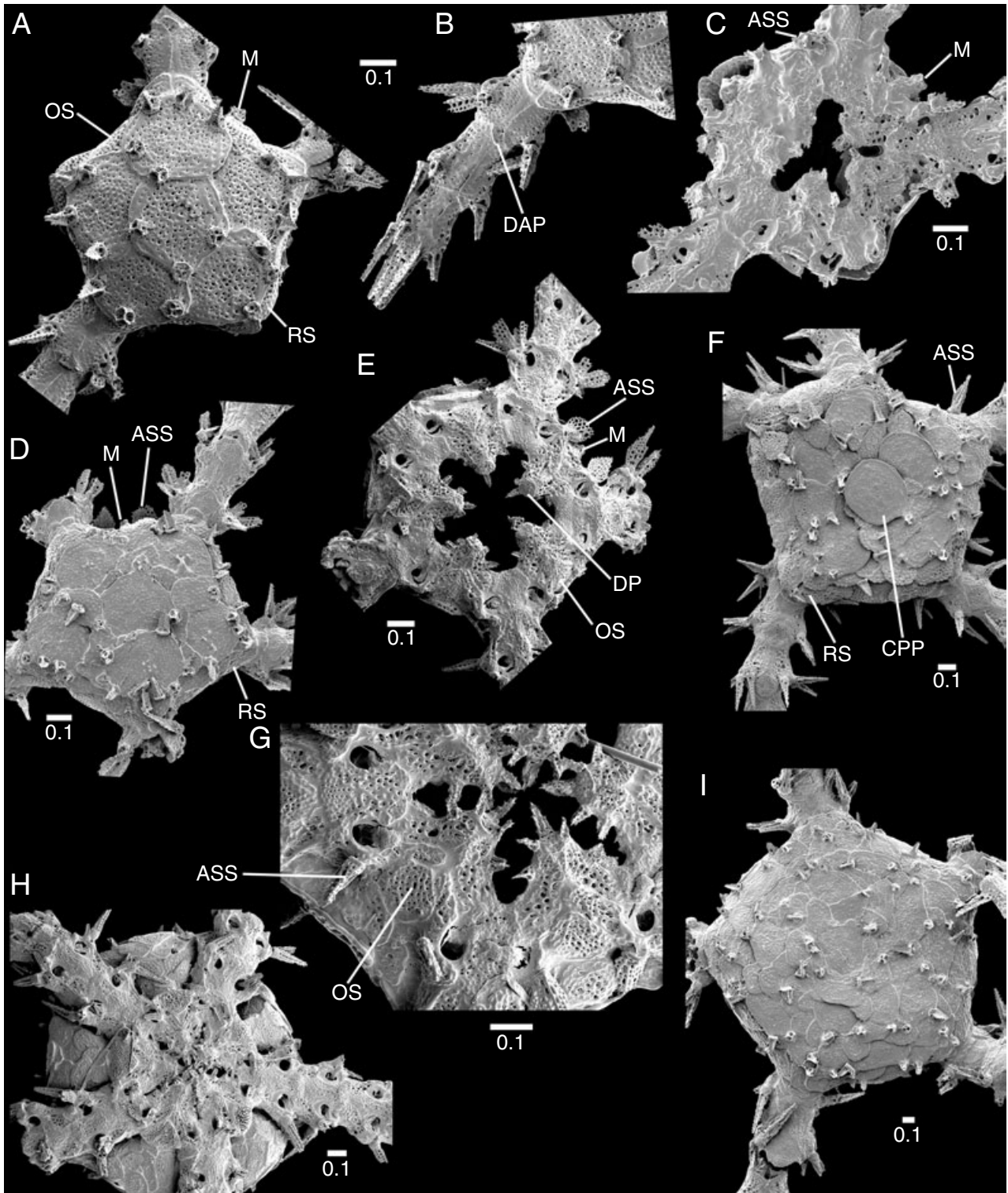
(Fig. 3A). The first arm segment bears a small, triangular dorsal plate with convex distal edge; each segment has two short conical spines to either side with longitudinal rows of round fenestrations (Fig. 3B). The integument of the ventral side could not be completely removed and handling the single animal to scan both sides caused additional damage such as loss of spines, but the remaining ASSs appear to be short multifid stumps. The oval DP bears a block-like serrated tooth and a conical MP at each side (Fig. 3C).

The next largest individuals found have a dd of 0.9 mm. There are three short flat arm spines with several rows of perforations on the most proximal segment, and two on the following segments. Additional dorsal plates have formed in an irregular pattern, partly overlaying the RPPs. All plates are almost imperforate (Fig. 3D). The ASs are narrow, the triangular OSs are about as long as wide and the M still bears its protrusion. The DP is wider than long, with convex proximal edge and distal angle, bearing a small conical papilla to either side. In the mouth angle a longer, spiniform papilla arises from the oral plate. The ASS is flat, pointed leaf-shaped with a wide rounded base, situated close to the disc edge, pointing outwards and visible also from the dorsal perspective (Fig. 3E).

With increasing size, the number of dorsal plates increases, the CPP remaining the largest for some time (Fig. 3F), although it is no longer obvious in the adult. The ASS changes shape to a simple conical spine (Fig. 3G). The number of MP increases until they form a row along the jaw edges, but there is no cluster of apical papillae as in *O. glacialis* (Fig. 3G, H). The dorsal disc scales are increasingly obscured by thick skin and scattered short spines (Fig. 3I). The TPo bears a small spiniform scale. From about 2 mm dd, adult characters can be used for identification.

A diagnostic character of *O. purpureus* is the hook-shaped distal arm spine, which could not be found in the postlarvae. However, as is often the case with Ophiomyxidae, most individuals were rather severely damaged and the distalmost tips of the arms were lost in the larger animals.

*Remarks:* *Ophioscolex purpureus* can readily be distinguished from *O. glacialis* by its flat habitus with horizontal arms, which may be explained by the presence of radial shields in *O. purpureus*. The size of plate fenestrations and the presence/absence of disc spines further distinguish the species from each other. Both can be distinguished from *Ophioscolex tripapillatus* Stöhr & Segonzac, in press, found off Iceland, which has a long spiniform tentacle scale in the postlarval stage and lacks disc spines.



**Figure 3.** *Ophioscolex purpureus* postlarval development. A–C, 0.6 mm dd postlarva; A, dorsal; B, arm dorsal; C, ventral; D, E, 0.9 mm dd postlarva; D, dorsal; E, ventral, note the leaf-shaped adoral shield spine; F, 1.5 mm dd postlarva dorsal; G, same ventral; H, 1.8 mm dd postlarva ventral; I, same dorsal. *Abbreviations:* CPP, central primary plate; DAP, dorsal arm plate; others as in Figs 1, 2. Scale bars in millimetres.

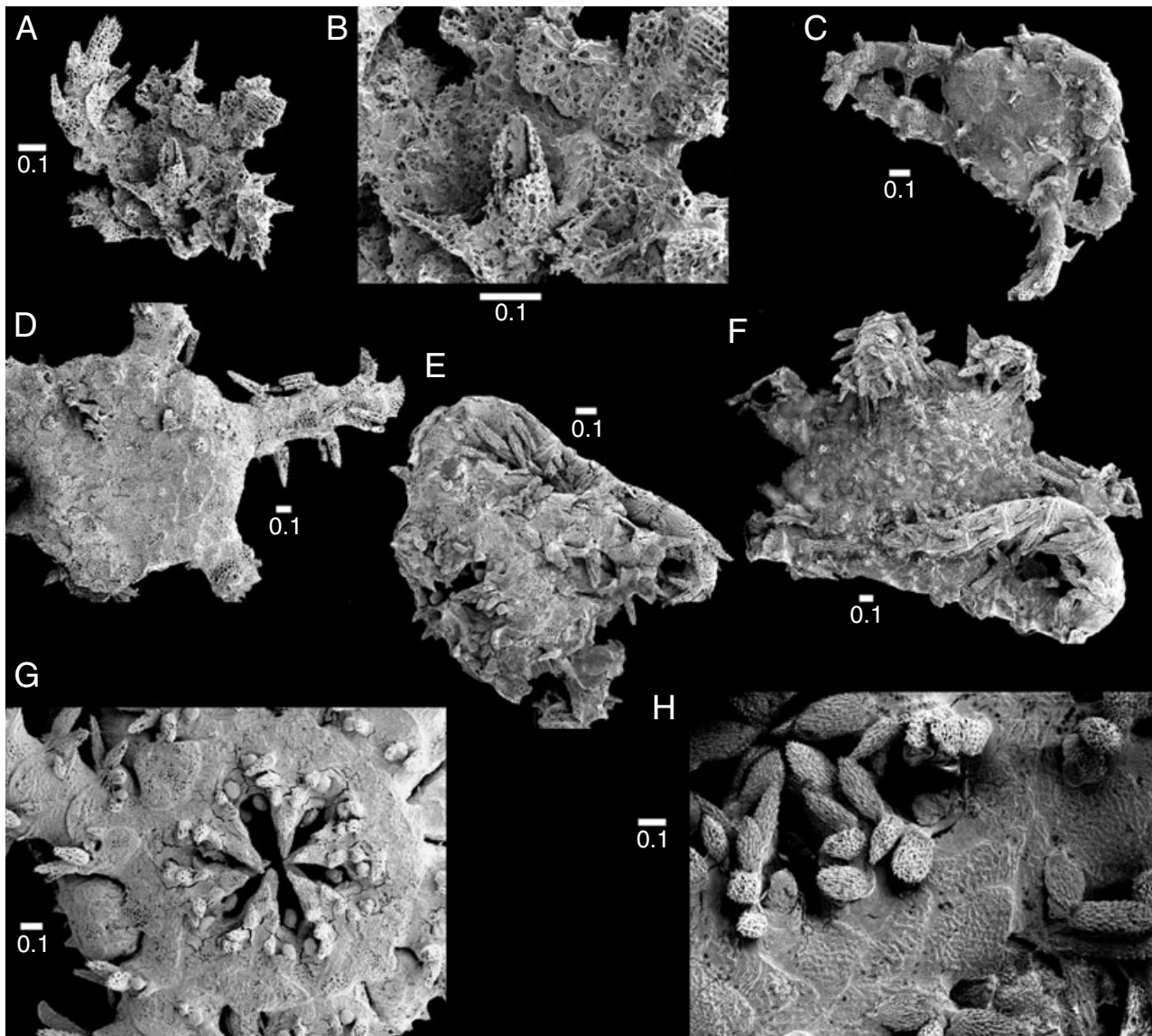


FAMILY OPHIACANTHIDAE PERRIER, 1891  
 SUBFAMILY OPHIACANTHINAE PATERSON, 1985  
*OPHIACANTHA ANOMALA* G.O. SARS, 1871  
 (FIG. 4A–H)

This hexamerous species is viviparous, with the embryos developing deeply embedded in the gonads (sometimes together with unidentified Myzostomatidae), not just lying in the bursae as in many other brooding species. All embryos are covered with thick skin and their disc is often compressed with arms vertical. The smallest embryo found measures 0.6 mm dd and its six arms consist of three segments and a flat-

tened TP with a blunt thorny distal end and large round fenestrations in irregular longitudinal rows (Fig. 4A). Several plates of different sizes and irregular shape form the dorsal disc, in a pattern which may consist of a CPP and six RPPs, but not a typical primary rosette (Fig. 4B). The plates bear no spines at this stage. The plate stereom is a meshwork of large irregular fenestrations. Each arm segment bears a strong serrated spine to either side. The jaws terminate in a pointed spiniform tooth.

At 0.9 mm dd and four arm segments, the dorsal disc plates have a more compact stereom with smaller round perforations and imperforate margins. Short



**Figure 4.** *Ophiacantha anomala* postlarval development, stages taken from brooding animal are termed embryo, free-living stages postlarvae. A, B, 0.6 mm dd embryo dorsal; C, 0.9 mm dd embryo dorsal; D, 1.3 mm dd embryo dorsal; E, 1.3 mm embryo ventrolateral; F, 1.6 mm dd; G, 2 mm dd postlarva ventral; H, 3 mm dd juvenile jaw. Scale bars in millimetres.

trifid disc spines with wide round base are distributed irregularly across the disc surface. There are two arm spines on each LAP, erect, and half as long as a segment (Fig. 4C).

From 1.3 mm dd, the dorsal disc is formed by numerous overlapping scales, among which the primaries are indistinguishable (Fig. 4D). The scales bear multifid stumps. There is a long pointed tooth and three conical MP, the distalmost arising from the AS (Fig. 4E). An increasing number of rugose granules obscure the disc scales at 1.6 mm dd (Fig. 4F).

The smallest free-living stages found have a dd of about 2 mm and can be identified using adult characters. The OSs are pentagonal, the M distinguishable as the largest one (Fig. 4G). The ASs are distally flaring, separating the OS from the first VAP. The VAPs are wider than long, with strongly convex distal edge, the first plate smaller than those following. There is a single pointed scale at each TPo. Later during development, additional MP are formed, which are pointed spiniform, erect, forming a cluster on the jaw (Fig. 4H). The ASs open in a wide angle at the proximal edge of the OS, no longer separating it from the arm.

*Remarks:* Upon dissection, fewer than 50% of the largest individuals carried embryos and rarely more than one per bursa, up to seven in total per individual, usually fewer. However, because of the rarity of the species and the damage necessary to extract the deeply embedded embryos, no quantitative analysis was conducted. Contrary to most other six-armed species, *O. anomala* does not reproduce asexually by fission.

#### SUBFAMILY OPHIOTOMINAE PATERSON, 1985

##### *OPHIOLIMNA BAIRDI* (LYMAN, 1883)

(FIG. 5A–H)

The smallest individuals found measure about 1.0 mm dd, with ten arm segments. The dorsal disc is formed by numerous imbricating plates with almost imperforate stereom, among which no primary rosette can be distinguished (Fig. 5A). Short conical, rugose spinelets are scattered across the disc surface, each standing on an opening surrounded by a circle of smaller holes. The distal portion of the RSs is just visible above the arm, the proximal part covered by disc scales. The LAPs are strongly striated with transverse ridges and rows of fenestrations, each bearing three spines, the dorsalmost of which is longer than an arm segment, the ventralmost about half as long (Fig. 5B). The rounded triangular DAP with obtuse proximal angle and convex distal edge shows weak striations; plates of the following segments are separated by the LAPs. The VAPs are striated, with proximal angle, convex distal edge and strongly concave lateral edges;

plates on following segments are separated by the LAPs (Fig. 5C). The first VAP is similar to the others, but with convex proximal edge. The TS is long, pointed and spine-like. The DP bears a spiniform pointed tooth and a similar MP to each side (Fig. 5D). The oral plate bears a wide low BS; adjacent oral plates are only parallel at their proximal ends, forming a wide angle distally, resulting in a jaw that is wider than long. ASs are longer than OS, separating it from the arm. The ASS is as long as a middle arm spine, pairs pointing towards each other, and not visible from above.

At 1.6 mm dd, the dorsal disc is formed by numerous overlapping scales, bearing a dense covering of short and sparsely distributed longer spines (Fig. 5E). The angle formed by adjacent oral plates has narrowed, forming a jaw that is longer than wide (Fig. 5F). The DP bears two spiniform MP1; there is a single conical MP2 on each edge of the oral plate replacing the BS, and proximal to the ASS a similar MP3 has formed on the AS (Fig. 5G). The ASS has shortened, but it is still longer than the MP, with which it forms a single row as the second TPo has moved close to the oral slit. The OS is triangular with convex distal edge, separated from the first VAP by the long ASs (Fig. 5F, G). The ventral disc is formed by small round overlapping plates with evenly distributed round perforations.

