Ophiuraster patersoni Litvinova, 1998 is the postlarva of *Ophiomyxa serpentaria* Lyman, 1883 (Echinodermata, Ophiuroidea)

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ABSTRACT
Ophiuraster patersoni Litvinova, 1998 is shown to be identical with the small postlarva of *Ophiomyxa serpentaria* Lyman, 1883, which is described here for the first time. The smallest individuals have an asteroid-like habitus with a disk diameter of 1.8 mm and short, not sharply set off arms. The whole animal is covered with thick, in small postlarvae transparent, skin, which thickens further with growth. The postlarvae are characterised by large primary plates, large, swollen lateral arm plates, the first of which surround the disk margin, and bare patches of skin on the interradial disk. The terminal arm plate is bulbous and hollow, in individuals of 2.5 mm it has a wide distal opening. The mouth papillae are flat and rugose as is typical for *Ophiomyxa* Müller & Troschel, 1840. Dorsal arm plates are absent in all stages, while ventral arm plates are present from about 2.0 mm disk diameter, as well as a small hook-shaped arm spine. Further disk growth is slower than the increase in arm length. Thus, individuals with 2.5 mm disk diameter have between 11 and 16 arm segments, two arm spines and two lateral mouth papillae. The large first lateral arm plates move ventrally during growth and probably later form the adoral shields. The taxonomic status of the remaining three species of *Ophiuraster* H. L. Clark, 1939 is discussed.

KEY WORDS
Echinodermata,
Ophiuroidea,
Ophiuraster patersoni,
Ophiomyxa serpentaria,
postlarvae,
development,
growth,
Atlantic Ocean.

RÉSUMÉ
Ophiuraster patersoni *Litvinova, 1998 est la postlarve d'*Ophiomyxa serpentaria *Lyman, 1883 (Echinodermata, Ophiuroidea).*
Il est démontré qu'*Ophiuraster patersoni* Litvinova, 1998 est identique à la petite postlarve d'*Ophiomyxa serpentaria* Lyman, 1883, qui est décrite ici pour la première fois. Les plus petits individus présentent la forme générale d'une astérie, avec un disque de 1,8 mm de diamètre et des bras courts peu différenciés du corps. L'animal tout entier est couvert d'une peau épaisse, transparente chez les petites postlarves, qui s'épaissit durant la croissance. Les postlarves sont caractérisées par des plaques primaires de grande taille, des brachiales latérales élargies, dont la première entoure la marge du disque, et sur le disque par des parties de peau nue en position interradiaire. La brachiale terminale est bombée et creuse et présente, chez les individus de 2,5 mm, une large ouverture distale. Les papilles buccales sont plates et rugueuses, ce qui est typique des *Ophiomyxa* Müller & Troschel, 1840. Les brachiales dorsales sont absentes à tous les stades, alors que les brachiales ventrales, ainsi qu'un petit piquant brachial en forme de crochet, sont présents sur les spécimens dont le diamètre du disque est d'environ 2,0 mm. La croissance du disque est plus lente que l'allongement des bras. Aussi les individus possédant un disque de 2,5 mm de diamètre ont-ils entre 11 et 16 brachiales, deux piquants brachiaux et deux papilles buccales latérales. Les premières grandes brachiales latérales se déplacent vers la face ventrale durant la croissance, pour probablement former à terme les boucliers adoraux. Le statut taxonomique des trois autres espèces d'*Ophiuraster* H. L. Clark, 1939 est discuté.

MOTS CLÉS
Echinodermata,
Ophiuroidea,
Ophiuraster patersoni,
Ophiomyxa serpentaria,
postlarves,
développement,
croissance,
océan Atlantique.

INTRODUCTION

The genus *Ophiuraster* H. L. Clark, 1939 includes ophiuroids with a relatively large flat disk from which the short wide arms are not sharply set off as in other ophiuroid genera. Hence, the habitus of this genus is superficially more similar to asteroids than typical ophiuroids. Indeed, *Ophiuraster patersoni* Litvinova, 1998 has been reported as a juvenile asteroid of the family Poraniidae Perrier, 1893 (Ringvold 1999). The disk margin of *Ophiuraster* is bordered by large, closely set plates. All four currently recognised species (*O. perissus* H. L. Clark, 1939; *O. symmetricus* Fell, 1958; *O. belyaevi* Litvinova, 1998 and *O. patersoni*) were described on single specimens. The size of these holotypes ranges from 1.9 mm disk diameter (dd) (*O. patersoni*) to 5.0 mm dd (*O. symmetricus*). All were collected at great depth between 725 (*O. symmetricus*) and 2312 m (*O. perissus*). The juvenile characters of these animals such as the small size, the short arms consisting of few segments, and the generally not well developed skeletal structures of disk, arms and oral frame were interpreted as paedomorphic by Vadon (1991), bearing great similarity to the genus *Ophiomastus* Lyman, 1878.

