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Archeterokrohnia Casanova, 1986, a junior synonym of *Heterokrohnia* Ritter-Záhony, 1911 (Chaetognatha), with a review of the species of *Heterokrohnia*

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ABSTRACT: The characters which have been advanced to separate *Archeterokrohnia* Casanova, 1986, from *Heterokrohnia* Ritter-Záhony, 1911, are discussed; they are considered to be insufficient to warrant the erection of a separate genus. A further argument against the separate status of *Archeterokrohnia* is the greater similarity of *Archeterokrohnia rubra* Casanova, 1986, to *Heterokrohnia longicaudata* Hagen & Kapp, 1986, than to *A. palpifera* Casanova, 1986. Various reasons are given for the retention of *H. longicaudata* in *Heterokrohnia* and against its transfer to *Archeterokrohnia*. The 13 species recognized and assigned to *Heterokrohnia* are reviewed; all characters used are tabulated and all species figured.

INTRODUCTION

When Casanova (1986a) described the new genus *Archeterokrohnia* Casanova, 1986, he noted that it was related to the genus *Heterokrohnia* Ritter-Záhony, 1911. Casanova pointed out three taxonomic characters separating *Archeterokrohnia* from *Heterokrohnia*. It will be shown that two of these do not belong exclusively to *Archeterokrohnia* and the third does not suffice to justify the erection of a new genus. Moreover, *A. rubra* Casanova, 1986, is more similar to *H. longicaudata* Hagen & Kapp, 1986, than to its congener *A. palpifera* Casanova, 1986. Therefore, it is here suggested to include *Archeterokrohnia* Casanova, 1986, in the genus *Heterokrohnia* Ritter-Záhony, 1911.

TAXONOMIC DISCUSSION

The characters differentiating *Archeterokrohnia* from *Heterokrohnia* are, according to Casanova (1986a), (1) the development (length) of the transverse trunk musculature,

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(2) the disposition (appearance) of muscle fibres, and (3) certain aspects (anatomy) of the genital apparatus.

(1) In *A. rubra* the transverse trunk musculature extends up to about 80 % of the trunk length (Casanova, 1986a), in *A. palpifera* up to about 90 % (Casanova, 1986c), whereas in most *Heterokrohnia* species it does not exceed two thirds of the trunk length (Ritter-Záhony, 1911; Marumo & Kitou, 1966; Dawson, 1968; Kapp & Hagen, 1985; Casanova, 1986b; Casanova & Chidgey, 1987); in *H. longicaudata* it also reaches 80 % of the trunk length (Hagen & Kapp, 1986). Thus, the character "length of transverse trunk musculature about 80 % of trunk length or more" is not restricted to *Archeterokrohnia* species, but being also present in the genus *Heterokrohnia* it cannot, therefore, be used as a character to differentiate between these genera.

(2) The appearance of the muscle bands which Casanova likened to those in the Thaliacea are not a genus-specific character of *Archeterokrohnia*, but a quite normal appearance of transverse musculature. I have observed such transverse musculature in *H. mirabilis* as well as in several *Eukrohnia* species.

(3) Casanova described two anatomical differences between the annex glands of *Archeterokrohnia* and *Heterokrohnia*. The annex glands are two symmetrical glands originating from the posterior inner part of each ovary, surrounding the intestine ventrally, and joining medio-ventrally (?) (Casanova, 1985). These glands are known to be present only in some *Heterokrohnia* species; their possible presence or absence and hence their structure in *A. palpifera* is not known, because the genital organs of Casanova's specimen were not developed. The joined annex glands of *A. rubra* possess a diverticle in the medio-ventral region, which is absent in *Heterokrohnia* species. The annex glands of *A. rubra* do not originate at the base of the ovaries, as they do in *Heterokrohnia*, but a short distance anteriorly. A third difference could be two swellings, one on each side of the annex glands. Casanova was not certain whether they were anatomical forms or only phases in the secretory cycle of these glands. Ventral ducts originating at the posterior inner ends of the ovaries, named annex glands by Casanova, are not restricted to the genus *Heterokrohnia*. Mawson (1944) reported tubes or ducts in several species of *Spadella*, which lead from each receptaculum seminalis. They pass the intestine ventrally just above the anus, end blindly at the mid-ventral mesentery or join one another, and they do or do not possess short anterior caeca (diverticula). Grassi (1883, in Ghirardelli, 1968) mentioned similar organs as ligaments in *Sagitta* species and I observed such ducts in several species of *Sagitta* and *Eukrohnia*. The described structural differences in the annex glands (place of attachment, diverticle, swellings) appear to be more of species-specific than of genus-specific quality; they are thus considered insufficient for the erection of a new genus.

