On the genus *Minutanemertes* SENZ, 1993

(Nemertini: Hoplonemertini)

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Abstract

The mesopsammic *Minutanemertes schifkoi* sp.n. from off Istria (Croatia) is described. The definition of the genus *Minutanemertes* SENZ, 1993, is adopted to the new species.

Key words: Nemertini, Hoplonemertini, *Minutanemertes*, *Minutanemertes schifkoi*, new species, morphology, typology, classification.

Zusammenfassung

Die mesopsammale Art *Minutanemertes schifkoi* sp.n. von der Küste Istriens (Kroatien) wird beschrieben. Die Definition der Gattung *Minutanemertes* SENZ, 1993, wird an die neue Art angepaßt.

Introduction

One specimen from a small number of interstitial hoplonemerteans collected off Rovinj (Istria/Croatia) is of interest. This is because it corresponds to the organisation of *Minutanemertes* SENZ, 1993, as currently defined incompletely. Because of this, *Minutanemertes* is re-investigated. In addition, some thoughts on the classification of the interstitial hoplonemerteans are provided.

Acknowledgements

Material and methods

The specimen was fixed in formol and embedded in paraplast. The series of sections (10 μm thick) have been stained with Kernechtrot-Pikroindigokarmin. The type material of the new species is deposited in the Museum of Natural History, Vienna.

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Minutanemertes schifkoi sp.n.

Holotype: NHMW-EV 3338, immature specimen, complete series of transverse sections; coast of Croatia off Rovinj; in sand; coll. Georg Schifko.

Etymology: The specific epithet is dedicated to Georg Schifko (Vienna) for providing the author with the material.

Diagnosis: Cephalic furrows present; rhynchocoel reaching to the posterior tip of the body; cephalic gland large (dorsal lobe reaching behind anterior margin of the brain); one pair of ocelli.

Description:

The specimen is about 1 mm long and cylindrical in cross section (diameter: 0.1 mm maximum). The body is whitish with one pair of ocelli somewhat in front of the brain (see below), with one pair of oblique cephalic furrows.

The epidermis is thick (up to 25 µm) and contains chordoid cells, as described for *Minutanemertes alba* SENZ, 1993 (see SENZ 1993a) and *Ototyphlonemertes antipai* MÜLLER, 1968 (see MÜLLER 1968). The epidermis rests on a delicate basement layer. No dermis is distinguishable.

The body wall musculature is weakly developed throughout the body. The longitudinal muscle layer is not split. In the preseptal area both muscle layers are very much reduced. No cephalic retractor muscle fibres could be detected. The inner circular muscle layer and its derivatives are absent.

The so-called "Zentralraum" is closed (for terminology see SENZ 1995). Hence, no large connective tissue compartments occur (Figs. 5, 6).

The rhynchodaeum opens subterminally and extends back to the proboscis insertion as a simple tube. The proboscis insertion lies somewhat in front of the brain. The septum is extremely reduced. The rhynchocoel extends back to the posterior end of the body. It is a simple tube lined by a very delicate musculature (Figs. 3 - 6). No interlacing of longitudinal and circular muscle fibres in the rhynchocoel wall exists. The proboscis is well developed and shows the typical monostiliferous organisation. Its anterior part (diameter up to 0.02 mm) consists of a thick glandular epithelium and a thin musculature. No individualised proboscis nerves are visible. The middle part of the proboscis consists of a muscle bulbus (Fig. 6) and the stylet bearing area. The stylet basis is a simple cylinder (Fig. 5; length: 40 µm; diameter: 16 µm). The central and accessory stylets are smooth (length of the reserve stylets: up to 30 µm). The base of each accessory stylet is swollen and knob-like. Two accessory stylet pouches are present, each containing two to three accessory stylets. The posterior part of the proboscis is well developed (diameter: up to 0.01 mm). No retractor muscle could be detected.