The postlarval development of the majority of the about 2000 described species of ophiuroids is still unknown. For some 20-30 species, most of them from the North Atlantic, postlarvae have been described in detail (Schoener 1967, 1969; Stancyk 1973; Hendler 1978; Muus 1981; Bartsch 1985; Webb & Tyler 1985; Sumida *et al.* 1998). These works showed that postlarvae often differ morphologically from the adults, which suggests great caution regarding the question of the existence of paedomorphic species until more juvenile forms have been identified and matched with their adult conspecifics.

Material collected by the BIOICE (Benthic Invertebrates of Icelandic waters) programme contained specimens of *O. patersoni*, which fit into a growth series of juvenile *Ophiomyxa serpentaria* Lyman, 1883. The postlarva of *O. serpentaria* will be described here for the first time, while *O. patersoni* is shown to be a junior synonym of *O. serpentaria*.

ABBREVIATIONS

BIOFAR	Investigations on the marine benthic fauna of the Faroe Islands;
dd	disk diameter;
KMBL	Kaldbak Marine Biological Laboratory, Kaldbak, Faroe Islands;
MNHN	Muséum national d'Histoire naturelle, Paris ;
NI	Icelandic Institute and Museum of Natural History, Reykjavik;
SMNH	Swedish Museum of Natural History, Stockholm;
stn	station number.

MATERIAL AND METHODS

Specimens of *O. serpentaria* were isolated from samples collected by BIOICE in the North Atlantic waters surrounding Iceland (Fig. 1). The animals were initially fixed in 4% formalin and later transferred to 80% ethanol. Postlarvae of different sizes were bleached in diluted household bleach (NaOCl), 1:1 bleach : tap water, for 5-20 secs, which was quickly washed off in water, and the animals were air-dried. They were then mounted on aluminium stubs using non-permanent spray-glue. After scanning the ventral side of the animals in a field emission scanning electron microscope (SEM) Hitachi S-4300, the glue was dissolved in butyl acetate, brushed off with a brush if necessary, and the specimens were then remounted with fresh glue to scan the dorsal side. The postlarvae were identified by tracing adult characters backwards from the largest to the smallest juveniles, building up a growth series. This method has been successfully used by previous authors (Webb & Tyler 1985; Sumida *et al.* 1998). The terminology used follows Sumida *et al.* (1998). Arm segments are counted from the first segment under the disk outwards to the last segment next to the terminal plate.

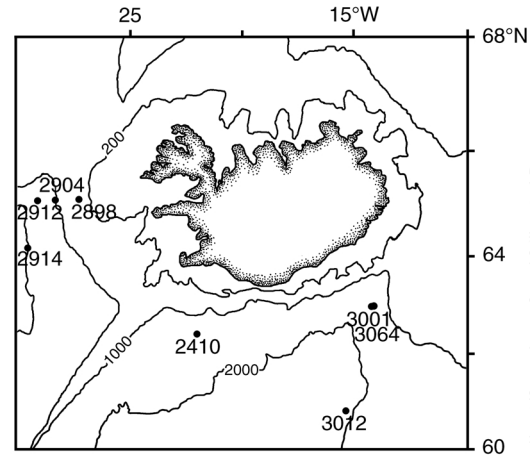

FIG. 1. — BIOICE collecting stations of *Ophiomyxa serpentaria* Lyman, 1883 (Iceland waters).

SYSTEMATICS

Family OPHIOMYXIDAE Ljungman, 1867
Genus *Ophiomyxa* Müller & Troschel, 1840

Ophiomyxa serpentaria Lyman, 1883
(Figs 2-4)

Ophiomyxa serpentaria Lyman, 1883: 274, pl. 8 figs 114-116.

Ophiodera serpentaria – Verrill 1899: 67.

Ophiodera serpentina – Koehler 1909: 203 (misspelling).

Ophiuraster patersoni Litvinova, 1998: 441.

MATERIAL EXAMINED (Table 1, Fig. 1). — **Off Iceland.** A total of 15 postlarvae and 25 adult specimens: stn 2410, 1 spec. on SEM stub (SMNH-46115); 2 specs in ethanol (SMNH-51874); stn 2898, 3 specs in ethanol (SMNH-51868); stn 3012, 2 specs on SEM stub (SMNH-51873); stn 2914, 2 specs in ethanol (SMNH-52035); remaining samples ethanol, lodged at NI (no catalogue numbers).

COMPARATIVE MATERIAL. — *Ophiuraster patersoni*, Bay of Biscay, BIOGAS 6, stn D586, N.O. *Jean Charcot*, 44°05'N, 4°19'W, 1950 m, 31.X.1974, holotype (MNHN EcOs 4895). — *Ophiuraster belyaevi*,

TABLE 1. — Collection data of *Ophiomyxa serpentaria* Lyman, 1883, from the BIOICE programme. Abbreviation: **pl**, postlarvae.