Casanova (1986a) mentioned a possibly fourth difference between the genera *Archeterokrohnia* and *Heterokrohnia* in his description of *A. rubra*, namely, the position of the ventral ganglion on the posterior half of the trunk instead of on the anterior half as in *Heterokrohnia* and other genera. Since a ventral ganglion has not yet been detected in *A. palpifera* or in *H. longicaudata*, a comparison is not possible at the moment. However, this character may not be of great importance, because the position of the ventral ganglion does show some variability in *Heterokrohnia* species.

Another argument for including *Archeterokrohnia* in the genus *Heterokrohnia* is the similarity between *A. rubra* and *H. longicaudata* which is greater than that between *A.*

rubra and *A. palpifera* (Table 1). The similarities between the characters compiled for the two species, *A. rubra* and *H. longicaudata*, in no way allow the drawing of a line of separation at the genus level.

Hagen & Kapp (1986) placed *H. longicaudata* after careful consideration in the genus *Heterokrohnia*. The species has a number of features characteristic of this genus: transverse musculature in trunk and tail, absence of eyes, two rows of teeth, one pair of

Table 1. Similarities between *H. longicaudata*, *A. rubra*, and *A. palpifera*

	H. longicaudata	*A. rubra*	*A. palpifera*
Length of trunk transverse musculature	about 80 % of trunk	about 80 % of trunk	about 90 % of trunk
Beginning of lateral fins	a short distance above the trunk-tail septum	a short distance above the trunk-tail septum	at or just above the trunk-tail septum
Lateral fins	without fin rays (few delicate ones)	without fin rays (some fibrils near the body)	completely rayed
Tail fin	without fin rays (few delicate ones)	without fin rays	completely rayed
Length of tail fin attachment	about 33 % of tail	about 35 % of tail	less than 20 % of tail
Oesophagus	reaching beyond the neck, coloured dark red-orange	reaching beyond the neck, coloured brick-red	not reaching beyond the neck, not coloured
Teeth	two rows of teeth	two rows of teeth	one row of teeth
Seminal vesicles	elongated epidermal structures	elongated epidermal structures	not known

moderately elongated lateral fins; also its rayless lateral fins and tail fin are very similar to those of *H. longidentata*; and, finally, the structure of its seminal vesicles corresponds with those of *H. fragilis* and *H. longidentata*. The same arguments are true for *A. rubra* and for the most part also for *A. palpifera*. On the strength of these characters the separate status of the genus *Archeterokrohnia* cannot be maintained.

The possibility of an alternate classification was examined, namely to recognize the genus *Archeterokrohnia* containing the three species *rubra*, *palpifera*, and *longicaudata*. These species have in common a long tail and a transverse trunk musculature that is longer than in all other species of *Heterokrohnia*. However, if the differences and similarities of all structures of all species in the genus *Heterokrohnia* are considered (see Table 2 and Figs 1 and 2a, b, c), these two morphological differences are not deemed sufficient to justify the creation of a new genus.

CONCLUSION

It was shown that only the species-specific differences in the anatomy of the annex glands (though only from one species) are left of the taxonomic characters Casanova (1986a, 1986c) used to distinguish *Archeterokrohnia* from *Heterokrohnia*. Also *A. rubra* and *H. longicaudata* are too similar to be separated at the generic level. Therefore, I propose to unite the genus *Archeterokrohnia* Casanova, 1986, with *Heterokrohnia* Ritter-Záhony, 1911, whereby the name of the former becomes a junior subjective synonym of *Heterokrohnia*, and the two species *A. rubra* Casanova, 1986, and *A. palpifera* Casanova, 1986, become *H. rubra* (Casanova, 1986), and *H. palpifera* (Casanova, 1986).

REVIEW OF THE SPECIES OF *HETEROKROHNIA*

Table 2 contains information available for the characterization of the species of *Heterokrohnia*. A total of 13 species is recognized. *H. mirabiloides* (Casanova & Chidgey, 1990) is considered to be synonymous with *H. mirabilis* (Kapp, 1991, this volume); *Archeterokrohnia palpifera* (Casanova, 1986c) and *A. rubra* (Casanova, 1986a) were transferred to *Heterokrohnia* (Kapp, present paper).

The information presented in Table 2 and Figures 1 and 2a, b, c may give the impression that the knowledge about the features listed and drawn is substantiated, but this is not true in all cases; therefore, the table and figures require some comments.

The structure of the seminal vesicles (elongate epidermal structure) of most species is not clear. Probably they are oval, slightly vaulted organs with vasa deferentia entering at their tops. Also the size and exact shape of the ovaries of most species are unknown, because most *Heterokrohnia* specimens found as yet are immature.

The exact contours of the lateral fins and the tail fin are not always known. It was recently recognized that the presence or absence of finrays is not an absolutely clear taxonomic character (see Kapp, 1991, this volume).

An illustration of the teeth of *H. involucrum* is not available, but Dawson (1968) described the teeth of *H. involucrum* as having the same form as *H. mirabilis* (Fig. 2a).

