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TAXONOMIC STATUS OF *NEOECHINORHYNCHUS AGILIS* (ACANTHOCEPHALA, NEOECHINORHYNCHIDAE), WITH A DESCRIPTION OF TWO NEW SPECIES OF THE GENUS FROM THE ATLANTIC AND PACIFIC MULLETS (TELEOSTEI, MUGILIDAE)

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Taxonomic Status of *Neoechinorhynchus agilis* (Acanthocephala, Neoechinorhynchidae), with a Description of Two New Species of the Genus from the Atlantic and Pacific Mullets (Teleostei, Mugilidae). Tkach, Ie. V., Sarabeev, V. L., Shvetsova, L. S. — The wide variability in morphological features, geographical and host ranges of mullet acanthocephalan parasite *Neoechinorhynchus agilis* (Rudolphi, 1819), raises the question of taxonomic status of this species. Rudolphi's type and Yamaguti`s voucher specimens, as well as our own material from the WW Pacific and NE Atlantic region were used herein to provide comparative morphological analysis. The study revealed three different species of *Neoechinorhynchus*, *N.* (*N.*) *agilis* and *N.* (*H.*) *personatus* Tkach, Sarabeev et Shvetsova, sp. n. in the Atlantic and *N.* (*H.*) *yamagutii* Tkach, Sarabeev et Shvetsova, sp. n. in the Pacific. Strong morphological and morphometric differences were found between three described herein species from different hosts and regions. The dividing of *N. agilis* into three species, two of them are new, provides a basis for the further revision of host-geographical records of mullet acanthocephalan parasites.

K e y w o r d s: Mediterranean, Azov-Black Sea, Northeast Atlantic, *Chelon labrosus*, *Mugil cephalus*.

Таксономический статус *Neoechinorhynchus agilis* (Acanthocephala, Neoechinorhynchidae), с описанием двух новых видов рода от кефалевых рыб (Teleostei, Mugilidae) Атлантики и Пацифики. Ткач Е. В., Сарабеев В. Л., Швецова Л. С. — Широкое географическое распространение, богатый список хозяев, а также значительная вариабельность метрических признаков акантоцефалы *Neoechinorhynchus agilis* (Rudolphi, 1819) ставит вопрос о таксономическом статусе этого вида. Для проведения сравнительного морфологического анализа был использован типичный материал Рудольфи и ваучерные экземпляры Ямагути, а также собственный материал, собранный в западной части Тихого океана и северо-восточной Атлантике. В результате исследования было обнаружено три вида акантоцефал *Neoechinorhynchus*, в том числе два вида из Атлантики: *N.* (*N.*) *agilis* и *N.* (*H.*) *personatus* Tkach, Sarabeev et Shvetsova, sp. n., и один вид из Тихого океана, *N.* (*H.*) *yamagutii* Tkach, Sarabeev et Shvetsova, sp. n. Описанные в работе виды хорошо различаются как морфологически, так и метрически. Разделение *N. agilis* на три вида, два из которых описаны впервые, является основой для дальнейшего пересмотра находок этой акантоцефалы из разных регионов и от разных хозяев.

К л ю ч е в ы е с л о в а: Средиземное море, Азово-Черноморский бассейн, северо-восточная Атлантика, *Chelon labrosus*, *Mugil cephalus*.

Introduction

According to the present evidence (Di Cave et al., 1997; Caillot et al., 1999; Dmitrieva, Gaevskaya, 2001; Merella, Garippa, 2001; Radujković, 2002; Jithendran, Kannappan, 2010; Shih et. al., 2010) *Neoechinorhynchus agilis* (Rudolphi, 1819) is a widely spread acanthocephalan of gray mullets in the Atlantic and Pacific Oceans. The species was originally described in *Mugil cephalus* L. in the Mediterranean, as a long worm with

smooth trunk and short proboscis. Rudolphi's (1819) description briefly outlined the characteristics of the worm external morphology and proboscis receptacle, and no measurements were provided. The subsequent Hamann's, Van-Cleave's and Meyer's redescriptions were largely incomplete (Yamaguti, 1935) and did not meet the requirements of the current conception of species description. Yamaguti (1935) provided a redescription of *N. agilis* based on material collected from *M. cephalus* from the Inland Sea and Pacific Coast of Japan. This description is still used widely by different authors in keys or reviews (Petrochenko, 1956; Yamaguti, 1963; Parukhin, 1975; Amin, 2002). Further, the most faunistic publications listed above provide records of this acanthocephalan species expanding the list of host species and the geographic distribution of *N. agilis* around the Holarctic (Petrochenko, 1956; Al-Hadilhri et al., 1980).

So, wide geographical and host ranges of *N. agilis,* as well as a considerable variability in morphological features of this species, such as anterior hook and body length (Yamaguti, 1935), have prompted herein the question of whether it is a single cosmopolitan species or a complex of morphologically similar species gradually defined by various researchers as one.

In the course of recent investigations of the parasite fauna of mullets, in the Japan Sea, the Bay of Biscay, the Mediterranean and the Azov-Black Sea region, we had the opportunity to collect and study a large number of specimens from the four host species. Our abundant material as well as Rudolphi's type and Yamaguti's voucher specimens, compared herein has shown that there were at least three different forms of *Neoechinorhynchus* occurring in mullet hosts, two of those in the NE Atlantic and one in the NW Pacific. Strong morphological and morphometric differences were revealed between the described specimens from different hosts and regions. The aim of the present study is to give a starting-point for the further revision of host-geographical distribution records of previously well known acanthocephalan parasite *N. agilis.*

Material and methods

Grey mullets, *Liza aurata* (Risso), *L. haematocheila* (Temminck et Schlegel), *Chelon labrosus* (Risso), *M. cephalus* L., were collected in the Sea of Japan, the NW Pacific and the Azov-Black Sea, the western Mediterranean and the Bay of Biscay in the NE Atlantic (table 1). Fish intestine and pyloric caeca were examined

Table 1. Zoo-geographical information on the specimens of *Neoechinorhynchus* used in the present study

Таблица 1. Зоогеографическое происхождение представителей *Neoechinorhynchus* исследованных в работе

