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The genera Myriochele and Myrioglobula (Polychaeta, Oweniidae) in Icelandic waters with the revision of type material of Myriochele heeri Malmgren, 1867, and the description of a new species

Julio Parapar<sup>a</sup>

<sup>a</sup> Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Facultade de Ciencias, Universidade da Coruña, A Coruña, Spain Published online: 21 Feb 2007.

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# The genera *Myriochele* and *Myrioglobula* (Polychaeta, Oweniidae) in Icelandic waters with the revision of type material of *Myriochele heeri* Malmgren, 1867, and the description of a new species

JULIO PARAPAR

Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Facultade de Ciencias, Universidade da Coruña, A Coruña, Spain

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#### Abstract

Based on the study of specimens previously identified as *Myriochele heeri* Malmgren, 1867 (Polychaeta, Oweniidae) in Icelandic waters collected during the BIOICE project, a redescription of this taxon is presented, a Pacific species—*Myriochele olgae* Blake, 2000—is reported, and one new species is described: *Myrioglobula malmgreni* sp. nov. *Myriochele heeri* is characterized by three short anterior uniramous chaetigers of similar length. The revision of the type series of *M. heeri* showed that the length of the anterior chaetigers and the chaetal composition is variable in the different specimens, thus demonstrating that more than one species is involved. Complementary anatomical (prostomial, foregut, and peristomial ciliary fields, ventral pharyngeal organ) and biological (food composition, tube ornamentation, body regeneration) observations from selected specimens are provided. Additions to the original description of *Myrioglobula islandica* Parapar, 2003a and an updated key to the species of Oweniidae recorded in Arctic and East Atlantic Boreal waters are also presented. Aspects on geographical distribution and phylogeny of the family are also discussed.

Keywords: BIOICE project, Iceland, Myriochele, Myrioglobula, new species, Polychaeta, Oweniidae

#### Introduction

In the family Oweniidae (Polychaeta), the most important taxonomic characters at genus level are to be found in the anterior end. The presence of structures such as a tentacular crown, a pair of palps, or a ventrally elongate oral slit surrounded by membranous lips, characterizes *Owenia* Delle Chiaje, 1842, *Myriowenia* Hartman, 1960, and *Galathowenia* Kirkegaard, 1959, respectively. A simple anterior end without any of those structures is found in *Myriochele* Malmgren, 1867 and *Myrioglobula* Hartman, 1967. Among the genus

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Correspondence: Julio Parapar, Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Facultade de Ciencias, Universidade da Coruña, Campus da Zapateira s/n, 15071 A Coruña, Spain. Email: jparapar@udc.es

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*Galathowenia* and the group *Myriochele/Myrioglobula*, relevant taxonomic characters for species discrimination are the number, relative length, and distribution of the anterior uniramous chaetigers, called "thoracic", and the relative length of the first biramous, "abdominal", elongated chaetigers (Blake 2000; Parapar 2003b, 2003c).

The genus *Myriochele*, with *Myriochele heeri* as type species, was established by Malmgren (1867) in a study of the polychaete fauna from Spitsbergian, Greenlandic, and Icelandic waters. From the description and illustrations provided by the author, the taxon is characterized by: (1) the three anteriormost chaetigers having no neuropodia [antica tria sat brevia uncinis destituta] and being of similar length [segmenta 4 antica setigera subaequans]; (2) chaetigers 6 and 7 of similar length (being the longest of the body); (3) the following chaetigers getting progressively shorter towards the hind part [VI et VII longissima aequalia, dein posteriora versus longitude sensimdecrescentia, in postrema parte conferta]. The author's reference to four anterior chaetigers of similar length instead of three was probably due to the application of a different chaetiger length concept (see Remarks to M. heeri type material).

Since the original description, *Myriochele heeri* has been recorded in numerous and very distant geographical areas: boreo-arctic waters (e.g. Malmgren 1867; Fauvel 1914, 1932; Berkeley 1930; Uschakov 1950; Blake and Dean 1973; Bellan 1978; Nilsen and Holthe 1985; Imajima and Morita 1987; Jirkov 2001), Antarctic and Subantarctic waters (e.g. Hartman 1966, 1978; Blake 1984; Gillet 1991; Cantone and San Filippo 1992), the Ivory Coast (Intès and Le Loeuff 1977) and particularly the Mediterranean Sea (e.g. Fauvel 1927; Bellan 1970; Amoureux 1976; Cognetti-Varriale 1980; Sardá 1986; Martín 1987).

Since Malmgren (1867), authors like Hansen (1882), Wollebaek (1911), Hartmann-Schröder (1971), Nilsen and Holthe (1985), Imajima and Morita (1987), and Hayward and Ryland (1995) have included original drawings (Figure 1). Some of these were copied by later authors such as Hartman (1966) and Jirkov (2001). As Berkeley (1949) stated "The figures [by Malmgren] have been generally copied in text-books".

In recent years a remarkable increase in the study of the diversity and speciation of Oweniidae, particularly in *Owenia* (Koh and Bhaud 2001; Koh et al. 2003) and small species of *Myriochele* and *Myrioglobula* (Blake 2000; Parapar 2003a, b, c), has occurred. In his revision of the material belonging to *Myriochele gracilis* Hartman, 1955, from the central and southern Californian shelf and slope, Blake (2000) redescribed the taxon and described a new species, *Myriochele olgae*, based on specimens belonging to the type material of *M. gracilis*. Recently, in a study of the oweniid material collected during the BIOICE program, a project focused on the distribution and abundance of the marine benthic fauna living around Iceland, Parapar (2003a) found *M. heeri* in numerous samples in a wide bathymetric and temperature range (Figures 2 and 6 as *M. heeri sensu lato*). Parapar (2003b) described two new species of this genus, *Myriochele robusta* and *Myriochele riojai*, from Antarctic material previously identified as *Myriochele heeri*, and Parapar (2003c) reestablished the Subantarctic taxon *Galathowenia australis* (Grube, 1866) from synonymy with *M. heeri*.

The study by Nilsen and Holthe (1985) on Arctic and Scandinavian Oweniidae was the first to report variability in the number of anterior uniramous segments among specimens of M. *heeri*. In recent years Blake (2000) and Parapar (2003a) also reported the existence of this variability in this species, with individuals with two or three uniramous anterior chaetigers equally present.