At 2.0 mm dd, dense granules and long spines completely obscure the disc scales. Granules have formed on the ventral disc scales and on the proximal end of the ASs (Fig. 5H). The row of MP consists of a small slightly pointed papilla on the DP, another similar papilla on the oral plate, a third on the distal AS and a larger, flat ASS. Each TPo bears a flat, pointed oval scale. Thus, all skeletal elements found in the adult are present and will only slightly change in shape or number during further growth.

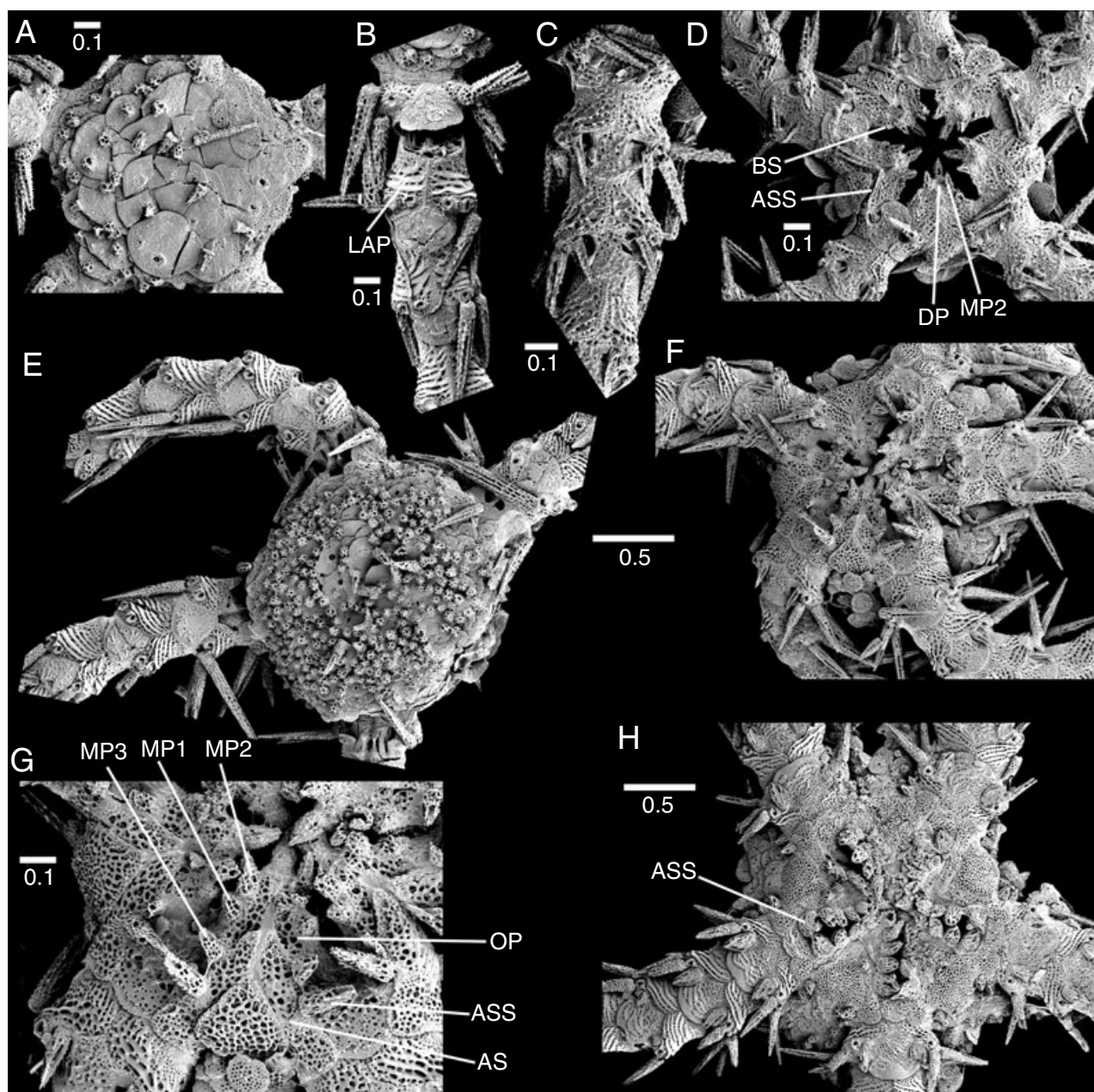
*Remarks:* *Ophiolimna bairdi* can be identified by the striated arm plates, which are visible in all stages studied here.

#### SUBFAMILY OPHIOLINTHACINAE PATERSON, 1985

##### *OPHIOMITRELLA CLAVIGERA* (LJUNGMAN, 1865)

(FIG. 6A–K)

This species broods its young in the bursae and often arms of juveniles can be seen extending from the slits. The smallest embryo found still inside an adult is already quite well developed with 0.6 mm dd and about six arm segments (Fig. 6A). This animal is aberrant in having a tetramerous symmetry with only four arms. The dorsal disc is formed by numerous round, overlapping scales, among which no primary rosette can be distinguished. The scales are perforated by round evenly distributed fenestrations. Strong trifid



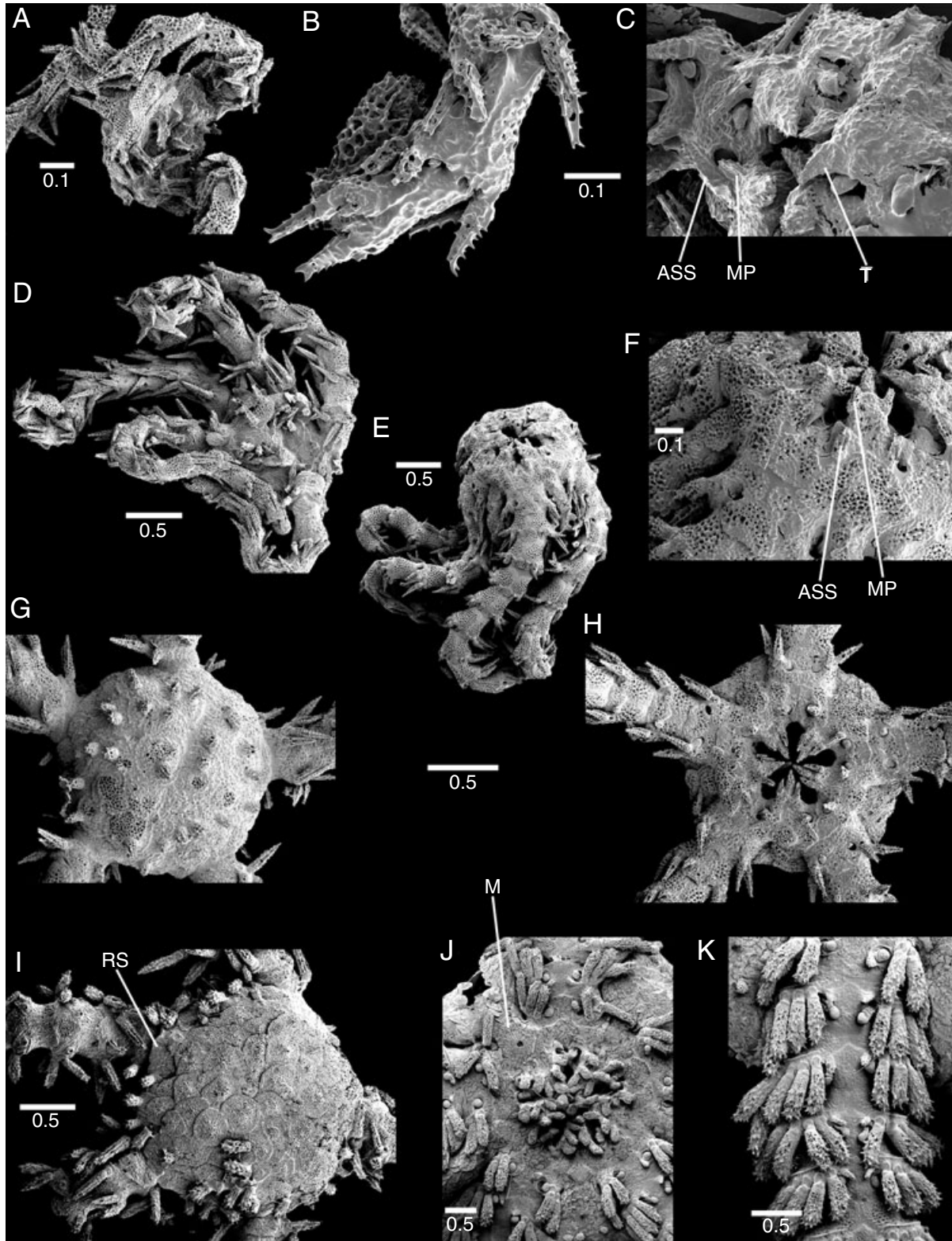
**Figure 5.** *Ophiolimna bairdi* postlarval development. A–D, 1 mm dd postlarvae; A, dorsal; B, arm dorsal; C, arm ventral; D, ventral; E, 1.6 mm dd postlarva dorsal; F, 1.6 mm dd ventral; G, same, jaw; H, 2 mm dd postlarva. *Abbreviations:* BS, buccal scale; MP, mouth papilla; OP, oral plate; others as in Figs 1, 2. Scale bars in millimetres.

spines are scattered across the scales. Each LAP bears three spines, the ventralmost of which is slightly hook-shaped with two terminal teeth and a double row of secondary teeth along its ventral edge (Fig. 6B). The TP is strong, somewhat swollen with an irregular pattern of fenestrations. The jaws bear a triangular sharply pointed tooth and what seems to be an MP on at least one jaw (Fig. 6C). The ASS is straight, not

tapering, with blunt end, pointing across the first VAP (Fig. 6C).

At 1 mm dd and 12 arm segments, additional disc scales have formed (Fig. 6D). A spine-like MP has formed to each side of the DP. A pointed spine-like scale covers each TPo.

At 1.3 mm dd, the DAP is shorter than half an arm segment, triangular, with convex distal edge. The ASS



**Figure 6.** *Ophiomitrella clavigera* postlarval development, specimens taken from brooding adult are termed embryo, free-living stages postlarvae. A–C, 0.6 mm dd embryo; A, dorsal; B, arm ventral; C, jaws; D, 1 mm dd embryo dorsal; E, 1.3 mm dd embryo ventral; F, same, jaws; G, 1.5 mm dd postlarva dorsal; H, same ventral; I, 2.1 mm postlarva dorsal; J, adult ventral; K, adult arm ventral. *Abbreviations:* T, tooth; others as in Figs 1, 2, 5. Scale bars in millimetres.

are rectangular, distally wider than proximally, their length 2.5× their greatest width. The OS is rounded triangular, with all edges convex. The ASS has shortened and moved closer to the mouth angle, pointing towards the slit (Fig. 6E, F).

The smallest free-living juveniles found have a dd of 1.5 mm and 13 arm segments. There seems to be a CPP, but all scales are of similar shape and size and it is unclear whether a primary rosette is present (Fig. 6G). Each LAP bears five serrated, tapering spines, but the hook shape of the ventral spine is no longer obvious. The ventral disc is formed of similar scales as the dorsal disc. The VAPs are almost square, with a concave notch in the distal edge; adjacent plates are widely separated by the LAPs. Tooth and MP have grown in length (Fig. 6H).

At 2.1 mm dd, rugose spinelets are scattered across the dorsal disc. The RSs are just visible above the arm, but hardly distinguished from the disc scales. There are six rugose arm spines (Fig. 6I), but they are still not as thick as in the adult. From about 3 mm dd, keys to adult specimens can be used.

In an adult of 5 mm dd the ASS is part of the row of MP and indistinguishable from them; one of the OSs is larger and identifiable by the hydropore in its centre (Fig. 6J). The arm spines are thick and strongly rugose (Fig. 6K).

#### FAMILY OPHIURIDAE LYMAN, 1865

##### SUBFAMILY OPHIURINAE LYMAN, 1865

#### *OPHIOPLEURA BOREALIS* DANIELSSEN & KOREN, 1877

(FIG. 7A–N)

The smallest postlarva in the samples has a dd of 0.6 mm and two arm segments. The disc is strongly domed with a large pentamerous CPP, surrounded by five smaller rounded triangular RPP with distal angle. In the inter-radial spaces the bulging ASs are visible. The first free arm segment consists of two inflated LAPs, which meet in midline, bearing a single smooth ventral spine each. The terminal arm segment is flask-shaped with inflated base and narrow distal part, round fenestrations running along its length (Fig. 7A). The DP is twice as wide as long, bearing a pointed tooth. A low BS is just visible on the oral plate edge. The first VAP is twice as long as wide, with proximal angle, concave lateral sides and straight distal edge. The swollen first ASs of two adjacent arms meet below the jaw (Fig. 7B). The M is visible dorsally in an inter-radius, projecting outwards with the pore opening ventrally at the tip of the plate (Fig. 7B).

At 0.8 mm dd, the round CPP is more than twice as large as the RPPs. Inter-radial plates (IR0) have formed as smaller rounded triangular disc plates above the RPPs (Fig. 7C). There are now four arm seg-

ments, still consisting of only LPs without DAPs. The M is still dorsal in position.

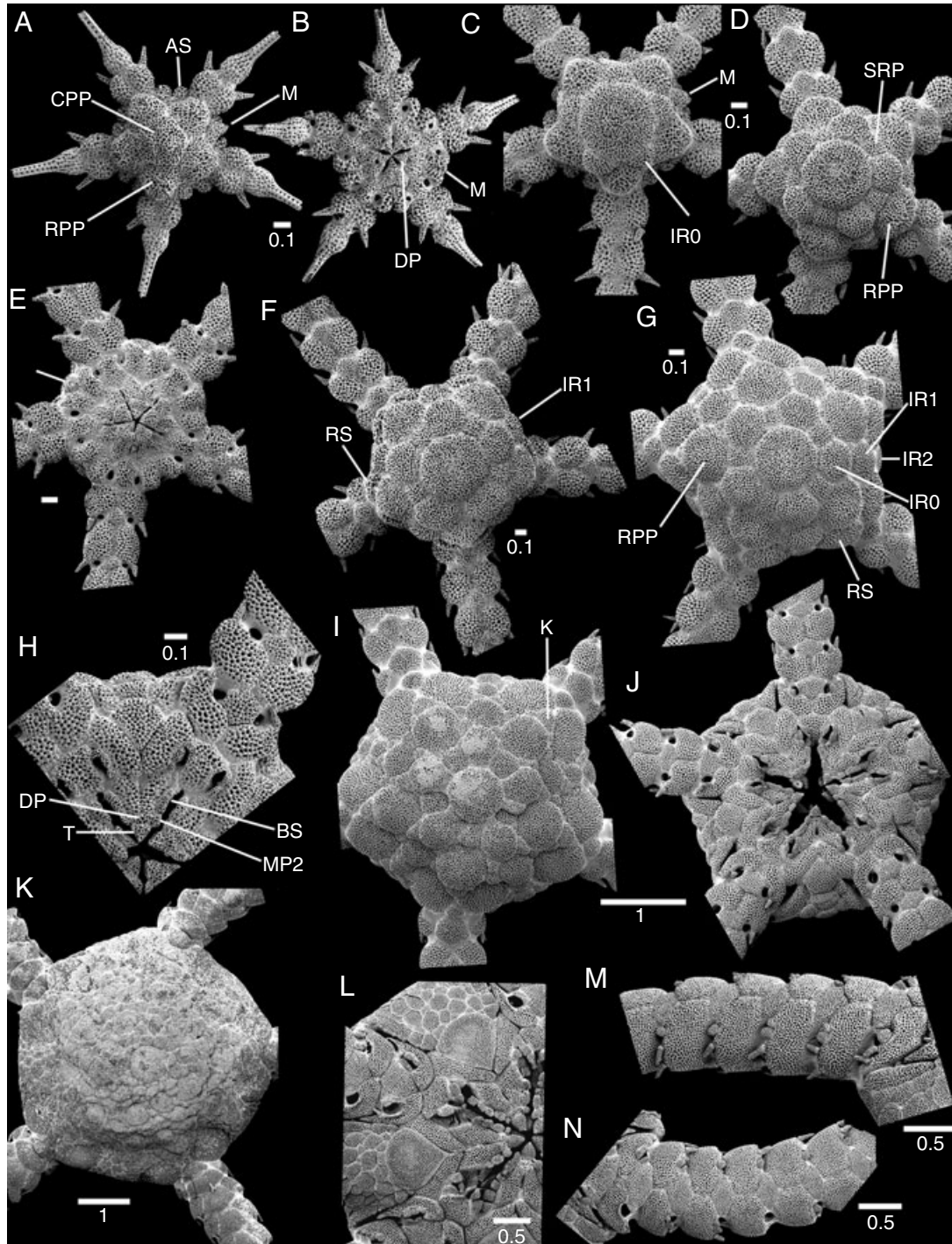
At 1 mm dd, the disc is about as high as wide. Additional smaller almost rectangular plates have formed as secondary radial plates between the IR0, the edges of the IR1 are visible between and below the RPPs, and the second to fourth arm segments bear triangular dorsal plates, longer than wide with convex distal edge, each DAP widely separated from the following plate by the LAPs (Fig. 9D). Short triangular VAPs with convex distal edge have appeared beyond the first segment, widely separated from each other by the LAPs. The M has migrated ventrally and forms the largest OS, with the other four just visible at the disc edge (Fig. 7E).

