Revision of the genus *Gephyrocrinus* Kœhler & Bather, 1902 (Echinodermata, Crinoidea, Hyocrinidae)

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Roux M. & Bohn J. M. 2010. — Revision of the genus *Gephyrocrinus* Kœhler & Bather, 1902 (Echinodermata, Crinoidea, Hyocrinidae). *Zoosystema* 32 (3): 425-437.

ABSTRACT
The species *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 (Echinodermata, Crinoidea, Hyocrinidae) is revised using additional information on arm and pinnule characters, ontogeny and intraspecific variation. The validity of the monospecific genus *Gephyrocrinus* is confirmed and its affinities are clarified and documented. It is known in northeastern Atlantic only at depths ranging from 1420 to 1968 m. Among hyocrinids, *Gephyrocrinus* belongs to the group of genera including *Calamocrinus*, *Dumetocrinus*, *Feracrinus* and *Ptilocrinus* which all bear the first pinnule on the fourth brachial. *Gephyrocrinus grimaldii* is remarkable in having a constant pattern of regularly alternating muscular (synarthries) and ligamentary (synostoses) articulations along the middle and distal arm, and small irregular lateral plates all along the pinnules. The proximal inflation of the genital pinnules in *Gephyrocrinus* is built with numerous lateral plates never in rows as in *Calamocrinus* and *Ptilocrinus*, unlike the H-shaped plates characteristic of several hyocrinid genera such as *Dumetocrinus*, *Feracrinus* and *Hyocrinus*. Long series of successive brachial pairs are also frequent among the genus *Hyocrinus*. Here, we interpret this character as an adaptive derived character independently appearing in different clades rather than as a synapomorphy. Arm branching occurs exceptionally at the fourth brachial in *Gephyrocrinus* and *Dumetocrinus*, whereas it never appears before the eighth brachial in *Calamocrinus*. Using pinnule architecture as the most discriminating character, *Gephyrocrinus* appears to have the closest affinities with *Calamocrinus* and *Ptilocrinus*.

KEY WORDS
Echinodermata,
Crinoidea,
stalked crinoids,
Hyocrinidae,
Calamocrinus,
Gephyrocrinus,
Hyocrinus,
Ptilocrinus.

RÉSUMÉ
Révision du genre Gephyrocrinus *Kœhler & Bather, 1902 (Echinodermata, Crinoidea, Hyocrinidae).*
L'espèce *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 (Echinodermata, Crinoidea, Hyocrinidae) est révisée en portant l'attention sur les caractères des bras et pinnules, l'ontogenèse et les variations intraspécifiques. La validité du genre monospécifique *Gephyrocrinus* est confirmée et ses affinités sont clarifiées et argumentées. Il n'est connu que dans le nord-est Atlantique, à des profondeurs comprises entre 1420 et 1968 m. Au sein des Hyocrinidae, *Gephyrocrinus* appartient à un ensemble de genres incluant aussi *Calamocrinus*, *Dumetocrinus*, *Feracrinus* et *Ptilocrinus*, chez lesquels la première pinnule est portée par la quatrième brachiale. *Gephyrocrinus grimaldii* se distingue par une très faible variation de l'organisation des parties médianes et distales des bras avec une alternance régulière d'articulations musculaires (synarthries) et ligamentaires (synostoses), et par la présence, tout au long des pinnules, de plaques latérales petites et irrégulières. La partie proximale enflée des pinnules génitales est dépourvue de plaques en forme de H qui sont présentes chez plusieurs genres de Hyocrinidae dont *Dumetocrinus*, *Feracrinus* et *Hyocrinus*. Elle est constituée de nombreuses plaques latérales jamais disposées en rangées, un caractère qui n'a été décrit que chez *Calamocrinus* et *Ptilocrinus*. De longues successions de brachiales unies par paires sont fréquentes au sein du genre *Hyocrinus*. Nous interprétons ici ce caractère plutôt comme une adaptation apparaissant indépendamment chez différents clades que comme une synapomorphie. Une ramification brachiale exceptionnelle se situe au niveau de la quatrième brachiale chez *Gephyrocrinus* comme chez *Dumetocrinus*, tandis que ces divisions n'apparaissent qu'à partir de la huitième brachiale chez *Calamocrinus*. En utilisant l'architecture des pinnules comme un caractère discriminant majeur, c'est avec *Calamocrinus* et *Ptilocrinus* que *Gephyrocrinus* présente les affinités les plus étroites.

MOTS CLÉS
Echinodermata,
Crinoidea,
crinoïdes pédonculés,
Hyocrinidae,
Calamocrinus,
Gephyrocrinus,
Hyocrinus,
Ptilocrinus.

HISTORICAL INTRODUCTION

Carpenter (1884) created the family Hyocrinidae for the small stalked crinoid *Hyocrinus bethellianus* Thomson, 1876, from the southern Indian Ocean. The species differed from other stalked crinoids known at the time in having large thin, spade-like radials and numerous short cylindrical stalk ossicles. It also had five slender unbranched arms with the first pinnule on Br6. Agassiz (1890) first described the large hyocrinid *Calamocrinus diomedae* Agassiz, 1890, from central eastern Pacific with branched arms and first pinnule on Br4, and followed that with a more detailed famous memoir (Agassiz 1892). *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 with five arms and first pinnule on Br4 was the first species of this family discovered in the Atlantic Ocean, off the Canary Islands (Kœhler & Bather 1902). A. H. Clark (1907) described a fourth species attributed to a fourth genus, *Ptilocrinus pinnatus*, from the northeastern Pacific. As the diagnosis of *Ptilocrinus* A. H. Clark, 1907 corresponded to the main characters of *Gephyrocrinus* Kœhler & Bather, 1902, Kœhler (1909) suggested the synonymy of the two genera, neglecting the fact that A. H. Clark (1907: 551) remarked "I was at first inclined to regard this as a second species of *Calamocrinus*". Could the three species, *C. diomedae*, *G. grimaldii* and *P. pinnatus*, belong to the same genus? Surprisingly, this question was never raised again. Later, several species with the first pinnule on Br4 were attributed to the genus *Ptilocrinus*, while *Calamocrinus* Agassiz, 1890 and *Gephyrocrinus* remained monospecific.

Table 1. — List of the specimens of *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 collected in northeastern Atlantic. Abbreviations: **N**, number of specimens; **stn**, station; **italics**, specimen numbers used in Table 2.