The foregut consists of an oesophagus (terminology sensu SENZ 1993b) (Fig. 2), stomach (Fig. 3), and pyloric tube (Fig. 4). The oesophagus opens into the rhynchodaeum. It is lined by a thin epithelium. Whether this epithelium is ciliary in the anterior part could not be detected. At the level of the ventral commissure of the brain the oesophagus is 20 µm in diameter. Behind the ventral commissure it transforms into the stomach (diameter: up to 80 µm). The stomach is a simple tube (no diverticula present) and lined by

a thick, ciliated epithelium. Posteriorly it merges into the pyloric tube (length: 90 µm; breadth: up to 50 µm). No foregut musculature is present. At its posterior end the pylorus opens into the dorsal wall of the midgut. Hence, the midgut is provided with a caecum (Fig. 4). Anteriorly, this caecum extends to the area of the maximum enlargement of the stomach (Fig. 3), i.e. the caecum extends to near the posterior end of the dorsal ganglia. However, at this level, the ventral ganglia already have transformed into the lateral nerve cord stem area. The caecum has neither terminal nor lateral diverticula. But, since the pyloric tube lies in a mid-dorsal furrow of the caecum, its lateral parts reach the rhynchocoel (Fig. 4). The midgut proper is a simple tube without lateral diverticula (Figs. 5, 6). This may alter when mature gonads are present.

The brain is comparatively large. At its anterior end, the brain consists of a thick compartment of nervous fibres, lined by ganglionic cells in its lateral and dorsolateral parts. Posteriorly a mid-ventral fissure of the fibrous core occurs, caused by ganglionic cells. Further back this fissure becomes bigger, and the posterior margin of the thick ventral commissure emerges. Simultaneously, both fibrous compartments split once more, forming the dorsal and ventral ganglia (Fig. 2). At this level, each fibrous core is uniformly lined by ganglionic cells. The dorsal ganglia are somewhat larger than the ventral. Posteriorly the dorsal ganglia end, whereas the ventral transform into the stem area of the longitudinal nerve cords. The dorsal commissure is thin and bridges both dorsal ganglia between the rhynchocoel and the dorsal lobe of the cephalic gland. Neither the inner nor the outer neurilemma could be identified histologically.

The lateral nerve cords lie adjacent to the body wall in a rather lateral position. Each cord consists of a single fibrous nerve core. Side stem muscles and neurochords are absent. The cephalic nerves are weakly developed, but clearly visible. One pair of nerves is present between the lateral margin of the brain and the body wall. These nerves enter the fibrous core of the brain at the level where each lateral part of the brain splits into dorsal and ventral ganglia. Foregut nerves, proboscis nerves and dorsal nerves could not be detected.

There is one pair of cephalic furrows (Fig. 1). Each furrow reaches from a dorsolateral position somewhat in front of the brain to a rather ventrolateral position in the anterior part of the preseptal area. The cerebral organ canal opens into the lateral part of the cephalic furrow. Somewhat behind its opening the canal turns backwards and ends a short distance in front of the brain. Anteriorly the thick canal (diameter: 17 µm) becomes lined by ganglionic cells, which are supplemented by glandular cells in the posterior area of the cerebral sensory organ proper. Due to these glandular parts the cerebral sensory organs are large, filling up the space between the dorsal and ventral lobe of the cephalic gland in front of the brain (Fig. 1). The posterior margin of each cerebral sensory organ lies adjacent to the anterior margin of the brain.