I examined the type specimens of seven species of *Heterokrohnia* described by Casanova (1986a, b, c) and Casanova & Chidgey (1987) at their depository, the Musée National d'Histoire Naturelle, Paris. There are some differences between Casanova's and my observations. In some specimens, not all organs were visible because of the strong and completely non-transparent musculature. This is especially true for the organs called annex glands by Casanova and the ducts connecting the annex glands to the tail cavities. In some cases, I could see the beginning of ducts at the inner posterior part of the ovaries (so, only the beginnings of these ducts were drawn).

I could not find the plates with a minutely dentated margin nor the posterior teeth nor the row of teeth on the palps which Casanova described for *H. palpifera*. Unfortunately, the small, easily destroyed, delicate type specimen did not permit much handling. Therefore, I give two drawings of the anterior part of the head (Fig. 2c), one after Casanova (1986c) and one of my own. Instead of teeth, I observed a number of roundish structures spread over the entire surface of the anterior part of the palps.

In the neck region of *H. rubra* I found, beside the transverse muscles, an almost wing-shaped structure on either side which I regard as muscles; they are perhaps necessary to bear the unusually large head of *H. rubra*.

Details taken from Casanova's descriptions are marked with asterisks in Table 2.

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Table 2. Taxonomic characters of the species of the genus *Heterokrohnia*

	Heterokrohnia bathybia Marumo & Kitou, 1966	*Heterokrohnia curvichaeta* Casanova, 1986	*Heterokrohnia davidi* Casanova, 1986	*Heterokrohnia fragilis* Kapp & Hagen, 1985
Habitus	stiff, opaque	slender, opaque	opaque	slender, translucent
Total length	up to 14.6 mm	up to 10.8 mm	up to 30.6 mm	up to 8.7 mm
Tail length	34–39 % of total length	43–44 % of total length	39–46 % of total length	34–38 % of total length
Lateral fins	rayed, beginning at a short distance below ventral ganglion	with some isolated rays, beginning about 1 ventral ganglion length below v.g.	rayless, beginning near end of ventral ganglion	rayed, beginning just below ventral ganglion
Tail fin	rayed, spade-shaped	only remnants present	rayless, oval	rayed, spade-shaped
Head	large	small, pear-shaped	large	
Apical gland cell complex	present	present	present	large
Knobs/plates				
Anterior teeth	up to 7, short and thick	up to 4, long, strong	9–12, short, conical	up to 5, small
Posterior teeth	up to 7, short and thick	3, small, distant from each other	11–16, long, slender	1 or absent
Hooks	up to 12, curved	6, strongly curved, amber-coloured	12–14, light brown	up to 9, juveniles up to 12, tips knee-shaped
Vestibular organs	swollen, with notches or large processes like prickly pears	slightly pronounced with small papillae	of irregular form (see drawing)	with long papillae
Corona ciliata	not observed	not observed	not observed	not observed
Neck canals	at both sides of neck	not observed	not observed	not observed
Alveolar tissue	on neck region	* 2 large cells (might be remains)	not observed	not observed

Transverse trunk musculature	extending to slightly below ventral ganglion	extending to middle of ventral ganglion	about two thirds of trunk length	extending to slightly beyond ventral ganglion
Transverse tail musculature	anterior quarter of tail	about anterior 15 % of tail	about anterior 20 % of tail	about anterior 20 % of tail
Oesophagus	see drawing			
Intestine	brick red			opaque
Ovaries	extending almost to ventral ganglion	very voluminous	nearly reaching ventral ganglion, slender	ovae smaller in anterior end than in basis
Seminal vesicles	remnants, touching lateral and tail fin	* elongated epidermal structures	elongated epidermal structures	elongated epidermal structures
Annex glands			* present and canal connecting a.g. and caudal coelom cavities	
Area of finding	Western North Pacific	Eastern North Atlantic	Eastern North Atlantic	Antarctic Ocean (Indian and Atlantic Sector)

Abbreviations: a.g. annex glands; v.g. ventral ganglion

Table 2 (continued)

	Heterokrohnia furnestinae Casanova & Chidgey, 1987	*Heterokrohnia heterodonta* Casanova, 1986	*Heterokrohnia involucrum* Dawson, 1968	*Heterokrohnia longicaudata* Hagen & Kapp, 1986
Habitus	strong	strong, opaque	more transparent than H. mirabilis	firm, opaque, skin transparent
Total length	up to 34 mm	up to 20 mm	up to 15.7 mm	up to 12.9 mm
Tail length	30–35 % of total length	43 % of total length	32–39 % of total length	56 % of total length
Lateral fins	rayed, beginning about 1 ventral ganglion length below v.g.	rayed, beginning about 1 ventral ganglion length below v.g.	rayed, beginning a little below ventral ganglion, narrower in the anterior third	with few isolated rays, beginning slightly above trunk-tail septum
Tail fin	rayed, spade-shaped	rayed, oval	rayed, spade-shaped	with few isolated rays, oval
Head				
Apical gland cell complex	present	present	gland reservoir at tip of head	present
Knobs/plates				
Anterior teeth	1–4, or absent, very small	4–7, very short, flat, beset with tiny teeth	up to 14, short, flat, like *H. mirabilis*	6–8, conical with broad base
Posterior teeth	5–11, long and thin	5–6, long, bent, anterior part beset with tiny teeth	up to 25, long, thin, like *H. mirabilis*	1, conical
Hooks	up to 14, inner edge with tiny serration	10–13, light brown	up to 11, like *H. mirabilis*	17–18, curved, slender, brownish
Vestibular organs	2 connected ridges, V-shaped, posterior one of irregular form (see drawing)	of irregular form, see drawing * 2 rows in juveniles		crescent-shaped with small, heterogeneously distributed papillae