A closer examination under light and scanning microscope of some BIOICE specimens previously identified as *Myriochele heeri* provided evidence that more than one species was



Figure 1. Representations of *Myriochele heeri* since its original description. (A) Malmgren 1867; (B) Hansen 1882; (C) Wolleback 1911; (D) Hartmann-Schröder 1971; (E) Nilsen and Holthe 1985; (F) Imajima and Morita 1987; (G) Hayward and Ryland 1995. All redrawn with permission from the original.

involved, characterized by the different length and the uniramous/biramous nature of the anterior body chaetigers. This situation led to the study of type material of *Myriochele heeri*, located at the Swedish Museum of Natural History, which proved also that two species were involved.

As a result of the revision of the type series of *Myriochele heeri*, *Myriochele olgae*, *Myrioglobula islandica*, and the revision of some material labelled as *M. heeri* collected during the BIOICE project and from other northern areas, a redescription of *M. heeri* is provided, the presence of *M. olgae* is confirmed for Icelandic waters, and a new species of *Myrioglobula* is described.

#### Material and methods

This study is based on 126 specimens from 18 benthic samples (Table I) collected during the BIOICE project around Iceland, previously identified as *M. heeri* (Parapar, 2003a). Additionally, the type series of two *Myriochele* and one *Myrioglobula* species were revised: *Myriochele heeri* Malmgren, 1867, Swedish Museum of Natural History, Stockholm (SMNH, five syntypes), *Myriochele olgae* Blake, 2000, National Museum of



Figure 2. Distribution maps of species. Sectors and BIOICE sampling sites of Myriochele heeri sensu lato and Myrioglobula islandica taken from Parapar (2003a).

Natural History, Washington, DC (USNM, holotype), and *Myrioglobula islandica* Parapar, 2003, Museo Nacional de Ciencias Naturales, Madrid (MNCN, five paratypes).

The type series of the new *Myrioglobula* species and the examined specimens of other BIOICE species, were deposited in the collections of the Icelandic Museum of Natural History (IMNH), Reykjavik (holotype and 11 paratypes) and Museo Nacional de Ciencias Naturales de Madrid (11 paratypes). For catalogue numbers see material examined section of the respective species.

The "Thoracic formula" (TF) (Parapar 2003a) and the "Relative length of thoracic chaetigers" (RLTC) (Nilsen and Holthe 1985) for first three segments are followed here.

Final drawings were created using Adobe Illustrator<sup>®</sup> software, based on hand drafts made with a camera lucida attached to an Olympus BX-40 stereomicroscope. With the exception of Figure 4C, all specimens were drawn using a cover glass. Specimens used for examination with scanning electron microscopy (SEM) were prepared by critical-point

Sampl	e Date	Latitude North	Longitude West	Water depth (m)	Water temperature (°C	Bottom
2065	2 July 1992	66.15	-17.60	198	3.8	Mud
2080	4 July 1992	67.38	-17.35	898.5	-0.6	
2081	4 July 1992	67.37	-17.38	895.5	-0.6	Mud
2100	6 July 1992	68.00	-19.42	1136.5	-0.6	
2152	9 July 1992	66.70	-20.05	148	5.1	Fine sand
2167	9 July 1992	66.33	-19.59	175.5	5.1	
2257	5 September 1992	63.24	-26.49	1210.5	4.1	Clay, shelly sand
2303	10 September 1992	63.06	-22.69	606	6.8	Muddy sand
2364	8 May 1993	64.58	-10.05	605.5	_	Sandy silt
2400	1 July 1993	63.13	-21.94	545.5	6.7	Sandy silt
2401	1 July 1993	63.12	-22.90	566	6.7	
2423	3 July 1993	63.17	-20.15	550	6.5	Sandy silt
2424	3 July 1993	63.17	-20.16	535	6.5	Coral
2474	5 July 1993	63.07	-21.59	812.5	5.5	Sandy silt
2480	11 July 1993	65.81	-23.92	62	3.6	Sandy silt
2575	15 July 1993	67.16	-24.32	797	-0.5	
2691	31 August 1994	64.44	-28.24	1187	3.7	Sand, silt and gravel
2700	2 September 1994	64.10	-27.83	1105	3.8	Sandy silt with gravel

Table I. Summarized data of BIOICE samples studied, where Myriochele heeri, M. olgae, and Myrioglobula malmgreni n. sp. were collected.

drying, coated with gold in a BAL-TEC SCD 004 evaporator, and examined and photographed under a JEOL JSM-6400 scanning electron microscope at the Servicios Xerais de Apoio á Investigación (SXAIN) of the Universidade da Coruña, Spain. Examination of food composition was done using chemical microanalysis by energy dispersive X-ray spectrometry, with Oxford Energy 200 equipment.

#### **Systematics**

#### Family OWENIIDAE Rioja, 1917

Genus Myriochele Malmgren, 1867

Myriochele heeri Malmgren, 1867, emended

(Figures 1, 2, 3B, 4A, B, 5, 6, 7A, 12, 13; Tables I, II)

Myriochele heeri Malmgren 1867, p 101-102, Table 7, Figure 37; Blake and Dean 1973,

p 37, Figure 2; Nilsen and Holthe 1985, p 21–22, Figures 3, 4, 11c–e; Parapar 2003a, p 283–284 [pro parte].

? Myriochele heeri: Imajima and Morita 1987, p 90-91, Figures 3a-k, 4e-h.

#### Type material

Swedish Museum of Natural History. The revised part of the collection consists of two jars. The first jar, labelled "SMNH—Type—5847 syntype(s). Myriochele heeri Malmgren, 1867. Svalbard, Vest Spitsbergen, Safe Haven. Leg. A. J. Malmgren 1864" has a vial inside labelled "Myriochele heeri # 905 (6518), S. C. Byers 4 Oct. 2002" with three specimens, one of them (Figure 3B) selected as lectotype (see below). The second jar, labelled "SMNH—Type—5848 syntype(s). Myriochele heeri Malmgren 1867. NW Greenland, Umanak, depth 455 m. Leg. C. T. Amondsen" also has a vial inside, labelled "Myriochele



Figure 3. Anterior end in ventrolateral view of three *Myriochele heeri* Malmgren, 1867 syntypes from the Swedish Museum of Natural History identified in this work as *M.* aff. *olgae* (A, C, D) and *M. heeri* (B). (A, B) SMNH 5847 (S. C. Byers' label 6518 # 905, specimens 1/3 and 3/3, respectively); (C, D) SMNH 5848 (S. C. Byers' label 6517 # 906, specimen 2/2), in left and right view. vpo, ventral pharyngeal organ. Scale bar: 1 mm.