At 1.2 mm dd, the RSs have begun to form beneath the RPPs (Fig. 7F). In addition to the BS on the oral plate there is a smaller MP at each lateral edge of the DP.

At 1.8 mm dd, IR2 have formed, and the RSs are now large and oval, pairs forming a wide angle, proximally separated by the RPP, distally by the first DAP, contiguous only at a narrow point (Fig. 7G). MP and tooth are as before, with ASs comma-shaped and OS teardrop-shaped (Fig. 7H). A ventral inter-radial disc plate, almost rectangular, that is wider than long, has formed distal to the OS, framed by narrow genital plates to each side. The second TPo lies outside the mouth slit and is surrounded by 3–4 small block-like scales. The following pores are scale-less.

At 2.6 mm dd, the dorsal disc scaling becomes increasingly complex; the k-plate has formed distal of the RPP. The primary plates are still distinguishable, but now widely separated by additional plates (Fig. 7I). The second TPo has moved close to the mouth slit and is now surrounded by 4–5 small scales. The third TPo bears a small papilla-like scale, whereas the following segments are still without TS. Bursal slits are present to either side of the first arm segment, bordered by a genital plate extending from the oral shield to the disc edge. Three additional ventral disc scales have formed at the disc edge. The second and following VAPs are wider than long, hexagonal with proximal and distal angles (Fig. 7J).

At 5 mm dd, the animals exhibit adult characters. The CPP is still distinct, but the other primary plates can no longer be distinguished among the many additional scales that have formed. The DAPs are wider than long with convex distal edge and contiguous on proximal segments, becoming more elongated distally. The skin thickens increasingly, obscuring the plates (Fig. 7K). There are three short arm spines and proximally two small round TSs, decreasing distally in number (Fig. 7M). The DP bears a large pointed tooth and a small round lateral papilla to each side. Four smaller block-like lateral papillae of about equal size



**Figure 7.** *Ophiopleura borealis* postlarval development. A, B, 0.6 mm dd postlarva; A, dorsal, note the high disc, swollen lateral arm plates and dorsal madreporite; B, ventral, note ventral hydropore at madreporite tip (between ASs); C, 0.8 mm dd postlarva dorsal, secondary inter-radial plates have formed above the radial primary plates (IR0); D, E, 1 mm dd postlarva; D, dorsal, secondary radial plates (SRP) have formed above the radial primary plates; E, ventral, the madreporite is now ventral; F, 1.2 mm dd postlarva dorsal; G, H, 1.8 mm dd postlarva; G, dorsal, secondary inter-radial plates (IR2) have formed below the first inter-radial plates (IR1); H, ventral, a second mouth papilla has formed on the dental plate; I, J, 2.6 mm dd juvenile; I, dorsal, the k-plate separates the radial shields proximally; J, ventral; K–L, 5 mm dd juvenile; K, dorsal, note the thick skin on the disc only partly removed; L, ventral; M, arm lateral, note two widely spaced short arm spines; N, arm ventral. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.

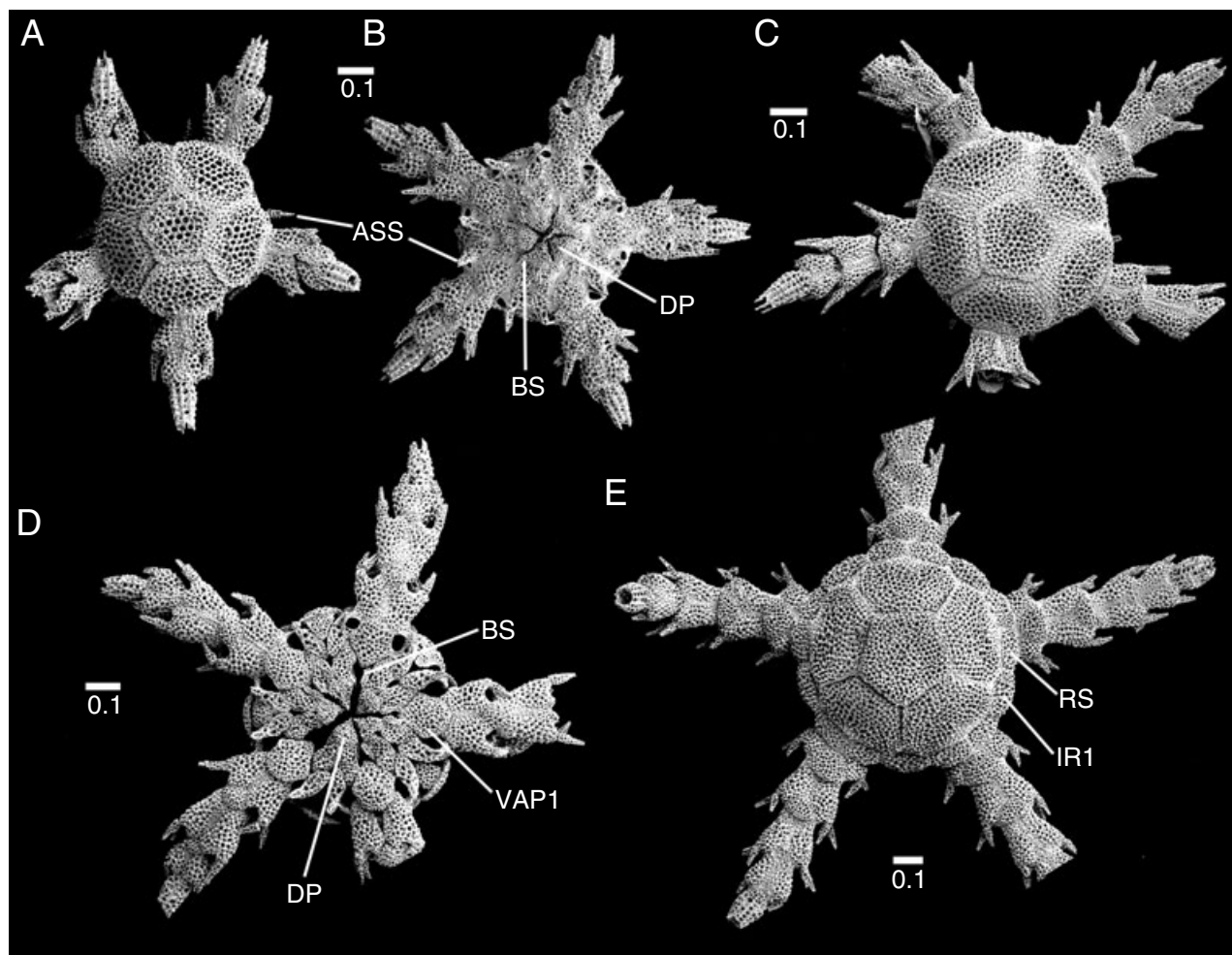
and shape have replaced the BS. The first TPo opens into the mouth slit. The large OS is teardrop-shaped and separated from the first LAPs by the narrow ASs. The ventral disc is covered by small, round, overlapping scales. The genital plate bears a row of small, round papillae. The genital slit does not fully extend to the disc edge (Fig. 7L). There are 1–2 small, round TSs on the proximal segments and three short addressed arm spines (Fig. 7M). The VAP is about twice as wide as long, with convex distal edge, separated from the following VAP by the large LAPs (Fig. 7N).

*Remarks:* The postlarvae of *O. borealis* are remarkably different from their adult conspecifics. They are, however, easily recognized among other species. The order of appearance of the dorsal plates differs from the general pattern as presented by Ludwig (1899) and later authors, who described the IR2 as forming

above the IR1. In *O. borealis* the IR2 forms at the disc edge below the IR1 and there is an early set of plates, here termed IR0, which have not been found in other species and are probably not homologous with the IR1. In addition, secondary radial plates form prior to the IR1 and together with the IR0 they form a circle above the RPPs, separating them from the CPP quite early in development.

*OPHIURA ALBIDA* FORBES, 1839  
(FIG. 8A–E)

The smallest postlarva previously described had a dd of 0.6 mm (Sumida *et al.*, 1998). The BIOIce material includes individuals of 0.4 mm dd and three arm segments (Fig. 8A). The dorsal disc is formed by the pentagonal CPP and five RPPs. The CPP has larger round



**Figure 8.** *Ophiura albida* postlarval development. A, B, 0.4 mm dd postlarva; A, dorsal, note the multilayered structure of the disc plates; B, ventral; C, D, 0.5 mm dd postlarva; C, dorsal; D, ventral, note the shape of the first ventral arm plate (VAP1); E, 0.7 mm dd postlarva. *Abbreviations:* as in Figs 1–2, 5. Scale bars in millimetres.

fenestrations in the centre and smaller further out, where they are overlaid by a second layer, while the plate margin is almost imperforate. In some individuals, the CPP is completely multilayered, with smaller perforations all over. There are two short appressed arm spines. The TP is slightly bulbous, hollow and terminating in several short thorns. The oval DP bears a pointed tooth and the oral plate bears a wide, block-like BS (Fig. 8B). The ASS sits on the distal end of the AS near the disc edge, pointing outwards and visible from above. The first VAP is slightly longer than wide, with proximal angle, straight lateral edges and convex distal edge. The second VAP is not even half the size of the first, triangular, wider than long, and with convex distal edge.

At 0.5 mm dd, and four arm segments, the edges of the RS are just visible above the arm and the IR1 has begun to form (Fig. 8C). The first DAP is rounded triangular, wider than long. A small OS can be seen at the disc edge between the distal parts of the ASs (Fig. 8D).

At 0.7 mm dd, the IR1 has formed (Fig. 8E). Larger individuals have been described in previous works. From about 3 mm dd, characters are close to the adult state.

*Remarks:* *Ophiura albida* postlarvae are quite similar to *O. robusta*, from which they can be distinguished by the stereom structure of the primary plates and the shapes of the TP, DAP and first VAP as discussed under that species.

*OPHIURA OPHIURA* (L., 1758)  
(FIG. 9A–H)

A detailed description of the development of this species was given by Webb & Tyler (1985). The smallest individuals in the BIOIce material have a dd of 0.3 mm, with a flat disc, and the arm consists of only the TP (Fig. 9A). The jaw bears a sharply pointed tooth and the ASS points outward (Fig. 9B).

At 0.5 mm and two arm segments, the dorsal disc is formed by the strongly domed pentagonal CPP and five RPPs, all of which have a complicated structure of fenestrations and an almost imperforate border (Fig. 9C). The M is clearly visible in a dorsal inter-radius. The LAPs are swollen, giving the animal a robust appearance (Fig. 9D). A second VAP has formed.

At 0.7 mm dd and four arm segments, the first DAP has formed (Fig. 9E). The proximal three arm segments bear small VAPs (Fig. 9F).

At 1.8 mm dd, the strongly domed CPP is the most distinguishing character (Fig. 9G). The CPP retains its domed shape until the animals are about 4 mm in dd (Fig. 9H). From about 3 mm dd, the animals can be

identified using keys to adults, bearing in mind that the characteristic pores separating the proximal VAPs are not distinct in small specimens.

*Remarks:* The Icelandic individuals of *O. ophiura* are characterized by a high disc in smaller postlarvae (but not the smallest) and a strongly domed CPP in larger animals, which is more prominent than in individuals from other areas. The LAPs are more swollen and bulbous than in previously described individuals (Webb & Tyler, 1985). These distinct features of *O. ophiura* postlarvae make them easily distinguishable from other sympatric species of *Ophiura*.

*OPHIURA ROBUSTA* (AYRES, 1851)  
(FIG. 10A–L)

The smallest individuals have a dd of 0.45 mm and three arm segments, the distalmost just beginning to form. The dorsal disc is formed by the pentagonal CPP and five RPPs (Fig. 10A). The CPP is perforated by larger round fenestrations in the centre and smaller ones peripherally. The first DAP is triangular, about as wide as long, with convex distal edge. There are two short addressed arm spines. The TP is about as long as an arm segment, terminating in several thorns. The DP is twice as wide as long and bears a triangular pointed tooth (Fig. 10B). The oral plate bears a low wide BS to each side. The OSs can be seen at the disc edge between the distal ends of the ASs, the M among them distinguishable from below by its large hydropore. The ASS is conical, pointing outwards with its tips just visible inter-radially from above. The first VAP is about twice as long as wide, with a spear-head shape and concave lateral edges.