Cruises	**Location**	**Depth**	**N**	**References**
Princesse Alice, 1901, stn 1123	27°41'N, 17°53'45"W	1786 m	1	*spec. PA1* (holotype), Koehler & Bather 1902
Princesse Alice, 1905, stn 2048	32°32'30"N, 17°02'W	1968 m	2	*spec. PA2 & PA3*, Koehler 1909
Thalassa, 1973, stn Z 452	48°39.0-41.5'N, 10°53.0-55.2'W	1420-1470 m	9	*spec.ThA to ThF*, Roux 1980
Discovery, stn 9042	42°15.0-17.8'N, 11°22.0-19.7'W	1541-1662 m	3	*spec. BM1 & 2*, A. M. Clark 1980
Poseidon, 129/3, stn 320	40°04,0'N, 09°56.0'W	1776 m	1	*specimen Pos*, this study
SEAMOUNT 2, 1993, stn DW 243	33°13.18'-13.47'N, 29°07.85'-08.24'W	1360-1420 m	1	*specimen Sm1*, this study
SEAMOUNT 2, 1993, stn DW 273	34°05.13'-04.96'N, 30°13.57'-13.81'W	1440-1490 m	1	*specimen Sm2*, this study

Introducing detailed characters of stalk articulations, Roux (1980) considered *Gephyrocrinus* as a subgenus of *Hyocrinus* Thomson, 1876 in the subfamily Hyocrininae with *Thalassocrinus* A. H. Clark, 1911, and placed the other genera (*Calamocrinus, Ptilocrinus,* and *Anachalypsicrinus* A. M. Clark, 1973) in the subfamily Calamocrininae A. M. Clark, 1973, which A. M. Clark (1973) initially erected for *Calamocrinus* only. Mironov & Sorokina (1998a, b) first recognized the importance of genital pinnule architecture for taxonomy and subdivided the Hyocrinidae into four subfamilies. They created the new genus *Dumetocrinus* Mironov & Sorokina, 1998 (Mironov & Sorokina 1998a) for *Ptilocrinus antarcticus* Bather, 1908 and placed *Dumetocrinus*, *Ptilocrinus*, *Calamocrinus* and *Gephyrocrinus* each in a different subfamily. *Gephyrocrinus* and *Hyocrinus* remained closely related within the subfamily Hyocrininae. Using information derived from an ontogenetic sequence of new specimens of *C. diomedae*, Roux (2004) suggested that all the genera with the first pinnule on Br4, i.e. *Calamocrinus*, *Gephyrocrinus* and *Ptilocrinus*, have very close affinities. He questioned the necessity of distinguishing subfamilies within Hyocrinidae, followed by Améziane & Roux (in press).

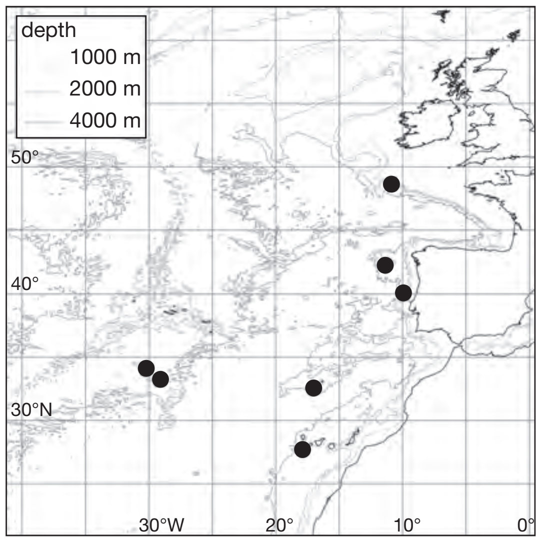

Fig. 1. — Location of stations in the northeastern Atlantic where specimens of *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 were collected (●).

MATERIAL AND METHODS

Material examined

The specimens collected in northeastern Atlantic are listed in Table 1. The holotype (NO *Princesse Alice*, cruise off Canaries) and two specimens (NO *Princesse Alice*, cruise off Madeira) are housed in the Prince Albert's collections of the Musée océanographique in Monaco with the catalogue numbers respectively 81.0866 and 81.114. The collections of the Muséum national d'Histoire naturelle, Paris house six specimens dredged by NO *Thalassa* in the Bay of Biscay (MNHN EcPs 245), and two specimens collected on the Mid-Atlantic Ridge during the cruise SEAMOUNT 2 (MNHN EcPs 10271 and MNHN EcPs 10272). The collections of the Natural

TABLE 2. — Main characters of *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 and their variation through ontogeny. Abbreviations: **BM1**, **2**, Natural History Museum London specimens; **PA1**-**3**, *Princesse Alice* specimens; **Pos**, *Poseidon* specimen; **Sm1**, **2**, SEAMOUNT specimens; **ThA**-**ThF**, *Thalassa* specimens; **Larm**, arm length; **Lpin**, maximum pinnule length; **Npin**, number of pinnules on each arm side; **Wb**, primibrachial width; **Wr**, radial upper width; **Dc**, diameter of aboral cup; **Hc**, height of aboral cup; **Dp**, proximal most diameter of stalk; **Dm**, minimum stalk diameter. Measurements in mm.

	Larm	Lpin	Npin	Wb	Wr	Wr/Wb	Dc	Hc	Hc/Dc	Dp	Dm
Sm1	6.1	2.4	1 (2)	0.88	1.1	1.25	2.1	1.9	0.90	0.5	0.3
BM1	> 5.6	2.9	2	1.0	1.3	1.27	2.4	2.3	0.93	0.6	0.4
ThB	12.2	5.6	3 (4)	1.35	2.0	1.48	3.6	3.2	0.88	1.3	0.6
Sm2	17.7	8.6	4 (5)	1.35	2.5	1.85	4.6	4.7	1.02	1.4	0.61
PA2	23	10.3	6 (7)	1.8	2.2	1.22	5.0	3.9	0.78	1.3	0.63
BM2	19.7	12.2	6 (7)	1.4	2.2	1.56	4.4	4.8	1.09	1.4	0.70
PA1	25.4	10.1	6 (7)	1.8	2.5	1.39	5.2	4.5	0.86	1.5	0.70
ThF	> 20	10.3	> 5	1.8	2.7	1.50	5.2	4.1	0.79	1.6	0.81
PA3	29.1	13.4	7 (8)	2.6	3.1	1.19	5.4	4.1	0.76	1.7	0.85
ThD	25.6	11.5	7 (8)	1.8	2.9	1.61	5.8	5.1	0.88	1.7	0.92
ThC	28.2	14.1	9	2.2	3.9	1.77	6.4	5.9	0.92	1.8	0.87
Pos	> 25.4	15.8	> 7	2.8	3.8	1.36	7.5	5.6	0.75	1.9	–
ThA	> 27	?	9	2.5	4.0	1.60	6.3	5.4	0.84	1.9	0.86
ThE		crown broken		2.4	3.6	1.50	6.4	6.4	1.00	2.0	0.88