Corona ciliata	not observed	not observed	on head and trunk	not observed
Neck canals	• in neck region, within alveolar tissue	not observed	at dorso-lateral margin of head	absent
Alveolar tissue	covering the whole body, similar to *H. involucrum*	absent	covering the whole body, well-developed on trunk and anterior tail segment	not observed
Transverse trunk musculature	extending to slightly below ventral ganglion	extending to lateral fins	extending to the anterior edge of lateral fins	about 80 % of trunk length
Transverse tail musculature	about anterior 30 % of tail	about anterior quarter of tail	about anterior third of tail	about anterior 11 % of tail
Oesophagus				elongated, dark orange-red
Intestine				voluminous, grey-yellow
Ovaries	not mature	slightly developed	immature	cob-shaped, numerous ovae of different size
Seminal vesicles	with oval basis distant from lateral fins, touching tail fin	elongated epidermal structures		elongated epidermal structures
Annex glands	• thicker at basis of ovaries, short canals connecting ovaries and tail coelom cavities	• present		absent
Area of finding	Eastern North Atlantic	Eastern North Atlantic	Arctic Ocean (Canada Basin)	Antarctic Ocean (Atlantic Sector)

Table 2 (continued)

	Heterokrohnia longidentata Kapp & Hagen, 1985	*Heterokrohnia mirabilis* Ritter-Záhony, 1911	*Heterokrohnia murina* Casanova, 1986	*Heterokrohnia palpifera* (Casanova, 1986)	*Heterokrohnia rubra* (Casanova, 1986)
Habitus	transparent	firm, transparent	opaque		
Total length	up to 12.2 mm	up to 33 mm	up to 38.5 mm	up to 7.1 mm	up to 22.5 mm
Tail length	36–41 % of total length	30–42 % of total length	28–42 % of total length	55 % of total length	50–52 % of total length
Lateral fins	rayless, with a few incomplete rays, with fine fibrils, beginning a little below ventral ganglion	rayed, with few rays, or rayless, beginning slightly below ventral ganglion, narrower in anterior part	incomplete rays in posterior part, beginning more than 1 ventral ganglion length below v.g.	completely rayed, beginning at trunk-tail septum	rayless, some fibrils near body, beginning about 1/2 ventral ganglion length below v.g.
Tail fin	rayless or with a few rays, with fine fibrils, fringe-shaped	rayed, with few rays, or rayless, spade-shaped	with incomplete rays, oval	rayed, fringe-shaped	rayless, oval
Head			apical part prolonged		large, broad
Apical gland cell complex	present or absent	present, small	present	slightly developed	present
Knobs/plates	up to 5 knobs			* 1 pair of plates with finely serrated margin	
Anterior teeth	absent	up to 17, short, flat	8–11, conical, bent	absent	4–12, conical, bent
Posterior teeth	up to 5, long	up to 35, long, partly bent	15–24, long, bent	* 5–6, small, short	2–8, bent, distant from each other
Hooks	up to 13, gently curved	up to 12, gently curved	12–14, dark brown	up to 18	12–15
Vestibular organs	collarlike structures with long papillae, a second row of small papillae	thick, with very small papillae	ridges with small papillae	vestigial, 1 pair of palps below, with * short conical teeth or other structures	2 pairs, anterior one with small papillae, posterior one vestigial

Corona ciliata	not observed	not observed	not observed	not observed	not observed
Neck canals	absent	in head and anterior trunk	not observed	not observed	not observed
Alveolar tissue	absent	on neck region	absent	not observed	not observed
Transverse trunk musculature	extending to end of ventral ganglion	reaching a little below ventral ganglion	extending to slightly below ventral ganglion	about 90 % of trunk length	about 80 % of trunk length
Transverse tail musculature	about anterior 20 % of tail	about anterior third of tail	in anterior quarter of tail	about anterior 16 % of tail	about anterior 13 % of tail
Oesophagus		elongated			elongated, brick-red
Intestine		orange-red			
Ovaries	club-shaped not fully mature	about a third of trunk length, ending in little bags	short, small ovae	not developed,	not mature
Seminal vesicles	elongated epidermal structures, slightly distant from lateral fins	slightly distant from lateral and tail fin, opening at mid-region	elongated epidermal structures	basis just below lateral fins	elongated epidermal structures
Annex glands	absent	ducts from basis of ovaries	• present; canals connecting ovaries with tail coelom cavities		originating a short distance above the end of the ovaries, • with a diverticle and 2 swellings
Area of finding	Antarctic Ocean (Indian and Atlantic Sector)	Antarctic Ocean (Indian and Atlantic Sector) Tropical East Pacific Atlantic (near Bermuda, Greenland Sea)	Eastern North Atlantic	Mediterranean (near Corsica)	Eastern North Atlantic

