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A NEW BENTHOPELAGIC SPECIES OF *HETEROKROHNIA* (CHAETOGNATHA) FROM THE NORTH ATLANTIC OCEAN

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ABSTRACT

A new species of *Heterokrohnia, H. mirabiloides,* is described from the "Discovery" collections made in the North-East Atlantic. It differs from the two other species of the *"mirabilis"* group mainly in the cephalic armature, particularly the posterior teeth which are much less numerous and bent at rigth-angle. Although *H. mirabiloides* is benthopelagic as are all the *Heterokrohnia* species, most specimens have been caught using benthic sampling gear (31 out of 33 specimens). On the other hand *H. mirabilis* has been found in both benthic and pelagic samples (14 and 19 specimens, respectively). It appears that *H. mirabiloides* is the shallowest living species of the genus because the great majority of specimens (24) have been found at depths between 1300 and 1400 m, whereas *H. mirabilis* appeared only in hauls below 2700 m.

RÉSUMÉ

Une nouvelle espèce d'*Heterokrohnia, H. mirabiloides,* est décrite des collections du "Discovery" dans l'Atlantique nord-est. Elle diffère essentiellement des deux autres espèces du groupe *"mirabilis"* par l'armature céphalique, notamment les dents postérieures beaucoup moins nombreuses et recourbées à angle droit. Bien que bentho-pélagique comme toutes les *Heterokrohnia, H. mirabiloides* a été capturée principalement dans les prélèvements benthiques (31 spécimens sur 33), tandis qu'*H. mirabilis* l'a été indifféremment dans les prélèvements benthiques et planctoniques (respectivement 14 et 19 spécimens). Enfin, *H. mirabiloides* est, semble-t-il, l'espèce la moins profonde du genre puisque présente en majorité dans des dragages entre 1300 et 1400 m (24 spécimens), alors qu'*H. mirabilis* n'apparaît qu'à partir de 2700 m de profondeur.

INTRODUCTION

In the 'Discovery' collections, several specimens of a *Heterokrohnia* species have been found that bear a superficial resemblance to *H. mirabilis* Ritter-Zahony, 1911. However, they differ from that species principally in the number and shape of the posterior teeth. When this material is compared with specimens of *H. mirabilis* caught either at the same station, or in the same area, it becomes clear that it belongs to a new species, which we have named *H. mirabiloides,* since it is closely related to, but distinct from, *H mirabilis.*

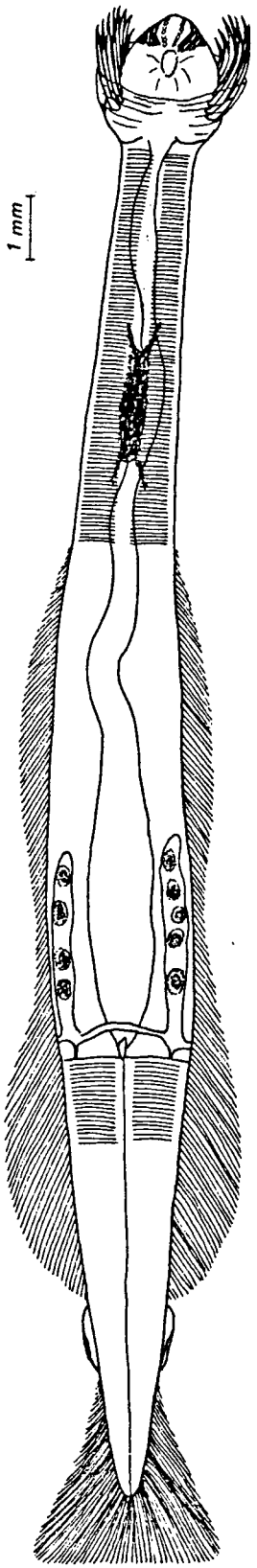

Fig. 1. *Heterokrohnia mirabiloides* n.sp. (ventral view).

Heterokrohnia mirabiloides n.sp.

(Figs. 1, 2, 3)

Material examined

Most of the specimens (31) were caught in six epibenthic trawls, five fished at depths between 1292 and 1404 m, and one between 3610 and 3646 m. Two other specimens came from pelagic hauls below a depth of 3100 m (Table I). Only those specimens that were in a good condition (18) have been measured.

Holotype: 1 specimen collected at "Discovery" st. 9779 (see table I for station details); length 22 mm; preserved in 5% formalin and presented to the Zoological Museum of the University of Amsterdam (no. ZMA VCH 2718).