Host	Locality*	Date	Number of specimens	Collected by
Unknown	Mediterranean (Unknown)	August 1817	4	Rudolphy
C. labrosus	MSP 38°10' N, 0°35' W	November 2001	2	Sarabeev
"	MJE 47° 50' N, 3° 53' W	August 2003	6	"
"	BBC 39°09' N, 0°15' E	June 2011	15	Tkach
M. cephalus	ISK (Unknown)	October 1927	3	Yamaguti
"	IST (Unknown)	July 1928	5	"
"	SBN (Unknown)	April 1935	4	"
"	ASK (Unknown)	April 1935	1	"
"	JKB 42°51' N, 133°40' E	June 2004	3	Shevtsova
"	JKB 42°51' N, 133°40' E	October 2011	5	"
"	AKS 45°34' N, 36°48' E	May 2004	39	Maltsev
"	AKS 45°34' N, 36°48' E	June 2005	1	Sarabeev
"	BSB 44°37' N, 33°31' E	September–November, 2005	8	"
"	MSP 38°10' N, 0°35' W	June 2005	28	"
L. haematocheila	JRD 43°20' N, 131°47' E	October, 2010	3	Shevtsova
"	AKS 45°34' N, 36°48' E	June 2004	1	Maltsev
"	AOE 46°36' N, 36°13' E	June 2004	2	Sarabeev
"	AKS 45°34' N, 36°48' E	September 2005	1	"
"	AUE 46°09' N, 34°48' E	October 2005	1	"
"	AME 46°26' N, 35°26' E	November 008	2	Tkach
L. aurata	AUE 46°09' N, 34°48' E	September 2004	1	Sarabeev
"	AKS 45°34' N, 36°48' E	July 2005	1	"
"	AUE 46°09' N, 34°48' E	July 2005	2	"
"	AUE 46°09' N, 34°48' E	October 2005	2	"

* Locality abbreviations: AKS, Azov Sea, Kerch Strait; AME, Azov Sea, Molochnij Estuary; AOE, Azov Sea, Obytochny estuary; ASK, Ariake Sea, Kyushu; AUE, Azov Sea, Utlutskij Estuary; BBC, Biscay Bay, Concarneau; BSB, Black Sea, Sevastopol Bay; ISK, Inland Sea, Kuki; IST, Inland Sea, Tarumi; JKB, Japan Sea, Kiyevka Bay; JRD, Japan Sea, Razdol'naya Delta; MJE, Mediterranean Sea, Jucar estuary, Cullera; MSP, Mediterranean Sea, Santa Pola Bay, Santa Pola; SBN, Suruga Bay, Numazu.

for parasites within the day of capture, or after freezing, and surveyed for infections with acanthocephalans under a stereomicroscope.

The worms were isolated from the intestine, washed in 0.8 % saline and after eversion of the proboscis fixed in 70% ethanol. Part of the fixed worms were stained in Delafield's Hematoxylin, washed in tap water, and differentiated and destained in acid alcohol. Then they were washed in tap water and blued in bicarbonate until the nuclei were sharply blue. The hematoxylin-stained slides were rinsed in tap water and placed in 70 % ethanol. Then they were transferred to eosin. Other acanthocephalans were stained in Mayer's acid carmine, and differentiated and destained in acid alcohol. Worms were next dehydrated in ascending concentrations of ethanol, cleared in dimethylphthalate and whole mounted in Canada balsam. Other specimens were mounted in glycerin-jelly, prepared with 0.5 g carbolic acid without staining.

In addition to this newly sampled material, the following material was examined: 13 voucher specimens mounted by Yamaguti from MPM, and 4 syntypes of *N. agilis*, from MFN (see below for abbreviations) (table 1).

The following museum abbreviations appear in the text: Shmalhausen Institute of Zoology, Kyiv, Ukraine (IZAN), National Museum of Natural History, Paris, France (MNHN), Meguro Parasitological Museum, Tokyo, Japan (MPM), Museum für Naturkunde in Berlin, Germany (MFN).

All measurements are in micrometers unless otherwise stated. Dimensions of internal organs and body represent their largest measurement and are designated as length (L) and width (W) in the tables. The trunk length does not include the neck, proboscis or male bursa. Eggs refer to fully developed ripe eggs measured in situ, through the body wall in uterus or vagina of the mature females.

The observations and illustrations were made using a Leica DM LB2 microscope. Measurements were taken with the help of an ocular micrometer.

Computations were calculated using R statistical program, version 3.1.0 for GNU/Linux.

Neoechinorhynchus* (*Neoechinorhynchus*) *agilis (fig. 1–11, table 2)

Redescription

General. Neoechinorhynchidae, Neoechinorhynchinae with characters of the genus. All shared structures proportionally larger in females than in males. Body almost cylindrical, normally widest at anterior one third of the body, tapering posteriorly. Trunk long, smoothly curved, robust. Body wall with reticular lacunar system, containing 6 dorsal and 2 ventral giant hypodermal nuclei. Proboscis short, nearly cylindrical, slightly wider than long. Hooks on proboscis arranged in 3 circular rows of 6 hooks each. Hooks in each row equal in size and shape, all rooted. Neck short, about one third in length of proboscis length. Long single-walled proboscis receptacle with cerebral ganglion at its posterior end. Anterior part of proboscis receptacle enclosed by thin neck ring. Lemnisci unequal, large, digitiform, posteriorly narrowing dramatically, not reaching to anterior testis in males. Shorter lemniscus uninuclear; longer lemniscus binuclear; both distant from anterior testis in males.

Male. Based on 5 mature individuals with sperm and 4 juveniles. Reproductive system occupying posterior half of body. Testes elongate oval, tandem, contacting or slightly overlapping each other. Anterior testis longer than posterior one. Syncytial cement gland elongate, with 8 giant nuclei, contiguous to posterior testis by its anterior end. Round to oval cement gland reservoir leading to 2 cement ducts. Genital pore terminal.

Female. Based on 10 gravid specimens and 6 juveniles (including 3 syntype specimens). Genital pore sub-terminal, ventral, connected with vagina by elongated canal. Accessory structure of papilla present, terminally to genital pore. Eggs cylindrical, elongate, without polar prolongation of fertilization membrane.

Taxonomic summary

Synonym. *Echinorhynchus agilis* Rudolphi, 1819.
Type host. Undefined.
Type locality. Spezia, Italy.
Other host. Thick lipped mullet, *Chelon labrosus* (Mugiliformes: Mugilidae).
Other localities. Atlantic: Bay of Biscay; Mediterranean: Gulf of Santa Pola, Júcar Estuary.
Site of infection. Intestine.
Type material. MFN E.1179, syntype.

