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Redescription and systematic discussion of *Amphiporus heterophthalmus* (Schmarda, 1859)

(Nemertea, Hoplonemertea, Monostilifera)

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The type material of *Amphiporus heterophthalmus* (Schmarda, 1859) is redescribed and illustrated. A reassessment of the classificatory status of the species indicates that *Amphiporus heterophthalmus* (Schmarda, 1859) should be transferred to the genus *Ischyronemertes* Gibson, 1990 as *I. heterophthalma* (Schmarda, 1859), comb. nov.

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Introduction

Schmarda (1859) described 17 new nemertean species. Since then only three of these species, *Emplectonema ophioccephala* (Schmarda, 1859), *Lineopsella trilineata* (Schmarda, 1859) and *Lineus atrocaeruleus* (Schmarda, 1859), became redescribed (see Wheeler 1934, Sánchez & Moretto 1984, Senz 1996a). Redescriptions of *Borlasia bilineata* Schmarda, 1859, *Lineus collaris* (Schmarda, 1859) and *Lineus schmardai* (Bürger, 1904) (= *Meckelia striata* Schmarda, 1859) will be provided by the author in a separate paper. The internal morphology of the remaining species remains unknown. Hence, from a modern point of view, these species cannot be classified in a satisfying way. In the present paper one of these species, *Amphiporus heterophthalmus* (Schmarda, 1859), is redescribed based on the type material.

Material and methods

The study is based on three complete specimens and the anterior fragments of two additional specimens. One of the complete specimens was fully sectioned, but only the anterior region of one of the other complete specimens was examined. The anterior fragments were completely sectioned. One of these fragments was longitudinally sectioned. The remaining series of sections are transverse sections. The material was embedded in 56° m.p., sectioned at 10 µm and stained by the Kernechtrot Pikroindigokarmin method.

Ischyronemertes heterophthalma (Schmarda, 1859), comb. nov.

Material examined: The study is based upon the syntypes deposited in the Naturhistorisches Museum in Wien: NHMW-EV 5179/3559, NHMW-EV 3560, NHMW-EV 3561, NHMW-EV 2562, NHMW-EV 16710.

External appearance. See Systematic discussion for original description by Schmarda (1859).

Body wall. The epidermis shows a typical hoplonemertean construction. Below it the dermis forms a well developed layer.

The body wall musculature is well developed, with outer circular, diagonal, longitudinal and inner circular muscle layer (Figs 1-4). The outer circular layer is as thick as the dermis. The diagonal musculature is a delicate layer. The longitudinal muscle layer is nowhere split. In front of the brain the major part of the longitudinal muscle layer bends inward to form the precerebral septum and the roots of the cephalic retractor muscles (Fig. 7). The remaining part of the longitudinal muscle layer reaches near the tip of the head as a thin layer. In the brain area and stomach area the inner circular muscle layer is well developed, forming a ventral and a dorsal plate, laterally interconnected by a meshwork of muscle fibres (Figs 1, 2). Several of these fibres correspond to dorsoventral muscles. The same arrangement occurs in the remaining foregut area and in the midgut area, although the inner circular muscle plates become incomplete and the dorsoventral muscles become well developed (Fig. 3).

Next to the rhynchocoel wall the inner circular muscle layer and the dorsoventral muscles cannot be separated from the rhynchocoelic circular musculature (Fig. 5; see also Systematic discussion).

Alimentary tract. The tubular oesophagus opens from the rhynchodaeum in the middle of the preseptal area. Its non-ciliary epithelium contains mucous cells. Behind the ventral commissure of the brain the oesophagus widens into the voluminous stomach. The stomach possesses deeply folded walls (Fig. 1). The stomach epithelium has a uniform construction throughout. Posteriorly the stomach continuously transforms into the long pylorus (Fig. 3). Some longitudinal muscle fibres lie adjacent to the oesophagus, stomach and anterior most part of the pyloric tube. In the postseptal area, the foregut is lined by dorsoventral muscles. Partly, these muscles are modified, forming an incomplete, weakly developed foregut circular musculature.