One pair of brown ocelli occurs adjacent to the posterior enlargement of the cerebral organs. Further sensory structures, including a frontal organ, are absent. The cephalic gland is well developed, consisting of a dorsal and ventral lobe (Fig. 1). Both lobes open to the exterior at the anterior tip of the preseptal area. The dorsal lobe extends behind the dorsal commissure of the brain (Fig. 2), but without extending behind the posterior margin of the brain.
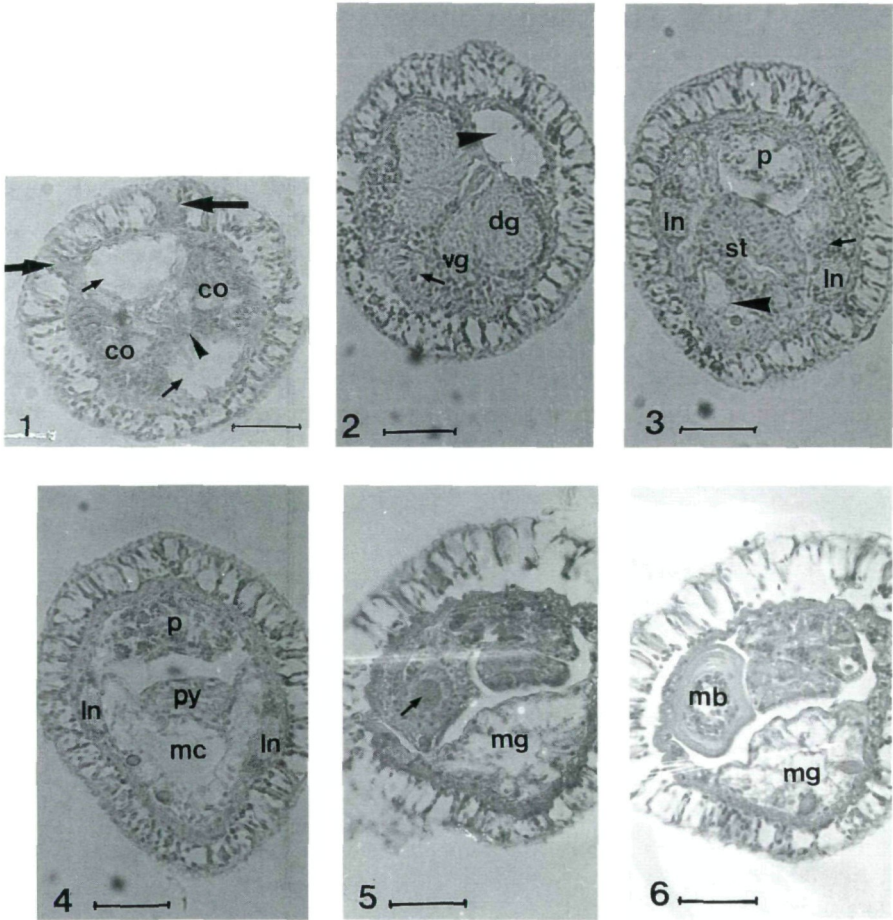
Figs. 1 - 6: Cross sections through *Minutanemertes schifkoi* sp. n.: (1) preseptal area; notice the large cephalic glands (→), the cephalic furrows (⟹), and the cerebral sensory organs lying adjacent to each other beneath the rhynchodaeum (➤); (2) brain area; notice the dorsal lobe of the cephalic gland (➤) and the transformation of the oesophagus into the stomach (→); (3) stomach area; notice the posterior end of the dorsal ganglion (→) and the anterior end of the midgut caecum (➤); (4) pylorus area; (5) midgut area; →: indicating base of the stylet; (6) midgut area. Abbreviations: co = cerebral sensory organ, dg = dorsal ganglion, ln = lateral nerve cord, mb = muscle bulbus of the middle part of the proboscis, mc = midgut caecum, mg = midgut, p = proboscis, py = pylorus, st = stomach, vg = ventral ganglion. Scale bares of all figs: 35 µm.

The vascular apparatus seems to be of the typical hoplonemertean organisation. It could not be studied in detail.

No signs of an excretory apparatus could be detected. Furthermore, there are no cells with a putative excretory function as known from *Ototyhplonemertes antipai* and *Minutanemertes alba* (see MÜLLER 1968, SENZ 1993a).

The specimen is immature. No signs of the reproductive apparatus are visible.

Discussion

Most of the interstitial hoplonemerteans belong to the family Ototyphlonemertidae (KIRSTEUER 1971, 1986, NORENBURG 1988). The remaining interstitial hoplonemerteans belong to the genera: *Albanemertes* SENZ, 1993 (*A. rovinjensis* SENZ, 1993); *Annulonemertes* BERG, 1985 (*A. minusculus* BERG, 1985); *Arenonemertes* FRIEDRICH, 1933 (*A. arenicolus* HYLBOM, 1991; *A. microps* FRIEDRICH, 1933; *A. minutus* FRIEDRICH, 1949); *Minutanemertes* SENZ, 1993 (*M. adiverticulata* SENZ, 1993; *Minutanemertes alba* SENZ, 1993); and *Prostomatella* FRIEDRICH, 1935 (*P. arenicola* FRIEDRICH, 1935) (see BERG 1985, FRIEDRICH 1933, 1935a, 1949, HYLBOM 1991, SENZ 1993a).