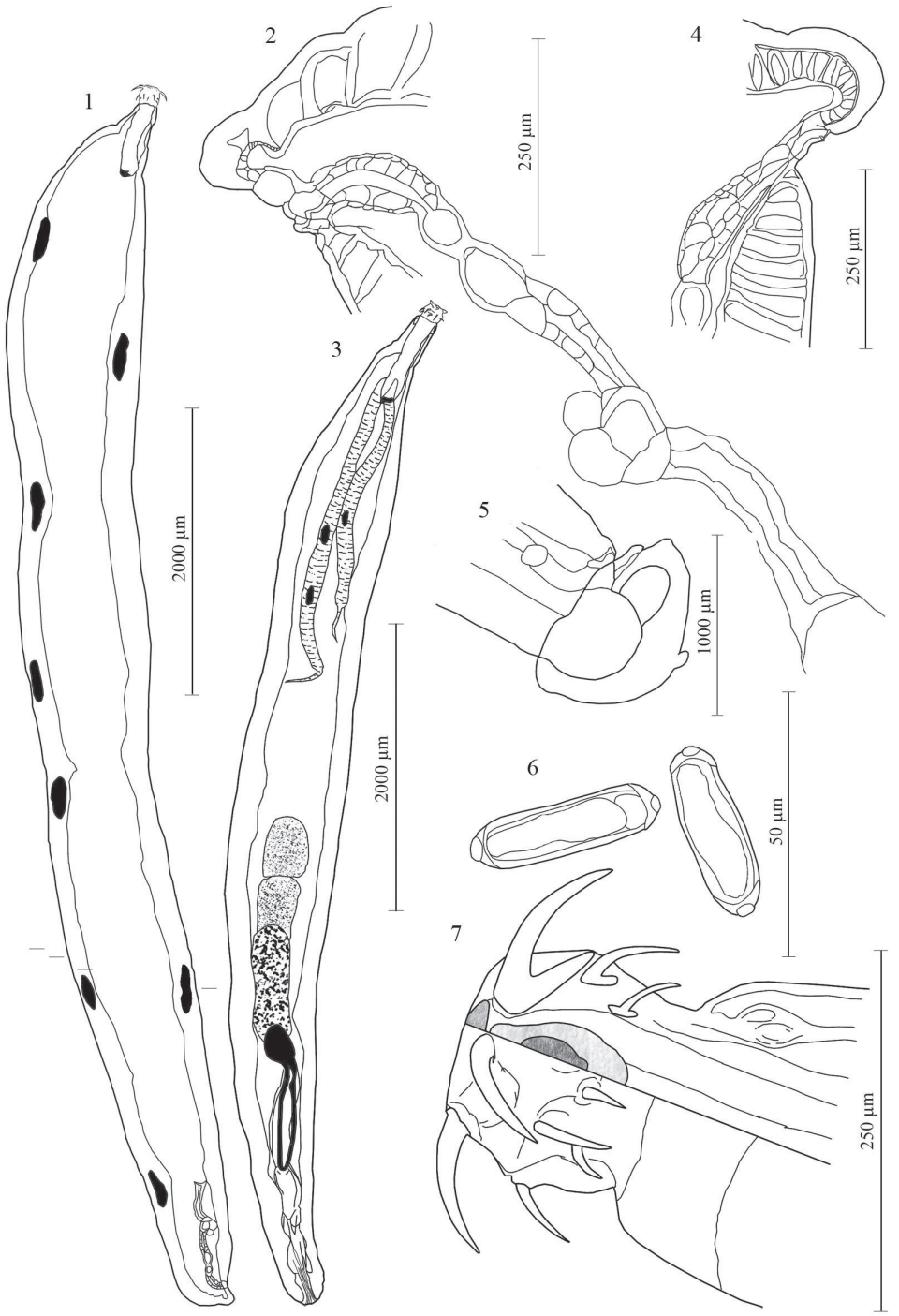

Fig. 1–7. Line drawings of the *Neoechinorhynchus (Neoechinorhynchus) agilis*. 1 — Female, entire ventral view. 2 — Female reproductive system, papilla everted minimally. 3 — Male, entire view. 4 — Female reproductive system, papilla everted maximally. 5 — Posterior end of female in section, papilla everted maximally, cement cap is present. 6 — Eggs from the body cavity. 7— Female proboscis in section, hooks with root system.

Рис. 1–7. Рисунки *Neoechinorhynchus (Neoechinorhynchus) agilis*. 1 — Общий вид самки. 2 — Женская половая система, папилла вывернута минимально. 3 — Общий вид самца. 4 — Женская половая система, папилла вывернута максимально. 5 — Задний конец самки в разрезе, папилла вывернута максимально, цементная крышечка присутствует. 6 — Яйца из полости тела. 7 — Хоботок самки в разрезе, крючья и корни.

Stored material. MFN 1–8; IZAN 9–15, voucher.
Etymology. Apparently *agilis* refers to the slender body of the worms.

Remarks

Rudolphi's (1819) description of *N. agilis* was based on nine specimens taken from the intestine of mullet fish at Spezia, Italy. According to Rudolphi (1819), the type specimens of the *N. agilis* were collected from *M. cephalus*, but at that time only three species of mullets were recognized from the Mediterranean, namely, *M. cephalus*, *L. aurata* and *L. saliens*, while *C. labrosus* was described only in 1827 (Risso, 1827). Therefore, we have no possibility to unambiguously identify the type host for

Table 2. Measurements of *Neoechinorhynchus* (*Neoechinorhynchus*) *agilis* from *Chelon labrosus*, Concarneau — Biscay Bay, France

Таблица 2. Размерные характеристики *Neoechinorhynchus* (*Neoechinorhynchus*) *agilis* от *Chelon labrosus*, Конкарно — Бискайский залив, Франция