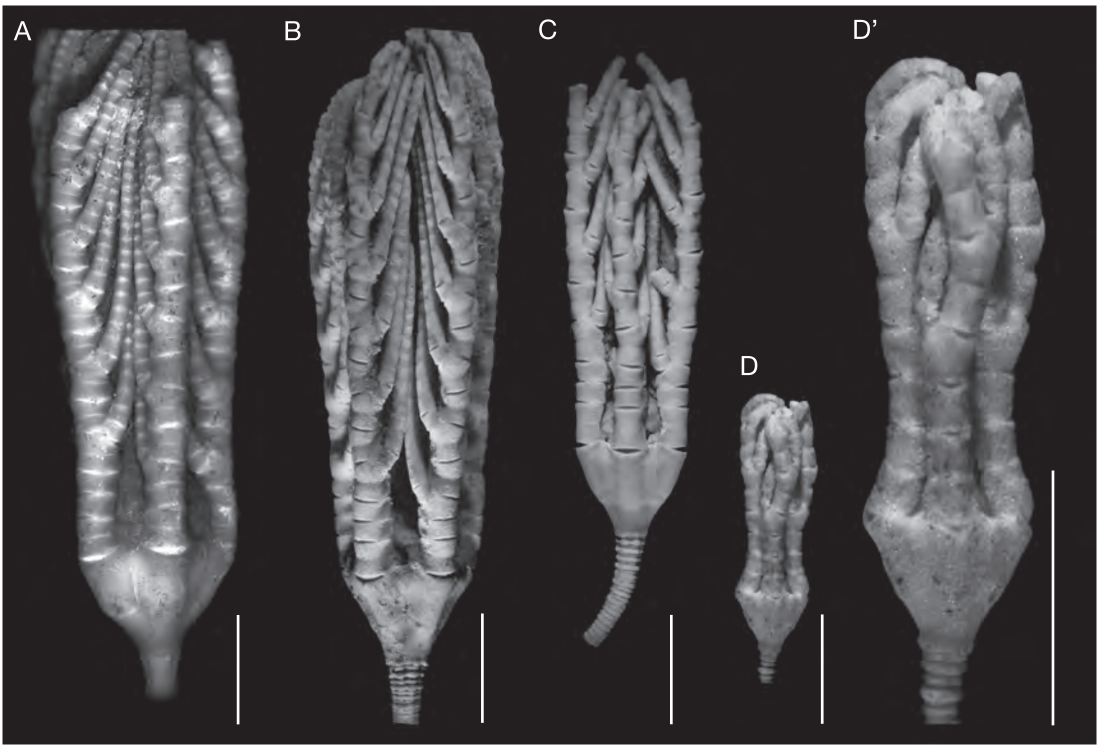

FIG. 2. — Ontogenetic sequence in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 from small juvenile at right to large specimens at left: **A**, *Poseidon* specimen (ZSM 20043141); **B**, *Thalassa* specimen (MNHN EcPs 245C); **C**, *Thalassa* specimen (MNHN EcPs 245F); **D**, **D'**, SEAMOUNT 2 specimen, Sm1 (MNHN EcPs 10271). Scale bars: 5 mm.

History Museum, London, house two specimens dredged off NW Spain by NO *Discovery* (BMNH 1977.3.15.30). The single specimen collected off Portugal by FS *Poseidon* is housed in the Bavarian State Museum Collection of Zoology in Munich (ZSM 20043141).

Methods

Many taxa of hyocrinids were described from one or very few specimens, and their variation and ontogeny frequently remains poorly documented. Consequently, taxonomy is not really based on any modern biological species concept and clear morphological criteria. So, here, we revise the description of *Gephyrocrinus grimaldii* using all available museum specimens to analyze intraspecific variations and ontogeny, and to give additional detailed information on arm and pinnule characters using scanning electron microscopy (SEM). For the descriptions, we refer to the terminology summarized by Roux *et al.* (2002). In arm pattern formulas, Arabic numbers correspond to the sequence of brachials from proximal to distal, and a non muscular articulation is indicated by a plus sign + (e.g., 1+2 3 4 5+6 indicates the first six brachials with the first and second and the fifth an sixth united by nonmuscular articulations). Brachial pairs or triplets are respectively two (a+b) or three (a+b+c) successive brachials united by nonmuscular articulations (synostoses). A free brachial displays two muscular articulations.

SYSTEMATICS

Family Hyocrinidae Carpenter, 1884

Genus *Gephyrocrinus* Kœhler & Bather, 1902

Species included. — Monospecific: *Gephyrocrinus grimaldii* Kœhler & Bather, 1902.

Amended diagnosis. — Five arms, rarely divided at IBr2ax; proximal arm pattern usually 1+2 3 4 5+6 7+8 with first pinnule on Br4, rarely on Br5. Proximal part of genital pinnules with numerous additional plates never in rows; distally with lateral plates on each side all along the pinnule. Tegmen inflated with subconical anal sac well developed on external side and taller than oral cone. Aboral border of basal ring flanged except in some larger specimens. Stalk with symplexies of 6-8 crenular units.

Remark

As discussed below, the middle and distal arm pattern usually with successive brachial pairs is interpreted as a specific adaptive character which is incorporated into the diagnosis of *G. grimaldii*.

Gephyrocrinus grimaldii Kœhler & Bather, 1902

Gephyrocrinus grimaldii Kœhler & Bather, 1902: 68-79, figs 1-4. — Kœhler 1909: 265, 266, pl. I, fig. 12 and pl. XXXII, figs 1-9. — A. H. Clark 1915: 160. — A. M. Clark 1973: 274; 1980: 208. — Roux 1977: 31; 1980: 33, 34, 40, fig. 1, pl. I figs 1-6. — Mironov & Sorokina 1998b: 30. — Roux *et al.* 2002: 816, 817, fig. 10c, d.

Hyocrinus (*Gephyrocrinus*) *grimaldii* – Roux 1980: 42; 1985: 481.

Amended diagnosis. — A relatively small species with crown length less than 30 mm, robust arms and pinnules without ornamentation, width of proximal brachials subequal. Pinnules mostly rigid except distalmost part, fewer than 10 on each arm side of each arm, and weakly differentiated from arms. Genital pinnules with numerous irregular polygonal lateral plates of nearly equal size in proximally inflated portion and with rarely conspicuous lanceolated cover plates distally. Middle and distal arm pattern usually with successive brachial pairs (e.g., a+b c+d e+f), rarely free brachials or triplets. Tegmen with about 12 or slightly more polygonal plates in each interradius; orals convex without projection; tubercles bearing hydropores on upper tegminal plates and oral base sometimes present, and food groove elevated above adjacent interradial surfaces forming a bridge between orals and Br4. Ratio of radial upper width to primibrachial width 1.2-1.8. Conical to weakly bowl-shaped aboral cup with trapezoidal radials; ratio of cup height to maximum cup diameter 0.7-1.0; basals fused. Proximalmost stalk diameter up to 2.0 mm; minimum stalk diameter up to 0.9 mm; proximal symplexies with chiefly galleried stereom and 6-8 small crenular units of 1 (rarely 2) crenulae; symplexies near the minimum stalk diameter with 6 or 7 well-developed crenular units of 1-2 crenulae and galleried stereom restricted to inner part of articular facet; crenularium of distal syzygies with radial or moderately labyrinthic pattern.