Figure 4. Anterior end of two *Myriochele* species studied in this work. (A, B) *Myriochele heeri* Malmgren, 1867 (BIOICE 2257) in lateral and ventral view; (C) *Myriochele olgae* Blake, 2000 (BIOICE 2152) in latero-ventral view (drawn without cover glass). In (B), the neck ciliated field is observed and notochaetae of chaetigers 4 and 5 are concealed by the body. Scale bars: 0.5 mm.



Figure 5. *Myriochele heeri* BIOICE 2423. (A) Anterior end, lateral view (right side); (B) chaetiger 13 with two types of notochaetae; (C) posterior end; (D) anterior end, latero-ventral view (left side); (E) head, showing mouth lips, glandular area, and the three ciliated fields; (F) detail of lateral ciliated field; (G) oral ciliated field inside mouth lips; (H) detail of oral cilia; (I) ventral hooks from chaetiger 17. In (A) and (D), first four chaetigers numbered. no1–5, notochaetae of chaetigers 1 to 5; ne4–5, neurochaetae of chaetigers 4 and 5; lno, long notochaetae; sno, short notochaetae; ncf, neck ciliated field; ga, glandular area; lcf, lateral ciliated field; ml, mouth lips; ocf, oral ciliated field.

*heeri* # 906, 2/2 specimen + tube (6517)" with two specimens supposedly also revised by S. C. Byers.

#### Additional material

*Icelandic Museum of Natural History.* BIOICE sample 2401 (13 specimens (spms); IMNH 4100); sample 2423 (six spms; IMNH 4101); sample 2424 (three spms; IMNH 4102); sample 2474 (one spm; IMNH 4103); sample 2691 (four spms; IMNH 4104).

Museo Nacional de Ciencias Naturales. BIOICE sample 2080 (one spm; MNCN 16.01/10532); sample 2257 (two spms; MNCN 16.01/10533); sample 2303 (seven spms; MNCN 16.02/10534); sample 2400 (six spms; MNCN 16.01/10535).



Figure 6. Relationship between bottom water temperature and water depth at sampling sites where *Myriochele* and *Myrioglobula* species were found. Data from *M. heeri sensu lato* and *Myrioglobula islandica* obtained from Parapar (2003a).



Figure 7. Three specimens from Greenland (USNM 51164) from Blake and Dean (1973). (A) *Myriochele heeri* in ventro-lateral showing the dorsolateral folds; (B) *Myriochele* indet. with the anterior end in process of regeneration and with ventral pharyngeal organ everted; (C) *Myriochele* aff. *olgae* in lateral view. dlcf, dorsolateral ciliary folds; vpo, ventral pharyngeal organ. Scale bars: 0.5 mm (A, B); 1 mm (C).

Characters	<i>Myriochele heeri</i> Malmgren, 1867	Myriochele heer Malmgren, 1867	i Myriochele olgae Blake, 2000	Myriochele olgae Blake, 2000	Myrioglobula malmgreni n. sp.	Myrioglobula islandica Parapar, 2003
Maximum length/ width (mm)	$10 - 12 \times 0.5$	$19 \times 1.08$	5–10×0.5	$7 - 8 \times 0.4 - 0.5$	$10 \times 0.6$	$10 \times 1.0$
No. of chaetigers	22-25	28	18-23	22	26-31	19
Arrangement of first three body segments	1:0-1:0-1:0	1:0-1:0-1:0	1:0-1:0-1:1	1:0-1:0-1:1	1:0-1:1-1:1	1:0-1:1-1:1
Relative length of first three anterior chaetigers	1-1-1.5	1-1-2	1-1.5-3	1-1-4	1-1.5(2)-5	1-2-4
Relative length of fourth chaetiger in relation with previous three	1.5–2	1.5	2 (1.5)	2	1.5	1.2
Relative length of fifth chaetiger in relation with fourth	1.5–2	1.5	1	0.8	1	2–3
Elongated chaetigers	4th–8th	4th–7th	4th-6th	4th	4th-6th (7th)	4th-6th
Reference	This study (BIOICE)	Type material (lectotype)	This study (BIOICE)	Type material (holoype)	This study (BIOICE)	Type material (holotype)

Table II. Comparison of some diagnostic characters of *Myriochele heeri*, *M. olgae*, *Myrioglobula islandica*, and *M. malmgreni* n. sp. (relative length of fourth and fifth chaetigers in *M. islandica* were taken from paratypes).

Swedish Museum of Natural History. BIOICE sample 2700 (nine spms; SMNH 83573).

National Museum of Natural History. East Angiak Island, Baffin Island region, Canadian Arctic Archipelago, st. 20A-B, 14 August 1968, 132–245 m depth (more than five spms; USNM 51164). Southern Baffin Bay between W. Greenland and East Baffin Island: 67°49'N, 60°46'W, st. 26A, 16 August 1968, 1920–1745 m depth (one spm; USNM 51165).

#### Description (based on lectotype of M. heeri) (Figure 3B)

Body short, 19 mm long and 1.08 mm wide, very much shrivelled longitudinally and posteriorly tapered. Head region not rounded probably because of fixation; distinctly set off from thorax by a constriction. Mouth forming a longitudinal slit in the antero-ventral part of the head region. Eye-spots not visible. First three chaetigers uniramous (TF=1:0-1:0-1:0), with RLTC=1-1-2, followed by 25 biramous chaetigers. Length of first four chaetigers: 0.18, 0.23, 0.38, and 1.13 mm, respectively. Fourth to sixth or seventh chaetigers increasing in length; fourth and fifth chaetigers about 1.5 and 2.5 times longer than thorax; sixth and seventh chaetigers the longest, about three times longer than thorax. Following chaetigers progressively decreasing in length, becoming crowded in prepygidial segments. Notopodia with a dorsal bundle of capillary chaetae and a ventral bundle of short and smooth acicular chaetae. Neuropodial tori narrow, with uncini arranged in irregular rows. Hooks with two teeth constantly arranged one above the other. Posterior end distally tapered, with segments highly compressed and pygidium contracted, appearing as two low lateral lobes.