Characters	Mature females					Mature males				
	Min	Max	Mean	SD	N	Min	Max	Mean	SD	N
Trunk L	5,950	8,949	7,535	964	10	5,855	8,044	6,692	847	5
Trunk W	900	1,160	1,032	80	10	650	930	792	109	5
Neck L	33	45	38.8	4	8	30	33	31.3	1.4	4
Neck W	110	140	126	9.7	9	120	128	125	3.5	4
Proboscis L	93	125	105	10.8	10	100	112	105	6.1	4
Proboscis W	140	168	150	8.6	10	133	150	141	7.2	4
Anterior hook L	93	110	99	5.7	10	100	100	100	–	2
Anterior hook W	15	17.5	15.3	0.8	10	12.5	15	14.5	1.1	5
Anterior hook root L	53	63	56	3.3	10	55	63	59	4.3	4
Anterior hook root W	15	17.5	15.5	1.1	10	15	15	15	–	4
Middle hook L	53	63	57	3.4	10	50	56	54	3.1	4
Middle hook W	7.5	10	7.8	0.8	10	5	7.5	6.3	1	4
Middle hook root L	17.5	25	21	2.4	10	15	25	18.8	4.8	4
Middle hook root W	5	7.5	6	1.3	10	7.5	17.5	10	5	4
Posterior hook L	43	50	46	3.2	10	45	50	47.5	2	4
Posterior hook W	5	7.5	6.1	1.1	10	5	6.5	5.3	0.6	4
Posterior hook root L	15	20	17.3	2.2	10	15	17.5	16.3	1.4	4
Posterior hook root W	5	7.5	5.3	0.8	9	5	5	5	0	4
Receptacle L	500	600	549	37	10	580	660	608	30.3	5
Receptacle W	100	180	131	23.8	10	120	180	154	21.9	5
Binuclear lemniscus L						2,200	2,900	–	–	2
Uninuclear lemniscus L						1,600	2,000	–	–	2
Anterior testis L						420	1,300	838	318	5
Anterior testis W						300	570	446	127	5
Posterior testis L						400	1,100	684	268	5
Posterior testis W						220	500	396	113	5
Cement gland L						780	1,100	934	133	5
Cement gland W						220	450	344	93	5
Reservoir cement gland L						260	370	308	43.2	5
Reservoir cement gland W						190	250	222	29.5	5
Uterine bell	350	700	534	148	4					
Uterus	250	525	368	97	7					
Vagina	225	275	246	17	9					
Egg L	36	40	38	1.5	15					
Egg W	10	12	10.9	0.9	15					
Papilla L	70	150	113	24	9					

Note. Abbreviations are given in Material and methods section.

Rudolphi's (1819) specimens. According to the present study *N.* (*N.*) *agilis* was recorded only from *C. labrosus*, which is proposed herein to be single typical host of this acanthocephalan parasite.

Examined herein type specimens of *N.* (*N.*) *agilis* (fig. 8–11) were stored in solution of ethyl alcohol. Specimens are in a temperate working condition, consistent, taut, their morphology is clear under light microscope and were discovered in temporary alcohol mounts. All four specimens are juveniles, three of those are females and one is in early development physiological age, with unclear sex.

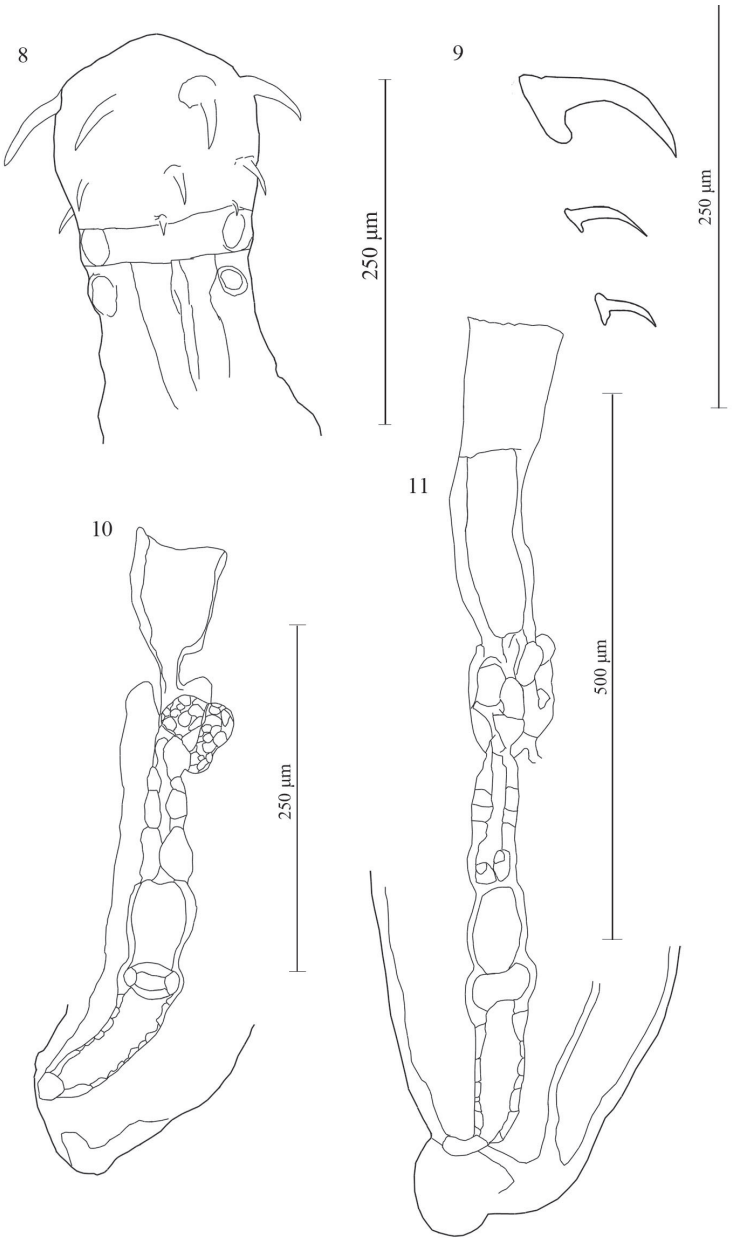

Fig. 8–11. Line drawings of the syntype specimens of *Neoechinorhynchus* (*Neoechinorhynchus*) *agilis*. 8 — Female proboscis. 9 — Female reproductive system. 10 — Hooks with root system. 11 — Female reproductive system.

Рис. 8–11. Рисунки синтипов *Neoechinorhynchus* (*Neoechinorhynchus*) *agilis*. 8 — Хоботок самки. 9 — Женская половая система. 10 — Крючья и корни. 11 — Женская половая система.

Morphological features and measurements of the examined types, such as proboscis arming, lemnisci and female genital system, corresponded well with the specimens collected in the present study from the Spanish and French localities.