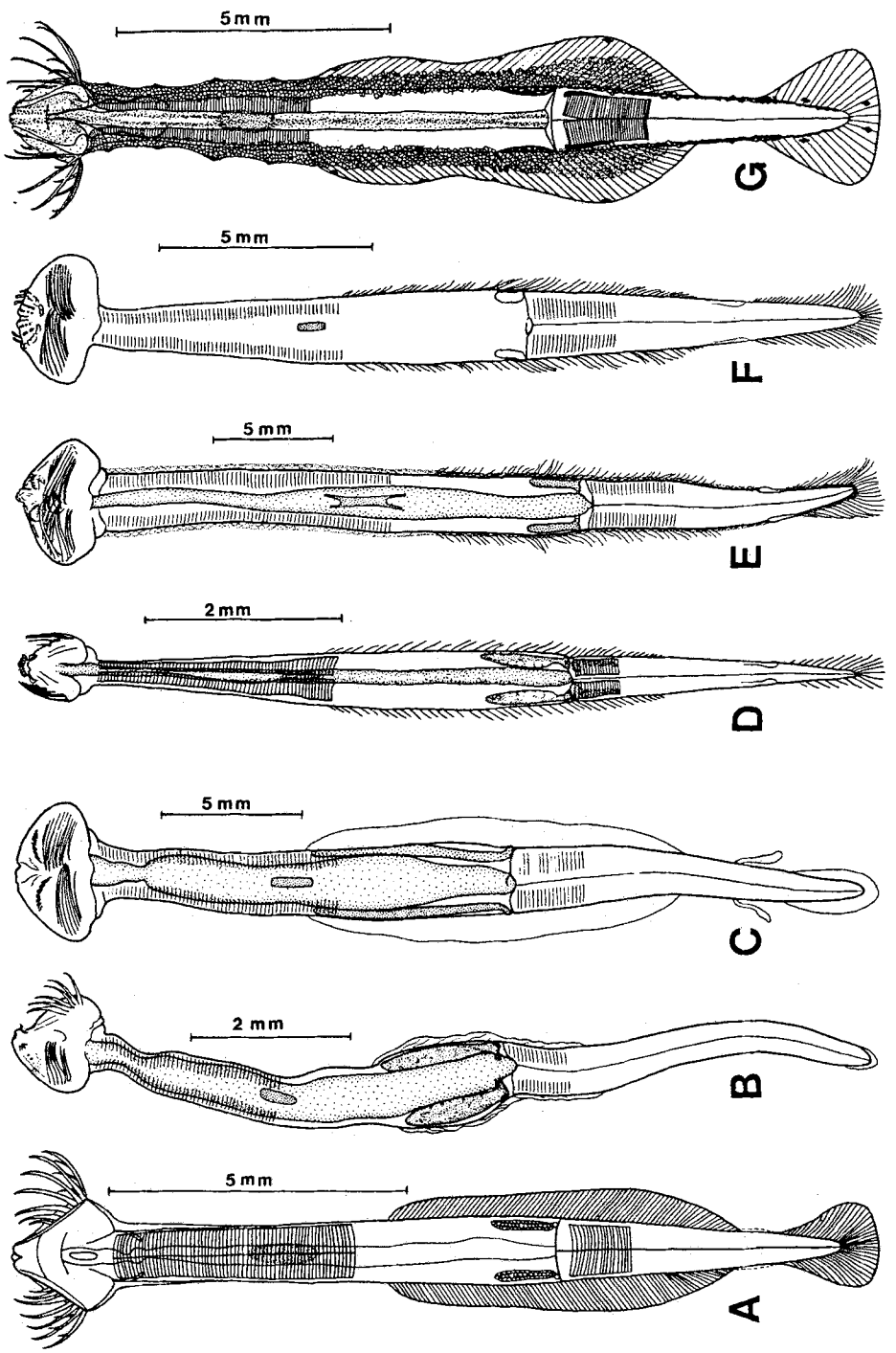

Fig. 1. Species of the genus *Heterokrohnia*, ventral view, if not indicated otherwise. A: *H. bathybia* Marumo & Kitou, 1966 (modified after Marumo & Kitou, 1966; dorsal view). B: *H. curvichaeta* Casanova, 1986. C: *H. davidi* Casanova, 1986. D: *H. fragilis* Kapp & Hagen, 1985 (dorsal view). E: *H. furnestinae* Casanova & Chidgey, 1987. F: *H. heterodonta* Casanova, 1986. G: *H. involucrum* Dawson, 1968 (modified after Dawson, 1968; dorsal view)