In the new material cerebral statocysts are absent and the foregut opens into the rhynchodaeum. Due to this it can be separated from the ototyphlonemertid nemerteans (cerebral statocysts present; NORENBURG 1988) and *Albanemertes* (rhynchodaeum opening into the foregut; SENZ 1993a).

Comparing the new material with the remaining interstitial taxa provides some problems.

Partly this is because of inadequate species descriptions, as for *Arenonemertes minutus*. FRIEDRICH (1949) (whose species description was hampered by the quality of the material at hand) hesitated placing this species within *Arenonemertes*. However, he did not change this later (FRIEDRICH 1955). Subsequently *Annulonemertes minusculus* BERG, 1985, became known, a species showing pseudosegmentation which is an apomorphic character within Nemertea, similar to that in *A. minutus*. Hence the question arises whether this similarity indicates close generic relationship, or depends on convergent evolution. As pointed out by BERG (1985; see also HYLBOM 1991 and NORENBURG 1988), several characters, differently developed in both taxa, seem to contradict a close generic relationship. However, neither the diagnosis of *Arenonemertes* sensu FRIEDRICH (1955), nor sensu HYLBOM (1991) includes unequivocal apomorphic characters, as demonstrated by the following analysis. The reduction of the midgut caecum and its diverticula (see Tab. 1) can be interpreted as being causally linked to the smallness of the body, such as reduction of the lateral midgut diverticula (see KIRSTEUER 1971, 1986). CORRÉA (1950) demonstrated increased enzymatic activity of the midgut proper in *Ototyphlonemertes brevis* CORRÉA, 1948, a putative compensation of the reduction of the diverticula and caecum. Hence, these characters have to be theorised as "Lebensform-Merkmale" sensu REMANE (1943). In other words, parallel and convergent evolution to ecological vicars (sensu SALTHE 1993) become intelligible explanations for similarity. It is worth noting that there are several non-interstitial hoplonemerteans showing characters interpreted above as "Lebensform-Merkmale" for interstitial hoplonemerteans (see Tab. 1). The characters "four ocelli present", "cerebral sensory organs simple", "rhynchocoel extending to posterior end of the body" are also known from other hoplonemerteans. Hence, a priori there is no necessity to interpret these characters as synapomorphic among the *Arenonemertes* species. Due to this, separation of *Annulonemertes* and *Arenonemertes* depends on the systematic weight given to the characters "rhynchocoel muscle layers interwoven or not" and "cerebral organ present or absent". *Annulonemertes* lacks cerebral organs and its rhynchocoel muscle layers are interwoven, in contrast to *Arenonemertes* (BERG 1985). According to GIBSON (1988) the muscle plan of the rhynchocoel wall is an important character in hoplonemertean syste-

Tab. 1: Comparison of the interstitial hoplonemerteans (without ototyphlonemertid nemerteans and *Albanemertes* SENZ, 1993), and some of the hoplonemerteans showing a similar morphology (see text)