We have to mention herein Van Cleave's (1919) redescription of the types of *N. agilis* as he examined two other male type specimens, which were not available for the present study. These data are of limited value because observations and drawings were made in alcohol and measurements of hooks were obtained for only those portions protruding beyond the proboscis wall (Van Cleave, 1919). All other data used in that re-examination were based on numerous specimens from European collections and European literature sources. Van Cleave marked noticeable variability of hooks measurements and ascribed this to interspecific variability. Following redescription of the species by Meyer (1932/1933) is incomplete and uninformative, drawings are too general and simplified, resembling any of *Neoechinorhynchus* species.

Amin (2002) arranged *Neoechinorhynchus* in two subgenera, which were differentiated primarily on features of the eggs. *N. agilis* was assigned to the subgenus *Hebesoma*, based on data by Yamaguti, 1935. The present study clearly shown that this species has eggs with concentric shells, while the polar prolongations of the fertilization membrane are absent. Therefore, it should be transferred to the subgenus *Neoechinorhynchus* as *N.* (*N.*) *agilis*.

N. (*N.*) *agilis* is distinguished from all other species of the genus by the following combination of characters: i) all proboscis hooks are equal in the length in each row, all hooks are rooted; ii) the neck ring is thin; iii) six dorsal and two ventral giant hypodermal nuclei are present; iv) lemnisci are markedly unequal and distant from the anterior testis; v) the male reproductive system occupies the posterior half of the body; vi) the posterior end of female posses a moderate caudal papilla. The latter feature is of particular value in distinguishing *N.* (*N.) agilis*. The latest revision by Amin defined 4 species of the subgenus *Neoechinorhynchus* with caudal papilla: *N.* (*N.*) *cylindratus* Van Cleave, 1913, *N.* (*N.*) *chelonos* Schmidt, Esch et Gibbons, 1970, *N.* (*N.) magnapapillosus* Johnson, 1969, *N.* (*N.*) *stunkardi* Cable et Fisher, 1961.

N. (*N.*) *agilis* differs from *N.* (*N.*) *stunkardi* and *N.* (*N.*) *chelonos* by the size of the caudal papilla (larger in *N.* (*N.*) *stunkardi* and smaller in *N.* (*N.*) *chelonos*); from *N.* (*N.*) *chelonos* and *N.* (*N.*) *stunkardi* by the equal size of the proboscis hooks in the each row (rather than lateral anterior proboscis hooks larger in the same row), from *N.* (*N.*) *cylindratus* by the presence of roots in the every row of hooks (rather than unrooted middle and posterior proboscis hooks); from *N.* (*N.*) *cylindratus* and *N.* (*N.*) *chelonos* by the smaller eggs (36–40 x 10–12 vs. 32–47 x 14–16, 46–50 x 20–22, 55–60 x 19–22, respectively) and from *N.* (*N.*) *magnapapillosus* and *N.* (*N.*) *stunkardi* by the larger eggs (36–40 x 10–12 vs. 28–36 x 14–22 and 24–26 x 15–17, respectively), from *N.* (*N.*) *magnapapillosus* and *N.* (*N.*) *stunkardi* by the absence of vacuoles in the acanthor. Moreover, it differs from *N.* (*N.*) *chelonos* by the absence of egg ornamentation and equatorial constriction in the outer membrane. Additionally *N.* (*N.) agilis* differs from *N.* (*N.) cylindratus* by having an attenuating trunk (rather than cylindrical and elongate, with almost parallel sides in the latter species), and from *N.* (*N.*) *stunkardi* by the straight trunk in the posterior end of the female (rather than posterior extremity swollen) (comparative data from Cable et Fisher, 1961; Amin, 2002).

The *Neoechinorhynchus* species listed above occur mostly in freshwater and brackish animals from North America. All compared species are known from the intestinal tract of turtle definitive hosts except *N.* (*N.*) *cylindratus,* which occurs in freshwater fish. Geographically and ecologically separated from the region of other *Neoechinorhynchus* spp. with caudal papilla, *N.* (*N.*) *agilis* seems to be first species of the genus with this feature outside North America.

We have made no attempt to compile the numerous records of *N.* (*N.*) *agilis* from different mullet fish because the present study suggests that the previous descriptions probably apply to different species of *Neoechinorhynchus*. Therefore it is impossible to ascertain

which of these early records actually correspond to *N.* (*N.*) *agilis*. Only Radujković (1989) supplemented the record of this species with drawings and a short list of characteristics and measurements. The drawings provided by Radujković (1989) conform with the morphological features specific for *N.* (*N.*) *agilis*. However, the description was based on parasites from three mullet hosts and therefore the morphometrical data are useless.