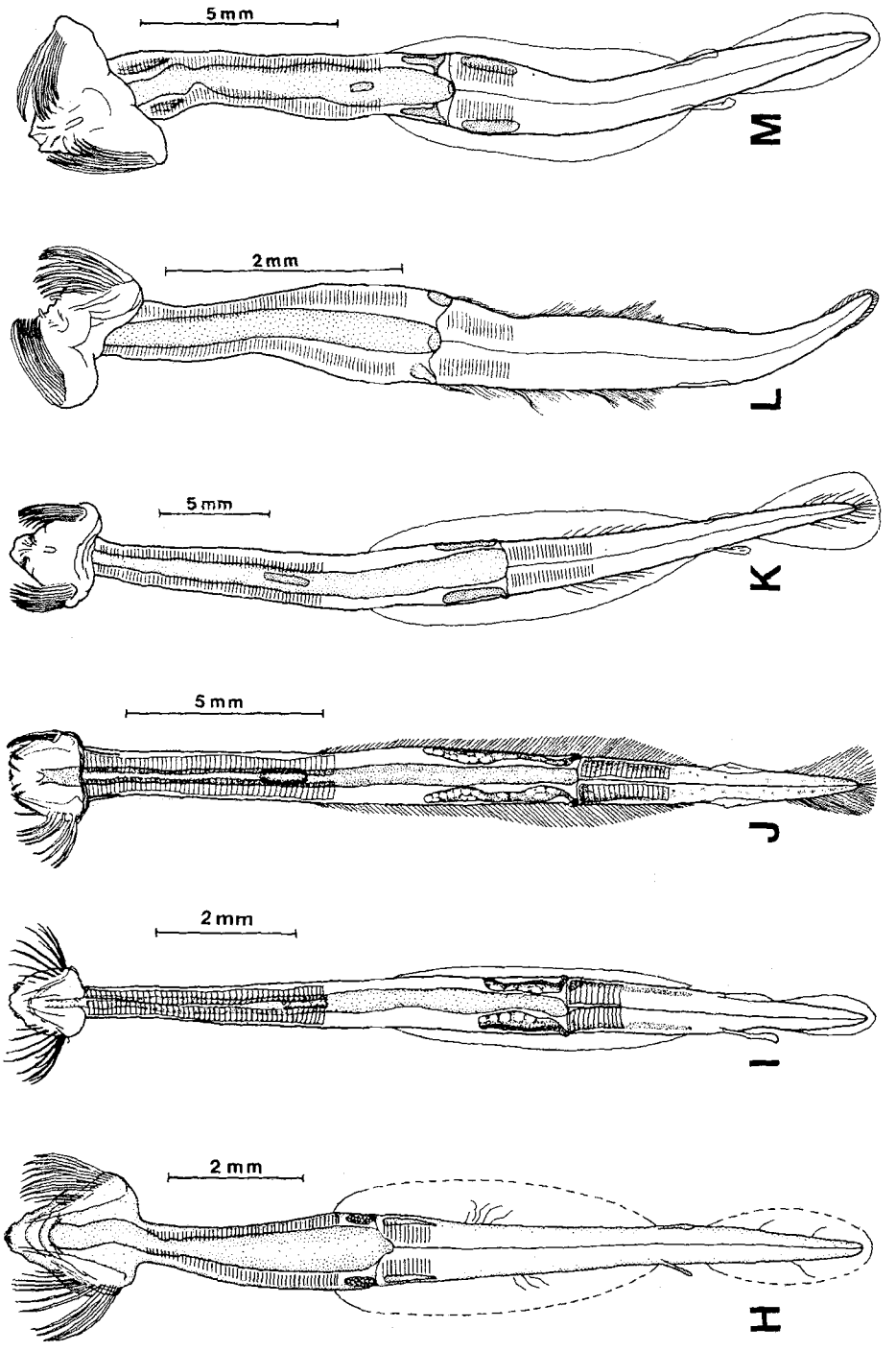

Fig. 1 (continued). H: *H. longicaudata* Hagen & Kapp, 1986 (dorsal view). I: *H. longidentata* Kapp & Hagen, 1985 (dorsal view). J: *H. mirabilis* Ritter-Záhony, 1911. K: *H. murina* Casanova, 1986. L: *H. palpifera* (Casanova, 1986). M: *H. rubra* (Casanova, 1986)