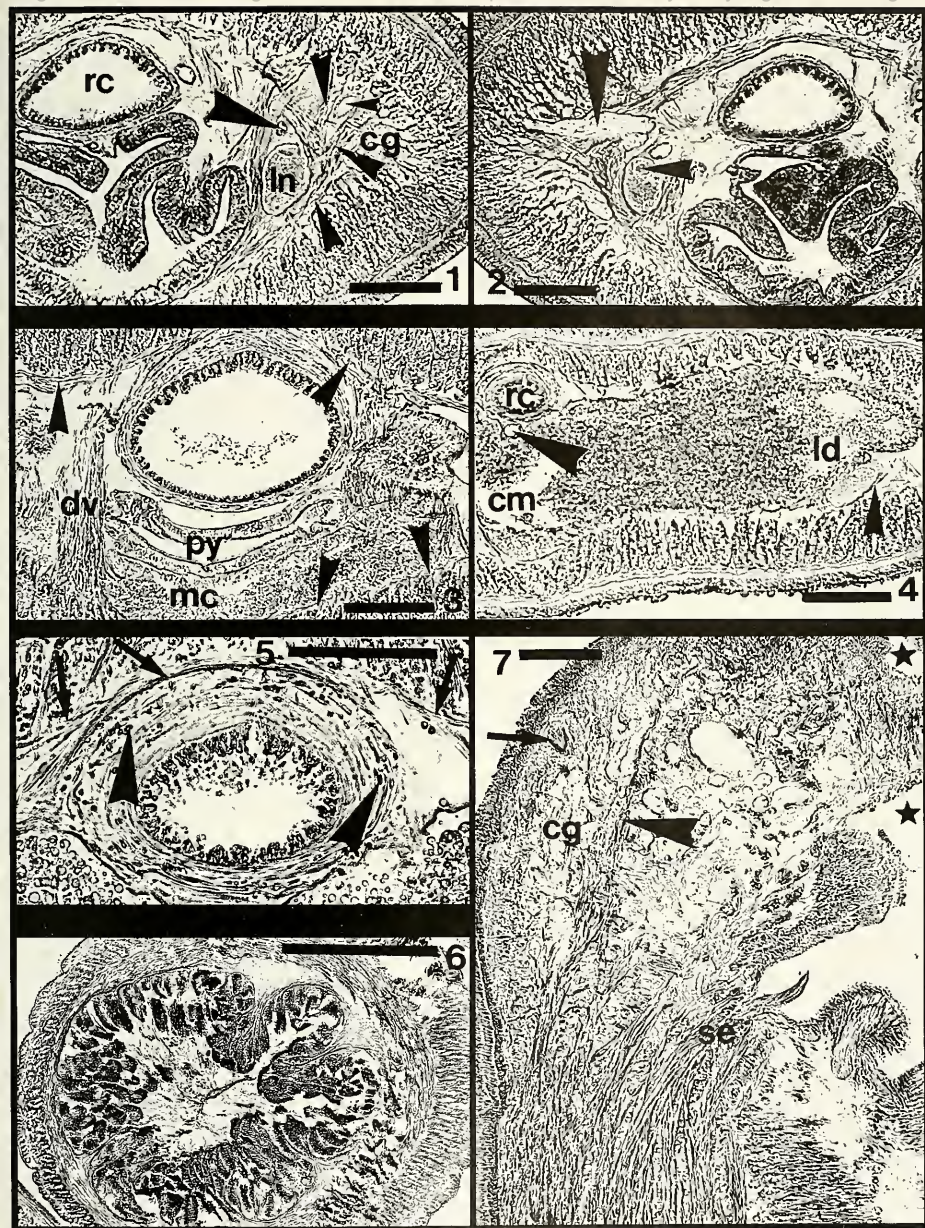
Posteriorly the pylorus opens into the dorsal wall of the midgut (Fig. 3). Hence a midgut caecum is formed. It is restricted to the posterior quarter of the pyloric area. The caecum ends in a long pair of terminal diverticula. These reach forwards into the stomach area, without reaching the brain. Lateral diverticula are absent. The lateral wall of the midgut caecum and the terminal diverticula is folded. These folds are associated with dorsoventral muscles. The main intestinal canal possesses deep lateral diverticula (Fig. 4).

Proboscis apparatus. The subterminal proboscis pore leads into a thin-walled rhynchodaeum the epithelium of which is neither ciliated nor glandular. Anteriorly to the oesophageal opening the rhynchodaeum is lined by an extremely delicate circular musculature. Behind the oesophageal opening this musculature becomes stronger. In front of the proboscis insertion it forms a muscular sphincter. The precerebral septum is closed. Several muscle fibres belonging to the septum extend anteriorly into the posterior preseptal area, forming a meshwork. This meshwork is traversed by the anterior most fibres of the inner circular muscle layer of the body wall.