Distribution. — Northeastern Atlantic from the north slope of the Bay of Biscay to Madeira (Roux 1985) and

TABLE 3. — Arm pattern variation in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902. ***Bolded italics***, free brachials; **underlined**, brachials bearing the first pinnule; **bold**, brachial triplets; **+**, synostosis uniting the two ossicles of a brachial pair.

1+2 ***3*** ***4*** 5+6 7+8 ***9*** 10+11 12+13 ***14*** 15+16 17+18 19+20…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 ***13*** 14+15 16+17…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14 ***15*** 16+17 18+19…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14 15+16 ***17*** 18+19…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14 15+16 17+18 19+20…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14 15+16…27+28 **29+30+31**…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14…19+20 **21+22+23** 24+25…
1+2 ***3*** ***4*** 5+6 7+8 9+10 11+12 13+14 **15+16+17** 18+19 20+21…
1+2 ***3*** ***4*** 5+6 7+8 9+10 **11+12+13** 14+15 16+17 18+19…
1+2 ***3*** ***4*** 5+6 7+8 **9+10+11** 12+13 14+15 16+17…
1+2 ***3*** ***4*** **5+6+7** 8+9 10+11 12+13 14+15 16+17 18+19…
1+2 3+4 ***5*** 6+7 8+9 10+11 12+13 14+15 16+17 ***18*** 19+20…
1+2 3+4 5+6 7+8 9+10 11+12 13+14 15+16 17+18…
1+2+3 4+5 6+7 8+9 10+11 12+13 14+15 ***16*** 17+18…
1+2+3 4+5 6+7 8+9 10+11 12+13 14+15 16+17 18+19…

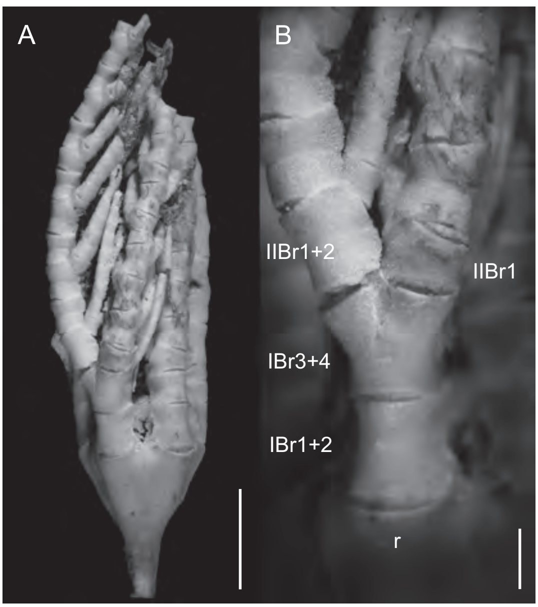

FIG. 3. — General view of the crown of the *Thalassa* specimen (MNHN EcPs 245A) (**A**) and enlargement of its arm ramification (**B**). Abbreviation: **r**, radial. Scale bars: A, 5 mm; B, 1 mm.

from the Canary Islands to the Mid-Atlantic Rise at depths ranging from (1360?) 1420 to 1968 m. The stalk fragment first identified as belonging to *Hyocrinus* by Carpenter (1884) and attributed to *Gephyrocrinus* by A. H. Clark (1915) came from a location in mid-Atlantic (01°47'N, 24°26'W, at a depth of 3330 m) significantly deeper than the depth range of *G. grimaldii* but corresponding to the depth range of *Hyocrinus*. A specimen attributed to *G. grimaldii* from off Newfoundland (Haedrich & Maunder 1985) was later described as *Ptilocrinus atlanticus* Roux, 1990, and transferred to *Anachalypsocrinus* by Mironov & Sorokina (1998b). So, specimens undoubtedly attributed to *G. grimaldii* have only been dredged in a relatively restricted area and depth range in the northeastern Atlantic (Fig. 1).

DESCRIPTION

All specimens characterized by small to medium size, robust arms and pinnules with thick brachials and pinnulars, widely separated inter-rays, conical aboral cup with basals fused, and usually large conspicuous ribs prolonging arm axis (Fig. 2). Proximal brachials subequal in width and height; following arm decreasing slowly and progressively in width. Muscular articulations becoming moderately oblique in mid and distal arm. Trapezoidal radials never forming an angle with the basal ring. Basals fused. Base of basal ring usually flanged; proximal stalk flexible and multilobated (Fig. 2B-D), both characters becoming inconspicuous in a few large specimens (Fig. 2A). Variation of the main external morphological characters that can be quantified (Table 2) are either related to growth (arm and pinnule lengths, number of pinnules on each arm side, and proximalmost stalk diameter) or independent. Variation not related to growth clearly observed at least for largest specimens with proximalmost stalk diameter more than 1.6 mm; ratios of primibrachial