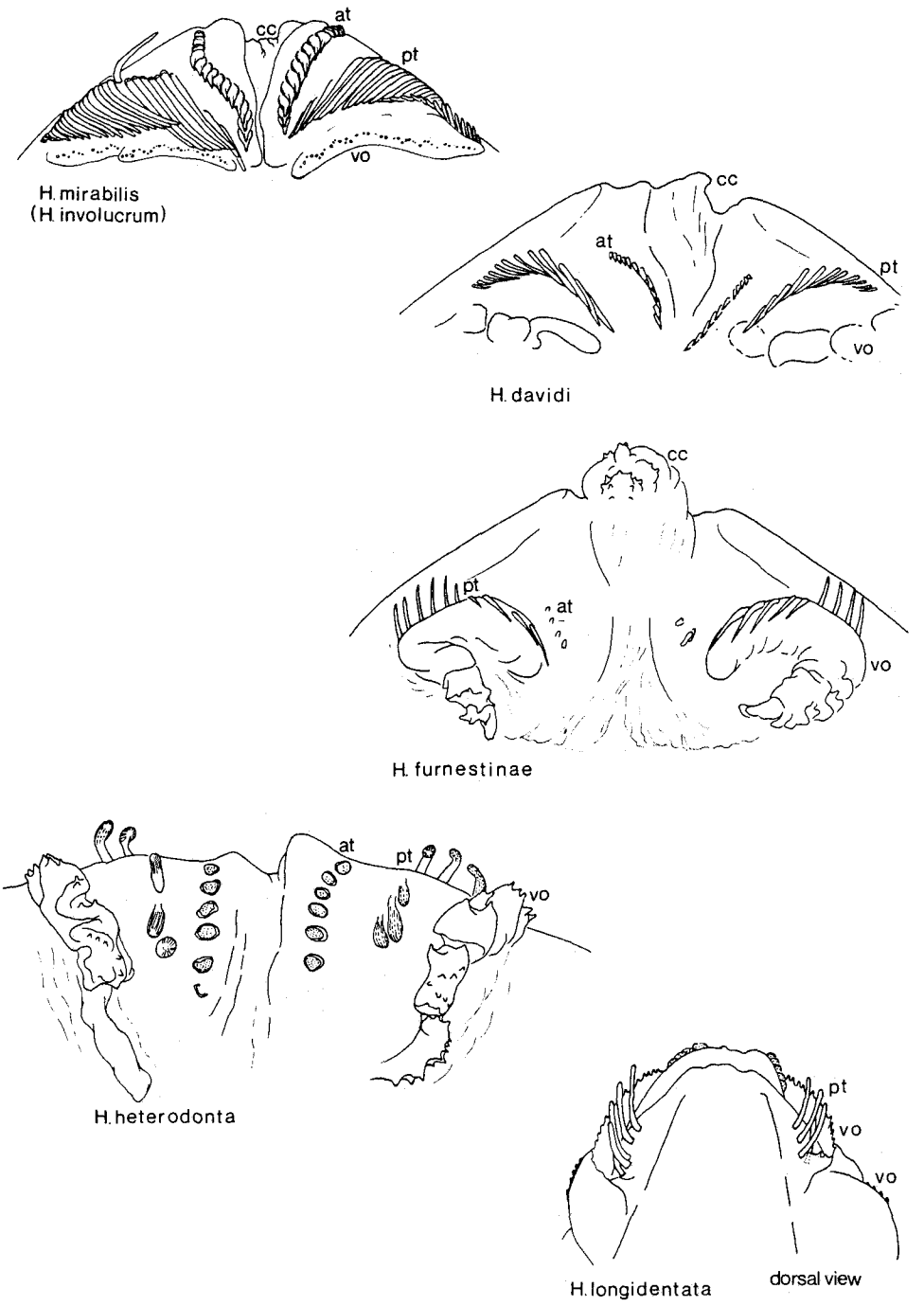

Fig. 2a. Different head armatures of *Heterokrohnia* species, ventral view, if not indicated otherwise. Abbreviations see Fig. 2c