Station No.	Collecting date	Coordinates	Depth	Temp.	Bottom	No. of specimens
2410	2.VII.1993	62°51'N, 21°43'W	1074 m	4.0°C	Silty sand	3 pl
2898	24.VIII.1996	65°29'N, 27°33'W	672 m	6.0°C		3
2904	24.VIII.1996	65°23'N, 28°21'W	1057 m	4.8°C	Silty sand	1 pl
2912	25.VIII.1996	65°10'N, 29°04'W	1456 m	3.9°C		1
2914	25.VIII.1996	64°54'N, 29°58'W	2005 m	3.2°C	Gravely sand	2 pl
3001	5.VII.1997	63°34.27'N, 14°54.96'W	690 m	4.7°C	Gravel, stones / boulders and coral	9
3012	7.VII.1997	61°22.31'N, 15°19.37'W	2139 m	3.3°C		9 pl
3064	10.VII.1997	63°43.63'N, 14°19.71'W	428 m	6.1°C	Coral	12

Kerguelen Islands, MD04, stn I106 CP258, 48°43'5"S 71°06'5"E, 925 m, 13.III.1975, holotype (MNHN EcOs 5839). — "Poraniidae", BIOFAR, stn 158, 61°58.3'N, 5°38.2'W, 322 m, 7.V.1988 (data from Nørrevang *et al.* 1994), 3 specs in ethanol (KMBL, no catalogue number).

REMARKS. — The dd among the studied postlarvae ranges from 1.8 to 2.5 mm, while the number of arm segments ranges from 2 to 16, with considerable variation in the larger individuals (Fig. 2). Adult specimens range from 16.0 to 25.0 mm dd, with arm lengths of 65.0 to over 100.0 mm. Unfortunately, the maximum arm length could not be determined, because all larger individuals are badly damaged with arms broken. All animals are covered with smooth thick skin, which obscures the plates.

DESCRIPTION

Postlarvae

The smallest individuals in the material have a dd of 1.8 mm with two arm segments, the first incorporated into the disk, the second free. Small additional plates indicating the beginning formation of the third segment are barely visible below the large, bulbous terminal plate bearing several short spines at its tip (Fig. 3A, B). The whole animal is covered with tough skin, which is transparent in the smallest specimens and difficult to remove without disintegrating the skeleton. The dorsal disk is formed by the large central disk plate, which is pentamerous and slightly raised in the centre. The surrounding five radial primary plates are equal in size and shape to the central plate. All primary plates are perforated by pentamerous fenestrations, giving them a honeycomb-like structure. The interradial areas are free of plates, covered only with skin, bordered by two large marginal plates, which extend onto the dorsal side. The radial plates are small, oval and separate. There are no dorsal arm plates, leaving the arm vertebrae visible in a naked furrow between the large and swollen lateral plates, which bear no spines. The arm plate is hollow with a distal opening (Fig. 3G). The mouth papillae are rugose, a single large, pointed apical papilla and a small lateral one to each side of the jaw, twice as wide as long. Distal to the paired jaws is a naked area, the oral shield has not yet formed. The first ventral arm plate is large and oval. The tentacle pore is obvious and scale-less, there are no arm spines yet.

At 2.0 mm dd the arms consist of five segments. A second flat, short lateral mouth papilla has just begun to form, as well as a single small hook-shaped ventral arm spine on the proximal segments, deeply embedded in the skin (Fig. 3C, D). The second and following ventral arm plates are less than half the size of the first plate, rounded triangular, with convex distal edge.

Between 2.0 and 2.5 mm dd, arm length increases, but no additional disk plates are formed (Fig. 2E-M).