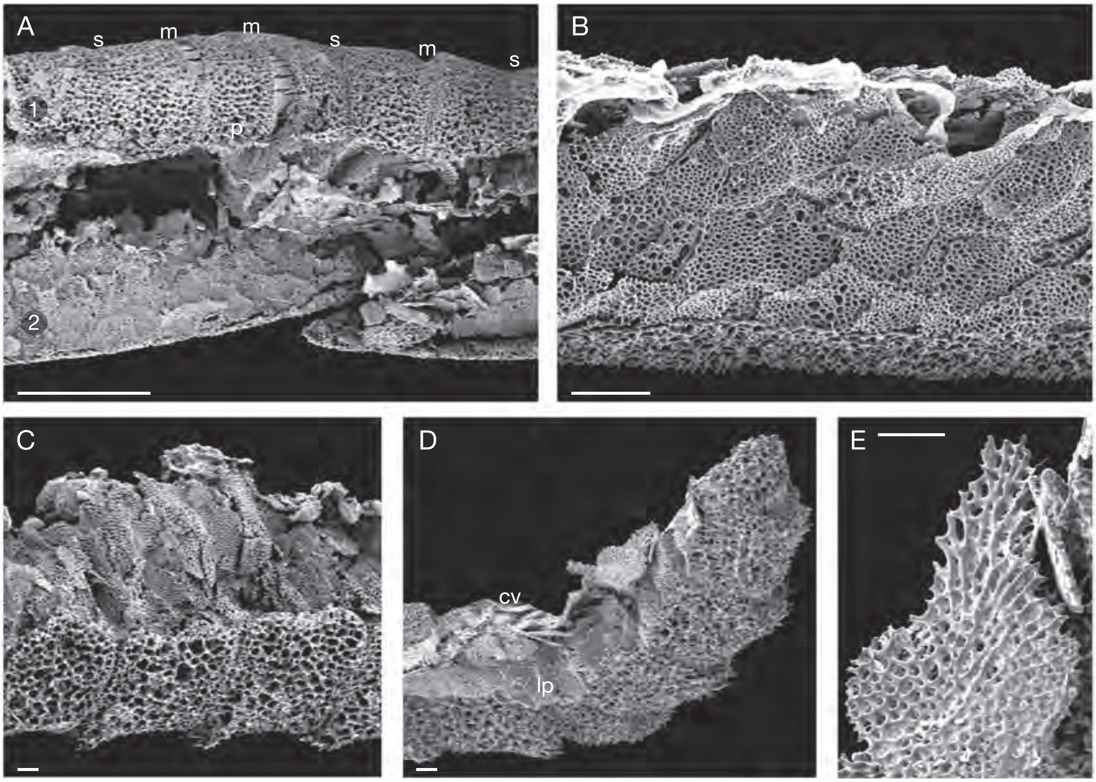

FIG. 4. — Architecture of pinnules in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902: **A**, fragment of arm with a few pinnules attached (**1**, lateral-aboral view of a pinnule; **2**, lateral-ambulacral view of a pinnule attached on the other arm side showing its proximal genital inflation); **B**, detailed lateral view of multiplated genital inflation; **C**, oblique-lateral view of genital inflation; **D**, distal end of a pinnule; **E**, cover plate. **A**, **C**-**E**, isolated fragments from *Thalassa* specimens (MNHN EcPs 245); **B**, isolated fragment from *Poseidon* specimen (ZSM 20043141). Abbreviations: **cv**, cover plates; **lp**, lateral plates; **m**, muscular articulation; **p**, proximalmost pinnular with its muscular articulation on arm at right; **s**, synostosis. Scale bars: A, 1 mm; B, 0.2 mm; C-E, 0.1 mm.

width to radial upper width and of cup height to maximum cup diameter are the most variable. In the smallest specimen, primibrachials jointed when crown closed, except in the anal inter-ray. Increase in primibrachial width slowing rapidly with growth relative to radial width (ratio ranging from 0.54 to 0.68), so that primibrachials are much narrower than radials and the inter-ray space much wider in larger specimens when crown closed.

Proximal arm pattern usually 1+2 3 4 5+6 (92.8% of 72 arms observed) with Br4 bearing first pinnule (95.8%). Three cases with first pinnule on Br5 and 1+2 3+4 5 6+7 (1 case) or 1+2+3 4+5 6+7 (2 cases). In two cases arm pattern 1+2 3+4 5+6 with first pinnule on Br4. Brachial triplets also observed in other arms at various places (one case each) from 1+2+3 to 29+30+31 (Table 3). Distal to brachial bearing first pinnule, usual pattern consisting of successive brachial pairs (i.e. a+b c+d) producing regular alternation of ligamentary (synostosis) and muscular (synarthry) articulations. Free brachials scarce and observed (one case each) at various places from Br5 to Br18 (Table 3). Patterns other than successive brachial pairs representing less than 1% of brachial articulations. Specimen ThA with arm division at IBr4ax (one case) with two branches of equal size and well-developed pinnules (Fig. 3); distal to axillary, series of brachial pairs beginning immediately (IIBr1+2) in the left branch and later (IIBr2+3) in the right one.