Paratypes: 2 specimens from the same station, presented to the British Museum (Natural History) (no. ZK 1989: 3: 1-2).

Type locality: "Discovery" station 9779, 49°20.7'N 12° 49.5'W, 24 April 1978, depth 1398-1404 m.

DESCRIPTION

The body is slender, with a well-marked neck. The maximum length observed was 25 mm, with the tail representing from 29.6 to 40% of the total.

The head is egg-shaped and bears small apical glands. There are 7-18 anterior teeth, which are flattened and roughly triangular in shape. The posterior teeth are slightly more numerous (10-20) and have a characteristic shape. They are bent at almost a right-angle at a third of their length, and are long and thin, such that their distal ends reach to the mouth opening. There are 8 to 10 hooks, clear amber in colour, the extremities of which are recurved. SEM studies of the teeth and hooks show: a) lamellar ornamentations and spines on the anterior teeth; b) spines and ribs on the posterior ones; and c) ribs on the hooks (Fig. 2). The vestibular organs are crest-shaped, showing a row of short papillae in the young specimens.

The lateral fins originate behind the ventral ganglion, at a distance equal to the length of the ganglion itself. They have an unusual shape, in that the anterior and posterior regions are well-developed, while the middle section is narrow. This certainly presages the total separation into anterior and posterior fins as found in *Sagitta* spp. The caudal fin is triangular in