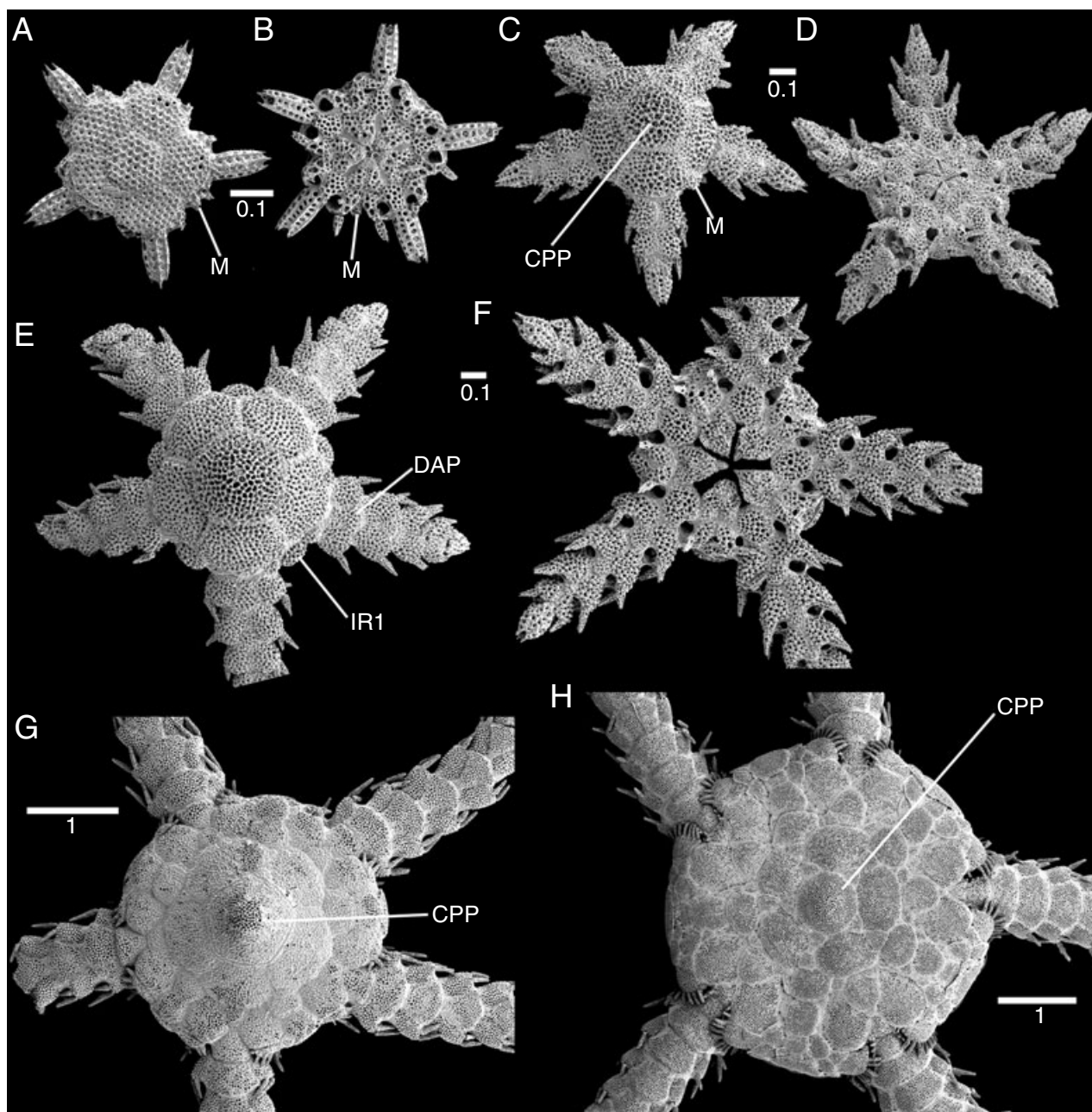
At 0.55 mm dd and still three arm segments, the RSs are just visible above the arm, below the edge of the RPP (Fig. 10C). The first DAP is longer than wide. The DP is slightly smaller, still not bearing a papilla (Fig. 10D).

At 0.85 mm dd, the IR1 has formed at the disc edge and the IR2 is a small triangle above the IR1, separating the RPPs at their distalmost end (Fig. 10E).

At 1 mm dd, the RSs are beginning to become separated distally by the proximal angle of the first DAP (Fig. 10F). The second and following DAPs are longer than wide, teardrop-shaped with convex distal edge and proximal angle. A lateral MP can be seen at the DP (Fig. 10G). Three ventral disc scales have formed distal of the OS. The ASS has decreased in size. The hydropore on the M is off-centre.

At 1.3 mm dd, the k-plate is present, separating the RSs proximally (Fig. 10H). An additional MP has formed at the proximal end of the oral plate next to the BS (Fig. 10I). At the first TPo there are two small oval TSs on the AS and a third on the first VAP; the follow-



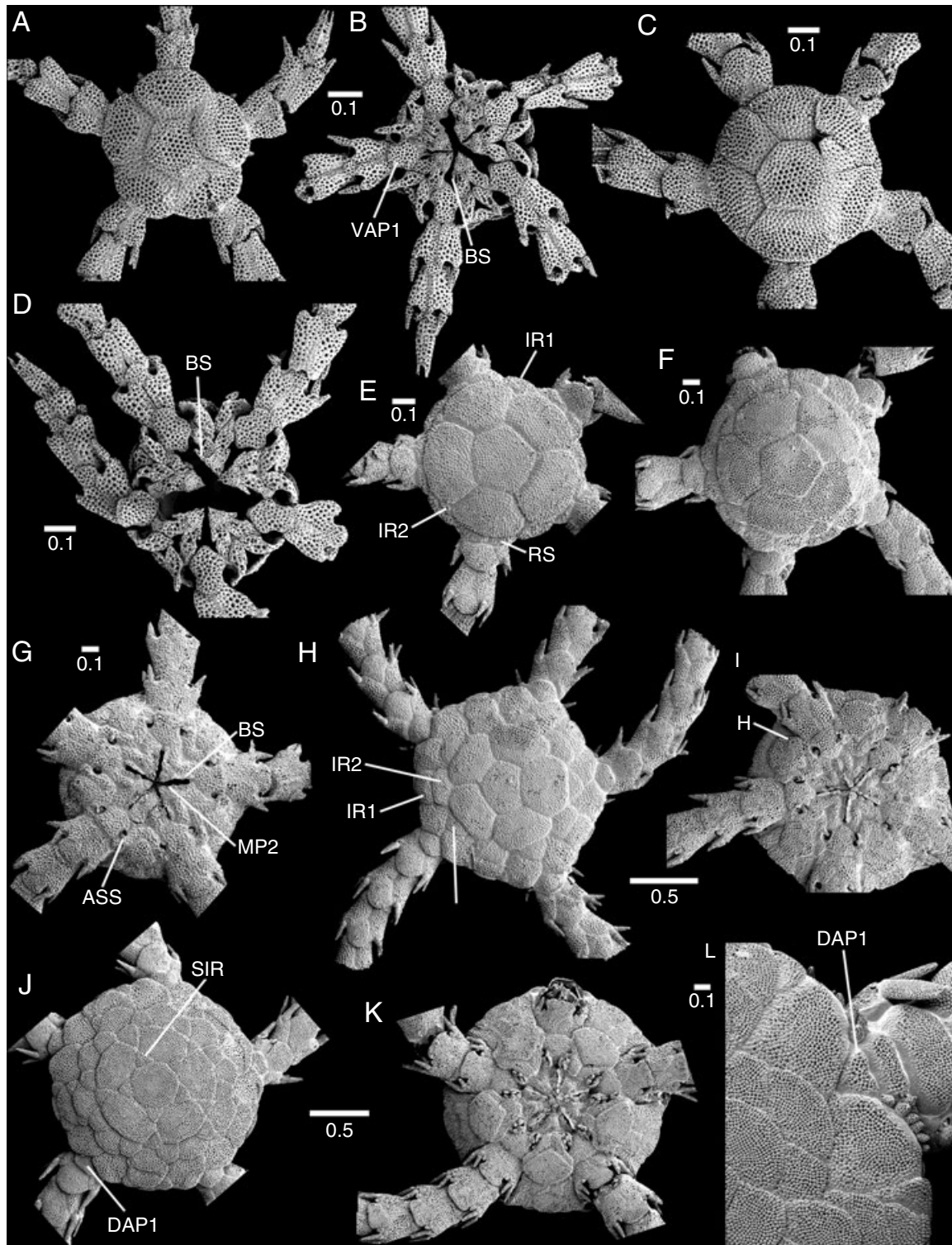


**Figure 9.** *Ophiura ophiura* postlarval development. A, B, 0.3 mm dd postlarva; A, dorsal, note the flat disc; B, ventral; C, D, 0.5 mm dd postlarva; C, dorsal, note the high disc, madreporite still dorsal; D, ventral; E, F, 0.7 mm dd postlarva; E, dorsal; F, ventral; G, 1.8 mm dd postlarva dorsal, note the domed central plate (CPP); H, 4 mm dd juvenile dorsal, the central plate is only slightly domed. *Abbreviations:* as in Figs 1, 3. Scale bars in millimetres.

ing TPoS bear a single oval TS. The ASs border the proximal angle of the OS, separating it from the first VAP. The OSs are about as wide as long with strongly convex distal edge. The hydropore has moved further to one side.

At 1.8 mm dd, many additional disc scales have formed, among them the SIRs below the CPP. The first

DAP has begun to attain a heart-shape (Fig. 10J). The DAPs of succeeding segments are now contiguous. The OS is wider than long, there are three smaller round MP, and the BS is twice as wide as long. The second TPoS lies outside the mouth slit, bordered by five small rounded scales. Following TPoS bear a single oval scale each (Fig. 10K).



**Figure 10.** *Ophiura robusta* postlarval development. A, B, 0.45 mm dd postlarvae; A, dorsal, note the structure of the plates; B, ventral, note the shape of the first ventral arm plate (VAP1); C, D, 0.55 mm dd postlarva; C, dorsal; D, ventral; E, 0.85 mm dd postlarva dorsal; F, G, 1 mm dd postlarvae; F, dorsal; G, ventral; H, I, 1.3 mm dd postlarvae; H, dorsal; I, ventral; J, K, 1.8 mm dd postlarvae; J, dorsal, note the heart-shaped first dorsal arm plate (DAP1); K, ventral; L, 2.9 mm dd juvenile dorsal, arm combs have formed and the DAP1 has its final heart-shape. *Abbreviations:* H, hydropore; k, k-plate; SIR, secondary inter-radial plate; others as in Figs 1–3, 5. Scale bars in millimetres.

At 2.9 mm dd, the first DAP has attained its final heart-shape (Fig. 10L), separating the RSs distally, while the k-plate separates them proximally. The arm comb papillae can be seen under the distal edge of the RS. There are three arm spines, the dorsalmost almost twice as large as the other two. Characters are now close to their adult state.

At 5 mm dd (not figured), the animals show fully adult characters. The CPP is still distinct, while the RPPs are no longer distinguishable. The DAPs are wider than long, overlapping so that their proximal angle is no longer visible. There are three lateral MP and a single tooth. The first TPo is surrounded by five TSs, the second TPo has two TSs, and all others only one. The OS is wider than long with straight distal edge. The VAPs are wider than long, with straight distal edge; following plates are separate.

*Remarks:* The smallest postlarvae of *O. robusta* are difficult to distinguish from *O. albida*. In mixed samples, the more slender habitus and the different structure of the primary plate stereom distinguish *O. robusta*. It is also somewhat further developed at smaller sizes with more plates present. The TP of *O. robusta* is longer and not as bulbous as in *O. albida* and the first VAP is longer and of a different shape. From just under 2 mm dd, the heart-shape of the first DAP becomes obvious. Although *O. albida* also may develop a heart-shaped first DAP, it is not as distinct as in *O. robusta*. Both species can be distinguished from *Ophiura sarsii* Lütken, 1858 by their distinctly smaller CPP.

FAMILY AMPHIURIDAE LJUNGMAN, 1867  
*AMPHIURA BOREALIS* (G.O. SARS, 1871)  
 (FIG. 11A–K)

This is a brooding species in which the embryos develop inside the bursae. The smallest free-living postlarvae found measure 0.7 mm dd, with five arm segments. The often high, circular dorsal disc is formed by transparent, irregularly rounded, overlapping scales of different sizes, with small round perforations (Fig. 11A). No primary rosette can be distinguished. The edges of the RSs are just visible above the arm. The DAPs are pentagonal, wider than long with a wide proximal angle and slightly convex distal edge. There are three arm spines of equal length, shorter than an arm segment. A BS is present at the oral plate edge, and infradental papillae (= MP2) on the DP, widely separated by the large pointed apical tooth; all papillae are rugose (Fig. 11B). The ASs are narrow, with concave inner edge, bearing a short conical spine next to the first TPo. The OS is triangular with convex distal edge. The VAPs are elongated pentagonal with obtuse proximal angle, straight

distal edge and concave lateral edges, except for the first VAP which is trapezoidal with straight lateral edges. The ventral disc is formed by a large round scale distal to the smaller OS and smaller plates to its sides.

At 0.8 mm dd and 6–9 arm segments, the number of disc scales has increased (Fig. 11C). The infradental papillae and BS have grown in size (Fig. 11D, E).

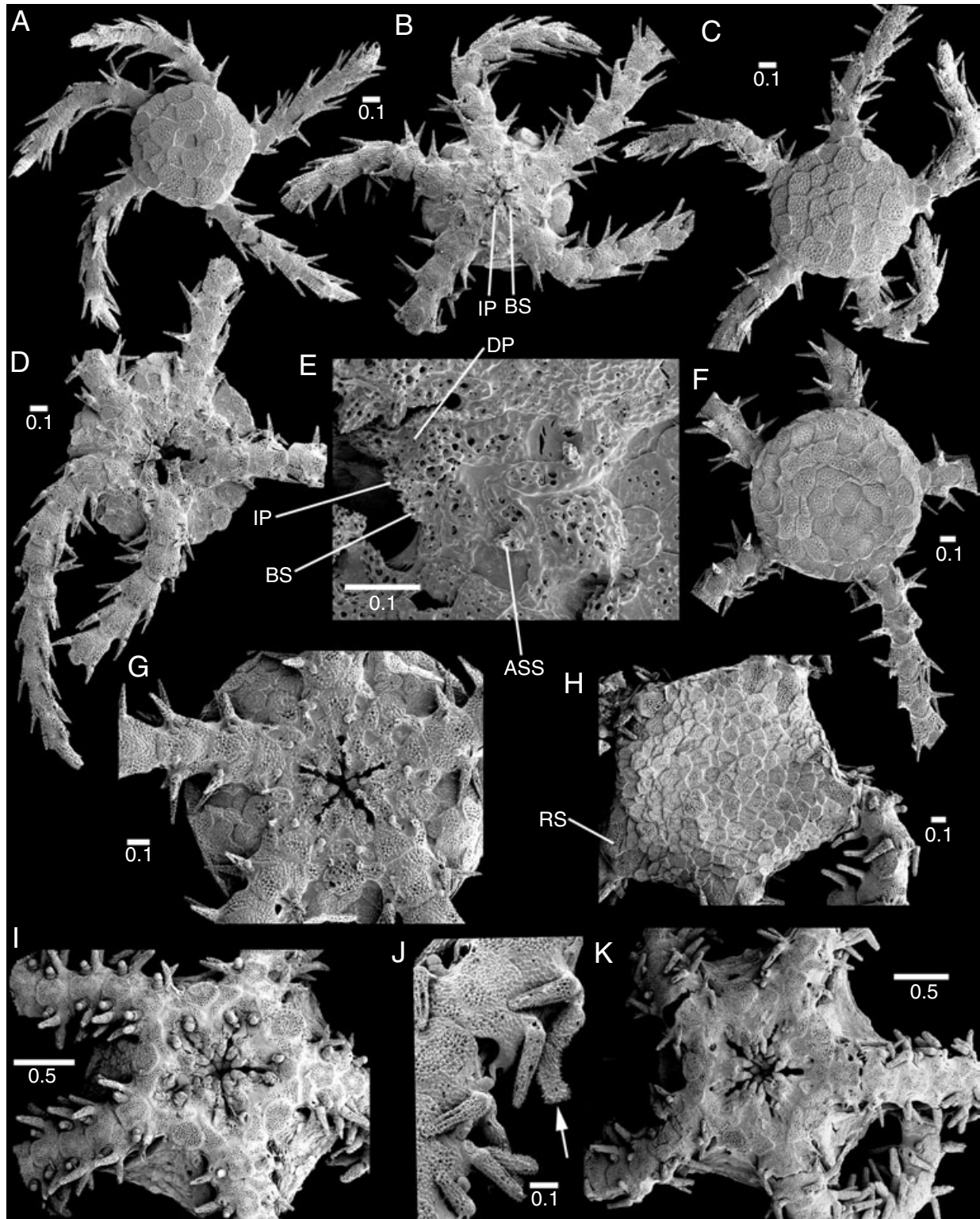
At 1.1 mm dd and up to 12 arm segments, the number of dorsal and ventral disc scales has increased further, the RSs are indistinguishable among them, and the infradental papillae are closer together than before (Fig. 11F, G).

At 2.0 mm dd, the RSs have formed, pairs separated by an elongated scale except at their distal ends (Fig. 11H). The infradentals have moved onto the proximal ends of the oral plates and the tooth is block-like (Fig. 11I). The OS has a rounded shape, wider than long, with wide obtuse proximal angle, convex on all edges. The ASS has disappeared. The ventral disc is covered with naked skin between the round scales.