The rhynchocoel extends backwards into the posterior half of the body, but does not reach the posterior end of the body by far. The rhynchocoel wall consists of a circular and longitudinal muscle layer, separated by a delicate connective tissue layer. The circular muscle layer is intermingled with several longitudinal muscle fibres (Fig. 5). In the posterior part of the rhynchocoel these fibres are somewhat more abundant. Several of the circular muscle fibres, intermingled with longitudinal muscle fibres, belong to the inner circular muscle layer of the body wall (see also above and Systematic discussion). Diverticula of the rhynchocoel are not present.

The proboscis shows a typical monostiliferous construction (see Senz, 1993a, for the use of the term 'monostiliferous'). Its anterior area, about 0.7 mm in overall diameter, contains three muscle layers (outer and inner circular, middle longitudinal) and about 20 proboscis nerves (Fig. 6). The middle part of the proboscis consists of the stylet apparatus bearing part and the muscle bulb, both separated by the diaphragm. The armature consists of a single stylet (shape: nail-like; surface: smooth; length:

Figs 1-7. *Ischyronemertes heterophthalma* (Schmarda, 1859), comb. nov. 1. Transverse section through the anterior stomach area; scale: 0.2 mm; cg: cephalic gland, ln: lateral nerve cord, rc: rhynchocoel, st: stomach, small arrow head: excretory tube, middle arrow heads: lateral meshwork of the inner circular musculature of the body wall, large arrows: vascular vessel. 2. Transverse section through the posterior stomach area; scale: 0.2 mm; small arrow head: accessory nerve of the lateral nerve cord, large arrow head: cephalic gland lobe. 3. Transverse section through the pyloric area; scale: 0.2 mm; dv: dorsoventral muscle, mc: midgut caecum, py: pylorus, arrow heads: inner circular muscle layer of the body wall. 4. Transverse section through the midgut area; scale: 0.2 mm; cm: central canal of the midgut, ld: lateral diverticulum of the midgut, rc: rhynchocoel, small arrow head:



inner circular muscle layer, large arrow head: dorsal vascular vessel. 5. Transverse section through the rhynchoceol; scale: 0.1 mm; arrow heads: longitudinal muscle fibres intermingled with the circular musculature enveloping the rhynchoceol wall, arrows: inner circular muscle layer of the body wall. 6. Transverse section through the anterior part of the proboscis; scale: 0.2 mm. 7. Longitudinal section through the anterior end of the body; scale: 0.2 mm. cg: cephalic gland, se: septum, asterix: rhynhodaedal tube, arrow: ocellus, arrow head: cephalic retractor muscle.

$\pm 125 \mu\text{m}$). It is mounted on a slightly conical basis (length: $\pm 80 \mu\text{m}$; diameter at the anterior end: $\pm 30 \mu\text{m}$; diameter at the posterior end: $\pm 37 \mu\text{m}$). Two reserve stylet pouches are present. The posterior part of the proboscis is longer than the anterior one and posteriorly connected to a retractor muscle.

Zentralraum-organisation and mesenchymate tissue. An open 'Zentralraum' is present, associated with voluminous ledges in the midgut area (for terminology see Senz 1995). In the stomach area the lateral meshwork of the inner circular muscle layer fibres is embedded in well developed amounts of mesenchymate tissue (Figs 1-3). In the midgut area considerable amounts of mesenchymate tissue are present in the lateral area of the ledges only.

Nervous system. The brain is enveloped by a thick outer neurilemma. The inner neurilemma is absent. In front of the commissures each half of the brain contains a fibrous core, dorsally, laterally and ventrally enveloped by ganglionic cells. Posteriorly the fibrous core enlarges, forming the thick ventral commissure. The dorsal commissure is much thinner than the ventral commissure. Behind the commissures the dorsal and ventral brain lobes start separating from each other. Just before separation is finished, a thin nerve leaves the dorsal lobe and enters the ventral one. In the lateral nerve cord, this nerve becomes the accessory nerve (Fig. 2). It is restricted to the foregut area (extending into the anterior most part of the midgut area). The lateral nerve cords have a posterior origin from the ventral brain lobes. They possess neither an inner neurilemma nor neurochords but contain side stem muscle fibres. The lateral nerve cords lie proximally to the inner circular muscle layer (Figs 1, 2, 4).

Sense organs. The ocelli show a regular pigment cup construction (Fig. 7) (for arrangement see below). The cerebral organs have a typical monostiliferous organisation and lie well in front of the precerebral septum (position somewhat variable due to contraction). The cerebral organ proper is enveloped by a delicate connective tissue layer only. Hence the shape of the organ also depends on the degree of contraction. However, the glandular part dominates in the anterior area of the organ, the ganglionic part in the posterior area. The short canals of the cerebral organs open into oblique epidermal furrows.