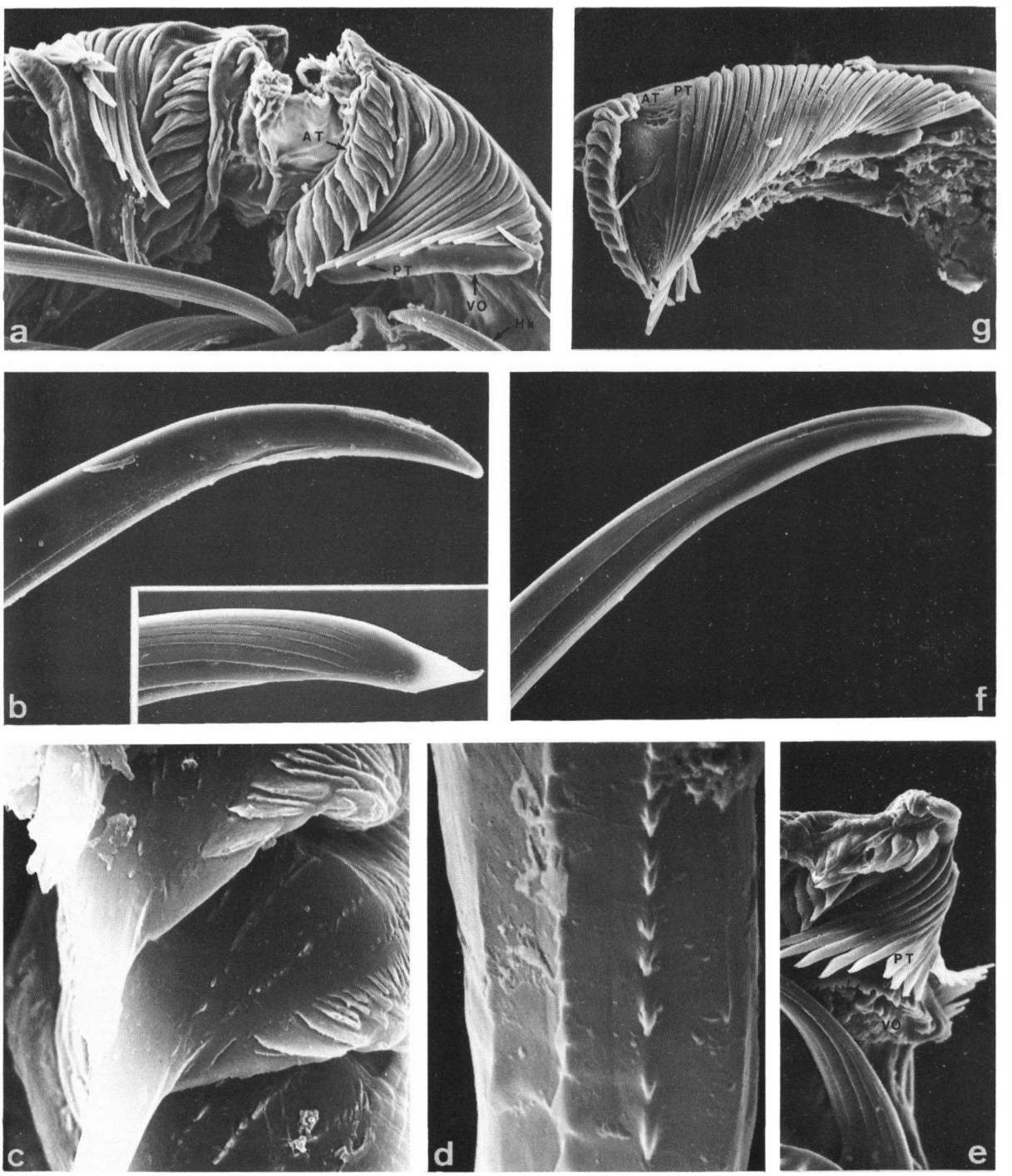

Fig. 2. S.E.M. photographs of the head armature of *Heterokrohnia mirabiloides* n.sp. (a-d) and *H. mirabilis* Ritter-Zahony, 1911 (e-g). a, anterior part of the head (ventral view), x130; b, anterior part of a hook (inset: tip of a newly formed hook), x 300; c and d, details of ornamentations on anterior and posterior teeth, x2000 and 6000 respectively; e, left side of anterior ventral part of head of a young specimen (recognizable by the small papillae on vestibular organs) showing the already numerous posterior teeth, x200; f, hook, x300; g, teeth, x150. Shrinkage after drying prevents a clear demonstration that the posterior teeth in *H. mirabiloides* are separated one from another (a). AT: anterior teeth, Hk: hooks, VO: vestibular organs.