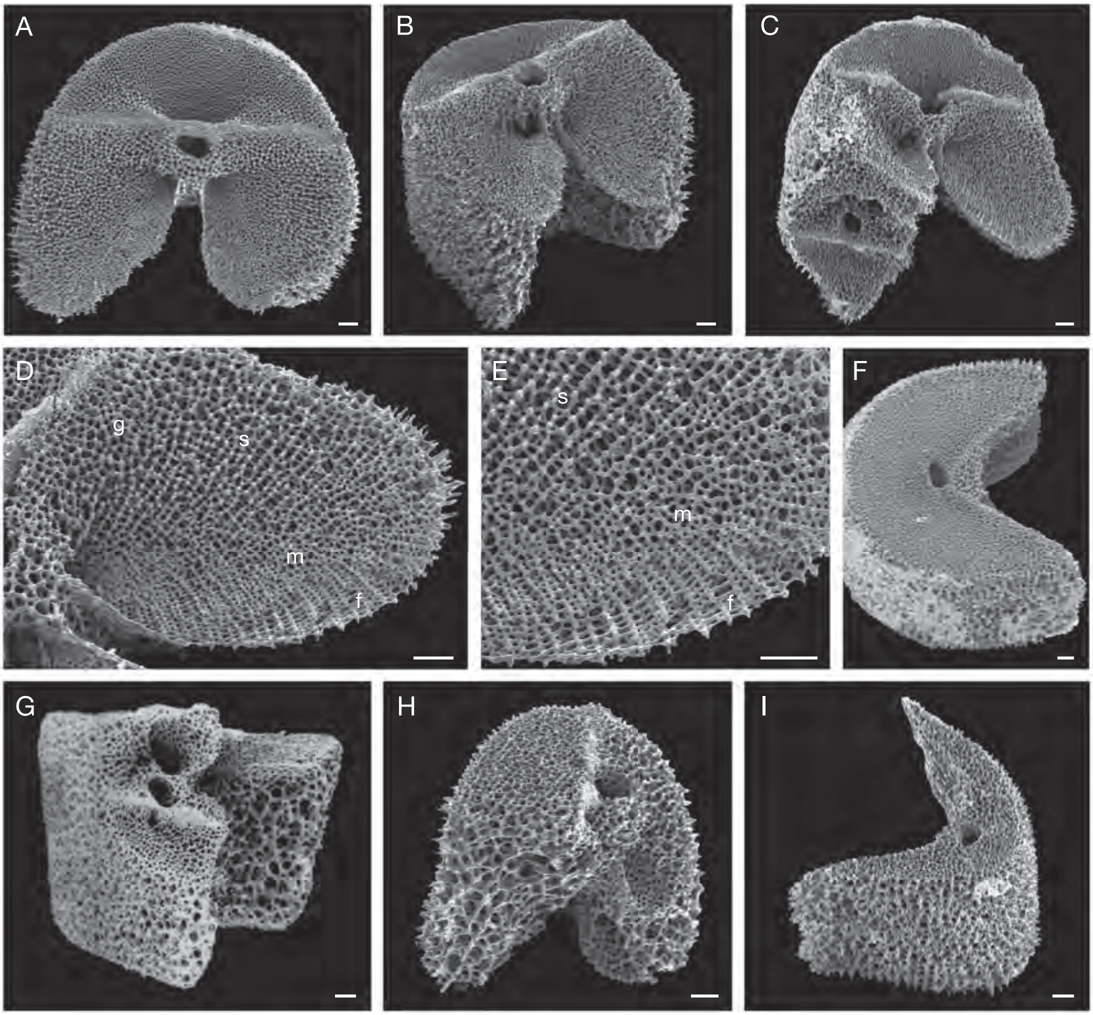

FIG. 5. — Brachial and pinnular ossicles in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902, isolated fragments from *Thalassa* specimens (MNHN EcPs 245): **A**, **B**, proximal muscular articulation (synarthry) of an hyposynostosial brachial; **C**, oblique-adambulacral view of episynostosial brachial with pinnule socket at left; **D**, **E**, adambulacral part of a brachial synarthry with inconspicuous boundary between inner ligament area (**g**, **s**) and muscle area (**m**, **f**); **F**, flat distal facet (synostosis) of hyposynostosial brachial; **G**, lateral-adambulacral view of an episynostosial brachial and its pinnule socket; **H**, proximal facet of the first pinnular (transverse muscular synarthry); **I**, oblique-aboral view of the third pinnular with synostosial articulations. Abbreviations: **f**, labyrinthic stereom with radial thickened frame; **g**, galleried stereom; **m**, thin layer of stereom with small irregular meshes; **s**, synostosial-like surface of labyrinthic stereom. Scale bars: 0.1 mm.

Proximal part of genital pinnules inflated (Fig. 4A) with numerous imbricating lateral plates not in rows (Fig. 4B, C). Irregular lateral plates present to the pinnule tip (Fig. 4D) and on the ambulacral face of arms. Cover plates usually variable and difficult to distinguish from lateral plates, lanceolate shape (Fig. 4E) only observed in distal part of pinnule.

Muscular brachial synarthries with prominent fulcral ridge allowing wide amplitude of movements (Fig. 5A, B). As in other hyocrinids (Holland *et al.* 1991), muscular and ligamentary areas of the adoral part of brachial facet not clearly delimited by galleried stereom associated with ligament. In *Gephyrocrinus grimaldii* (Fig. 5D, E), galleried stereom only present

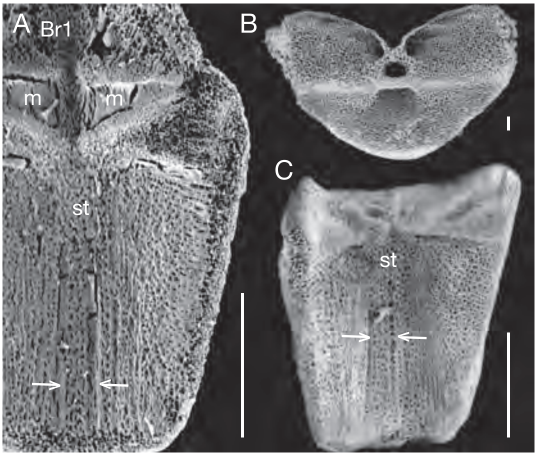

FIG. 6. — Radial and first brachial (Br1) in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902, isolated fragment from *Thalassa* specimens (MNHN EcPs 245): **A**, ventral view of radial articulated with Br1 (uppermost part) with preserved dry soft parts; **B**, **C**, ossicles dissociated and clean up using sodium hypochlorite; **B**, proximal facet of IBr1; **C**, slightly oblique ventral view of radial. **Arrows**, pair of radial nerves (**A**) and corresponding grooves underlined by large stereom meshes (**B**). Abbreviations: **m**, muscles; **st**, labyrinthic stereom covering radial nerve grooves. Scale bars: 1 mm.

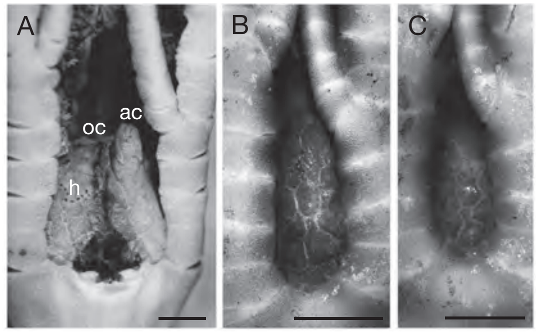

FIG. 7. — Tegmen of *Gephyrocrinus grimaldii* Kœhler & Bather, 1902: **A**, *Thalassa* specimen (MNHN EcPs 245F), general view with one arm removed; **B**, **C**, *Poseidon* specimen (ZSM 20043141) with inflated tegmen showing large tegminal plates; **B**, anal interradius; **C**, non-anal interradius. Abbreviations: **ac**, anal cone; **oc**, oral cone; **h**, hydropores. Scale bars: A, 1 mm; B, C, 2 mm.

near ambulacral side of fulcral ridge. Ligament mainly attached to labyrinthic stereom covered by small globular extensions as in synostosial stereom (Macurda *et al.* 1978). Muscle attached either to thin layer of labyrinthic stereom of small meshes or to stereom with radially thickened frame near facet outer edge (Fig. 5E). All brachial synostoses with flat undifferentiated facets (Fig. 5F). Pinnule on episynostosial ossicle of brachial pair (Fig. 4A); pinnule socket (Fig. 5C, G) located ventrally with fulcral ridge parallel to the brachial fulcral ridge in proximal arm. Pinnule articulation with arm a transverse muscular synarthry with a symmorphy that produces a convex pinnular facet (Fig. 5H). Two proximalmost pinnulars united by classical muscular synarthry and following pinnulars by flat synostoses (Fig. 5I). Muscular synarthry articulating primibrachial to radial wider than high and symmetrical (Fig. 6B). Inner surface of radial (Fig. 6B, C) with two radial nerves running in parallel grooves covered by labyrinthic stereom in the distal part of radial only (Fig. 6A, C), as previously observed by Gislèn (1939) in *Ptilocrinus*.

Tegmen reaching Br4-5 in medium-sized specimens and inflated to Br6-7 and not attached to first pinnule in the largest one. Subconical anal sac located near external border of tegmen and taller than oral cone (Fig. 7A). Tegminal plates polygonal and convex (Fig. 7B, C), usually about 12 or slightly more per interradius (except anal interradius), up to 18 in specimen BM2. Hydropores frequently inconspicuous except at base of oral plates as in the holotype; a few specimens showing series of conspicuous hydropores open at top of small tubercles in upper half of tegmen (Fig. 7A). Orals always well developed, convex and smooth, usually bearing one tubercle with hydropore at base.