#### Description of Icelandic specimens

Body short, 10-12 mm long and 0.4-0.5 mm wide, 22-25 chaetigers. First three body chaetigers short and uniramous (TF=1:0-1:0), shorter than wide, with relative length 1-1-1(1.5) (Figures 4A, B, 5A, 12); fourth to sixth or seventh chaetigers increasing in length. Fourth chaetiger, first biramous, 1.5-2 times thoracic length. From chaetiger eight, body segments decreasing in length. Notopodia with long capillary chaetae and short acicular chaetae (Figure 5B); neuropodial hooks with two apical teeth located one above the other (Figure 5I); pygidium with two low lateral lobes (Figure 5C).

Two ciliated fields distinct using SEM at head level in BIOICE specimens: a front lateral field dorsal to the mouth lips and a neck field ventral to the mouth lips (Figures 4B, 5D–F). Oral cilia present on the inner side of the mouth lips (Figure 5E, G, H).

Tube with cylindrical middle part and long tapering ends, covered by sponge spicules or sand grains depending on bottom nature (Figure 13).

#### Remarks

As Malmgren did not define holotype or paratypes and S. C. Byers, who revised the collection in 2002, created no lectotype or paralectotypes, the syntype proposed herein as lectotype for *Myriochele heeri* (Figure 3B) was selected for three reasons:

- 1. Both TF and RLTC are in accordance with Malmgren's original description (see Introduction) and the general body appearance traditionally assigned to this taxon in classical literature (see Figure 1).
- 2. The vial # 5847 with specimens from Spitzbergen, according to Byers' notes, probably belongs to the original Malmgren types.
- 3. Even though it is wrinkled, it is in better condition than the other two specimens from Malmgren's collection also assigned by the author to this species.

The three specimens in vial # 5847 of the *M. heeri* type series correspond to two species. One of them (Figure 3A) has an asymmetric second anterior chaetiger giving rise to an anterior region with two uniramous chaetigers on the right side and only one on the left side (TF=1:0-1:0(1:1)-1:1). Relative length of thoracic chaetigers, RLTC=1-1-3, with chaetigers 4–6 of similar length, the fourth being about 1.5 times longer than the sum of the preceding. The mouth is widely open with the ventral pharyngeal organ everted. This specimen corresponds to those identified as *Myriochele* aff. *olgae* from the BIOICE material (see below).

The other two specimens correspond to *M. heeri*: TF=1:0-1:0; RLTC=1-1-1.5(2) with chaetigers 4–6 increasing in length, the fourth being about 1.75 times the sum of the preceding. One of them is damaged (not illustrated) and the other, which was selected as lectotype (Figure 3B), is much wrinkled longitudinally.

In vial # 5848 of the *M. heeri* type series, one specimen is damaged (not illustrated, corresponding to *M. heeri*), but the other is in good condition, again with asymmetric anterior chaetigers and RLTC=1-1.5-3.5; this specimen is assigned again to *M.* aff. *olgae* (Figure 3C, D).

Malmgren's assumption that the four anterior chaetigers, instead of three, are of similar length (see Introduction) was probably due to a different concept in chaetiger delineation. Considering the relative proportions of anterior chaetigers to be of high taxonomic relevance, a clear delimitation of them is a matter of great importance. Following Blake (2000), who stated that in oweniids parapodia are located at the anterior border of segments (even though this is difficult to discern in *Myriochele*, a genus without clear segment delineation—but easily observed in *Myriowenia*; see Blake 2000, Figure 5.7), a large fourth chaetiger is revealed in this species. Nevertheless, the assumption of a middle position of the parapodia in the chaetiger, which is the generalized case in polychaetes and the idea probably assumed by Malmgren, led to the view of a short fourth chaetiger.

As was previously noted, the number and relative length of anterior body chaetigers are traditionally considered to have crucial taxonomic value for species discrimination in the genus *Myriochele*, with *M. heeri* characterized by the presence of three short uniramous chaetigers of similar length, while specimens with two uniramous chaetigers represent a different species (see below).

Myriochele gracilis Blake, 2000 from off California and Myriochele riojai Parapar, 2003 from Bransfield Strait (Antarctica) share with Myriochele heeri two of the most relevant diagnostic characters in Myriochele systematics and qualifies them as very close species. These characters are the thoracic formula, TF=1:0-1:0-1:0, and the relative length of thoracic chaetigers, RLTC=1-1-1(1.5). Nevertheless, Myriochele gracilis differs from M. heeri in the prostomial shape—domed dorsally and with numerous small papillae in M. gracilis and without these characters in M. heeri—and the length of the first abdominal chaetigers—increasing in length from fourth to seventh or eighth in M. heeri and all of consistent length in M. gracilis. Myriochele riojai differs from M. heeri both in known geographic distribution (Antarctic versus Arctic and Boreo-Atlantic waters), by its body size (10-12 mm versus 23 mm), and by the position and number of notopodial acicular chaetae (much more numerous and present from the first chaetiger in M. riojai).

Although no specimens were examined, the descriptions and illustrations provided by Imajima and Morita (1987) of Japanese specimens of M. *heeri* (Figure 1F) leave little doubt about their correct identification. No specimens with two thoracic chaetigers were referred to by the authors.

The material collected by Blake and Dean (1973) consists of two vials. Vial # 51165 contains one damaged indeterminable specimen and vial # 51164 contains nine specimens out of their tubes and about 16 still inside. Among the former, five have the characteristics here accepted for *M. heeri* (Figure 7A), one is regenerating the anterior end (*Myriochele* indet., Figure 7B), and three, although in general appearance similar to *M. heeri*, belong to *M.* aff. *olgae* (Figure 7C), with TF=1:0-1:0-1:1 and RLTC=1-1-2. One specimen identified as *M. heeri* shows the dorsolateral ciliary folds semi-everted (Figure 7A) and the specimen identified as *Myriochele* indet. also shows the pharyngeal organ everted (Figure 7B), as in *Myriochele* aff. *olgae* from SMNH 6518 (Figure 3A).

#### Distribution

The revised material of *M. heeri* reveals an Arctic and Boreo-Atlantic distribution. With the only exception of a specimen collected on the northern coast (sector a) from sample 2080 (898.5 m depth and  $-0.6^{\circ}$ C), the specimens from the BIOICE project were collected in sector b (southwest coast–Reykjanes Peninsula) in warm waters (3.8–6.8°C) and at depths ranging from 535 to 1210.5 m (Figures 2, 6 as *M. heeri sensu stricto*).