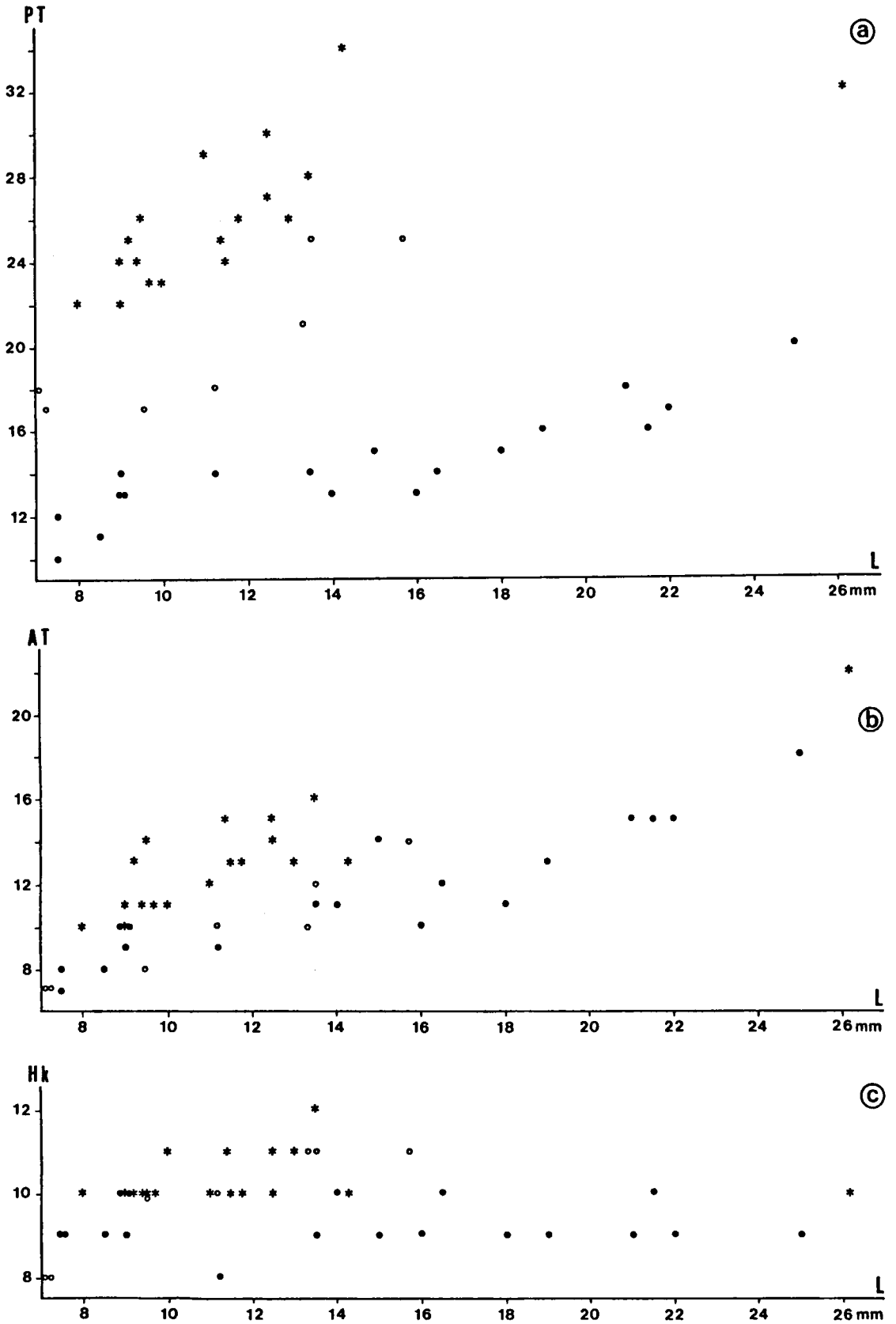

Fig. 3. Number of posterior teeth, PT (a), anterior teeth, AT (b) and hooks, Hk (c), of the three species of *Heterokrohnia* of the *"mirabilis"* group plotted against total length, L. *H. mirabiloides* (black dots), *H. mirabilis* (asterisks); data for *H. involucrum* (open circles) are those of Dawson (1968).

shape. All the fins are provided entirely with rays.

The anterior transverse musculature of the trunk starts at the neck and ends on a level with the origin of the lateral fins, thereby extending for about 45% of the length of the trunk. The transverse musculature of the tail segment represents from 17-19% of the total tail length.

Neither a collarette nor intestinal diverticula are present.

No specimens have mature ovaries, but a few slightly developed ovaries were noted. These were short (up to 3 mm in length), flattened and leaf-shaped; each opens at the apex of a body swelling. Ova are few, small, and aligned in a row. The annex gland, which connects the two ovaries and girdles the intestine ventrally, is clearly visible. In one specimen, the duct connecting each ovary to the corresponding coelomic caudal cavity contains spermatozoa, while the cavities themselves are filled with sperm. The seminal vesicles, which in the larger specimens are represented only by traces, are separated from both the lateral and caudal fins, and open laterally.

Comparisons with other species

Among all the known species of *Heterokrohnia, H. mirabiloides* is most closely related to *H. mirabilis* and *H. involucrum* Dawson, 1958, on the basis of the shape of the anterior teeth and lateral fins. These two characters distinguish these three from all other *Heterokrohnia* species, such that we can refer to a *"mirabilis"* group which recognizes the close affinities of its members, much the same as certain groupings in the genera *Sagitta, Eukrohnia* and *Spadella.*

In all three species the lateral fins originate behind the ventral ganglion, at a distance equal to the length of the ganglion, where the transverse musculature of the trunk ends. Thus, for this character, there is no difference between the species. This would appear to be at variance with the original description of *H. mirabilis,* as Ritter-Zahony (1911) illustrated the transverse musculature as extending beyond the ventral ganglion, while the lateral fins were shown to originate at the posterior end of the ganglion. However, a re-examination of the original material by Kapp (personal communication) confirms our observations.

The lack of a collarette in *H. mirabiloides* seems to distinguish this species from *H. involucrum,* which has a well-developed collarette extending from the neck to the end of the tail. However, often this tissue is very fragile and could have been lost during collection, as frequently happens with specimens of *H. curvichaeta* Casanova, 1986. However, if a collarette was present in *H. mirabiloides* one would have expected some trace of it in one of the 33 specimens observed, unless the benthic dredges damage specimens too much.

The examination of the cephalic armature shows that *H. mirabiloides* differs from the other two species (Fig. 3). This is best exemplified by the number of posterior teeth.

Since *H. mirabilis* also does not possess a collarette, we will consider in more detail how *H. mirabiloides* differs from it. The number and shape of the posterior teeth, as described above, is the best criterion by which the two species may be distinguished immediately. As regards the number of posterior teeth, in *H. mirabiloides* there are between 10 and 20 teeth, as compared with 22 to 34 in *H. mirabilis,* at the same total body length of > 7.5 - 8 mm. Usually, for equally sized animals, the latter species has more than twice the number of teeth than the former. *H. involucrum* occupies an intermediate position, having between 17 and 25 teeth. As regards the shape of the teeth, in *H. mirabiloides* they are strongly bent, thin and separated one from another, as is also the case in *H. murina* Casanova, 1986. This situation contrasts with that of *H. mirabilis,* where the teeth are almost straight, thinner and in close contact with each other. There is thus a possibility that young *H. mirabiloides* and *H. murina* (T.L. < 8 mm) can, on the basis of the posterior teeth, be confused. However, the anterior teeth of the former, which have not yet developed their characteristic triangular shape, are narrow, but definitely flattened, whereas those of the latter are clearly conical.