	1	2	3	4	5	6	7	8	9	10	11	12	13
interstitial hoplonemerteans													
Annulonemertes minusculus	#	0	-	-	#	+	-	+a	-	+	+b	I	A
Arenonemertes microps	-	4	+	+	+c	+	+	+	+	+	+	I	B
Arenonemertes minutus	+	0	?	+	?	?	-	?	?	+	?	I	C
Arenonemertes arenicolus	-	4	+	+	-	-d	-	?	+	-	+	I	D
Minutanemertes alba	-	0	+	-e	+	+	-	-	-	+	-	I	E
Minutanemertes adiverticulata	-	4	+	-	+	+	.	-	-	+	-	I	E
Prostomatella arenicola	-	4	+	+f	+	+	-	-	+	?	+	I	FG
Minutanemertes schifkoi sp.n.	-	2	+	+	#	+	-	-	+	?	-	I	
non-interstitial hoplonemerteans													
Nemertellina oculata	-	4	-	-	+	+	-	-	-	+	+	II	H
Nemertellina canea	-	4	-	-	+	+	-	-	-	+	?	II	H
Nemertellina minuta	-	4	-	-	+	+	-	-	-	+	?	II	F
Nemertellina tropica	-	4	-	-	+	+	-	-	-	+	+	III	I
Nemertellopsis pacificus	-	0	+	+g	#	+h	-	?	-	?	?	II	J
*Nemertellopsis typica**	-	?	+	+g	+	+i	+	+	-	+	+	II	K
*Nemertellopsis macrodasys**	-	4	+	+g	+j	-	+	+	-	+	+	II	H
Nemertellopsis cephalotrichiformis	-	0	+	+g	+j	-	-	-	-	+	+	IV	H
Paraminutanemertes minutus	-	4	+	+	?	+	+	+	?	+	?	II	HE

(1) pseudosegmentation present (#), restricted to posterior body (+) or absent (-); (2) number of ocelli; (3) cerebral sensory organs absent (-), adjacent to the brain (+), not reaching to the brain (-); (4) cephalic furrows present (+) or not (-); (5) cephalic gland absent (-), restricted to the pre-septal area (+) or reaching behind the anterior margin of the brain (#); (6) oesophagus present (+) or not (-); (7) midgut caecum with diverticula (+) or not (-); (8) midgut caecum reaching the brain (+) or not (-); (9) rhynchocoel reaching to the posterior end of the body (+) or not (-); (10) gonadial area absent in the anterior midgut area (+) or not (-); (11) protonephridial excretory apparatus present (+) or not (-); (12) biotope: I interstitial, II Zostera-Ulva-region, III on coral, IV in mud; (13) literature: A: BERG (1985), B: FRIEDRICH (1933), C: FRIEDRICH (1949), D: HYLBOM (1991), E: SENZ (1993a), F: FRIEDRICH (1935a), G: NORENBURG (1993), H: FRIEDRICH (1935c), I: KIRSTEUER (1965), J: FRIEDRICH (1970), K: FRIEDRICH (1936).

(a) the caecum is short, although reaching the brain; (b) rudimentary developed; (c) the cephalic gland consists of a dorsal and ventral lobe; only the ventral one reaches to the brain; (d) the term oesophagus is somewhat vaguely defined in nemerteanology (SENZ 1993b); so far as can be concluded from the micrographs 9a and 9b in HYLBOM (1991), the foregut in the brain area resembles the definition of "oesophagus" sensu SENZ (1993b) in several respects; (e) only rudimentary cephalic furrows present; (f) annular cephalic furrow; (g) little developed; (h) oesophagus little developed; (i) according to FRIEDRICH (1936: fig. 11), no information in text; (j) interrupts septum dorsally and/or ventrally.

* Species transferred to *Tetrastemma* by FRIEDRICH (1955) but listed as *Nemertellopsis* spp. by GIBSON (1995).

matics. But, SENZ (1993c) suggests in his analysis of hoplonemertean systematics, that the character "rhynchocoel wall muscle layers intermingled" developed at least several times within the hoplonemerteans. Hence, it is open to question whether this character is a good argument for separating *Arenonemertes* from *Annulonemertes*. Summing up, there is only a single character (presence or absence of the cerebral sensory organ) to separate *Arenonemertes* and *Annulonemertes*. In the case of *Arenonemertes minutus*, this is of particular importance, because of pseudosegmentation, present in this species and in *Annulonemertes*. Due to this, *Arenonemertes* will be defined on the basis of *A. microps* and *A. arenicolus*. *A. minutus* will be discussed separately.