Myriochele olgae Blake, 2000

(Figures 2, 3A, C, D, 4C, 6, 7C, 8, 9, 12, 13; Tables I, II) Myriochele olgae Blake 2000, p 111–113, Figure 5.5.



Figure 8. *Myriochele olgae* BIOICE 2065. (A) Anterior end, anteroventral view (right side) of a contracted specimen; (B) notopodium of chaetiger 16 showing two types of notochaetae; (C) hooks of first neuropodium; (D) posterior end; (E) detail of cilia from anus ciliated field; (F) anterior end, ventral view of a non-contracted specimen; (G) detail of two types of notochaetae of chaetiger 6; (H) view of mouth with food remains; (I) detail of food (diatom frustules); (J) ventral view of three anterior chaetigers showing limit of neck ciliated field; (K) detail of cilia from neck ciliated field; (L) detail of cilia from mouth ciliated field. In (A) and (F), chaetae of first four chaetigers numbered. no1–4, notochaetae; ncf, neck ciliated field; acf, anus ciliated field.

Myriochele heeri Malmgren 1867, p 101–102, Table 7, Figure 37; Blake and Dean 1973, p 37, Figure 2; Parapar 2003a, p 283–284 [pro parte]. Myriochele heeri: Nilsen and Holthe 1985, p 21–22, Figures 3, 4, 11c–e [? pro parte].

#### Type material

*National Museum of Natural History.* North Pacific Ocean, USA, California, Santa Maria Basin, off Point Sal, 145 m (holotype; USNM 186431).

#### Additional material

Icelandic Museum of Natural History. BIOICE sample 2575 (five spms; IMNH 4105); sample 2700 (three spms; IMNH 4106).

*Museo Nacional de Ciencias Naturales.* BIOICE sample 2065 (five spms; MNCN 16.01/10536); sample 2080 (four spms; MNCN 16.01/10537); sample 2081 (one spm; MNCN 16.01/10538); sample 2100 (nine spms; MNCN 16.01/10539); sample 2152 (13 specimens; MNCN 16.01/10540); sample 2167 (three spms; MNCN 16.01/10541);



Figure 9. (A–C) *Myriochele* aff. *olgae* with asymmetric biramous second chaetiger BIOICE 2423: (A) anterior end, lateroventral view (left side); (B) first neuropod in second chaetiger; (C) detail of hooks of first neuropod piercing the epidermis. (D–I) *Myriochele* aff. *olgae* from BIOICE 2424: (D) anterior end of a recently broken specimen; (E) posterior end with only neuropodial hooks; (F) specimen regenerating anterior end; (G) anterior end in ventral view of a specimen with a supernumerary fourth chaetiger (arrow); (H) posterior end in lateral view; (I) pigidial ciliated field. In (A), chaetae of first chaetigers numbered. no1–3, notochaetae of chaetigers 1 to 3; ne2–3, neurochaetae of chaetigers 2 and 3; sno, short notochaetae; lno, long notochaetae; ncf, neck ciliated field, acf, anus ciliated field.

sample 2364 (seven spms; MNCN 16.01/10542); sample 2480 (one spm; MNCN 16.01/10543).

#### Description based on Icelandic specimens

Body short, 5-10 mm length and 0.5 mm wide, 18-23 chaetigers. First two body chaetigers uniramous; third biramous (TF=1:0-1:0-1:1), first and second shorter than wide and third longer than wide, with increasing length (RLTC=1-1(1.5)-3) (Figures 4C, 8A, F, 12). Fourth to sixth chaetigers (second to fourth abdominal) elongated and of similar length; fourth about two (1.5) times as long as the sum of three previous chaetigers. Following chaetigers decreasing in length. Notopodia with long capillary chaetae and short acicular chaetae (Figure 8B, G); neuropodial hooks with two apical teeth located one above the other (Figure 8C); pygidium with two low lateral lobes (Figure 8D).

As in *M. heeri*, ciliated fields associated with head and mouth distinct (Figure 8F, J–L); a dense ciliated anal field observed at the pigidium (Figure 8D, E); food remains, possible diatom frustules, present inside the mouth of one specimen (Figure 8H, I).

Tube with cylindrical middle part and long tapering ends, covered by sponge spicules or sand grains depending on bottom nature (Figure 13).

#### Distribution

*Myriochele olgae* was originally described from the East Pacific coast of North America (California) and is now reported from Iceland. In Icelandic waters, the species seems to be restricted to sector a on the north coast (Figure 2) at a wide depth (198–1136.5 m) and temperature  $(-0.6-5.1^{\circ}C)$  range (Figure 6).

#### Remarks

The investigation of the holotype of *Myriochele olgae* (USNM 186431) showed that the general body shape, size, number of chaetigers, and thoracic formula of the specimen are completely in agreement with the Icelandic specimens (Table II). The only difference was in the relative length of the anterior biramous chaetigers; in the holotype chaetiger 3 is about four times longer than the uniramous chaetigers (chaetigers 1 and 2) and chaetiger 4 is the longest of the body, the following being shorter. In Icelandic specimens chaetiger 3 is about three times longer than uniramous chaetigers and an increasing length is observed from the fourth to sixth chaetigers. In both cases chaetiger 4 is about two times longer than the first three chaetigers combined. In my opinion, those differences are not significant enough to describe a new species.

Specimens named *Myriochele* aff. *olgae* from BIOICE samples 2423 and 2424 (Figure 9) show some abnormal characters such as: (1) asymmetrical second biramous chaetiger with left neuropodial hooks partially piercing the epidermis (Figure 9A–C); (2) anterior end broken or in process of regeneration (Figure 9D, F); (3) a supernumerary second biramous chaetiger (Figure 9G); and (4) last chaetigers without notopodia (Figure 9E). Cilia associated with pygidial lobes were also seen (Figure 9H, I).

Unlike *M. heeri*, in which the principal taxonomic characters (number of uniramous/ biramous anterior chaetigers and their relative length) seem to be consistent, the Icelandic specimens of *Myriochele olgae* show a high variability in the presence of asymmetric anterior chaetigers and differences in the relative chaetiger length (see above). This variability would correspond to decapitation due to predation or an asexual reproduction process by bipartition, a reproductive strategy previously reported by Parapar (2003a) in the BIOICE oweniids *Galathowenia fragilis* (Nilsen and Holthe, 1985) and *Galathowenia oculata* (Zachs, 1923).