From about 2.2 mm dd, the middle arm spine is flattened and slightly wider than the other two, with serrated edges (Fig. 11J). This is the first indication of the often axe-shaped, flattened, second ventralmost arm spine that is characteristic of this species. The ventral inter-radial disc is now covered with skin and scattered small round scales with large round perforations not extending to the scale edge (Fig. 11K). Lateral MP have just begun to form at the oral plate. The infradentals are close together, but on several jaws a third tooth is placed between them, which can also be seen in larger animals (Fig. 11K). These specimens can be identified using keys to adults.

Adult characters (not figured) include four arm spines, the second ventralmost axe-shaped, and two lateral MP above the BS. The dorsal disc is covered by small, round, imbricating scales, the RS is almost semicircular, 2.5× as long as wide, length about one-fifth of the dd, pairs contiguous only at their distal end, and separated by two narrow wedge-like plates and a proximal round plate. The DAP is wider than long, oval, with proximal edge more convex than distal edge. The occurrence of the axe-shaped spine varies between individuals, and arms and arm segments in the same individual. Often, the second ventralmost spine on the most proximal segments is only slightly flattened with serrated edges, while the fully axe-shaped spines are found further out on the arm.

*Remarks:* Postlarvae of *A. borealis* can be distinguished from other species by the lack of a primary rosette, which gives the dorsal disc a conspicuously different appearance with quite uniform scalation.



**Figure 11.** *Amphiura borealis* postlarval development. A, B, 0.7 mm dd postlarvae; A, dorsal; B, ventral, note the infradental papillae (IP = MP2); C, D, E, 0.8 mm dd postlarvae; C, dorsal; D, ventral; E, jaw, note that the IP form on the dental plate (DP); F, G, 1.1 mm dd postlarvae; F, dorsal; G, ventral; H, I, 2 mm dd postlarva; H, dorsal, note the radial shields (RS); I, ventral, note the IP on the oral plates; J, K, 2.5 mm dd juvenile; J, arm ventral, note the hatchet-shaped spine (arrow); K, ventral. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.

*AMPHIURA CHIAJEI* FORBES, 1843  
(FIG. 4A–O)

The smallest individuals available have a dd of 0.4 mm and one arm segment. The dorsal disc is formed by the CPP and five RPPs, all of which are perforated by large round fenestrations which continue onto the plate margins (Fig. 12A). The arm segment bears a simple spine; the TP terminates in several short thorns and is perforated by longitudinal rows of holes. The large DP bears a small sharply pointed tooth, the BS is present, and the ASS sits close to the disc edge, pointing outwards (Fig. 12B). The paired ASs are contiguous along their proximal halves, running parallel with the arms, slightly curving around the first TPo. The OS is just beginning to form at the disc edge, and the M just visible from above with a pointed projection. The first VAP is longer than wide, with proximal angle, convex distal edge and slightly concave lateral edges.

At 0.6 mm dd and 3–4 arm segments, the dorsal disc is still formed by the primary rosette. The plate fenestrations are smaller than in the youngest animals, smallest in the centre of the CPP (Fig. 12C). The plate margins are almost imperforate. DAPs are present on the first three segments, rounded triangular, with convex distal edge, and plates on following segments are widely separated by the LAPs. There are two conical arm spines half as long as a segment. The OS has moved to the ventral side (Fig. 12D).

At 0.9 mm dd and about ten arm segments, the IR1 and IR2 are present, but it is unclear which is which (Fig. 12E). The RSs are wider than long and contiguous, their proximal edges under the RPP. There are now three erect arm spines, about as long as an arm segment. A pair of small, round infradental papillae has formed on the DP, separated by the triangular pointed tooth (Fig. 12F). The narrow ASs are strongly curving inwards with a concave proximal edge around the first TPo, their distal edge bordering the lateral proximal edge of the angle of the OS. The OS is teardrop-shaped, longer than wide. The short ASS sits at the proximal end of the concave part of the AS, pointing towards the first VAP. The VAPs of the second and following segments are of similar shape and size as the first VAP. Two short, wide, ventral disc scales have formed near the disc edge, distal of the OS. The bursal slits have begun to form at the disc edge.

At 1.4 mm dd, the k-plate is present, separating paired RSs at their proximal end, and several small additional plates have formed inter-radially (Fig. 12G). The infradental papillae have moved closer together, and the ASS is close to the mouth slit and has flattened with a blunt tip. The OS is now wider than long, with straight or slightly convex distal edge (Fig. 12H). The ventral disc is covered with small,

overlapping plates. The bursal slits are clearly visible.

At 2.0 mm dd, numerous additional disc scales have formed, but the primary rosette is still clearly distinguishable (Fig. 12I). The semicircular RSs are separated proximally by the wedge-shaped k-plate. The DAPs are triangular with convex distal edge, slightly wider than long, with plates on following segments nearly touching. The infradentals have moved onto the proximal ends of the oral plates, the ASS is an oval papilla wider than long and the BS lies deeper in the mouth slit (Fig. 12J). The second TPo has moved closer to the mouth slit.

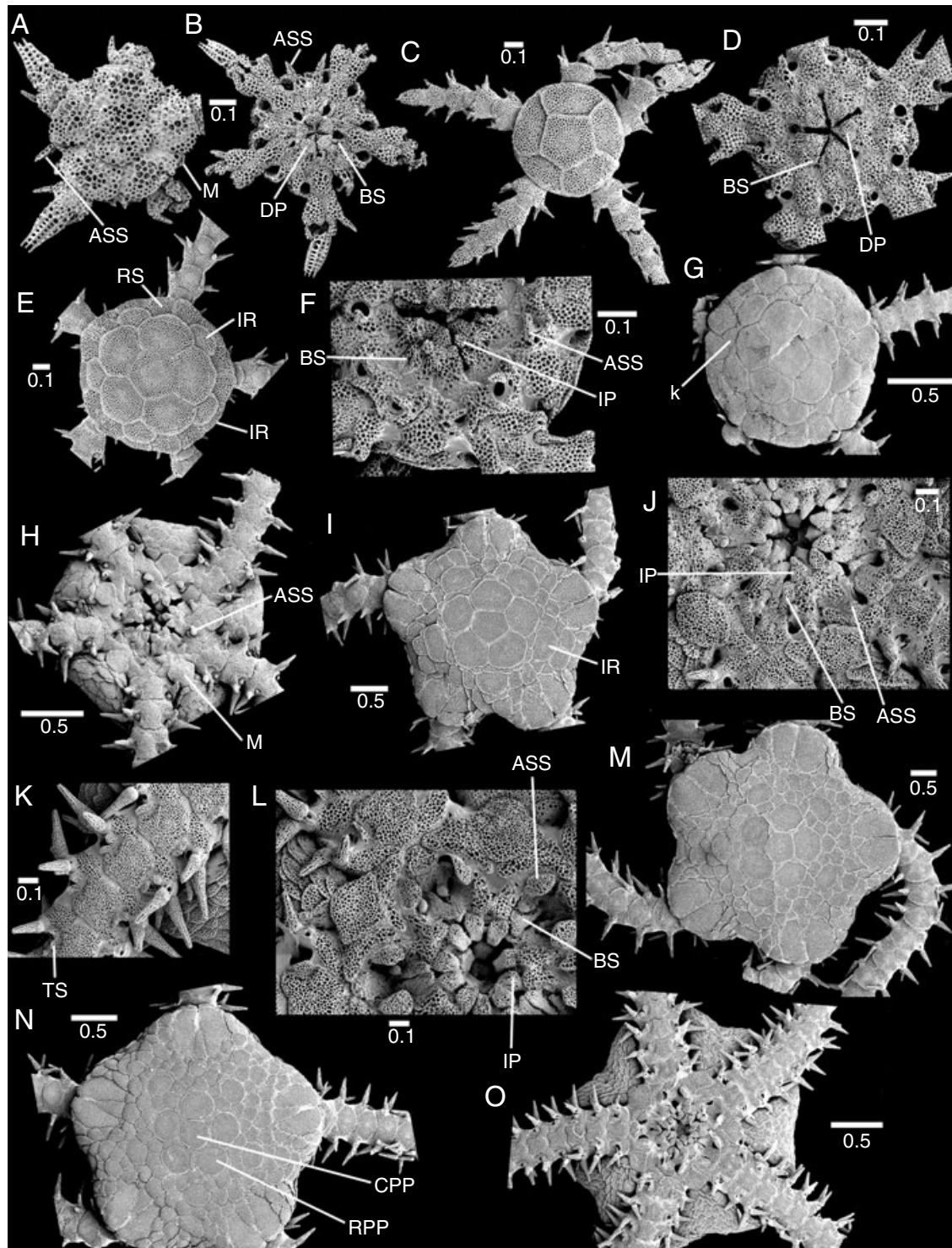
At 2.4 mm dd, additional small disc scales and wedge-shaped SIRs have formed (Fig. 12M). Two tentacle scales have formed along the arm, except on the most distal segment (Fig. 12K). The second TPo is now in the mouth slit and the ASS has grown to a wide scale (Fig. 12L). The BS has moved deeper on the oral plate and the infradentals are close together. Characters are now close to the adult state.

At 3 mm dd, the number of dorsal and ventral disc scales has increased further and the RSs are elongated (Fig. 12N). ASS and infradentals have grown (Fig. 12O).

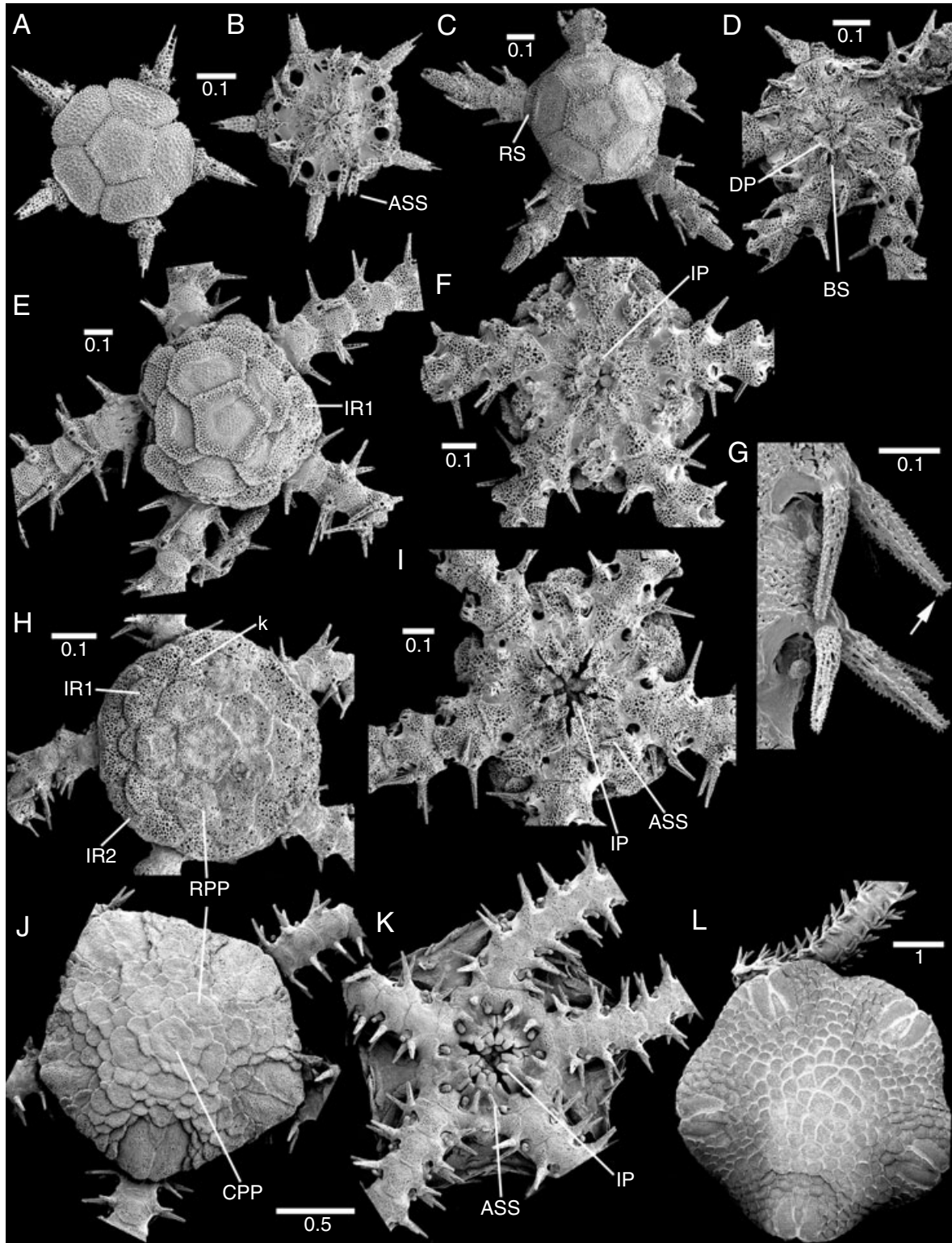
*Remarks:* Postlarvae of *A. chiajei* can be distinguished from *A. filiformis* by the uniform, non-bordered structure of the dorsal disc scales. The narrow, imperforate plate margins are only noticeable after removal of the integument. The smallest postlarvae have larger plate fenestrations, which distinguish them from the almost solid disc plates of the smallest postlarvae of *A. filiformis* (see below), and a more pointed tooth. Additionally, the disc scales of *A. chiajei* are larger and fewer in number than in individuals of *A. filiformis* of similar size and the primary rosette remains distinguishable in all stages.

*AMPHIURA FILIFORMIS* (O.F. MÜLLER, 1776)  
(FIG. 4A–L)

The smallest animals found have a dd of 0.35 mm and the arms consist of only the TP. The dorsal disc is formed by the CPP and five RPPs, all of which are almost imperforate with a pattern of small round granules on the surface, except for the plate margins, which are perforated with round fenestrations (Fig. 13A). The TP is tapering, perforated by irregularly distributed small holes, and bears two short and a longer terminal thorn. The ventral disc conforms with Hendler's (1988) stage 2. There is a single rather large, flat, triangular, pointed tooth, a BS on the oral plate and the long ASS next to the large first TPo points outwards and is visible from above at the disc edge (Fig. 13B).



**Figure 12.** *Amphiura chiajei* postlarval development. A, B, 0.4 mm dd postlarvae; A, dorsal, note the large fenestrations of the primary plates; B, ventral; C, D, 0.6 mm dd postlarvae; C, dorsal; D, ventral; E, F, 0.9 mm dd postlarva, E, dorsal, note the inter-radial plates (IR); F, ventral, note the infradental papillae (IP = MP2) on the dental plate (DP); G, H, 1.4 mm dd postlarvae; G, dorsal, note the k-plate (k); H, ventral, the adoral shield spine (ASS) has transformed into a flat scale; I, J, 2.0 mm postlarvae; I, dorsal; J, ventral, IP have moved onto oral plates; K–M, 2.4 mm dd juvenile; K, arm ventral, note the tentacle scales (TS); L, ventral; M, dorsal; N, O, 3 mm dd juvenile; N, dorsal; O, ventral. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.



**Figure 13.** *Amphiura filiformis* postlarval development. A, B, 0.35 mm dd postlarvae; A, dorsal, note the solid plate stereom; B, ventral; C, D, 0.5 mm dd postlarva; C, dorsal, note the multilayered plate margins; D, ventral; E, F, 0.6 mm dd postlarva; E, dorsal; F, ventral, note the infracradental papillae (IP = MP1); G, 1 mm dd postlarva arm ventral, note the serrated middle arm spine; H, I, 1.3 mm dd postlarva; H, dorsal; I, ventral; J, K, 1.6 mm dd postlarva; J, dorsal; K, ventral; L, 5 mm dd adult. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.