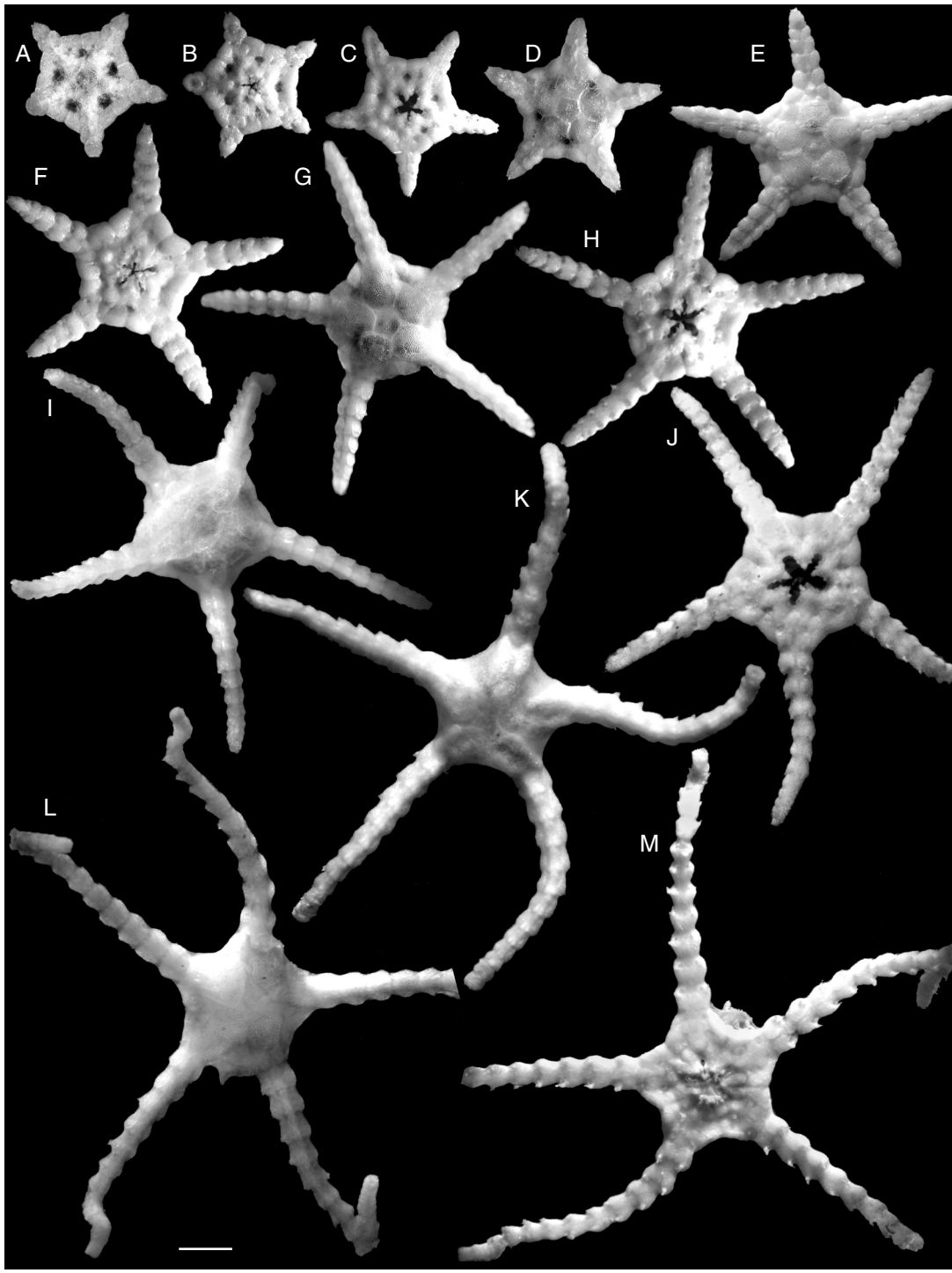

FIG. 2. — Growth series of postlarval *Ophiomyxa serpentaria* Lyman, 1883, dorsal and ventral aspects; **A**, **B**, dd 1.8 mm, 2 as, stn 3012; **C**, **D**, dd 1.9 mm, 3 as, stn 3012; **E**, **F**, dd 2.2 mm, 7 as, stn 2914; **G**, **H**, dd 2.3 mm, 9 as, stn 2914; **I**, **J**, dd 2.5 mm, 11 as, stn 3012; **K**, dd 2.5 mm, 13 as, stn 2410; **L**, **M**, dd 2.5 mm, 16 as, stn 3012. Abbreviations: **as**, arm segments; **dd**, disk diameter; **stn**, BIOICE station number. Scale bar: 1 mm.