Cephalic gland, cephalic musculature and frontal organ. The frontal organ is a small pit opening into the dorsal wall of the rhynchodaeum, near its opening to the exterior.

The cephalic gland, it consists of typical basophilic lobules, is by far the dominating organ in the preseptal area. Behind the septum it extends to the posterior end of the foregut in a lateral position (Figs 1, 2). Typically the postseptal part of the cephalic gland lies distally to the lateral meshwork of the inner circular muscle layer. Exceptionally it extends proximal of this meshwork (Fig. 2).

In the preseptal area the lobules of the cephalic gland are intermingled with the anterior cephalic musculature. This musculature is a derivative of the body wall and rhynchodaeal musculature (see Senz 1993b). Several of its fibres form an incomplete circular musculature enveloping the proximal part of the cephalic gland and the rhynchodaeum. Occasionally this musculature is in direct contact with the rhynchodaeal circular musculature proper.

Vascular apparatus. The vascular apparatus has a typical monostiliferous construction. Characters of particular interest are: no extra cerebral vessels are present; the mid-dorsal vessel emerges from the right lateral vessel and lacks a vascular plug; numerous valves are present; throughout the midgut area there are commissures between the longitudinal vessels. In the foregut area the lateral vessels lie proximally to or within the lateral meshwork of the inner circular muscle layer (Figs 1, 2).

Excretory apparatus. The excretory apparatus extends from immediately behind the brain to the posterior end of the foregut area. Most of the collecting tubules lie distally to the lateral meshwork of the inner circular muscle layer (Fig. 1). They show no regional differentiation (diameter somewhat variable). The single pair of efferent ducts lies in the stomach area. The nephridiopores have a dorsolateral position.

Reproductive apparatus. One of the specimens examined histologically is a male. The testes are small and no gonoducts are present. They are distributed dorsally, laterally and ventrally to the lateral midgut diverticula. The anterior most gonads occur in the posterior foregut area. The remaining specimens examined histologically contain small immature gonads (distribution as in the male). Their sex could not be determined.

Systematic discussion

Original description by Schmarda (1859: 41): '*Ommatoplea heterophthalma*. Schmarda. Char.: Corpus depressum teniaeforme. Linea mediana alba. Caput indistinctum, apice acuminatum. Oculi in lineis transversis. Der abgeplattete, fast bandförmige Körper ändert seine Form nur wenig. Seine Farbe ist roth mit einer weissen Rückenlinie. Der Bauch ist blassroth. Seine Länge 60 mm, Breite 4 mm. An dem zugespitzten Koptheile stehen zwei Augen und in einiger Entfernung rückwärts sieben in einer Längsline, hinter welcher drei in Form eines Dreiecks stehen. Die Oeffnung des Rüssels ist terminal. Dieser ist seiner ganzen Länge nach mit nesselartigen Organen bedeckt. Die Stilette haben die Form einer Lanzette mit lang ausgezogener Spitze. Stiller Ocean, unter Steinen bei Auckland an der Küste von Neu-Seeland.'

All references to this species, published in the mean time, depend on the information provided by Schmarda (1859). Bürger (1895: 27) notices: '[*Ommatoplea heterophthalma* Schm. Neuseeland stellt eine Metanemertine vor (*Amphiporus* oder *Eunemertes* [= *Emplectonema* Stimpson, 1857])'. However, in 1904 Bürger interprets *O. heterophthalma* as a valid species of *Amphiporus* Ehrenberg, 1831. Gibson & Crandall (1989: 459) designate *Amphiporus heterophthalmus* as a *nomen dubium* and notice: 'A strikingly marked species, *A. heterophthalmus* remains poorly characterised morphologically'.

So far no valid diagnosis of *Amphiporus* can be provided (see Gibson & Crandall 1989). But, the following character combination, present in *A. heterophthalmus*, indicates that this species cannot be incorporated within *Amphiporus* (see Friedrich 1955 and Gibson 1982 for *Amphiporus*): inner circular muscle layer of the body wall well developed; midgut caecum short and provided with long terminal diverticula; mid-dorsal vessel without vascular plug; rhynchocoel does not reach the posterior end of the body; lateral nerve cord with anterior accessory nerve; cephalic gland reaching to the posterior end of the foregut. The only described hoplonemertean genus provided with this character combination is *Ischyronemertes* Gibson, 1990 (see Gibson 1990). The diagnosis of this genus is in accordance with the here provided description of *A. heterophthalmus*, despite of the characters: length of the rhynchocoel; structure of the rhynchocoel wall musculature; vascular apparatus provided with commissures in the midgut area.