From about 0.5 mm dd, the number of arm segments varies. With two arm segments, the RSs are visible above the arm. With three arm segments, a rounded triangular DAP with convex distal edge is present on the second arm segment (Fig. 13C). The margins of the CPP and the RPPs are wider than before, multilayered, and higher than the centre of the plate. The second arm segment bears two spines on each side, shorter than a segment. A second VAP has formed, twice as long as wide, lateral edges strongly concave, proximal angle and concave distal edge (Fig. 13D). Inter-radially at the disc edge, the OSs are just visible, but the M is still not distinguishable. With seven arm segments, five segments have a DAP, the first one being as wide as the arm and twice as wide as long, the following decreasing in size.

At 0.6 mm dd, the animals correspond to Hendler's (1988) stage 3, the IR1 is clearly visible below the RPPs, and the infradental papillae have appeared on the DP (Fig. 13E). The OS is arrowhead-shaped, with the angle between the narrow ASs (Fig. 13F). The bursal slits are beginning to form at the disc edge. The first VAP is long triangular with straight edges. The second and following VAPs are twice as wide as long with proximal angle, slightly convex distal edge and deeply concave lateral edges.

At about 0.8 mm dd, according to Hendler (1988), the ASS has migrated to the distal end of the jaw (distal oral plate in Hendler, 1988). In the present material, no animal of this size was found.

At 1 mm dd, there are three arm spines, the middle one of which is serrated along its edges and shows the first sign of the axe-shape that is characteristic of this species (Fig. 13G).

At 1.3 mm dd, the CPP and RPPs with their thicker borders are still clearly visible. Both IR1 and IR2 are present, the distal plate smaller than the proximal plate, suggesting that the IR2 formed below the IR1 (Fig. 13H). A small triangular k-plate separates the RSs at their proximal end. These additional disc plates are perforated all over with many round fenestrations in contrast to the primary plates, which are perforated in the centre and on the periphery, with an imperforate area in between. The infradentals have moved onto the proximal oral plates and they have grown in length (Fig. 13I). The second TPo has moved closer to the mouth slit. Several ventral disc scales have formed.

At 1.6 mm dd, the CPP and RPPs with their bordered structure are just barely distinguishable among the many additional overlapping disc scales (Fig. 13J). The ventral disc is partly covered with naked skin, embedded with scattered scales (Fig. 13K). The ASS has grown in length. The most widely used character to separate *A. filiformis* from *A. chiajei* is the naked

ventral disc and its presence makes the animals identifiable using keys to adults.

In adults, the primary plates are no longer distinguishable (Fig. 13L).

*Remarks:* The postlarvae of *A. filiformis* are characterized by the distinct border on the primary plates, distinguishing them clearly from the other species of *Amphiura*. Small specimens are often more transparent than the sympatric *A. chiajei* and the plates are slightly reflective.

#### FAMILY OPHIACTIDAE MATSUMOTO, 1915

##### *HISTAMPICA DUPLICATA* (LYMAN, 1875)

(FIG. 14A–D)

The smallest individuals found measure 1.5 mm dd and the dorsal disc is formed by the primary rosette, wide RSs, secondary radial plates, the k-plate and several IRs (Fig. 14A). All disc scales are evenly perforated by small round fenestrations; the primary plates have a wide, thickened, perforated border and a perforated centre, but an imperforate area in between. Triangular DAPs, about as wide as long, separated from the following plate, are present on all arm segments. There are three conical arm spines, the dorsal-most of which is as long as a segment. The oral plate bears a wide BS, and a flat, triangular, pointed tooth arises from the short DP (Fig. 14B). The ASs are distally flaring, separating the teardrop-shaped OS from the LAP. A conical ASS is present near the second TPo, some distance from the oral slit.

At 2.9 mm dd, the animals possess adult characters with numerous disc scales. The tooth is block-like, wider than long, the DP bears a small round oral papilla followed by two larger round papillae on the oral plate and a third similar one on the AS, probably homologous to the ASS (Fig. 14C).

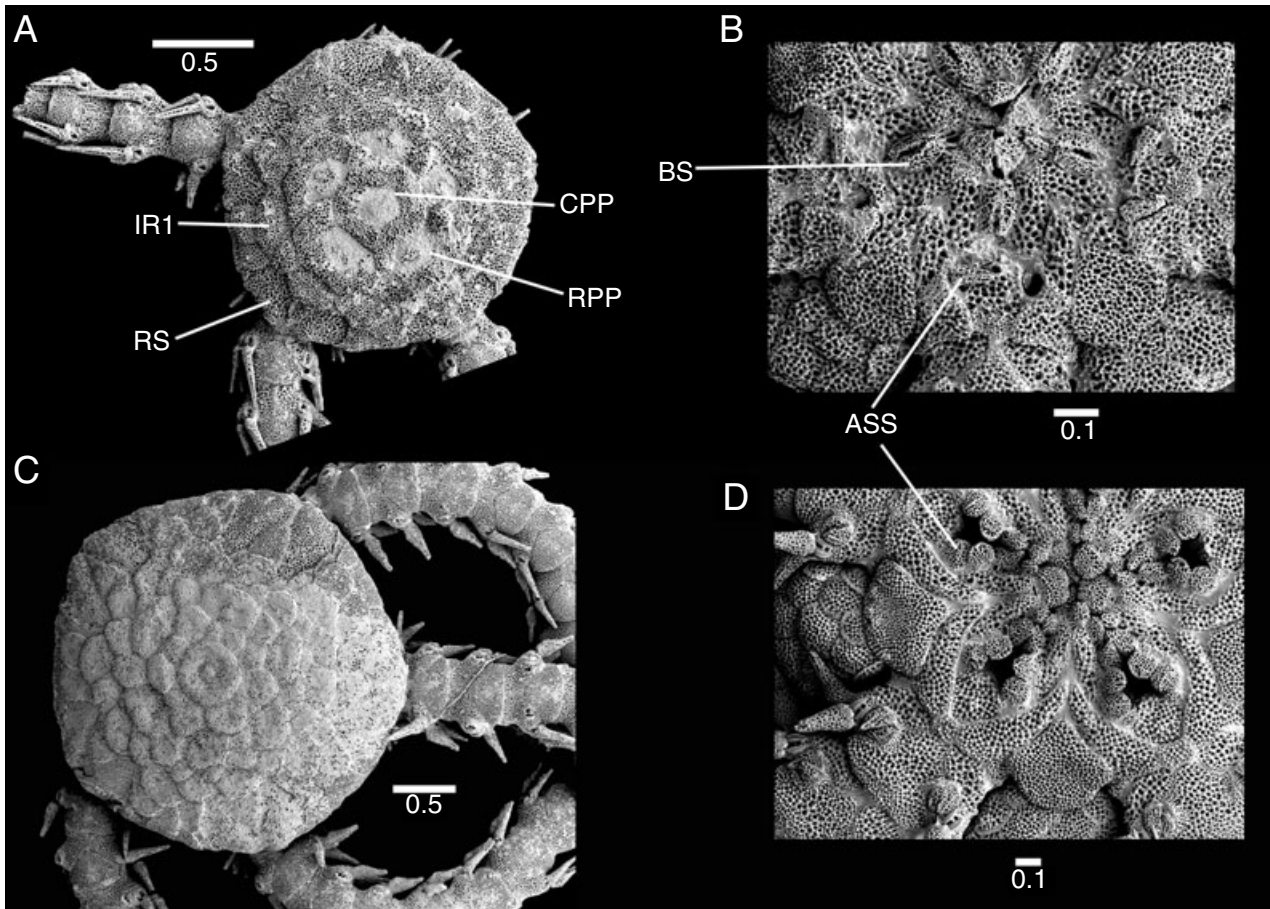
*Remarks:* Although few and only relatively large juveniles were found, the great similarity to *A. filiformis* is obvious. The primary plates have a similar bordered structure and the tooth of the small postlarvae is also quite similar in both species. In the BIOIce material both species have not yet been found in sympatry, with *H. duplicata* mainly occurring below 1000 m depth and *A. filiformis* being restricted to the upper 300 m (my unpubl. data). Off the Swedish west coast, *H. duplicata* does not occur, which eliminates the possibility of error in the identification of *A. filiformis* postlarvae from that area.

#### *OPHIOPUS ARCTICUS* LJUNGMAN, 1867

(FIG. 15A–H)

The smallest individual found measures 0.55 mm dd, with a single arm segment and the TP (not figured).





**Figure 14.** *Histampica duplicata* postlarval development. A, B, 1.5 mm dd postlarva; A, dorsal, note the thicker plate margins; B, ventral; C, D, 2.9 mm dd juvenile; C, dorsal; D, ventral. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.

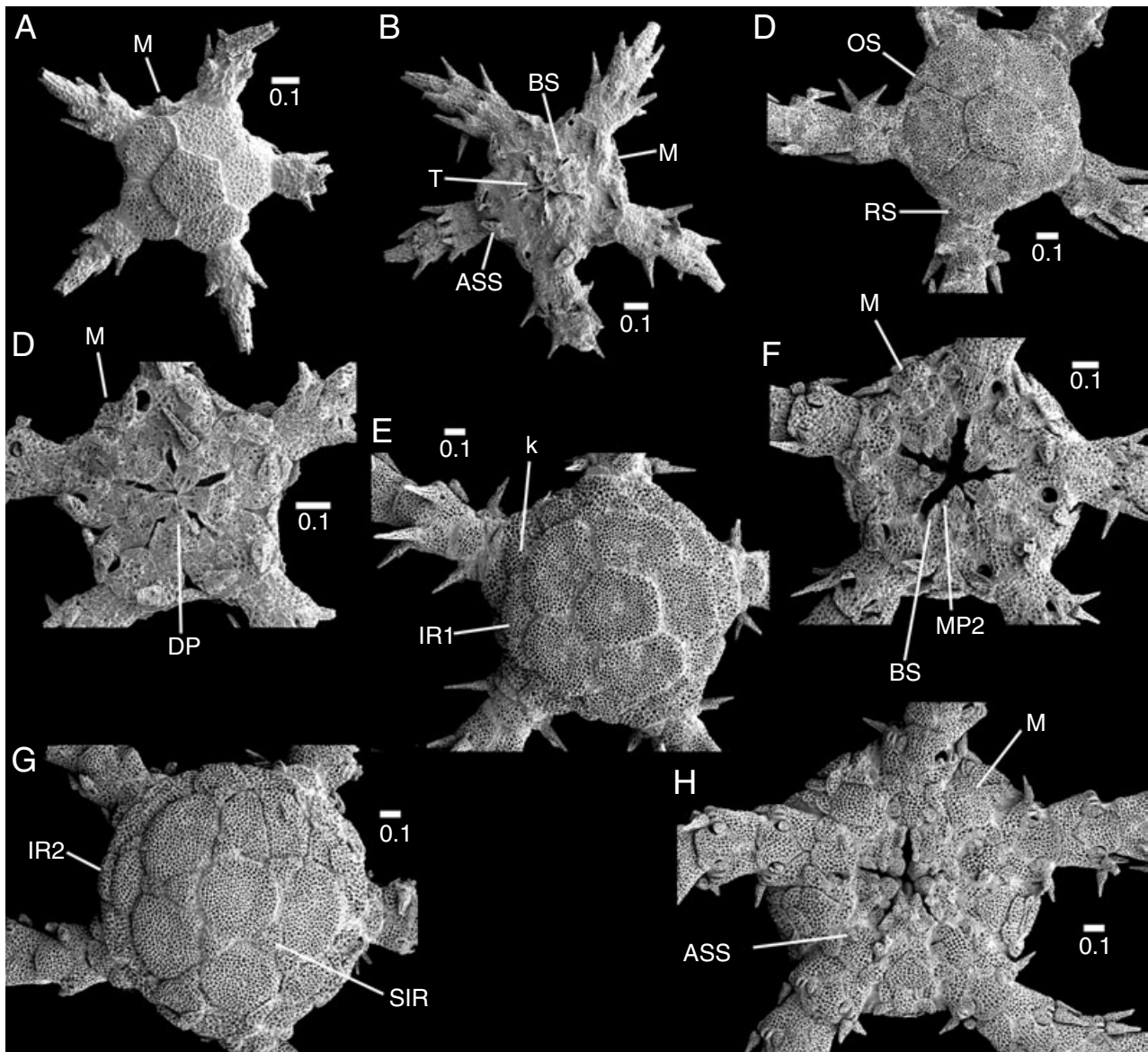
The dorsal disc is domed, formed by the evenly perforated plates of the primary rosette, M protruding in an inter-radius. The tooth is minute, and a low BS is present on the oral plate. The ASS is flat triangular, pairs pointing towards each other across the first VAP.

At 0.7 mm dd, the postlarvae have two arm segments, each bearing two spines on either side (Fig. 15A). The CPP is distinctly pentagonal, overlapping the rounded pentagonal RPPs. The TP is strong, hollow, tapering and ending in short thorns. At the disc edge, between the ASSs, the OSs can be seen, the M with a protruding cone ending in the hydropore. The tooth is wide and flat, triangular. The oral plate bears a wide low BS (Fig. 15B). The ASS is wide and flat triangular, pairs pointing towards each other, not visible from above. The TPo on the arm bears a conical pointed scale. The first VAP is elongated pentagonal, with proximal angle, concave lateral edges and straight distal edge.

At 0.9 mm dd and three arm segments, the RSs are just visible above the arm (Fig. 15C). The DAP on the first two segments is rounded triangular, longer than wide with slightly convex distal edge. The OSs are triangular, wider than long, still close to the disc edge, separated from the first VAP by the ASs (Fig. 15D). The base of the flat ASS is almost as wide as the spine is long. The second and following VAPs are of similar size and shape as the first VAP.

At 1.3 mm dd, the IR1 have formed below the RPPs and the IR2 at the disc edge, and the k-plate is present (Fig. 15E). Additional inter-radial scales are forming next to the IR1. The MP2 has formed on the DP (Fig. 15F).

At 1.4 mm dd, triangular SIRs have formed at the edge of the now round CPP (Fig. 15G). The first DAP is smaller than the following plates, its proximal part covered by the RSs. There are three conical arm spines, about half a segment long. A small round MP3 has formed on the oral plate proximal to the BS



**Figure 15.** *Ophiopus arcticus* postlarval development. A, B, 0.7 mm dd postlarva; A, dorsal, note the projecting madreporite; B, ventral, note the wide flat tooth (T); C, D, 0.9 mm dd postlarva; C, dorsal; D, ventral (a stray arm spine lies on a jaw); E, F, 1.3 mm dd postlarva; E, dorsal, note k-plate (k) and first inter-radials (IR1); F, ventral, note the second mouth papillae (MP2) on the dental plate; G, H, 1.4 mm dd postlarvae; G, dorsal, note the secondary inter-radial plates (SIR); H, ventral. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres.

(Fig. 15H). The MP on the DP have moved closer together. The ASS has transformed into a round scale close to the mouth slit. The ventral disc is formed by small round overlapping plates. The OS is teardrop-shaped, still separated from the arm by the long narrow ASSs. There is no bursal slit. Each TPO bears a single round scale. From about 2 mm dd, keys to adults can be used.

In adults (not figured), the ASS has grown into a large round scale and becomes part of the row of MP,

and the BS forms a leaf-like pointed papilla. Numerous small scales cover the dorsal disc; the CPP is much larger.

*Remarks:* The small postlarvae of *O. arcticus* have a compact appearance with distinctly straight plate edges. The order of appearance of the IR1 and IR2 is opposite to that in *Ophiura*, but similar to *Ophiopleura*. The shape of the tooth is similar to small *A. filiformis*.