#### Myrioglobula malmgreni sp. nov.

(Figure 2, 6, 10A–C, 11, 12; Tables I, II) Myriochele heeri: Parapar 2003a, p 283–284 [pro parte].

#### Type material

*Icelandic Museum of Natural History.* Holotype (IMNH 4112); 11 paratypes (IMNH 4107/ 4111 and 4113).



Figure 10. Anterior end of two *Myrioglobula* species studied in this work. (A, B) *M. malmgreni* n. sp. in lateral (left) and ventral view (holotype, IMNH 4112); (C) *M. malmgreni* n. sp. (paratype, IMNH 4107) in latero-ventral view; (D, E) *M. islandica* Parapar, 2003 (paratype, MNCN 16.01/9023) in ventral and lateral (left) view. In (B), notochaetae of chaetigers 3 and 4 are concealed by the body. Scale bars: 0.5 mm.



Figure 11. (A–G) *Myrioglobula malmgreni* n. sp. BIOICE 2401 (paratype, MNCN 16.01/10544): (A) anterior end, ventral view; (B) mouth opening with oral ciliary field; (C) detail of oral cilia; (D) detail of mouth ciliary fold; (E) first and second neuropodia; (F) notopodia of segment 6; (G) hooks from fourth chaetiger. (H–L) Specimen from BIOICE 2303 (paratype, IMNH 4110): (H) anterior end, lateral (right) view; (I) detail of head; (J) anterior chaetigers, lateral view; (K) notopodia of chaetiger 5; (L) lateral slit at fourth chaetiger. In (A) and (E), chaetae of first chaetigers numbered. no1–4, notochaetae of chaetigers 1 to 4; ne2–4, neurochaetae of chaetigers 2 to 4; ncf, neck ciliated field; ocf, oral ciliated field.



Figure 12. Schematic diagrams of anterior end organization, in ventral view, of species studied in this work, showing chaetal composition and relative length of anterior chaetigers. Drawings not at same scale.

Museo Nacional de Ciencias Naturales. Eleven paratypes (MNCN 16.01/10544-47).

#### Additional type material

Museo Nacional de Ciencias Naturales. Myrioglobula islandica Parapar, 2003, five paratypes (MNCN 16.01/9023) (Figure 10D, E).

#### Type localities

Northern Icelandic coast: BIOICE sample 2080 (one paratype; IMNH 4107). Iceland– Faeroe Passage: BIOICE sample 2364 (one paratype; IMNH 4108). Southern coast– Reykjanes Peninsula: BIOICE sample 2167 (three paratypes; IMNH 4109); sample 2303 (four paratypes, one on SEM stub; IMNH 4110–4111); sample 2400 (holotype and two paratypes; IMNH 4112–4113); sample 2401 (one paratype on SEM stub; IMNH MNCN 16.01/10544); BIOICE sample 2423 (three paratypes; IMNH MNCN 16.01–10545);



Figure 13. Some examples of *Myriochele heeri* (2257–2700) and *Myriochele olgae* (2065–2700) tubes collected in different localities in the BIOICE project. Scale bar: 1 mm.

# sample 2424 (four paratypes, IMNH MNCN 16.01/10546); BIOICE sample 2474 (three paratypes; IMNH MNCN 16.01/10547).

#### Diagnosis

First chaetiger uniramous; second and third biramous (TF=1:0-1:1-1:1). Relative length of three anterior chaetigers (RLTC) 1-1.5(2)-5, fourth to sixth (seventh) chaetigers of similar length, fourth about 1.5 times as long as three previous chaetigers. Following chaetigers decreasing in length. Notopodia with long capillary chaetae and short acicular chaetae; neuropodial hooks with two apical teeth located one above the other; pygidium with two low lateral lobes.

#### Description based on holotype (Figure 10A, B)

Body short, 10 mm long and 0.6 mm wide, with 28 chaetigers, nearly cylindrical, and posteriorly tapered. A longitudinal mid-dorsal, ventral and lateral slit present along the body (Figure 11H, J, L). Head region rounded and distinctly set off from thorax by a constriction (Figure 10A-C). Eve-spots not visible. First chaetiger uniramous; second and third biramous (TF=1:0-1:1-1:1) (Figure 10A, B, 11A, H–J), with relative length 1-1.5(2)-5, followed by 25 biramous chaetigers. Fourth chaetiger 1.5 times as long as the sum of preceding chaetigers (Figure 12). Fourth to sixth or seventh chaetigers of more or less similar length. Following chaetigers showing a progressive decrease in length. Notopodia with a dorsal bundle of capillary chaetae and a ventral bundle of short and smooth acicular chaetae from the third chaetiger (Figure 11F, K). Notopodial acicular chaetae about half the length of the capillaries (Figure 11K), with distal half abruptly tapered. Neuropodial tori narrow and nearly rectangular, with uncini arranged in three to four irregular rows in anterior segments (Figure 11E) to four to five in middle ones. Hooks with two long and slender teeth constantly arranged one above the other (Figure 11G). Posterior end distally tapered, with final segments highly compressed; pygidium consisting of two low lateral lobes.

Cilia associated with head (neck ciliated field and oral cilia) also present in specimens studied with SEM (Figure 11B–D, I).

Tube with cylindrical middle part and long tapering ends, covered with sand grains.

#### Distribution

Iceland. Although specimens of this new species were found in the three sectors studied, most were found in sector b off the southwest coast of the Reykjanes Peninsula (Figure 2) in temperate waters  $(5.5-6.8^{\circ}C)$  at moderate depths (535 and 812.5 m) (Figure 6).

#### Remarks

*Myrioglobula malmgreni* n. sp. differs from *Myrioglobula islandica* Parapar, 2003, a species recently described from Icelandic waters, in: (1) head of *M. islandica* larger and quadrangular instead of rounded (Figure 10D, E); (2) body shape large and robust in *M. islandica*, small and slender in *M. malmgreni*, which is very similar in general appearance to *Myriochele heeri* and *M. olgae*; (3) body dorso-ventrally flattened in *M. islandica* (as in *M. japonica*) especially in posterior chaetigers, and rounded in *M. malmgreni*; (4) dorsal chaetae

more numerous in *M. islandica* than in *M. malmgreni*; (5) both absolute and relative length of anterior chaetigers different, longer in *M. islandica*.