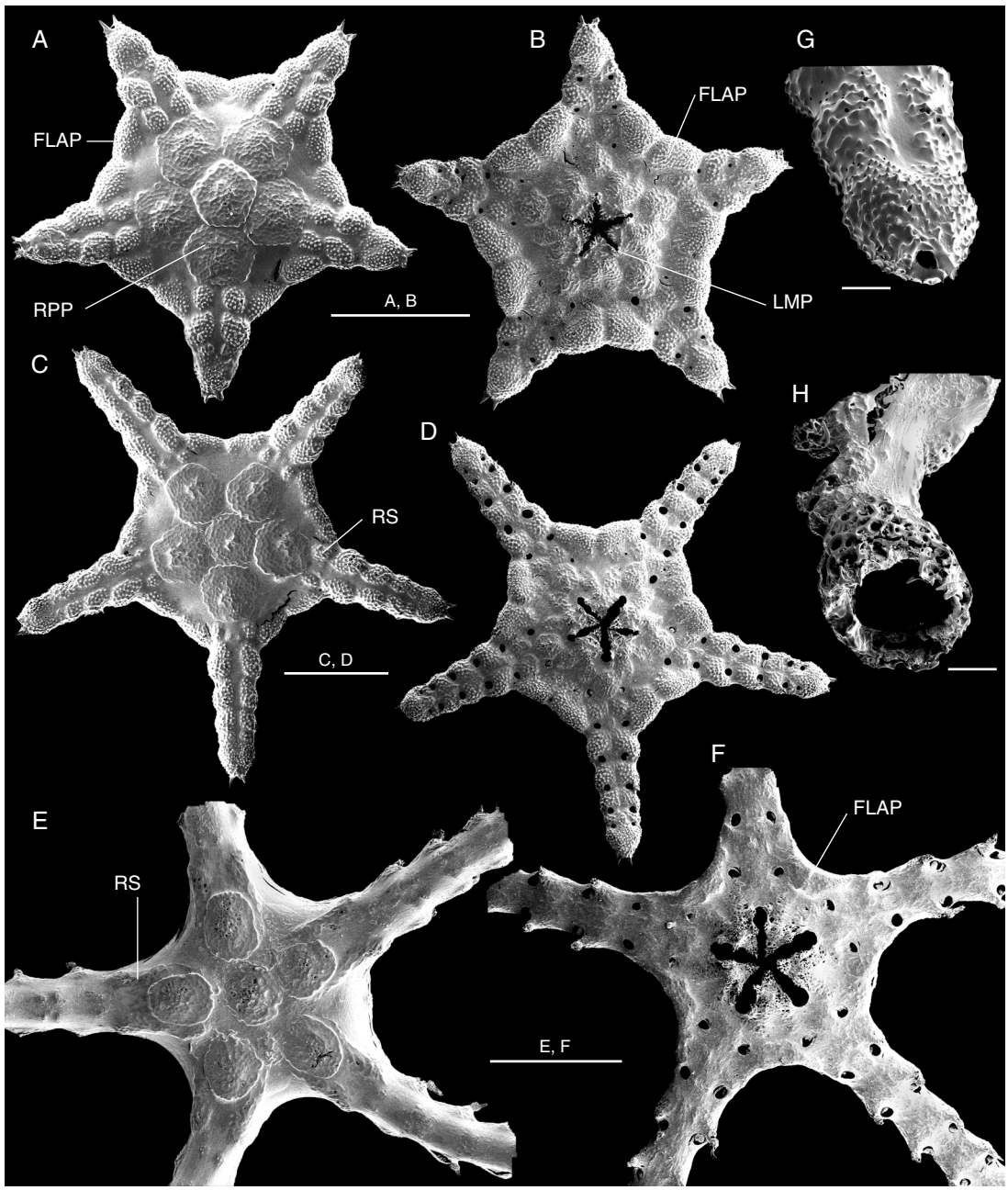

FIG. 3. — Scanning electron micrographs of postlarvae of *Ophiomyxa serpentaria* Lyman, 1883; **A**-**F**, dorsal and ventral aspects; **A**, **B**, dd 1.8 mm; **C**, **D**, dd 2.0 mm; **E**, **F**, dd 2.5 mm; **G**, **H**, swollen, hollow terminal arm segments with dd 2.0 and 2.5 mm. Skin partially removed. Abbreviations: **dd**, disk diameter; **FLAP**, first lateral arm plate; **LMP**, lateral mouth papillae; **RPP**, radial primary plates; **RS**, radial shields. Scale bars: A-F, 1 mm; G, H, 0.1 mm.

From a dd of about 2.2-2.5 mm, disk growth is slowed down in favour of arm growth. Thus, there are individuals with different arm length, but the same dd (Fig. 2I-M). In the largest of these postlarvae, with arm length of about 5.0 mm and 16 segments, the marginal disk plates have moved to the ventral side, leaving the dorsal interradial areas naked (Fig. 3E, F). The primary plates are still obvious, but they have separated from each other and are more oval instead of pentamerous and no longer raised in the centre. The radial shields are long and narrow, separated by a primary plate at their proximal end and never meet. There are two separate lateral mouth papillae in addition to the large apical papilla, flat, serrated and slightly pointed. The skin has thickened and is no longer transparent. There are no dorsal arm plates. The terminal arm segment is still inflated and hollow, with a wide opening (Fig. 3H). Each lateral arm plate bears two small hook-shaped spines (Fig. 4A, B).

Unfortunately, the size series is discontinuous with a gap between about 2.5 and 16.0 mm dd, which makes it impossible to follow the complete development of the skeleton.