The anterior teeth in *H mirabiloides* are also less numerous than in *H. mirabilis,* as are the hooks (Fig. 3b, c), which vary in number from 8 to 10 in the former and from 10 to 12 in the latter. Their shapes also are different, being more hooked at their tips in the former (Fig. 2b, f). Finally, the musculature is thicker in *H. mirabiloides,* making anatomical observations

Table I Number of specimens of *Heterokrohnia mirabilis* and *H. mirabiloides* caught in different benthic and planktonic samples in the "Discovery" collections. The former are arranged in depth order.

Station	Date	Position	Depth (m)	Gear	*H. mirabilis*	*H. mirabiloides*
51403 # 1	25/3/82	51°37.7'N 12°59.8'W	1292-1314	BN1.5/3M	-	1
# 2	25/3/82	51°37.4'N 12°59.2'W	1317-1325	"	-	1
# 4	26/3/82	51°37.7'N 12°59.6'W	1319-1333	"	-	3
51420 # 1	2/4/82	51°37.3'N 12°58.6'W	1326-1328	"	-	11
9779	24/4/78	49°20.7'N 12°49.5'W	1398-1404	"	-	8
10112 # 3	10/9/79	50°19.9'N 13°26.9'W	2740-2755	"	1	-
10141 # 1	3/10/79	24°34.8'N 19°40.7'W	3460-3470	SBN	4	-
8976	5/8/76	32°54.4'N 11°38.5'W	3610-3646	BN2.4/5	4	7
10145 # 1	4/10/79	24°53.2'N 20°43.5'W	4250-4260	SBN	4	-
11262 # 15	10/7/85	31°13.2'N 25°03.9'W	5432-5432	BN1.5/3M	1	-
9541 # 22	20/4/77	20°12.5'N 21°37.7'W	3870-3740 (20-100 m.a.b.)	RMT1	3	-
9801 # 86	20/5/78	41°45.8'N 16°58.4'W	2900-3100	RMT1M/2	6	-
# 87	"	41°46.1'N 16°52.7'W	3100-3300	RMT1M/3	1	1
# 88	"	41°52.6'N 17°03.7'W	3700-3900	RMT1M/1	1	-
# 90	"	41°56.8'N 17°12.6'W	3300-3500	RMT1M/3	2	-
# 91	21/5/78	42°04.2'N 17°02.4'W	4300-4520	RMT1/M1	-	1
# 92	"	42°09.6'N 16°48.6'W	1610-4320	RMT1M/2	1	-
11121 # 20	4/6/84	41°36.0'N 21°43.9'W	4006-4021 (10-25 m.a.b.)	RMT1M/1	3	-
# 22	"	41°42.1'N 21°47.7'W	3976-3991 (40-55 m.a.b.)	RMT1M/3	1	-
# 23	5/6/84	41°22.5'N 21°44.3'W	4004-4021 (10-27 m.a.b.)	RMT1M/1	1	-

more difficult.

Many species have been confused under the name *H. mirabilis*. Ritter-Zahony (1911) in his description of that species produced a table showing the number of posterior teeth for his eight specimens, of which only the first three now are considered to belong to that species. Two of the others probably belong to *H. longidentata* Kapp & Hagen, 1985, as the latter authors discuss. As for the single specimen described as *H. mirabilis* by Tchindonova (1955), which came from the Kurile Trench, it is more likely to be *H. mirabiloides* on the basis of the number of teeth, although the number of hooks is a little high despite the large size of the specimen (36 mm). Casanova (1986a) also doubted this author's identification. In addition, of the two Antarctic specimens mentioned by David (1958) only the larger is *H. mirabilis* for, as the author himself admitted, the poor condition of the specimens made identification difficult. However, this larger specimen establishes the maximum size of *H. mirabilis* (33 mm) with certainty. Lastly, we note that Dawson (1968) also considered the possibility of confusion with *H. involucrum*: "since the main characteristic differentiating *H. involucrum* from *H. mirabilis* is the presence of a collarette, mishandled specimens [of *H. involucrum*] could be stripped of their collarette and consequently be identified as *H. mirabilis*.".

The main characters of the species of the *"mirabilis"* group are presented in Table II.