Nevertheless, the same problems occur, when *Arenonemertes* is compared with *Minutanemertes* and *Prostomatella*. For example *Minutanemertes* and *Arenonemertes* correspond in "Lebensraum-Merkmalen" and differ in characters of uncertain systematic value (see Tab. 1), such as the length of the rhynchocoel. The most striking character in this respect is the absence of the protonephridial excretory apparatus in the *Minutanemertes* species. On the one hand, the presence of this apparatus in *Arenonemertes* cannot be interpreted as an apomorphic character. That is because an excretory apparatus belongs to the plesiomorphic condition within hoplonemerteans, and there is no reason for arguing, that the excretory apparatus in *Arenonemertes* developed independently of this character. On the other hand, absence of this apparatus is known from quite a number of nemerteans, among others the interstitial hoplonemerteans *Ototyphlonemertes* DIESING, 1863, and *Otonemertes* DAWYDOFF, 1937 (NORENBURG 1988).

The new material even increases the problems illustrated so far. This is because it shares several characters with *Minutanemertes* (among others: "no excretory apparatus distinguishable"), but is similar to *Arenonemertes* and *Prostomatella arenicola* in the characters "cephalic furrows present" and "rhynchocoel reaching to posterior end of the body".

So far, it seems as if these problems primarily stem from the many problems in hoplonemertean systematics in general (CRANDALL 1993, GIBSON 1988, 1990, SENZ 1993c, SUNDBERG 1990), and the putative large number of convergences ("Lebensform-Merkmale"), due to the involved ecological vicar, that is apomorphic for nemerteans. Current nemertean systematics react on this problem (not only in the case of interstitial hoplonemerteans, but of nemertean systematics in general) by discussing the validity of phyletic versus cladistic methods (GIBSON 1990, MOORE & GIBSON 1993, SUNDBERG 1990, 1993). MOORE & GIBSON (1993: 100) reflect on the importance of taking convergent evolution in nemerteans into account: "In conclusion, it would be dangerously misleading to assume that convergent evolution was a rare phenomenon in any nemertean group. We must therefore choose a method of classification which does not implicitly assume that resemblance is more likely to be due to common ancestry than to convergence. We believe that the traditional [= phyletic] method, emphasising the assessment of all available characters, is the one which has the best chance of revealing true evolutionary relationships". Furthermore, MOORE & GIBSON (1993: 91) argue for a "controlled and disciplined subjectivity". On the other hand, it is the aim of cladistic analysis to minimise this subjectivity by mathematical (quantitative) methods. Without question, the cladistic analysis gets credit from its ability to take parsimony into account.

However, in the author's opinion, in the current situation even an ideal combination of phyletic and cladistic methods seems to be hampered in its ability to produce meaning-

ful systematic conclusions. The reason therefore is provided by the character matrices, as used in modern nemertean systematics. This is, characters are defined as phenotypic entities, without any attempt to incorporate a systems approach into the analysis. In other words, although functional interdependency of the phenotypically defined characters is taken into account (as far as possible, MOORE & GIBSON 1993, but see SUNDBERG 1990, 1993), these interdependencies are not related to the body plan, defined as an individuality sensu the systems theory (SAUNDERS 1984, and literature therein). But, as shown by modern evolutionary biology this step further is necessary in order to understand evolution of a complex structure, e.g. the body plan (WAKE & al. 1983; SALTHE 1993). Furthermore, modern evolutionary biology demonstrates that the epigenetic landscape, that provids the individuality of a body plan, essentially is a non-linear system (ALBERCH 1982, HINCHLIFFE 1991). Hence, phenotypically divergent characters may be "similar" from the viewpoint of the epigenetic landscape. Due to this non-linearity it is not possible to determine the systematic value of a character by any method not taking the systems approach into account. Because of this, even if one takes every character of a body plan into account, but neglects the individuality of the body plan sensu the systems approach, no valid systematic conclusion seems possible.

Summing up, as long as nothing is known on the body plan of nemerteans sensu the systems approach, in the author's opinion, conclusions on the systematics of nemerteans are problematical (at best). Due to this, the analysis of the interstitial hoplonemerteans provided in this paper is a typological interim statement. The named taxa are not proposed to designate monophyletic groups of descendants, but terms useful for sorting our knowledge, taken as basis for the phylogenetic analysis dealing with the systems approach.