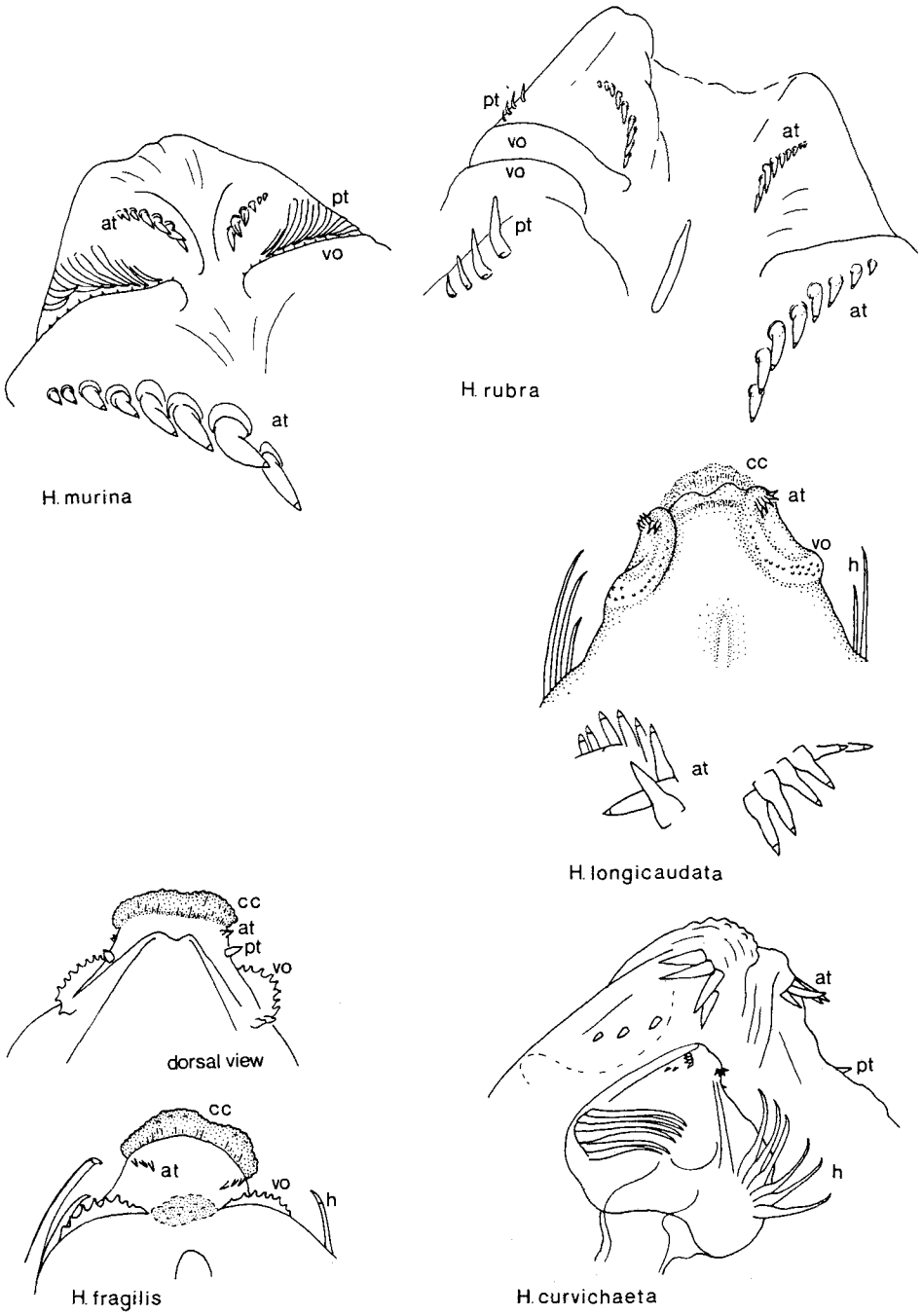

Fig. 2b. Different head armatures of *Heterokrohnia* species, ventral view, if not indicated otherwise, and details of anterior or posterior teeth of *H. murina*, *H. rubra*, and *H. longicaudata*. Abbreviations see Fig. 2c

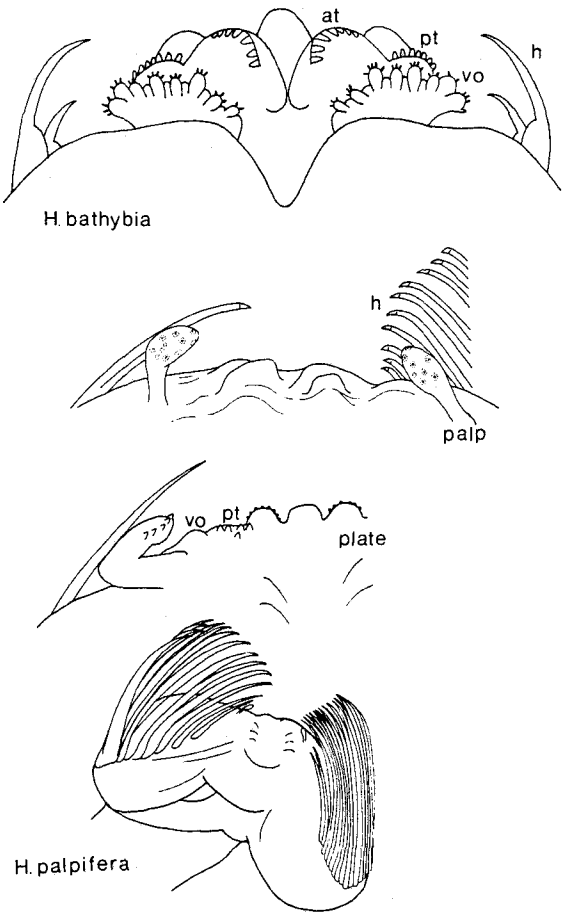

Fig. 2c. Different head armatures of *Heterokrohnia* species, ventral view. *H. bathybia*: modified after Marumo & Kitou (1966). *H. palpifera*: middle figure modified after Casanova (1986c), for further explanations see text. at = anterior teeth, cc = apical gland cell complex, h = hooks, pt = posterior teeth, vo = vestibular organs