Stalk relatively gracile; length 78 mm in the single complete specimen (ThD). Diameter decreasing rapidly from 1.7 to 1.1 mm in the proximal 5 mm below aboral cup, and reaching minimum (0.92 mm) at 17 mm, increasing slowly to 1.42 mm at 2 mm before the distal end, and rapidly to 1.48 mm in the few last columnals indicating the proximity of the attachment disk. Proximal columnals thin, multilobated and with variable thickness and diameter (as in Figure 2A, C, D) providing maximum flexibility. In largest specimens, proxistele more regular and cylindrical (Fig. 2B). Columnals increasing in thickness and becoming cylindrical (Fig. 8A) or weakly barrel-shaped in middle and distal stalk of large specimens (Fig. 8B, C); ratio of columnal height to diameter up to 0.7 in proximal mesistele, decreasing to <0.6 in distal stalk and <0.5 in distalmost columnals. Middle stalk articulations (symplexies) of young specimens with ligament area (areola) predominating, and 6 or 7 crenular units of 1 short crenula restricted to outer border of facets (Fig. 8A, D). In larger specimens, well-developed crenularium restricting areola to facet centre (Fig. 8B, E); up to 8 crenular units of 2 crenulae in proxistele of largest specimens; radial crenulae variable, more or less regular in size and form. Distal articulations with thin syzygial crenularium predominating (Fig. 8C), varying from a radial to labyrinthic pattern, and juvenile symplexial pattern with 6 or 7 crenular units preserved in facet centre (Fig. 8F).

DISCUSSION

After their very fine and complete description of the holotype, Kœhler & Bather (1902) concluded that *Gephyrocrinus grimaldii* is characterized by fused basals; brachial pairs united by synostosis; food groove elevated above the adjacent interradial surfaces of the tegmen forming a bridge (*gephyro* = bridge) between orals and Br4, which exposes a membrane without lateral plates, and tegminal plates without hydropores. They pointed out that one arm with 1+2+3 4+5 6+7 and the first pinnule on Br5 differed from the others with the first pinnule on Br4 and a proximal pattern 1+2 3 4 5+6 7+8. The current study shows hydropores frequently present on tegminal plates, and a narrow range of variation in arm articulation pattern relative to that of several other species of Hyocrinidae (Mironov & Sorokina 1998b; Roux & Pawson 1999; Roux 2004; Améziane & Roux in press). The proximal arm pattern is usually 1+2 3 4 5+6 (about 90%) and about 95% of arms have the first pinnule on Br4. When the first pinnule is on Br5, the proximal arm pattern is never 1+2 3 4+5 as is usual in *Thalassocrinus* or *Anachalypsicrinus* and frequent in *Ptilocrinus*. The presence of patterns with 1+2 3+4, brachial triplets at various places along the arm, and usually a+b c+d e+f, etc., to the distal end, suggests possible affinities with the genus *Hyocrinus*, particularly with three Pacific Ocean species, *H. biscoiti* Roux, 2004, *H. cyanae* Bourseau, Améziane, Avocat & Roux, 1991, and *H. giganteus* Roux & Pawson, 1999. However, *G. grimaldii* differs from *Hyocrinus* in usually having the proximal arm pattern 1+2 3 4 5+6, first pinnule on Br4 (never on Br6), a more developed anal cone, and numerous small additional lateral plates in genital pinnules not in rows and without H-shaped ossicles. These four characters suggest that *Gephyrocrinus* is closely related to *Calamocrinus* and *Ptilocrinus* (*sensu* Mironov & Sorokina 1998b), two genera known only in the Pacific and South Indian oceans. Which characters have the greatest phylogenetic significance?

According to Mironov & Sorokina (1998b), articulation patterns in the middle and distal arm are related to arm flexibility. The regular alternation of synostoses and muscular articulations increases arm rigidity in small species with relatively short arms such as *Gephyrocrinus grimaldii*. In large species with long arms such as *Hyocrinus biscoitoi* or *H. giganteus*, the same pattern allows moderate arm flexibility and relatively dense pinnulation (Roux 2004: fig. 5) while in small species of *Hyocrinus* like *H. foelli* Roux & Pawson, 1999, frequent brachial triplets give the filtration fan greater rigidity with more widely spaced pinnules (Roux & Pawson 1999: plate IV). Moreover, multiplication of synostoses facilitates autotomy of just a short arm fragment in case of predation by fishes. Development of numerous synostoses allowing autotomy is usually assumed to be a derived character that appears mainly in post-Paleozoic crinoids (Moore & Teichert 1978). Thus, middle and distal arms with successive brachial pairs seem to be an adaptive derived character present in different hyocrinid clades rather than a synapomorphy. It can be used in taxonomy at the species level only.

The proximal arm pattern has less adaptive significance especially in taxa with an inflated tegmen developed to Br4 or beyond, and it is usually taxonomically significant in the other stalked crinoid families (Roux *et al.* 2002). If the interpretation of brachial pairs as derived character is correct, the most derived pattern is 1+2 3+4 5+6 as usual in *Hyocrinus*. As a consequence, the predominating proximal arm pattern 1+2 3 4 5+6 shared by *Calamocrinus*, *Dumetocrinus*, *Feracrinus*, *Gephyrocrinus* and *Ptilocrinus* is a symplesiomorphy without phylogenetic significance. In these five genera, development of

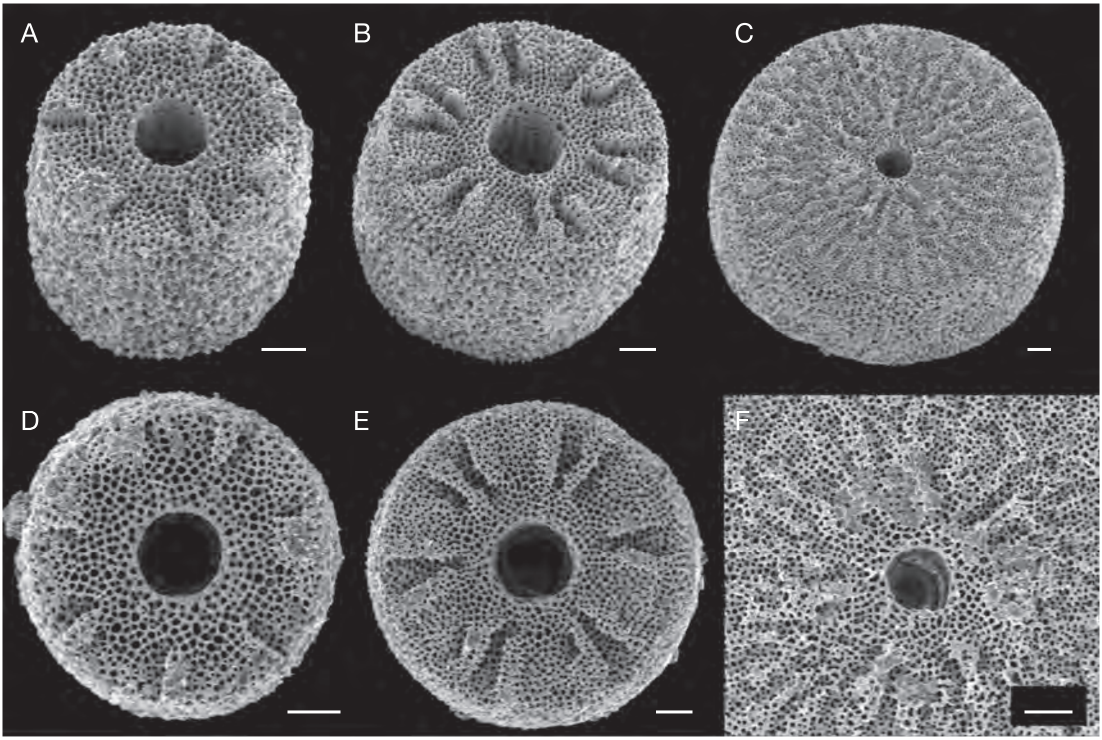

FIG. 8. — Stalk articulations in *Gephyrocrinus grimaldii* Kœhler & Bather, 1902 from stalk fragments associated with *Thalassa* specimens (MNHN EcPs 245): **A**-**D**, symplexy in the proximal mesistele (near the minimum stalk diameter) of a young specimen; **B**-**E**, symplexy in the mesistele of a large specimen; **C**-**F**, distal syzygy of the same stalk; **F**, juvenile symplexial pattern preserved in syzygy centre. Scale bars: 0.1 mm