## FAMILY OPHIOTHRICIDAE LJUNGMAN, 1867

*OPHIOTHRIX FRAGILIS*

(ABILDGAARD, IN O.F. MÜLLER, 1789)

(FIG. 16A–N)

The postlarvae of this species were collected on adult conspecifics (Fig. 16A). The smallest individuals found measure 0.34 mm dd, with two arm segments. The high dorsal disc is formed by the large, flat, pentagonal CPP, and twice as wide as long RPPs (Fig. 16A, B). All plates have only a small number of scattered minute perforations in their otherwise solid stereom. Each LAP bears a large hook-shaped spine on a protruding articulation ridge. LAPs are evenly perforated by small holes. The TP is quite small and hollow, about half as long as the hooks of the distal segment. The DAP is triangular, slightly wider than long, with convex distal edge and proximal angle, almost imperforate. Large triangular plates are visible inter-radially at the disc edge. The DP bears a tricuspid tooth (Fig. 16C). The comma-shaped AS bears no spine. The first VAP is trapezoidal, longer than wide. OSs are not visible.

At 0.55 mm dd and four arm segments, few short trifid spines have formed on the inter-radial OSs (Fig. 16D). The proximal angle of the DAP is rounded off and the most proximal arm segment bears two straight spines instead of hooks, perforated by rows of small holes. The hooks of the distalmost segment are only half the size of those of the previous segments (Fig. 16E). Remaining hooks have a large terminal tooth and two secondary teeth along their ventral edge. A short spine has formed dorsal to the hooks (Fig. 16F). In the middle of the proximal edge of the tooth, a sharp thorn has formed (Fig. 16G). Two additional teeth have formed on the DP dorsal to the first. OSs are beginning to form at the disc edge.

At 0.8 mm dd and 10–11 arm segments, the distal half of the RSs can be seen above the arm, perforated by numerous small holes (Fig. 16H). A small IR2 has formed below the IR1 at the disc edge. The DAPs are longer than wide, triangular with convex distal edge and rounded proximal angle. The OSs are triangular, wider than long, with convex distal edge (Fig. 16I). The VAPs are rectangular, with straight to concave distal edge and concave lateral edges.

At 1.1 mm dd, the wide wedge-shaped k-plate has appeared (Fig. 16J). The first tooth papillae have formed on some DPs (Fig. 16K), apparently by fragmentation of the teeth.

At 1.3 mm dd, the dorsal disc is covered with numerous bifid and trifid spinelets (after removal of the integument only visible at the disc edge; Fig. 16L). The proximal arm segments bear four erect spines with several thorns along their length, the dorsalmost half as long as the others (Fig. 16N). Only the distal

segments still bear hooks. Each DP bears several papillae instead of teeth (Fig. 16M). The appearance of tooth papillae clearly identifies the animals as Ophiotrichidae and in areas with no other species of the family, identification is unambiguous at this early stage.

In adults, only the ventralmost arm spine remains a short hook; all teeth have been replaced by papillae.

*Remarks:* *Ophiotrix fragilis* is identifiable in all growth stages by its characteristic arm hooks and the large imperforate CPP. The teeth appear to fragment during growth to form the tooth papillae. Postlarvae of this species, which has a planktotrophic larva, often aggregate on unrelated adult conspecifics (MacBride, 1907).

## FAMILY OPHIICOMIDAE LJUNGMAN, 1867

## SUBFAMILY OPHIICOMINAE LJUNGMAN, 1867

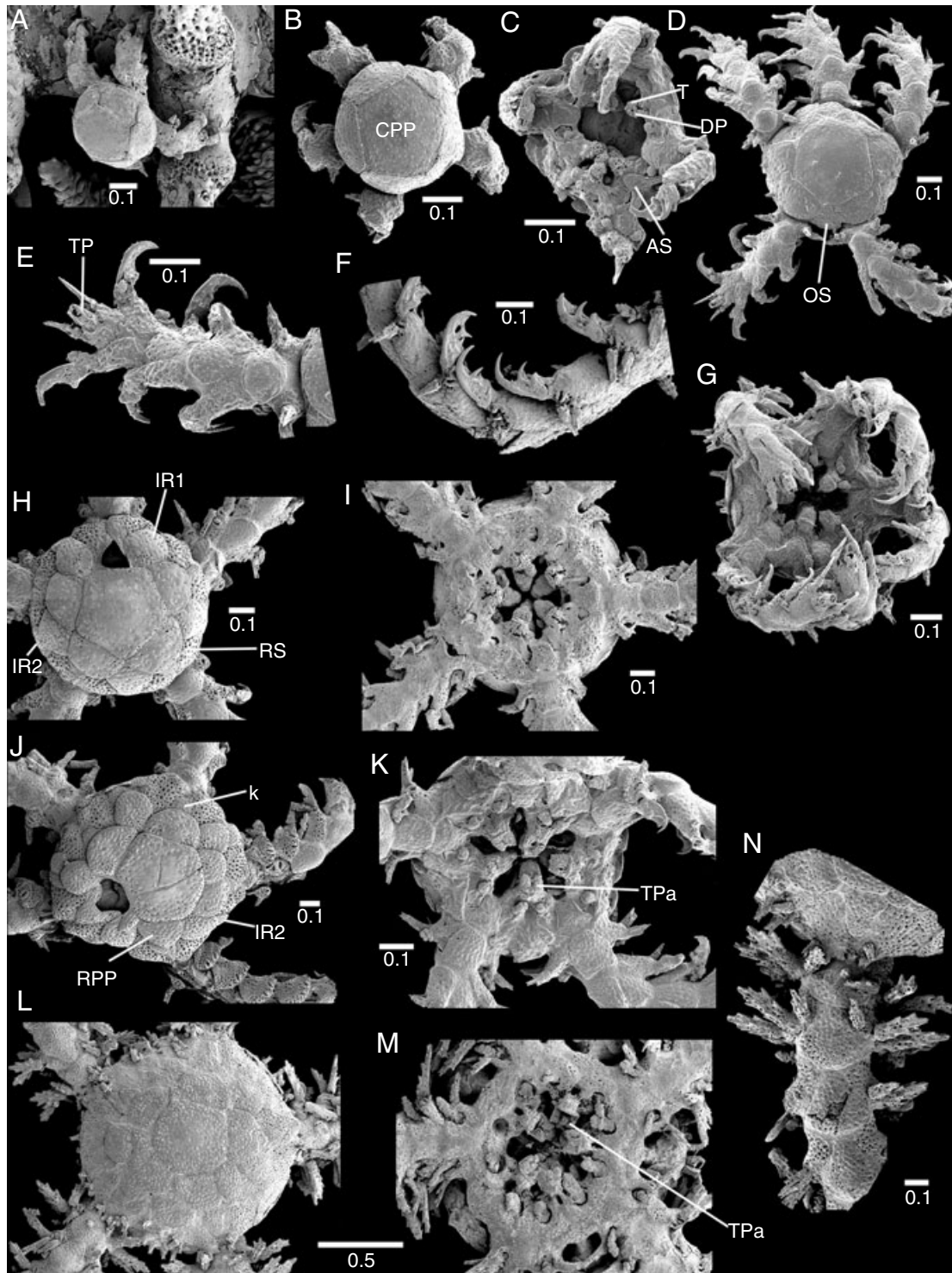
*OPHIICOMINA NIGRA*

(ABILDGAARD, IN O.F. MÜLLER, 1789)

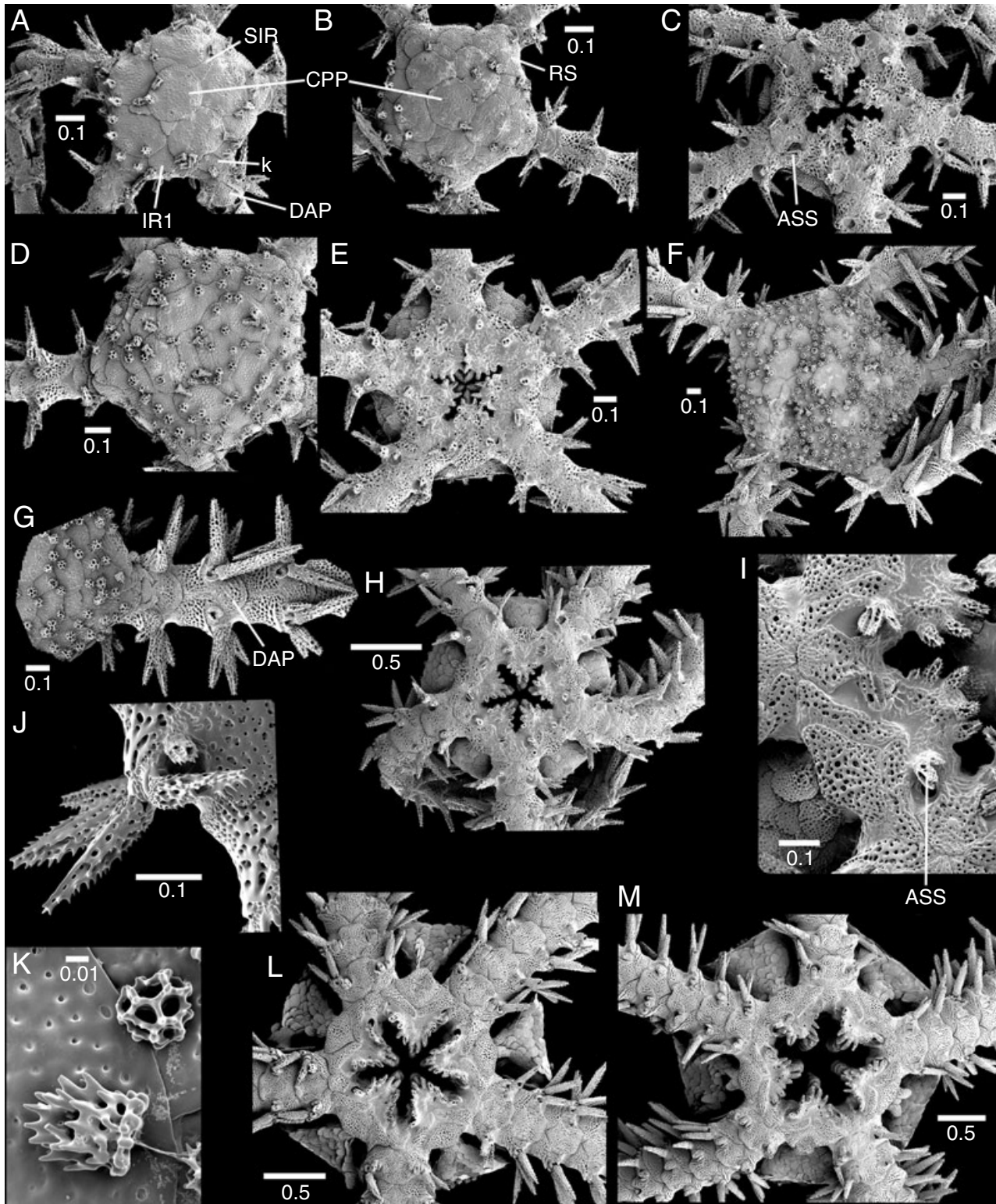
(FIG. 17A–M)

All stages studied here had a dark brown, almost black colour, which makes them unique among the species found at the Swedish west coast and thus easily identifiable. The smallest specimens available measure 0.7 mm dd with seven arm segments. The dorsal disc is formed by the round CPP and five RPPs, triangular SIRs, IR1 and the round k-plate above the distal ends of the RSs (Fig. 17A). All plates are almost imperforate, except for small holes on their margins particularly under a disc spine. The disc spines are conical and rugose. Each LAP bears three erect serrated spines. The DAP is triangular, slightly wider than long, with strongly convex distal edge, and adjacent plates separated by the LAPs. Another individual of 0.7 mm dd has fewer SIRs, and slightly larger IRs (Fig. 17B). The MP are rugose and spiniform, one on the DP and another on the oral plate, both half as long as the spine-like tooth (Fig. 17C). On some jaws a third lower papilla is present on the distal end of the oral plate. There is a strong, rugose ASS in the middle of the concave edge of the long distally flaring AS. The OS is teardrop-shaped, wrapped around the raised edge of the oral frame. Several round evenly perforated scales form the ventral disc. On the proximal arm segments, the TPo bears a single small rugose scale, which does not cover the pore. The VAPs are longer than wide, with convex distal edge, proximal angle and deeply concave lateral edges. The first VAP is similar to the others except for a convex proximal edge. Adjacent plates are separated by the LAPs.

At 0.9 mm dd, the number of disc scales has increased considerably. Most disc spines are shorter granules, but some are still conical spines, all of which



**Figure 16.** *Ophiothrix fragilis* postlarval development. A–C, 0.34 mm dd postlarvae; A, on arm of adult; B, dorsal, note the large central plate (CPP); C, ventral, note the tricuspid tooth; D–G, 0.55 mm dd postlarvae; D, arm dorsal, note the small terminal plate (TP) and large hooks; F, arm lateral; G, ventral; H, I, 0.8 mm dd postlarvae; H, dorsal, radial shields (RS) and inter-radial plates (IR1, 2) have formed; I, ventral; J, K, 1.1 mm postlarvae; J, dorsal, note the k-plate; K, ventral, note the first tooth papillae (TPa); L–N, 1.3 mm postlarvae; L, dorsal with numerous disc spines; M, ventral with additional TPa; N, arm dorsal, note the serrated shape of the proximal dorsal spines. *Abbreviations:* as in Figs 1–3, 5. Scale bars in millimetres. Some dorsal plates have fallen off due to the bleaching process (H, J).



**Figure 17.** *Ophiocomina nigra* postlarval development. A, B, two 0.7 mm dd postlarva dorsal, note that only one has secondary inter-radial plates (SIR); C, 0.7 mm dd postlarva ventral; D, E, 0.9 mm dd postlarvae; D, dorsal; E, ventral; F–H, 1.4 mm dd postlarvae; F, dorsal; G, arm dorsal; H, ventral; I–K, 1.6 mm dd postlarva; I, jaw, note the scale-like adoral shield spine (ASS) and the second smaller scale proximal to it; J, arm spines, note the serrated edges; K, disc granules are strongly rugose; L, 2.4 mm juvenile; M, 3 mm dd juvenile. *Abbreviations:* as in Figs 1–3, 10. Scale bars in millimetres.

are rugose (Fig. 17D). The oral plates bear two MP, the distal one lower and wider than the proximal papilla (Fig. 17E).

At 1.4 mm dd, the numerous dorsal disc scales are partially obscured by rugose granules (Fig. 17F). There are now four strongly serrated arm spines, the dorsalmost being the longest, longer than an arm segment (Fig. 17G). Of the RSs only the distal edge is visible beneath the disc scales. The MP on the DP have moved closer towards each other, forming an apical pair below the first tooth (Fig. 17H). The TS is flat, oval and covers the pore. Bursal slits are visible above the arm. Numerous round overlapping scales form the ventral disc.

With increasing size, the number of disc granules (Fig. 17K) increases until the dorsal disc is completely covered. At 1.6 mm dd, the ASS has moved to the oral plate and a small papilla has formed on the proximal side of the ASS (Fig. 17I). The ASs are long, pairs forming a wide angle. The OS is twice as wide as long with slightly protruding distal edge. The first VAP is smaller than the others, hexagonal with straight edges. On the first 'true' arm segment a second smaller TS has formed. The arm spines are pointed with strongly serrated lateral edges (Fig. 17J).

At 2.4 mm dd, the ASS and its adjacent papilla have been incorporated into the row of lateral MP, thus counting a total of five, with the apical pair close together, ventral to the first tooth (Fig. 17L). The ventral disc is covered with round, imbricating scales with small round perforations, bearing no granules.