Adults

The smallest individuals showing adult characters have a dd of 16.0 mm, arm length 65.0 mm. The dorsal disk plates are no longer present, instead small, round, thin plates lie deep in the smooth skin. The large marginal plates are no longer discernible and from the material at hand it is not clear what became of them. Dorsal arm plates are not obvious, but small thin plates are embedded in the skin. The mouth papillae are flat, rugose and glassy, four to each side and a single apical papilla (Fig. 4C). There is a round oral shield, with two long, distally slightly flared adoral shields (Fig. 4C). The ventral arm plates are longer than wide and contiguous. The arm spines are covered with thick skin, three on the proximal part of the arm, rugose at their distal end, shorter than an arm segment (Fig. 4D). Distally the spines turn into hooks with a small terminal tooth and two larger lateral teeth (Fig. 4E). Each tube foot emerges from a well developed skin sheath, which is supported by two long, thin, flat plates (Fig. 4F). There is no tentacle scale. All adult specimens had broken arms, a single intact arm was regenerating, but lacked the swollen terminal segment found in the juveniles.

REMARKS

The holotype of *O. patersoni* has been dried, which has caused the skin to collapse, revealing the underlying plates, but obscuring its affinity with Ophiomyxidae. The three "Poraniidae" are quite similar to the specimens studied in this work, with slightly wider arms and smaller interradial areas of naked skin. Two specimens have a dd of 1.8 mm and four arm segments, the third animal has 1.9 mm dd and five arm segments. They appear more compact than the specimens from Iceland. Measurement of dd must be taken with caution in this species because of the large areas of skin unsupported by skeletal plates, which allows for a great amount of flexibility and variation in size. The disk size in larger postlarvae is also affected when the large marginal plates move ventrally. Adults larger than 16.0 mm dd all had the dorsal disk more or less torn off or dissolved.

DISCUSSION

The ophiuroid skeleton continues to develop well beyond metamorphosis and most features characterising adult specimens are absent in small juveniles (Ludwig 1881). All juveniles observed in this study are covered by thick skin, which distinguishes them from all previously described juveniles. This thick skin is a diagnostic character of Ophiomyxidae, clearly indicating the familial association of these specimens. The ophiuroid fauna of the North Atlantic is well known and includes only four species of Ophiomyxidae occurring near Iceland (Paterson 1985), *Ophioscolex purpureus* Düben & Koren, 1846, *Ophioscolex glacialis* Müller & Troschel, 1842, *Ophiophrixus spinosus* (Storm, 1881), and *O. serpentaria*. *Ophioscolex* Müller & Troschel, 1842 and *Ophiophrixus* H. L. Clark, 1915 can be