a pinnule on Br4 is a derived character relative to their absence in *Hyocrinus* in which the first pinnule is usually on Br6, rarely on Br5 (Améziane & Roux 1994).

In *Gephyrocrinus*, the single case of arm branching was interpreted by Roux (1980) as the result of a transformation of the first pinnule into an arm, the third brachial (IBr3) becoming axillary. Despite the discovery of numerous new hyocrinid specimens during the two last decades, no first pinnule has ever been found on Br3. Moreover, a detailed re-examination of this branched arm shows that the so-called axillary is formed by three ossicles (Fig. 3B). The proximal one (IBr3) is triangular and united by synostoses to the first ossicle of each branch. These two distal ossicles are fused together by their inner sides creating an imperfect axillary (IBr4ax), and each bears a pinnule on its outer side. Thus, the proximal arm pattern is 1+2 3+4ax rather than 1+2 3ax. Moreover, on the same crown, an other arm displays 1+2 3+4 which documents that regeneration after autotomy at the synostosis 3+4 during early ontogeny is possible with an axillary replacing Br4 bearing the first pinnule. In fact, there is no evidence of pinnule transformation into an arm.

Calamocrinus differs mainly from other hyocrinids in having numerous arm divisions from IBr8 to IBr15, never at Br4 which usually bears the first pinnule. At each division, one branch is always larger than the other (Agassiz 1892; Roux 2004). According to Gislèn (1924), arm divisions and pinnules are assumed as homologous. The ramification observed in *G. grimaldii* is in place of the first pinnule, the two branches displaying equal development. In a complementary description of the type series of *Dumetocrinus antarcticus*, John (1937: 7) noted one case of arm division: "An unpublished drawing prepared for Dr Bather shows the arm bifurcating at the fourth brachial, and that the two branches were of equal size". As in *G. grimaldii*, the first pinnule is usually on Br4 in *D. antarcticus*. The case of rudimentary arm ramification described in middle arm of *Feracrinus* is related to abnormal pinnule regeneration in adult individuals (Améziane & Roux in press). Thus, *Gephyrocrinus* and *Dumetocrinus* share the ability to develop exceptional true arm division at IBr4 while in *Calamocrinus* all the rays divide but never before IBr8.

Is arm branching a useful character for phylogenetical reconstruction? The case of arm branching described above in *Gephyrocrinus* in which axillary results in the fusion of two brachials bearing a pinnule, is either a derived character or an abnormal regeneration during early ontogeny. In a small juvenile of *Calamocrinus*, pinnules strongly resemble arms (Roux 2004), and, in the adult, arm division with one branch larger than the other suggests that the smallest branch results from the transformation of a young pinnule into arm during ontogeny. As a consequence, arm branching in *Calamocrinus* could be a derived character too, but with another ontogenetic trajectory than in *Gephyrocrinus* or *Dumetocrinus*. However, it is not useful for hyocrinid phylogeny in the current state of our knowledge.

The single character that distinguishes *Gephyrocrinus* from *Calamocrinus* and *Ptilocrinus* and all the other hyocrinid genera is the extension of lateral plates all along the pinnule. If lateral plates restricted to the proximal part of the genital pinnules and development of H-shaped plates forming a rigid box around the gonad are derived characters, as suggested by Mironov & Sorokina (1998b), *Gephyrocrinus* could display the most archaic architecture of pinnules among the family Hyocrinidae. In the genus *Ptilocrinus*, the number and arrangement of lateral plates in proximal part of genital pinnules varies (Mironov & Sorokina 1998b). *Ptilocrinus brucei* Vaney, 1908 displays numerous small lateral plates not in rows as in *Gephyrocrinus* but more regularly arranged (Vaney & John 1939; Mironov & Sorokina 1998b). In fact, genital expansion is most similar in *Calamocrinus* and *Gephyrocrinus*.

CONCLUSION

The architecture of pinnules and the proximal arm pattern of *Gephyrocrinus grimaldii* here described differ strongly from those of the genus *Hyocrinus* and show close affinities with *Calamocrinus* and *Ptilocrinus*. *Gephyrocrinus* and the two latter genera share several main characters such as first pinnule on Br4, anal cone taller than oral cone, and proximal expansion of genital pinnules without H-shaped plates. However, *Calamocrinus* and *Ptilocrinus* have pinnules with lateral plates restricted to the proximal half of each pinnule whereas in *Gephyrocrinus* lateral plates are present along the entire pinnule. Arm division occurs in all rays at Br8 or beyond in *Calamocrinus*, is exceptionally present at Br4 in *Gephyrocrinus* and *Dumetocrinus*, and is unknown in *Ptilocrinus*. The validity and affinities of the genus *Gephyrocrinus* are now clearly documented. At the present state of our knowledge, it remains highly speculative to establish phylogenetic hypotheses within the Hyocrinidae because of the complex mosaic of characters displayed by the different genera, the heterogeneity of descriptions which require revisions, and the absence of any fossil record of crowns. However, *Calamocrinus*, *Gephyrocrinus* and *Ptilocrinus* seem to have the most archaic architecture of pinnules currently known among hyocrinids.

Acknowledgements
We would like to thank Andrew Cabrinovic for access to the collections housed in the Natural History Museum, London, Nadia Améziane for access to the collections housed in the Muséum national d'Histoire naturelle, Paris and Michèle Bruni for information on the specimens housed in the Musée océanographique de Monaco. We also wish to thank Xavier Drothière (University of Reims), Marc Eléaume, Gérard Mascarell and Gabrielle Zimmerman (Muséum national d'Histoire naturelle, Paris) for technical assistance. The manuscript benefited from reviews and useful suggestions by Charles G. Messing (Nova University, Oceanographic Center, Florida) and Alexander N. Mironov (P. P. Shirshov Institute of Oceanography, Moscow).

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Submitted on 6 October 2009;
accepted on 17 February 2010.