At 3 mm dd, additional apical MP can be seen below the apical pair (Fig. 17M), an indication of the apical cluster of the adult, making this the smallest size at which keys for adults can be used. Each TPo bears a pair of one smaller and one larger, flat, oval scale. The VAP are contiguous, slightly overlapping on the proximal segments, with straight distal edge. The AS is long and narrow, almost horizontal to the jaw, bordering the proximal angle of the OS, without separating it from the first LAP. The OS is twice as wide as long, with a low protrusion in the middle of the distal edge.

*Remarks:* This shallow-water species can easily be identified in all growth stages by its dark brown to black colour, already present in small postlarvae, and its granulated dorsal disc. The genus *Ophiocomina* has been argued to belong within the Ophiacanthidae instead of the Ophiocomidae (Wilkie, 1980), but this has been refuted by Baker & Devaney (1981). The serrated spines and rugose disc granules and mouth papillae certainly bear closer similarities to Ophiacanthidae than to Ophiocomidae. However, small stages of Ophiocomidae were not available for comparison, leaving this question undecided. In addition, the Ophiacanthidae has been suggested to be paraphyletic

(Smith *et al.*, 1995), which makes the systematic status of *O. nigra* even more difficult to understand. Until this question is resolved it is retained in the Ophiocomidae.

## DISCUSSION

### GENERAL COMMENTS

The main skeletal features of ophiuroids develop over an extended period of time after metamorphosis (Ludwig, 1881, 1899; Clark, 1914). Among the skeletal elements of the arm, the terminal plate appears first, while all later arm segments are formed at the proximal end of the terminal plate, leading to the well-known fact that the distal segments are younger and less differentiated than the proximal segments. In the youngest postlarvae, only a single modified arm segment lies under the disc, but during growth, additional segments may be incorporated into the disc. The youngest arm segments consist of only the lateral plates, which meet above and below. The ventral arm plate usually appears earlier than the dorsal plate, and the number of arm spines is lower in younger segments. Additional arm spines are formed in ventrodorsal direction, the ventralmost spine being the oldest according to Ludwig (1899), although the ventral spine usually is the smallest and could be argued to be the youngest. Further studies of the growth of the lateral plates and development of arm spines are necessary to decide this. Tentacle scales develop independent of arm spine development. The jaws are present in the smallest postlarvae, but the number of teeth, tooth papillae and mouth papillae increases during development. Oral shields, including the madreporite, appear on the dorsal side of the disc, and move later to the ventral side, gradually assuming their final shape (Ludwig, 1899; this study). This is particularly obvious in *Ophiopleura borealis*, whereas the madreporite and oral shields are more lateral at the disc edge in other species. All species examined in this study and previous works follow this general developmental pattern, which was established by the earliest studies. The development of the dorsal disc scalation and mouth papillae are less conservative and show considerable variation among taxa (see below).

### PHYLOGENETIC COMPARISONS

#### *Dorsal disc plates*

Previous studies have reported that the first interradial plates on the dorsal disc form distal to the circle of primary radial plates and that the second interradial plates form proximal to the first (Ludwig, 1899; Schoener, 1967, 1969; Webb & Tyler, 1985; Sumida *et al.*, 1998). This appears to hold true for all studied

species of *Ophiura*, but is more doubtful in other genera. Because most species have not been studied from laboratory reared material, continuous size series are rarely available. Thus, the observed skeletal changes between postlarvae of different sizes are subject to interpretation, because the history of each individual plate cannot be determined. Assuming that the smaller of two plates, of which only one was present in a younger stage, is the newly formed plate, the second inter-radial plate can be identified proximal to the first plate in *Ophiura robusta* (this study) and other species of *Ophiura* (Webb & Tyler, 1985; Sumida *et al.*, 1998). However, under the same assumption, the second inter-radial plate must form distal to the first in *Ophiopleura borealis*. In *Amphiura filiformis* and *Amphiura chiajei* the proximal plate is slightly larger than the distal plate, suggesting the same condition as in *Ophiopleura borealis*, but slightly smaller growth stages are required to confirm this conclusion. In *Ophiopus arcticus* the proximal plate is considerably larger than the distal plate in all stages where both are present, suggesting that also in this species the second inter-radial plate forms distal to the first. Upon examination of the pictures of *Ophiactis abyssicola* in Sumida *et al.* (1998) and my own material of that species the same observation is made, but the available data on *Ophiopholis aculeata* are inconclusive (Sumida *et al.*, 1998). However, Ludwig (1899) describes the second inter-radials as appearing proximal to the first in *Ophiactis asperula* (Philippi, 1858) and *Ophiactis kroeyeri* Lütken, 1856, suggesting that this pattern is either not genus specific or that indeed *O. abyssicola* develops in the same way. In *Ophiothrix fragilis*, the second inter-radial appears to form distal to the first; data on Ophiacanthidae and *Ophiocomina nigra* are insufficient to answer this question.

In *Ophiopleura borealis*, a set of inter-radial plates (IR0) forms proximal to the primary radial plates prior to the appearance of the first inter-radial plates (IR1, IR2) discussed above. Later, secondary radial plates form between the IR0, completely separating the primary radial plates from the central plate. This pattern is similar to that found in *Amphipholis squamata* as described by Ludwig (1881), but it is unique among the species studied since.

Several species show patterns of dorsal disc scalation, which deviate even more from the generalized type. The primary rosette is lacking in *O. glacialis*, *A. borealis*, *O. anomala*, *O. bairdi* and *O. clavigera*. In *O. glacialis*, the primary plates of the newly settled postlarva are of different sizes and irregular shapes, later forming a circle of seven plates around a central plate, but this pattern disappears later and no radial shields can be distinguished. In *Amphiura borealis* all disc scales are of similar shape and size, which makes it impossible to identify inter-radial plates or any of

the other common plate types except the radial shields, which, however, are difficult to distinguish until quite late in development. In the remaining species without primary rosette, the development of additional plates does not follow a well-defined order, although size and shape may vary. These observations show that the development of the dorsal disc scalation is quite variable and may not be a reliable character for phylogenetic inferences.

The plate stereom has been shown to be valuable for the identification of small stages (Sumida *et al.*, 1998). This is particularly evident in the genera *Ophiura* and *Amphiura*, where the stereom structure and size of fenestrations are important characters for distinguishing closely related species.

#### *Mouth papillae*

The mouth papillae are composed of the block-like buccal scale, the adoral shield spine and a varying number of additional papillae forming on the oral plates. The buccal scale is here regarded as the first mouth papilla in accordance with Sumida *et al.* (1998), because the adoral shield spine becomes part of the row of papillae quite late in development. A buccal scale has been found in all examined Ophiuridae, Amphiuridae and in Ophiactidae with the exception of *Ophiopholis aculeata* (L., 1767), whereas it is lacking in *Ophioscolex*, *Ophiothrix fragilis* and *Ophiocomina nigra* (this study; Webb & Tyler, 1985; Hendler, 1988; Sumida *et al.*, 1998). Among Ophiacanthidae so far only *Ophiolimna bairdi* has a buccal scale. When present, the buccal scale is formed during metamorphosis and is visible in the earliest postlarva (Ludwig, 1881; Hendler, 1978). In Amphiuridae and in *Ophiactis abyssicola*, the buccal scale is retained as a low, wide scale deep in the mouth slit (Hendler, 1988; Sumida *et al.*, 1998), whereas in *Ophiura*, *Ophiopleura borealis* and *Ophiolimna bairdi* it is not clear whether it decreases in width or splits into several smaller papillae. In *Ophiopus arcticus*, the buccal scale forms a block-like distal papilla on the oral plate, but its development in *Histampica duplicata* is unclear. The absence of the buccal scale may be ancestral for Ophiuroidea because it is lacking in the basal taxa (Smith *et al.*, 1995) Ophiomyxidae, Ophiacanthidae and possibly Euryalida, but it has probably been reduced secondarily in Ophiothricidae and in *Ophiopholis*.

In *Ophiura* the second mouth papilla develops on the proximal end of the oral plate (Webb & Tyler, 1985; Sumida *et al.*, 1998). In *Ophiopleura borealis*, the second mouth papilla clearly forms on the edges of the dental plate. It is not clear whether it later moves onto the oral plate making room for another much smaller papilla or whether it grows more slowly than the other papillae and stays on the dental plate. In Amphiur-

ridae, the second papilla also forms on the edges of the dental plate (Hendler, 1988; this paper) and moves subsequently to the proximal edge of the oral plate forming the infradental papillae. In *Ophiolimna bairdi*, *Ophiomitrella clavigera*, *Ophiacantha anomala* and *Ophiocomina nigra* the second papilla overlaps between dental plate and oral plate in larger postlarvae, probably originating on the proximal end of the oral plate. The available material is, however, insufficient to decide this, lacking the smallest stages.

The adoral shield spine is homologous with the arm spines (Hendler, 1988) and is usually present in the youngest stage. In most species, this spine changes shape and becomes part of the series of mouth papillae. In *Ophiura* it forms the first of the numerous tentacle scales at the second pore. *Ophiopleura borealis* is one of few species lacking the adoral shield spine, and the papillae associated with the second tentacle pore form at about the same time as the second mouth papilla, before tentacle scales begin to form along the arm. The absence of the spine may be a derived state as arm spines are present in early *O. borealis* and even species lacking tentacle scales, such as *Ophiocolex glacialis*, possess adoral shield spines. In *O. glacialis*, the adoral shield spine remains similar to regular arm spines, suggesting that this is the ancestral state. The adoral shield spine and all other mouth papillae are lacking also in *Ophiothrix fragilis*, and in *Ophiothrix angulata* (Say, 1825) according to Clark (1914).

#### Teeth

The newly metamorphosed postlarva usually has a single tooth and additional teeth are formed dorsal to the first on the dental plate. The first tooth usually differs in shape from the other teeth and is more or less tricuspid in postlarvae of Ophiactidae, Ophiothricidae and Amphiuroidae, with the exception of *Amphiura chiajei*, which has a smaller, sharply pointed triangular tooth. In Ophiuridae the teeth are triangular with a sharp point, whereas Ophiomyxidae and Ophiacanthidae have spine-like teeth at least as postlarvae. In *Ophiothrix*, the teeth appear to divide and shorten to form the tooth papillae, beginning with the ventral-most tooth. This must be a highly derived condition. These similarities across families suggest that the overall shape of the first tooth is a rather conservative character, valuable for the analysis of phylogenetic relationships between higher-level taxa. Clark (1914) regarded spine-like teeth as ancestral and other shapes as derived. Indeed, the shape of the teeth supports the classification proposed by Smith *et al.* (1995), according to which Ophiomyxidae and Ophiacanthidae are basal taxa within the order Ophiurida. However, the position of the Euryalida as sister taxon

to Ophiurida is not supported and few euryalid postlarvae have been described. To determine this, more species need to be analysed.

#### Madreporite and oral shields

The point of origin of the madreporite in ophiuroids and its bearings on interclass relationships have been subject to discussion, because adult ophiuroids generally have a ventral madreporite, whereas it is usually dorsal in asteroids. Hendler (1978) suggested *in situ* formation of the madreporite in its final ventral position. Sumida *et al.* (1998) were able to show that the oral shields and thus the madreporite form interradially at the disc edge and migrate to their final location during development. This is particularly evident in *Ophiopleura borealis*, where the madreporite first appears as a quite large dorsal inter-radial plate. Mortensen (1912) remarked on the 'sudden' ventral appearance of the madreporite in *A. loveni*, which curiously lacks all other oral shields. The small sample of *A. loveni* postlarvae available does not include intermediate stages that would allow any conclusion on the point of origin of its madreporite, which may form *in situ*. Apart from this possible exception, a dorsal origin of the madreporite is general for ophiuroids, indicating affinities with asteroids. A ventral madreporite is one of the characters used to delimit the class Ophiuroidea, but the increasing ontogenetic evidence suggests that this character is no longer valid, which demonstrates the importance of including all life-stages in systematic analyses.

#### REPRODUCTION AND RECRUITMENT

All stages studied here originate from bottom samples and thus represent settled life-stages. In species with planktotrophic larvae, the newly metamorphosed postlarva may spend some time in the plankton before settling on the seafloor, as has been shown in *Ophiocten gracilis* (G.O. Sars, 1871), which settles at 0.6 mm dd (Sumida *et al.*, 2000). The smallest bottom-living stage is found in postlarvae with arms consisting of only the terminal plate, such as in *Ophiura sarsii* (Sumida *et al.*, 1998), *Ophiura ophiura* and *Acrocnida brachiata* (Webb & Tyler, 1985). In all other free-living species studied so far, the smallest stage found has at least one arm segment in addition to the terminal plate. Among these species, planktotrophic (pluteus-) larvae are known for *O. albida*, *O. robusta*, *O. ophiura*, *A. filiformis*, *A. chiajei*, *O. fragilis* and *O. nigra* (Mortensen, 1897, 1901; Narasimhamurti, 1933; Thorson, 1934, 1946; Fenaux, 1963). Smaller stages may thus exist also for these species, but possibly they stay in the plankton until the first arm segment has developed. According to Hendler (1975), species with



planktotrophic larvae produce eggs of less than 0.2 mm diameter. The large size of the postlarva and the large yolky eggs (0.6–0.8 mm; Mortensen, 1912) of *A. loveni* suggest lecithotrophic development, possibly a bottom-living vitellaria, because the species is not brooding. Planktotrophic development has not been reported for Ophiomyxidae and Ophiacanthidae (McEdward & Miner, 2001), suggesting that not only the brooding *O. anomala* and *O. clavigera* but also *O. bairdi*, *O. glacialis* and *O. purpureus* have lecithotrophic larvae.

Hendler (1988) suggested that the scalation of the disc might be useful to infer the mode of reproduction and that the lack of a primary rosette may suggest abbreviated development. Among the species lacking a primary rosette, *A. borealis*, *O. anomala* and *O. clavigera* are brooding, while *O. glacialis* and *O. bairdi* are non-brooding. According to Thorson (1936), *O. glacialis* has a pelagic lecithotroph larva with abbreviated or direct development and relatively large yolky eggs of 460–510 µm diameter. However, several species with eggs of similar size and mode of development, such as *O. borealis*, *O. arcticus*, *Ophiacantha bidentata* (Retzius, 1805) and *Ophiomusium lymani* Wyville-Thomson, 1873 (compiled in Pearse, 1994), have typical primary rosettes. Thus, growing evidence suggests that the scalation of the disc of ophiuroid postlarvae is unrelated to reproductive mode.

Mortensen (1920) found it impossible to distinguish the youngest stages of *A. chiajei* from *A. filiformis* and his attempts to rear the (then unknown) larvae of *A. chiajei* were not successful. Most probably, his samples consisted only of *A. filiformis* as recruitment events are rare in *A. chiajei*, with up to 12 years between settlements, despite a lifespan of about 15 years and repeated spawning (Buchanan, 1967). It is a common species at the Swedish west coast, occurring in sympatry with *A. filiformis* over a depth range of at least 7–110 m, according to the collection records at the Swedish Museum of Natural History, Stockholm, and in contradiction with Buchanan's (1964, 1967) observations of a sharp depth separation of the two species off Northumberland. However, only few postlarvae of *A. chiajei* were available for examination from museum samples, most of them collected at Tjärnö Marine Biological Laboratory (TMBL) in 1998. Collecting efforts at TMBL in November 2001 and 2002 yielded juveniles only of *A. filiformis*, whereas in 2003 a small number of *A. chiajei* postlarvae were obtained, indicating that recruitment indeed is rare in *A. chiajei* but more common than previously thought. In contrast, the shorter-lived (3–4 years, Buchanan, 1964; but see Muus, 1981) *A. filiformis* shows recruitment events every year. The recruitment periodicity of the other species described here is largely unknown, but the increasing number of descriptions of juvenile

stages being published should supply much needed support to population studies.

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