Curiously, Myrioglobula malmgreni n. sp. is, regarding its general body shape, much more similar to the Icelandic specimens of Myriochele olgae and Myriochele heeri than to Myrioglobula islandica, the biramous organization of chaetiger 2 being the only relevant character that separates it from the two Myriochele species.

#### Etymology

This species is named in honour of A. J. Malmgren, Finnish zoologist of the second half of the 19th century, pioneer in the study of taxonomy of Icelandic polychaetes, who originally described *Myriochele heeri*, type species of the genus.

#### Key to species of Oweniidae

Nilsen and Holthe (1985) described a new oweniid species (Galathowenia fragilis as Myriochele) for Boreo-Arctic waters, and presented emended descriptions of all four species known from the area up to that date: Owenia fusiformis Delle Chiaje, 1842, M. heeri, Myriochele danielsseni Hansen, 1879, and Galathowenia oculata (Zachs, 1923) (as Myriochele). Parapar (2003a), from material collected during the BIOICE expeditions, confirmed the presence of all of them in Icelandic waters and described a new species, Myrioglobula islandica. In the present work, the description of Myriochele heeri is emended and one new species is described.

Although a key for Icelandic oweniids was recently presented by Parapar (2003a), the important additions and changes to Oweniid taxonomy in Arctic and East Atlantic boreal waters presented in this work and in Koh et al. (2003), which reinstated the taxon *Owenia assimilis* (Sars, 1851) and described the two new *Owenia* Delle Chiaje, 1842 species; *O. polaris* Koh, Bhaud and Jirkov, 2003 and *O. borealis* Koh, Bhaud and Jirkov, 2003, justify the presentation of a new key. *Owenia fusiformis* is not included because its geographical distribution, according to these authors, is probably more meridional (Mediterranean Sea). Koh et al. (2003) differentiated this species from *O. polaris* and *O. borealis*, among other characteristics, by a larger tentacle crown, with a "length of crown" to "length of thorax" ratio of 1:1 instead of 1:2 in both new species.

Key to species of Oweniidae from Arctic and East Atlantic boreal waters

1.	Cephalic region with tentacular crown Owenia	ı 2
-	Cephalic region without tentacular crown	4
3.	Collar oblique and without angle at level of lateral notch. Owenia assimilis (Sars, 185	1)
_	Collar not oblique and with open angle (120°) on lateral notch	3
3.	Hooks of median part of torus of first abdominal segment forming a $45^{\circ}$ angle with longitudinal body axis	03
_	Hooks of median part of torus of first abdominal segment forming a $0-20^{\circ}$ angle with longitudinal body axis	03

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4.	One thoracic chaetiger
_	Two or three thoracic chaetigers
5.	Body long and robust, quadrangular in section, first three chaetigers long, with notochaetal bundles well separated; RLTC=1:2:4
_	Body short and slender, circular in section, first three chaetigers short, with notochaetal bundles close to each other; RLTC=1:1.5(2):5
6.	Head region anteriorly truncated with overlapping membranous oral lips; abdominal notopodia with capillary chaetae only; teeth of uncini more or less arranged in an oblique row
_	Head region anteriorly not truncated without overlapping membranous mouth lips; abdominal notopodia with capillary and acicular chaetae; teeth of uncini not arranged in an oblique row
7.	Thorax with a fine transverse slit between first and second chaetigers; head without eye-spots or dorsal pigmented band; scales of capillary chaetae short; teeth of hooks more or less in an oblique position; pygidium with five to six lobes
_	Without thoracic transverse slit; a pair of ventrolateral eye-spots and dorsal pigmented band in head region in some populations; scales of capillary chaetae slender; teeth of hooks located side by side at different levels; pygidium with two lobes
8.	Head region anteriorly rounded; teeth of uncini arranged one above the other . 9
_	Head region sub-conical, with rounded tip and dorsolateral sulcus; teeth of uncini arranged side by side
9.	Three anterior uniramous chaetigers (TF=1:0-1:0)
_	Two anterior uniramous chaetigers (TF=1:0-1:0-1:1) Myriochele olgae Blake, 2000

## Discussion

### Species discrimination

The low number of characters with taxonomic relevance for species discrimination in oweniids and particularly in the genus *Myriochele* (see Table II), linked to the high variability observed in some of them for various reasons (genetic, predation, reproduction process, fixation artefact, etc.) occasionally makes it difficult to establish a clear criterion for species discrimination. I follow Blake's (2000) proposal in giving high taxonomic value to the relative length of anterior body chaetigers (considered consistent within a single species), but using it with care, keeping in mind, in order to avoid unnecessary creation of new species, the fact that this is a soft character that would be affected by body contraction.

Koh and Bhaud (2001) and Koh et al. (2003) gave great significance to characters such as tooth orientation in hooks and size of scale covering of capillary notochaetae in *Owenia* taxonomy. In my opinion, such hard characters are insufficiently studied in *Myriochele*, and would need more attention in future studies perhaps in the framework of a worldwide revision of the genus.

#### The ciliature

Since the work of Watson (1901), who found that Owenia fusiformis uses its ciliated tentacular crown for feeding, works on the ciliated epidermis in oweniids have been mostly limited to this species. Dales (1957) described the tentacle structure, and Gardiner (1978) demonstrated that its oral epithelium consists mostly of unspecialized monociliated cells, which is unique among the Polychaeta, more similar to the epithelia of lophophorates or primitive deusterostomes than to the epithelia of other polychaetes. Rieger (1976), who reported unspecialized monociliated cells also in some Gastrotricha and Gnatostomulida, considered this structure as a primitive feature among Metazoa, and since it is of widespread occurrence among the Archicoelomates, Gardiner (1978) considered that, as far as the epidermis is concerned, Owenia preserves the original condition of the common ancestor to the Archicoelomates and the Polychaeta. Dales (1957) proposed that the tentacular cilia in O. fusiformis are used not only for the production of water flow in a suspension-feeding microphage guild, but also for surface deposit feeding, a trophic strategy later corroborated by Gambi (1989) and Desroy et al. (1997). Recently, Purschke and Tzetlin (1996) studied the ciliary folds from the dorsolateral walls of the foregut in 26 species belonging to 16 polychaete families and revealed that it consists of ciliated cells, usually associated with gland cells and with no intrinsic muscular system. These folds, protruded by contractions of the musculature of the body wall in the anterior part of the body, and making contact with the substratum during food uptake, were recorded in the oweniid Galathowenia oculata (as Myriochele) associated with a characteristic "ventral pharyngeal organ" composed of bulbous muscle (see Purschke and Tzetlin 1996, Figures 10B, 11, 12A). The observations made in the present work on several specimens seem to confirm the presence of this ciliary fold in the foregut of Myriochele heeri. Also, the illustrations of this species provided by authors such Hartmann-Schröder (1971) and Nilsen and Holthe (1985) seem to show the presence of the ventral pharyngeal organ in their specimens (Figure 1D, E). The presence of what I termed "ciliary fields" in the prostomium of BIOICE specimens of M. heeri and M. olgae would also be related to some kind of sensory perception perhaps linked to food selection which, at least in Icelandic M. olgae, seems to be composed mainly of diatoms (Figure 8H, I). The analysis of their fine structure, biological role, and phylogenetic relevance is beyond the scope of this study.