Ecology and speciation

Heterokrohnia species are known now to be deep benthopelagic animals (Casanova, 1986a; Casanova & Chidgey, 1987). It appears that the first species to be described, *H. mirabilis*, also is that which has the least association with the sea bed, since it is

Table II Diagnostic characters for the species of the genus *Heterokrohnia* of the *"mirabilis"* group.

	Heterokrohnia mirabilis Ritter-Zahony, 1911	*Heterokrohnia involucrum* Dawson, 1986	*Heterokrohnia mirabiloides* n.sp.
Total length	to 33 mm	to 15.7 mm	to 25 mm
Tail percentage	32.3 - 39.5%	31.6 - 38.9 %	29.6 - 40%
Beginning of lateral fins	behind ventral ganglion at a distance equal to the length of ventral ganglion	like *H. mirabilis*	like *H. mirabilis*
Anterior teeth	to 22, short and flat	to 14, like *H. mirabilis*	to 18, like *H. mirabilis*
Posterior teeth	to 34, almost straight, long and thin	to 25, like *H. mirabilis*	to 20, very bent, long and slightly thicker
Hooks	to 12, gently curved	to 11, like *H. mirabilis*	to 10, thicker and more curved
Vestibular organs	thick, smooth organs, juveniles with small papillae	?	like *H. mirabilis*
Collarette	absent	covering the whole body	absent (?)
Transverse musculature in trunk	reaching the level of the beginning of lateral fins	like *H. mirabilis*	like *H. mirabilis*

sometimes caught higher in the water column, although usually not far from the bottom. This association with the sea bed was suspected by Dawson who wrote: "All of the seven *Heterokrohnia mirabilis* were found in three bottom trawls ... pulled to the surface with the mouth of the net open, ... [thus although] *H. mirabilis* may have been collected in midwater ... their absence in plankton hauls suggests that they were collected at or very close to the bottom."

Examination of Table I reveals that there are differences in the bathymetric distribution of *H. mirabiloides* and *H. mirabilis.* Firstly, *H. mirabiloides* has been found at shallower depths than *H. mirabilis.* This is particularly evident in the samples from the epibenthic sledge hauls, where the former species is well represented (24 specimens) in five samples at depths between 1292 and 1404 m, whereas *H. mirabilis* has not been found in any hauls at depths less than 2740 m. However, a few specimens of *H. mirabiloides* have been found at greater depths (Table I), but only individual specimens have been found in two planktonic hauls (RMT1), one at ca. 2200 and the other at ca. 1000 m above the bottom. In contrast, the majority of the specimens of *H. mirabilis* have been caught within the water column (19 as against 14 in epibenthic sledge samples - Table I), at depths as far as 2600 m from the bottom. This would appear to indicate that this species is less constrained to a near-bottom existence than *H. mirabiloides.* Another indication for this is the fact that *H. mirabiloides* has been found only in epibenthic sledge hauls at depths of ca. 1300-1400 m, despite the large number of planktonic hauls carried out at similar depths and in similar areas.

Thus, it appears that we have another example of vertical segregation in congeneric species, as found in other groups of pelagic marine animals (e.g. Baker, 1970; Pugh, 1974; Angel, 1986). A similar situation has been described recently for two pairs of deep-living planktonic chaetognath species (Casanova, 1986b). He found that off the southern Atlantic coast of tropical Africa, *Eukrohnia hamata* and *E. bathy-*

pelagica are found below 150 m, whereas the related blind species, *E. macroneura* and *E. flaccicoeca,* which have evolved from the other two, live below 800-900 m.

Geographical distribution

Taking into account, on the one hand, the above remarks concerning the possibility of previous confusions in the identification of the species of the *"mirabilis"* group and, on the other hand, the paucity of sampling in the depths of the oceans, it is not surprising that the zoogeography of these species is little known. It appears that *H. mirabiloides* is not uncommon in the eastern Atlantic, and probably also has been found in the Kurile Trench, in the North pacific, as discussed above.

H. mirabilis has an extensive distribution. It is known with certainty from the Antarctic (Ritter-Zahony, David, op.cit.), the Arctic (Dawson, op.cit.), the Bermuda area of the western Atlantic (Pierrot-Bults, 1982) and off Cap Blanc (Mauritania) (Casanova, 1986a), where the present samples also show that it is common. It has also been mentioned from a station in the Pacific, off the Central American coast (Bieri, 1959).

The third species, *H. involucrum* has been described from 5 stations in the Arctic (Dawson, op.cit.).

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