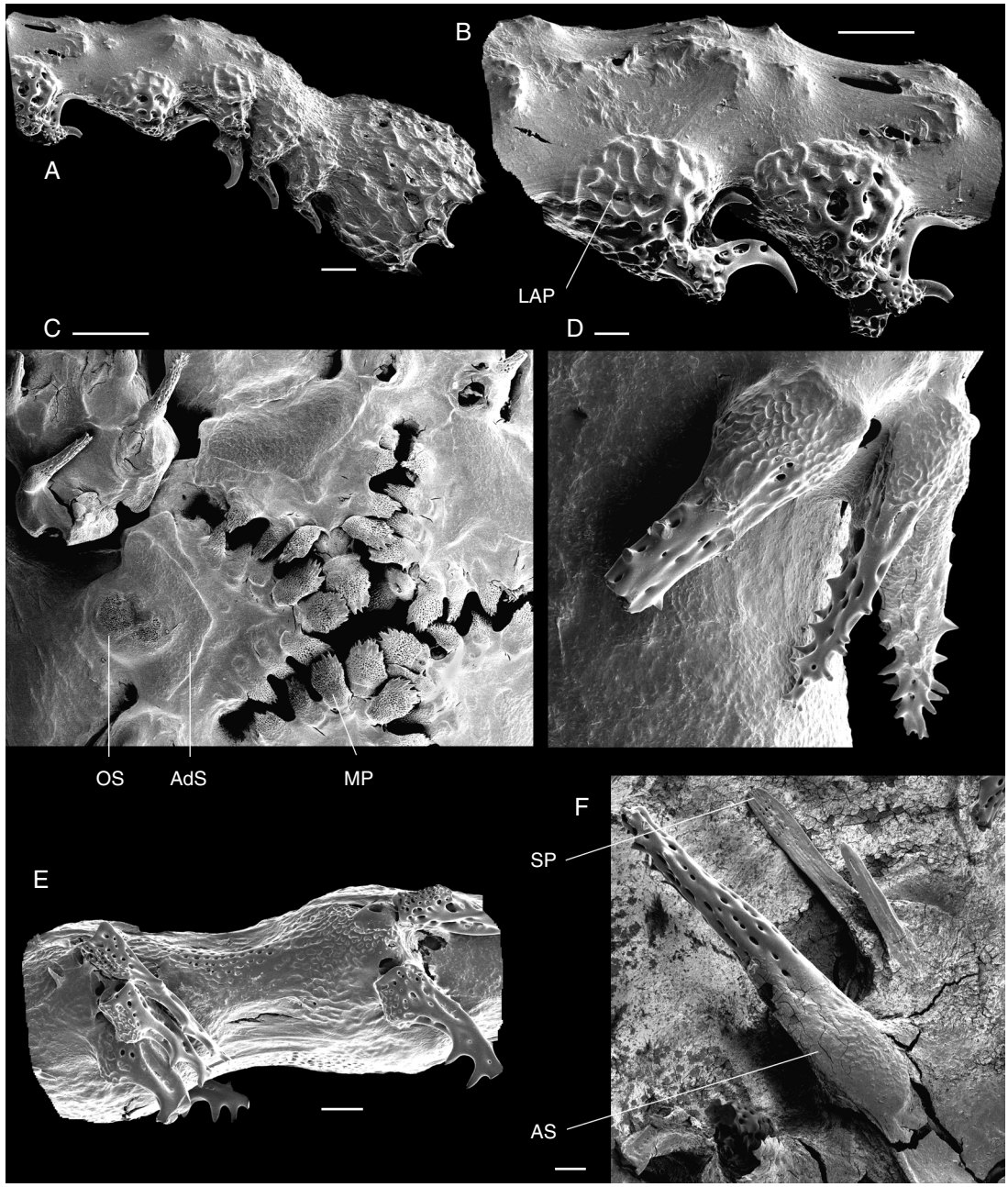

FIG. 4. — *Ophiomyxa serpentaria* Lyman, 1883, scanning electron micrographs; **A**, distal postlarval arm with swollen terminal segment; **B**, postlarval arm, lateral plates and spines; **C**, adult, mouth; **D**, adult, proximal arm spines; **E**, adult, distal arm spines; **F**, adult proximal arm spine and long, flat tentacle scales. Skin partially removed, disk diameter of postlarva 2.5 mm, of adult 16 mm. Abbreviations: **AdS**, adoral shield; **AS**, arm spine; **LAP**, lateral arm plate; **MP**, mouth papillae; **OS**, oral shield; **SP**, sheath plate. Scale bars: A, B, D-F, 0.1 mm; C, 1 mm.

distinguished from *Ophiomyxa* by their spine-like mouth papillae (Mortensen 1927), which in *Ophioscolex* are recognisable already in small postlarvae (unpublished observation), while *Ophiomyxa* has flat, rugose mouth papillae. The larger postlarvae described in this work have a typically ophiomyxid skin and flat, rugose mouth papillae, clearly matching only *O. serpentaria* among the species occurring in the area. Additionally, while the arm spines are hook-shaped on the distal part of the arm in adults of both *O. serpentaria* and *O. purpureus*, the latter has short spines on the dorsal disk scales, which are absent in *O. serpentaria* and the specimens of this study. The smaller postlarvae can be connected to the larger individuals by the thick skin, the size and shape of the dorsal disk plates, which are present in all specimens, and the shape of the arm hooks, present in all but the smallest individuals. Additionally, the large marginal plates can be distinguished in all juveniles, although they have moved ventrally in the largest individuals. Thus, despite the large gap in the size series between 2.5 and 16.0 mm dd, all animals can clearly be matched to *O. serpentaria*.

Ophiuraster has been positioned within the Ophiuridae Lyman, 1865, which do not possess a thickened skin. The family is characterised by short, smooth appressed arm spines and block-like mouth papillae (Paterson 1985). Hook-shaped arm spines are rarely found in this family. Examination of the holotypes of *O. patersoni* and *O. belyaevi* revealed the thickened skin and rugose mouth papillae, indicating their affinity with Ophiomyxidae. Both species differ in many characters from the two previously described species *O. perissus* and *O. symmetricus*. The dorsal disk is formed mainly of the large primary plates, the narrow radial shields, and only few small additional plates. The mouth papillae are undeveloped and oral shields are lacking. The arms are short and dorsal plates are lacking. All of these character states are clearly juvenile as recognised by Litvinova (1998), while other characters like the skin-covered areas of the disk and arms and the open dorsal furrow between the lateral arm plates were interpreted by her as apomorphic specialisations. She explained the absence of dorsal arm plates with resorption, ignoring that small ophiuroid postlarvae usually lack these plates, which develop later during ontogeny (Ludwig 1881). Besides the asteroid-like habitus, only a single character is shared by all four species, namely the large plates surrounding the disk margin, which were interpreted as radial shields by Clark (1939) and as first lateral arm plates by Fell (1958), while Litvinova (1998) suggested the term marginal interradial plates. These large plates form a continuous row with the lateral arm plates and like them they move to the ventral side in the larger postlarvae of *O. serpentaria* (Fig. 2F), suggesting that they are probably not identical with the small, thin dorsal marginal disk plates found in the adult (Mortensen 1933). Instead, the postlarval marginal plates of *O. serpentaria* and probably *O. belyaevi* most likely are lateral arm plates. Unfortunately, no individuals of intermediate size between the largest juveniles presented here and adults of about 16.0 mm dd have yet been found. Hence, the skeletal development cannot be followed all the way. However, Hendler (1978) showed that the first lateral arm plates in ophiuroids are homologous to the adoral shields. The absence of adoral shields in the postlarvae of *O. serpentaria* and the ventral migration of the marginal plates would be consistent with them transforming into adoral shields.