According to Gibson (1990) in *Ischyronemertes* the rhynchocoel is restricted to the anterior half of the body. In *A. heterophthalmus* the rhynchocoel extends into the posterior half of the body but without reaching the posterior end of the body by far. In several hoplonemertean genera the rhynchocoel reaches to the posterior tip of the body (Friedrich 1955).

In *Ischyronemertes* the rhynchocoel wall musculature consists of two separate muscle layers (longitudinal and circular) (Gibson 1990). In *A. heterophthalmus* longitudinal muscle fibres are intermingled with the circular musculature enveloping the rhynchocoel. It remains open to question, whether these muscle fibres actually belong to the longitudinal musculature of the rhynchocoel wall. First, there is a well demarcated longitudinal muscle layer next to the endothelium of the rhynchocoel wall. Second, the discussed longitudinal muscle fibres are intermingled with the inner circular musculature of the body wall adjacent to the rhynchocoel wall as well. It is worth noting that a well developed inner circular body wall muscle layer, as present in *A. heterophthalmus* and *Ischyronemertes*, is an unusual

Tab. 1. Characters that can be used to distinguish the known species of *Ischyronemertes* Gibson, 1990.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
<i>Ischyronemertes albanensis</i>	-	-	-	d	++	p	d	-	-	ar	a
<i>Ischyronemertes erythrophleps</i>	+	+	-	vl	++	p	v	-	-	ar	a
<i>Ischyronemertes tetraphthalma</i>	+	-	+	d	+	a	v	-	-	ar	a
<i>Ischyronemertes heterophthalma</i>	+	+	+	vl	-	a	d	+	+	au	b, c

I oesophagus with (+) or without gland cells (-); II stomach epithelium regionally differentiated (+) or with uniform construction throughout (0); III stomach walls deeply folded (+) or little folded (0); IV cephalic gland lobules pass brain dorsally (d), laterally (v) or ventrally (l); V ocelli in four groups (++) , four separate ocelli forming corner of trapezium (+) or arranged in another way (-); VI glandular component of cerebral sensory organs predominantly anterior (a) or posterior (p); VII nephridiopores dorsolateral (d) or ventrolateral (v); VIII vascular apparatus with (+) or without valves (-); IX foregut with (+) or without longitudinal muscle fibres (-); X distribution: Albany region (Western Australia) (ar), Aukland (New-Zealand) (au); XI reference: a Gibson (1990), b Schmarda (1859), c this paper.

character within Monostilifera. Due to this the whole complex of circular and longitudinal muscle fibres is somewhat enigmatic from a phylogenetic viewpoint.

Hence, the presence of the transverse commissures of the vascular apparatus is the only distinct difference between *A. heterophthalmus* and the diagnosis of *Ischyronemertes* by Gibson (1990). Summing up there are characters indicating that *A. heterophthalmus* should be transferred to *Ischyronemertes*, and characters seemingly contradicting this viewpoint.

Contemporary hoplonemertean classification provides no rules, allowing to solve this problem in an unequivocal way. This is because supraspecific hoplonemertean taxa are based on the existence of a unique combination of characters, a method unlikely to lead to monophyletic taxa (Sundberg, 1993, but see also Moore & Gibson 1993).

It is beyond the scope of the present paper to provide a meaningful starting point for systematisation. However, it has to be the aim of the present paper to classify *A. heterophthalmus* in a way that is commensurable with the remaining hoplonemertean classification. Because of this the character combination method is used, since it is the method dominating in hoplonemertean classification so far (see also Senz 1996b).

Due to this *A. heterophthalmus* is transferred to the genus *Ischyronemertes*. First, this is possible because of the above mentioned characters present in both taxa. Second, the modification of the diagnosis of *Ischyronemertes* (see above) triggered because of the incorporation of the redescribed species still allows to define this genus in a meaningful way, if compared to the diagnosis of the remaining hoplonemertean genera.

So far three *Ischyronemertes* species have been distinguished: *I. albanyensis* Gibson, 1990; *I. erythropleps* Gibson, 1990; *I. tetrophthalma* Gibson, 1990. Tab. 1 summarises several of those characters (not discussed so far) separating *I. heterophthalma* from the remaining *Ischyronemertes* species.

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