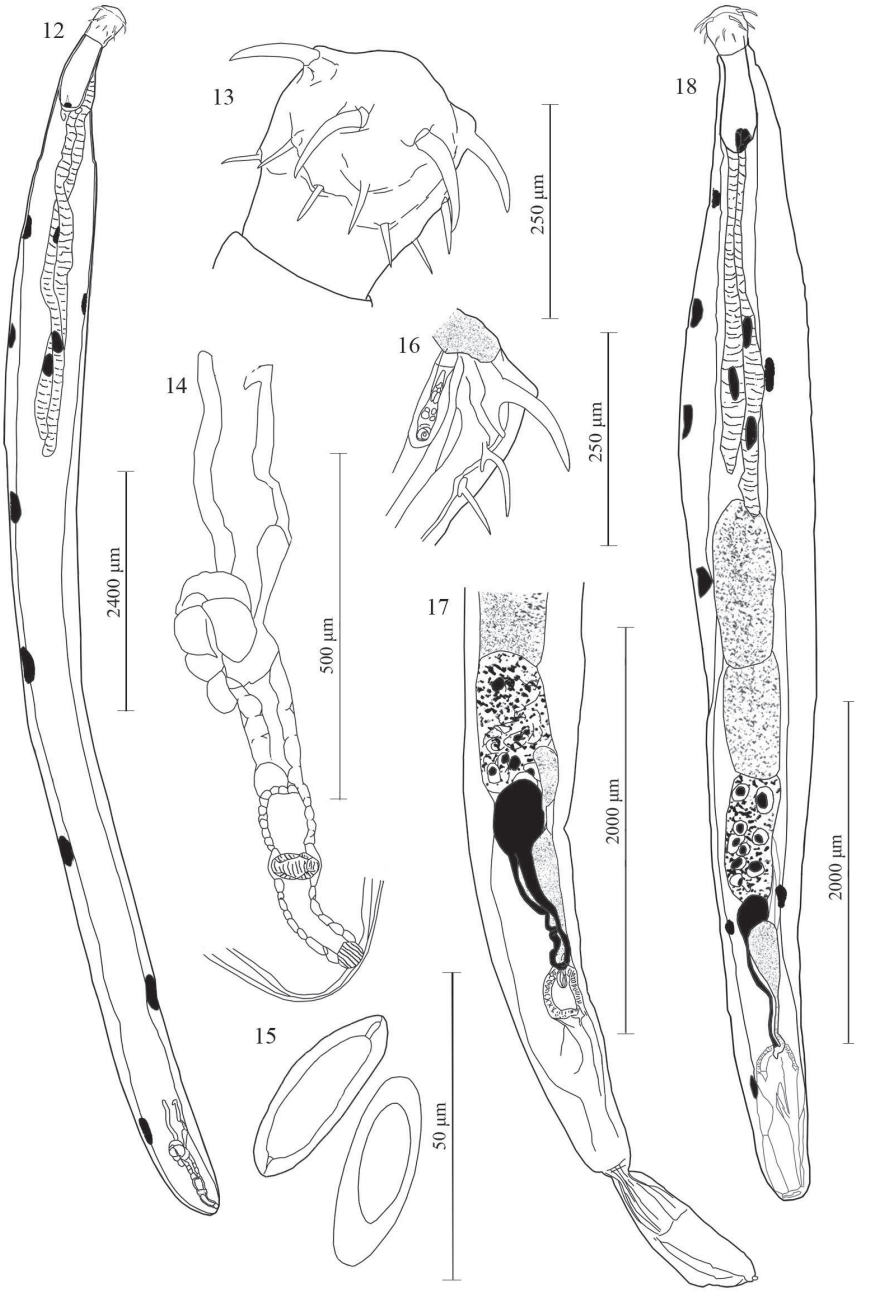

Fig. 12–18. Line drawings of the *Neoechinorhynchus* (*Hebesoma*) *personatus* sp. n. 12 — Female, total view. 13 — Female reproductive system. 14 — Eggs from the body cavity. 15 — Female proboscis in section, hooks with root system. 16 — Female proboscis. 17 — Male reproductive system, bursa everted. 18 — Male, entire view.

Рис. 12–18. Рисунки *Neoechinorhynchus* (*Hebesoma*) *personatus* sp. n. 12 — Общий вид самки. 13 — Женская половая система. 14 — Яйца из полости тела. 15 — Хоботок самки в разрезе, крючья и корни. 16 — Хоботок самки. 17 — Мужская половая система, бурса вывернута. 18 — Общий вид самца.

Table 3. Measurements of *Neoechinorhynchus* (*Hebesoma*) *personatus*, Azov-Black Sea, Ukraine

Таблица 3. Размерные характеристики *Neoechinorhynchus* (*Hebesoma*) *personatus*, Азово-Черноморский регион, Украина

Characters	Mature females					Mature males				
	Min	Max	Mean	SD	N	Min	Max	Mean	SD	N
Trunk L	6,283	12,852	8,559	1,736	26	5,236	10,948	6,541	1,239	19
Trunk W	480	910	695	112	23	400	1,000	680	131	16
Neck L	75	137	95	15.4	21	75	100	85	9.5	17
Neck W	150	238	195	28.8	24	133	220	171	27.1	17
Proboscis L	130	280	178	32.2	22	105	200	160	29.3	17
Proboscis W	190	275	229	23.8	22	156	250	201	25.8	17
Anterior hook L	123	157	137	8.9	24	125	155	136	7.7	19
Anterior hook W	22	30	24.9	2	24	19	27.5	22.8	2.3	20
Anterior hook root L	60	80	70.9	4.7	24	53	75	64.8	4.9	20
Anterior hook root W	16	24	18.6	1.9	22	15	20	18.8	1.6	18
Middle hook L	74	100	85.3	6.5	22	75	97.5	85	5	17
Middle hook W	10	13	10.9	1	23	9	12.5	10.4	0.9	17
Middle hook root L	20	33	28.5	3.3	21	25	34	28.3	2.5	17
Middle hook root W	6	13	7.2	1.9	21	6	10	7.5	1.6	16
Posterior hook L	60	83	73.5	5.5	22	63	85	74.	5.3	15
Posterior hook W	7	10	7.9	0.9	22	7	10	8	0.8	15
Posterior hook root L	17	34	21.9	5	11	16	32	20.5	5.9	12
Posterior hook root W	4	10	6	2.2	11	4	9	5.8	2.3	10
Receptacle L	560	870	724	81.2	25	580	840	676	67.9	18
Receptacle W	70	300	233	59.8	24	100	300	189	60.2	18
Binuclear lemniscus L	2,520	4,300	3,506	536	20	1,980	4,300	3,037	559	18
Uninuclear lemniscus L	2,200	4,080	3,183	499	16	1,500	4,100	2,828	580	17
Anterior testis L						410	1,740	896	334	15
Anterior testis W						160	560	296	94	15
Posterior testis L						420	1,330	803	277	19
Posterior testis W						150	550	270	88	19
Cement gland L						470	1,400	829	284	18
Cement gland W						150	390	259	60	18
Reservoir cement gland L						190	570	303	89	20
Reservoir cement gland W						90	240	174.5	41.2	20
Uterine bell	237	650	369	8,501	17					
Uterus	175	330	238	1,610	25					
Vagina	160	300	208	1,808	26					
Egg L	30	34	31.6	1.6	30					
Egg W	9	11	10	0.7	30					

Note. Abbreviations are given in Material and methods section.

Neoechinorhynchus* (*Hebesoma*) *personatus Tkach, Sarabeev et Shvetsova, **sp. n.**
(fig. 12–18, table 3)

Description

General. Neoechinorhynchinae, with characters of the genus. All shared structures proportionally larger in females. Body normally cylindrical, widest at anterior half, gradually tapering toward anterior end and attenuating posteriorly, arched ventrally. Trunk long, smooth curved, robust. Body wall with reticular lacunar system containing 6 dorsal and 2 ventral giant hypodermal nuclei. Proboscis short, nearly cylindrical, slightly wider than long. Hooks on proboscis arranged in 3 circular rows of 6 hooks each. Hooks in same row equal in size and shape, all hooks with developed roots. Anterior hook semifalciform, stout and massive, middle hook of same shape, shorter and thinner, basal hook shortest

and more spine-shaped. Neck short, approximately three times shorter than proboscis. Proboscis receptacle as single-walled sac with cerebral ganglion at its posterior end. Lemnisci digitiform, large, slightly unequal, much longer than proboscis receptacle, reaching the anterior testis in males. Shorter lemniscus uninuclear; longer lemniscus binuclear.