According to the original descriptions of Clark (1939) and Fell (1958) respectively, the holotypes and only known specimens of both *O. perissus* and *O. symmetricus* are larger (dd 4.0 mm) than *O. patersoni* (dd 1.9 mm) and *O. belyaevi* (dd 3.0 mm) and their skeletons are well developed. Their disks are covered with many plates, there are adoral and oral shields and several mouth papillae. Dorsal and ventral arm plates as well as tentacle scales and arm spines are present, but they lack bursal slits. These character states indicate that the former two individuals have developed farther than the holotypes of Litvinova's (1998) two species. They may still be juveniles, because most plates are small and bursal slits usually develop later in ontogeny, but that

cannot be decided with the single specimens known so far. However, it is clear that they belong to a different family than *O. patersoni* and *O. belyaevi*. Since *O. patersoni* is similar in all respects to the smaller postlarvae of *O. serpentaria*, it is a junior synonym of that species. *Ophiuraster belyaevi* is only slightly more developed than *O. patersoni* and it probably is the postlarva of another *Ophiomyxa*, yet to be identified and matched to its juvenile.

The superficial similarity of the small postlarva of *O. serpentaria* with Asteroidea has led to a misidentification of three individuals from the Faroe Islands as juvenile Poraniidae (Ringvold 1999). In this case, ophiuroid characters such as the closed ambulacrum were overlooked, but the reexamination of these specimens confirmed their identity as *O. serpentaria* postlarvae.

Among ophiuroid postlarvae, *O. serpentaria* is unusually large with a dd of 1.8 mm in the smallest, probably recently settled individuals. In comparison, the smallest postlarvae of other species described so far, such as *Ophiura sarsii* Lütken, 1858, *Ophiura carnea* M. Sars, 1857, *Ophiura ljungmani* (Lyman, 1878), *Ophiocten affinis* (Lütken, 1858), and *Ophiactis abyssicola* (M. Sars, 1861), have a dd of 0.4-0.7 mm (Sumida *et al.* 1998). None of these species exhibits a habitus so similar to asteroids as *O. serpentaria*, although the smallest postlarva of *O. sarsii* with barely 0.4 mm dd has a proportionally large, often domed, disk and relatively short arms, but its small size and the skeletal structure of the thin arms clearly distinguish it as an ophiuroid. It has been suggested that postlarval size may indicate the reproductive mode of the species (Hendler 1975). The larva of *O. serpentaria* is unknown, but the size of the smallest postlarva falls well within the reported range of 0.6-5.0 mm dd for species with direct development (Hendler 1975). However, there are no indications of *O. serpentaria* brooding its young in any of the adult specimens examined, some of which contained mature gonads, but no young, and no previous author has suggested it to be viviparous.

The postlarvae of *O. serpentaria* collected off Iceland and the specimen of *O. patersoni* from the Bay of Biscay were all found at depths greater than 1000 up to over 2000 m, while adults were mainly found shallower than 1000 m and never together with postlarvae, which would suggest different depth preferences between adults and juveniles, possibly related to temperature (3-6°C, Table 1). However, the three individuals from the Faroes were collected at 322 m and 6.6°C (Nørrevang *et al.* 1994; Ringvold 1999), contradicting this hypothesis. The distribution of *Ophiomyxa serpentaria* is limited to the SE North Atlantic from SW Iceland to the Faroe Channel and southward to the Bay of Biscay at depths of 450-2440 m (Mortensen 1933; Einarsson 1948; Paterson 1985), which confers with the localities of postlarvae. The species appears to be restricted to the warmer areas south of the Greenland-Iceland Faroe-Ridge. In general, *O. serpentaria* appears to be a rather rare species, found in only eight out of several hundred BIOICE samples and in small numbers, which stresses the importance of large-scale surveys such as BIOICE.

The case of *O. patersoni* illustrates the lack of knowledge on ophiuroid development and the importance of ontogenetic studies for the understanding of ophiuroid systematics. More species, particularly among those which have been described as paedomorphic, may turn out to be the juveniles of others. When more postlarvae have been described, phylogenetic analyses will be possible and ontogeny is expected to contribute important information on the relationships between species and within and between higher taxa.

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