#### Tube ornamentation

Although the general shape of the tube was revealed as a valuable tool to identify genera in Icelandic oweniids and proposed as a simple tool to separate groups of species in broad benthic studies (see Parapar 2003a, p 287–288), it proves to be useless in species discrimination of *M. heeri*, *M. olgae*, and *M. malmgreni* n. sp. specimens. Therefore, as was previously noted with regard to the relative length of anterior biramous chaetigers, tube ornamentation should also be used with care in taxonomic species descriptions and

identification routine. Observations on BIOICE material (Figure 13) show variability in material used in tube construction (sand grains and sponge spicules) depending on the geographic area and the bottom type. At one single station an important selection in the material used is observed, only one of the two normally used elements, mineral/organic, being dominant in each case. This selection seems to be more accentuated in *Myriochele heeri* than in *Myrioglobula malmgreni* in which the use of sand grains of different colour, and probably also of different nature, seems to be more widespread. Koh et al. (2003) also considered the value of using tube structure as a good taxonomic criterion, but only if it is used with prudence, admitting that only through experimentation with living specimens it could be demonstrated that differences observed are species specific. However, they affirmed that at similar bathymetry and sediment, differences in tube aspect among *Owenia* species coincide with differences in body, which suggest that grain choice is specific and could be used as a taxonomic character. This could not be confirmed among *Myriochele* species.

#### The geographic distribution

In my opinion, the presence of M. heeri both in the Mediterranean Sea, East Atlantic temperate coast, and in the Southern Ocean should be corroborated. I agree with Nilsen and Holthe (1985) on the reported distribution of this species: "The distribution is uncertain, as this is the species under which several *Myriochele* species have been lumped for long periods". Therefore, I consider more correctly for this species a restricted geographic distribution, such as "widely distributed polychaete in northern seas" (Berkeley, 1949) particularly in Boreo-Arctic waters "with the southern limit on the French coast of the British Channel" (Dauvin 1986). This consideration is supported by the revision of the Oweniidae of the Iberian Peninsula by Martín (1989), who revised some material from the Mediterranean Sea, and affirmed that most parts of the records of this species—perhaps with the exception only of the Cognetti-Varriale (1980) material from the Tyrrhenian Sea—correspond to Galathowenia oculata. The revision of specimens initially named M. heeri in worldwide areas will probably result in the erection of new species, as in Cantone and Di Pietro (2001) and Parapar (2003b) for Antarctica, and the resurrection of Psammocollus australis Grube, 1866, in the genus Galathowenia by Parapar (2003c), a species for many years considered a synonym of Myriochele heeri.

In relation to the Icelandic distribution (Figure 2), even though none of the species into which *M. heeri s. lat.* divides were clearly restricted to a well-defined geographic area or water mass, a different pattern of distribution could be outlined. *Myriochele heeri s. s.* and *M. malmgreni* n. sp., are well restricted to south of the Greenland–Iceland–Faeroe (GIF) Ridge (sector b), associated with north Atlantic warm waters, while *M. olgae* is mainly present on northern coasts (sector a) linked to cold waters from the Arctic Ocean.

#### Phylogeny of the family

Sene-Silva (2002), in a phylogenetic analysis of Oweniidae, concluded that while *Owenia* Delle Chiaje, 1842, *Myriowenia* Hartman, 1960, and *Myrioglobula* Hartman, 1967 are monophyletic groups, *Myriochele* Malmgren, 1867 and *Galathowenia* Kirkegaard, 1959 are paraphyletic. Although a taxonomic study of both genera is still needed, the differences among them are, in my opinion, well established in the recent literature (see Blake 2000),

hence the paraphyly proposed by Sene-Silva (2002) is perhaps due more to incomplete or inexact descriptions than to the real nature of the taxa. Sene-Silva's results were determined by two facts: first, the characterization of some species only from bibliographic resources and not from the direct study of the specimens and, second, the lack of a strict application of the concepts of Myriochele/Galathowenia in species nomination. The author reproduces the species names used in the original articles, without taking into account if they support (e.g. Nilsen and Holthe 1985; Hartmann-Schröder and Rosenfeldt 1989; Fiege et al. 2000) or not (Imajima and Morita 1987; Blake 2000; Parapar 2001) the synonymy Myriochele/ Galathowenia, giving rise to a list of taxa without a common taxonomic criterion. Considering Galathowenia as a valid taxon, besides G. scotiae (Hartman, 1978) and G. oculata (Zachs, 1923), the species named M. joinvillensis Hartmann-Schröder and Rosenfeldt, 1989, M. fragilis Nilsen and Holthe, 1985, M. pygidialis Hartman, 1960, and M. logicollaris Hartmann-Schröder and Rosenfeldt, 1989 should also be included in the genus Galathowenia (see Parapar 2003c); under these circumstances the monophyly of both genera would be much more plausible (see Sene-Silva 2002, Figure 2), probably even with the addition of newly described species in recent works such as Koh et al. (2003) or Parapar (2003a, 2003b, 2003c). The only problematic species would be M. danielsseni Hansen, 1879, in which the side-by-side disposition of teeth in hooks is more similar to Myrioglobula antarctica Hartman, 1967 (see Hartman 1967, p 140–150, Figure 43) than to Myriochele.

In addition, the above-mentioned similarity between *Myrioglobula malmgreni* n. sp. and *Myriochele olgae* would support the idea of considering *Myrioglobula* a probable junior synonym of *Myriochele* which was already proposed by Blake (2000). In Sene-Silva's cladogram, the species belonging to *Myriochele* or *Myrioglobula*, with the commented exception of *M. danielsseni*, form a monophyletic clade.

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