Male. Based on 22 mature individuals with sperm. Reproductive system occupying posterior part of body, about three fifths of body length. Testes large, elongate oval, tandem, contacting or slightly overlapping each other. Anterior testis longer than posterior one. Syncytial cement gland elongate, with 14–16 giant nuclei, contiguous to posterior testis by its anterior end. Rounded cement gland reservoir leading to 2 cement ducts. Sperm ducts on ventral side of testis swelling posteriorly, then constricting to form common sperm duct at level of cement reservoir. Saefftigen s pouch dorsal, elongate, at level of common sperm reservoir. Genital pore terminal.

Female. Based on 27 adult specimens. Genital system occupying 8–16 % of trunk length. Uterus with composite uterine complex between uterus and uterine bell. Ripe eggs elliptical, with polar prolongation of fertilization membrane. Genital pore subterminal, just ventral to posterior extremity.

Taxonomic summary

Type host. *Mugil cephalus* L.
Other hosts. *Liza haematocheila, L. aurata.*
Type locality. Azov-Black Sea region.
Other localities. Mediterranean Sea.
Site of infection. Intestine, pyloric caeca occasionally.
Type material. MFN 1 (holotype male), MFN 2 (allotype female), MFN 3–15 (paratypes), IZAN 16–30 (paratypes).
Etymology. From Latin *personatus* — masked, referring to the long term of erroneous identification as *N. agilis*.

Remarks

N. (*H.*) *personatus* sp. n. is distinguished from other species of the genus by the following combination of characters: i) the body wall contains six dorsal and two ventral giant hypodermal nuclei; ii) all hooks are equal in size in each row, decreasing progressively in length posteriorly, all hooks are rooted; iii) lemnisci are subequal, reaching the anterior testis; iv) the cement gland is not appreciably longer than either testis; v) the gonopore of adult female is subterminal, just ventral to the posterior extremity.

The new species shares the latter four features with *N.* (*N.*) *strigosus* Van Cleave, 1949, *N.* (*N.*) *villoldi* Vizcaino, 1992, *N.* (*N.*) *rigidus* Van Cleave, 1928 and *N. (N.) chilkaensis* Podder, 1937 (Amin, 2002). However, several distinct morphological and morphometrical characters allow differentiating these species. Additionally to the differences in the number of hypodermal nuclei *N.* (*N.*) *personatus* sp. n. differs from *N.* (*N.*) *strigosus* by having the cement gland contiguous to the posterior testis and smaller eggs (28–34 x x 8–11 vs. 53–72 x 26–31); from *N.* (*N.*) *chilkaensis, N.* (*N.*) *rigidus* and *N.* (*N.*) *villoldi* by having larger proboscis hooks (anterior 120–155, middle 72–97.5, posterior 63–85 in males, 120–157, 74–100, 60–83 in females vs. 65–70, 35–45, 26–30 in males, 68–78, 33–40, 30–35 in females, 60–75, 45–54, 42–48 in males, 60–81, 36–63, 45–60 in females and 25–29, 24–28, 19–23 in males; 27–35, 23–28, 19–30 in females, respectively); further, from *N.* (*N.*) *chilkaensis* by the rooted hooks in every row and the larger eggs (28–34 x 8–11 vs. 18–19 x 12–13). *N.* (*N.*) *personatus* sp. n. occurs sympatrically with *N.* (*N.*) *agilis* and differs from the latter species by the longer hooks (122.5–155 anterior, 72.5–97.5 middle, 63-85 posterior, in males, 120–157, 74–100, 60–83 in females rather than 87.5–102.5, 50–