According to this, *Arenonemertes* (only *A. microps* and *A. arenicolus* taken into account) can be defined as a taxon of hoplonemerteans showing only gross correspondence to the interstitial environment (see genus diagnosis by FRIEDRICH 1955). On the basis of this gross correspondence, the remaining three taxa show different pecularities: the taxon *Prostomatella* shall be reserved for those interstitial hoplonemerteans showing a well developed body wall musculature and locomotion by "Stemmschlängeln" (see FRIEDRICH 1935b); *Annulonemertes* is characterised by pseudosegmentation; *Minutanemertes* is characterised by the reduction of the protonephridial excretory apparatus.

Annulonemertes minutus cannot be classified so far in a satisfactory way, because of lack of data on its anatomy (table 1). It has to be left as an uncertain *Arenonemetes* species. Here it is of importance that pseudosegmentation in *Annulonemertes* and *Arenonemertes minutus* show considerable morphological differences (BERG 1985, FRIEDRICH 1949). Hence, it cannot be concluded, that the term pseudosegmentation means the same in both taxa.

Due to above, the new material can be placed within *Minutanemertes* because of the lack of a protonephridial excretory apparatus.

Up to now *Minutanemertes* has been represented by two species, *Minutanemertes adiverticulata* and *M. alba* (see SENZ 1993a). Both species are separated by characteristics of the epidermis, the excretory apparatus, the midgut diverticula and the dorsal commissure of the brain (SENZ 1993a). A further difference, not pointed out by SENZ (1993a), is the absence of ocelli in *M. minuta* and presence of four ocelli in *M. adiverticulata*. Furthermore, *M. alba* is somewhat misleadingly described in SENZ (1993a) so far as

concerns the cephalic furrows. Sensu SENZ (1993a) distinct cephalic furrows are absent in *M. alba* and no cephalic fissure is visible in life. Although this is correct, the epidermis is modified to a varying degree at the opening of the cerebral sensory organ canal. In one *M. alba* specimen this area has an extension, similar to that of the cephalic furrow in *M. schifkoi*. In this area the epidermis is thinner than the surrounding, and provided with significantly longer cilia. Hence, the presence of a rudimentary cephalic furrow is proposed. From the species known so far the new one can be separated due to the cephalic furrows, the large cephalic gland with the dorsal lobe reaching behind the anterior margin of the brain, the rhynchocoel reaching to the posterior tip of the body, and the presence of one pair of ocelli (Tab. 1).

Without question the definition of *Minutanemertes schifkoi* sp.n. is hampered because only one immature specimen is known. Nevertheless, a satisfying diagnosis of the species, also allowing re-identification is possible, also if taking intraspecific variability and contraction into account. The most characteristic feature of the new species is the large cephalic gland. Although there is some variability in the size of the cephalic gland in *Minutanemertes alba* and *M. adiverticula* (pers. obs.), the situation in these species can be strictly separated from the one in *M. schifkoi* sp.n. Furthermore there are no indications that a large cephalic gland is a juvenile character. The same is true for the character "rhynchocoel extending to the posterior end". Given, that the specimen is not full grown and the rhynchocoel does not reach to the posterior end finally, this would not alter the generic placing of the species advocated in the present paper. According to NORENBURG (1988) the number of ocelli varies in not yet described *Annulonemertes* species from none to four. But, as far as it is known from the remaining hoplonemerteans, the character "none, one or two pairs of ocelli developed" is a good diagnostic character.

Because of the new material, the original diagnosis of *Minutanemertes* (see SENZ 1993a) has to be re-investigated.

Revised diagnosis of the Genus *Minutanemertes* SENZ, 1993:

Free living monostilifereans, cephalic furrows present or absent; body wall muscle layers reaching far anterior in the preseptal area; body wall longitudinal muscle layer not split; septum much reduced; rhynchocoel extends full length of the body or to the midbody at least; muscle layers of the rhynchocoel wall not intermingled with each other; rhynchocoel diverticula absent; oesophagus present; midgut caecum without diverticula and not reaching to the brain; lateral nerve cords simple; cerebral sensory organs large, reaching to the anterior margin of the brain; statocysts absent; protonephridial excretory apparatus absent; sexes separate.

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