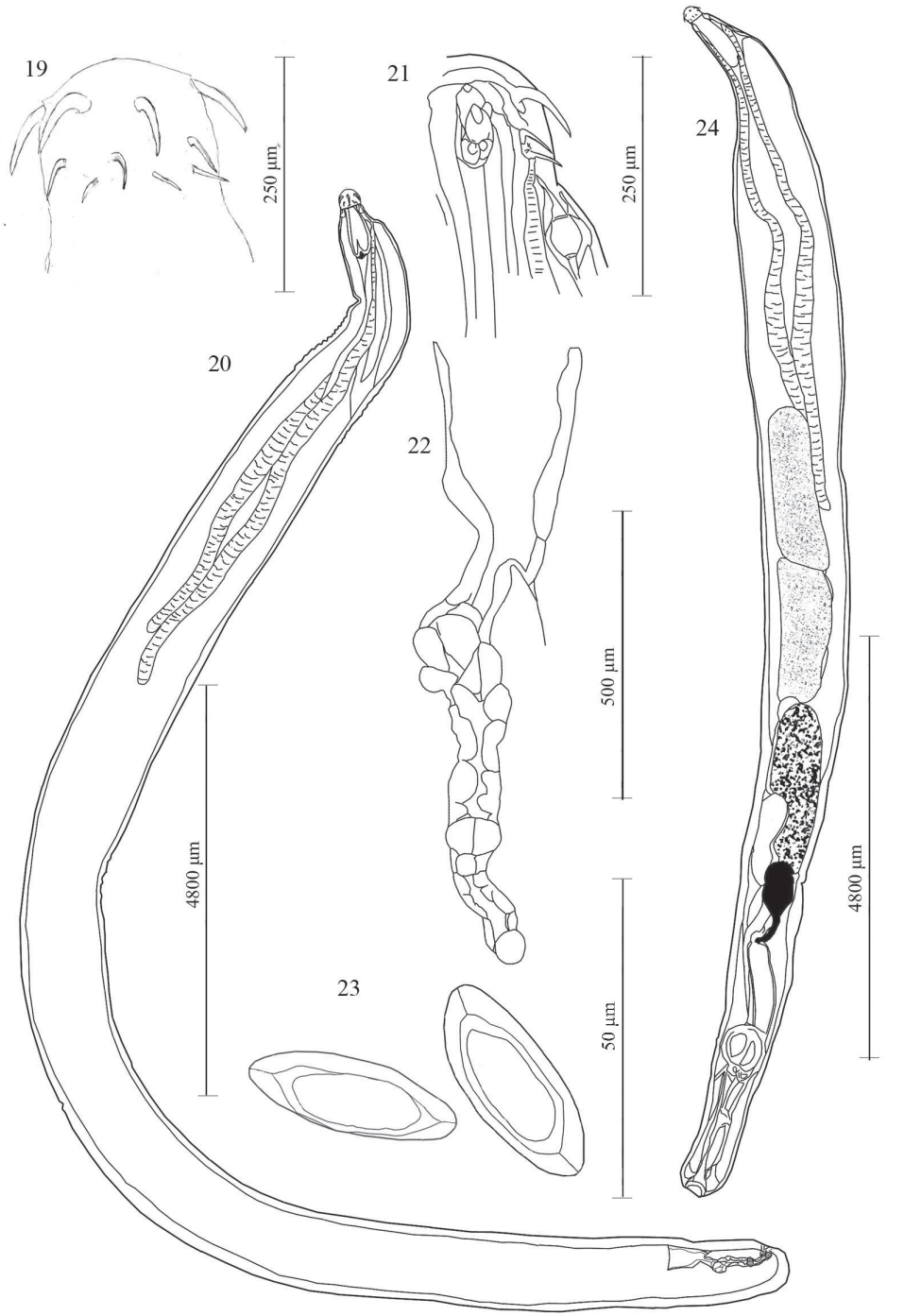

Fig. 19–24. Line drawings of the *Neoechinorhynchus* (*Hebesoma*) *yamagutii* sp. n. 19 — Female proboscis. 20 — Female, total view. 21 — Male proboscis in section, hooks with root system. 22 — Female reproductive system. 23 — Eggs from the body cavity. 24 — Male, entire view.

Рис. 19–24. Рисунки *Neoechinorhynchus* (*Hebesoma*) *yamagutii* sp. n. 19 — Хоботок самки. 20 — Общий вид самки. 21 — Хоботок самца в разрезе, крючья и корни. 22 — Женская половая система. 23 — Яйца из полости тела. 24 — Общий вид самца.

Table 4. Measurements of *Neoechinorhynchus* (*Hebesoma*) *yamaguti*, Inland Sea, Suruga Bay, Ariake Sea, Japan

Таблица 4. Размерные характеристики *Neoechinorhynchus* (*Hebesoma*) *yamaguti*, Внутреннее море, залив Суруга, море Ариаке, Япония

Characters	Mature females					Mature males				
	Min	Max	Mean	SD	N	Min	Max	Mean	SD	N
Trunk L	10,800	24,705	17,550	5,371	7	6,953	18,360	11,813	4,351	6
Trunk W	570	1,100	858	196	6	600	1,100	805	231	6
Neck L	17.5	40	26.7	8.8	6	15	38	27.1	7.7	6
Neck W	113	200	147	33.6	6	95	188	140.4	40.6	6
Proboscis L	103	185	130	30	6	105	1,150	122	19.1	6
Proboscis W	125	183	152	25.5	6	110	205	156	37.1	6
Anterior hook L	78	105	94	9.2	6	83	115	102	11.8	6
Anterior hook W	15	19	17.7	1.5	6	17	19	18	0.9	6
Anterior hook root L	42	58	50	5.8	6	48	55	49.9	2.7	6
Anterior hook root W	12	16	14.2	1.3	6	10	15	12.5	2.7	6
Middle hook L	36	58	48.7	7.8	6	48	60	52.8	5.4	6
Middle hook W	5	8	6.5	1.1	6	5	7	6	0.9	6
Middle hook root L	14	18	16	1.3	6	15	18	16.8	1.2	6
Middle hook root W	4	6	4.7	0.8	6	4	6	5	0.6	6
Posterior hook L	34	55	40.2	8	6	36	56	43.3	7	6
Posterior hook W	4.5	7	5.6	0.9	6	4.5	7	5.4	0.9	6
Posterior hook root L	11	14	13	1.2	5	13	17	14.2	1.6	6
Posterior hook root W	3	4	3.7	0.6	3	3	4	3.6	0.6	5
Receptacle L	460	760	625	106	6	430	850	596.7	152	6
Receptacle W	100	250	169	64.8	6	90	280	167.5	75	6
Binuclear lemniscus L	3,640	6,340	4,524	1,074	5	2,200	5,800	3,988	1,506	6
Uninuclear lemniscus L	3,350	5,800	4,156	1,003	5	1,800	5,500	3,655	1,494	6
Anterior testis L						530	1,850	1,222	506	6
Anterior testis W						250	540	387	105	6
Posterior testis L						450	1,630	1,030	425	6
Posterior testis W						200	590	385	149	6
Cement gland L						600	1,870	1,328	466	6
Cement gland W						320	580	470	103	6
Reservoir cement gland L						280	620	473	112	6
Reservoir cement gland W						200	500	350	98	6
Uterine bell	250	650	536	158	6					
Uterus	140	387	265	96	7					
Vagina	57	237	146	63.3	7					
Egg L	26	29	27.3	1.5	15					
Egg W	10	10	10	–	15					

Note. Abbreviations are given in Material and methods section.

57.5, 37.5–50 in males, 87.5–110, 45–62.5, 15–20 in females in *N.* (*N.*) *agilis*, respectively), different position of the lemnisci in relation to the anterior testis (extending to the anterior testis rather than not reaching in *N.* (*N.*) *agilis*), the terminal position of the gonopore in females and absence of genital papilla (rather than the gonopore subterminal and the papilla present in *N.* (*N.*) *agilis*) (comparative data from Amin, 2002).

Neoechinorhynchus* (*Hebesoma*) *yamagutii Tkach, Sarabeev et Shvetsova, **sp. n.**
(fig. 19–24, table 4)

Description

General. Neoechinorhynchidae with characters of *Neoechinorhynchus.* Trunk long, cylindrical, curved ventrally, widest at anterior one third of the body, robust, walled. Body

wall with 6 dorsal and 2 ventral giant hypodermal nuclei. Proboscis short, cylindrical, slightly wider than long. Hooks of proboscis arranged in 6 spiral rows of 3 each. In each row, hooks equal in size and shape, all hooks with developed roots. Anterior hook semifalciform, longer and stouter than others. Middle hook shorter and thiner, one-half of anterior one. Basal hook subequal to middle hooks. Neck short, between one third and one sixth shorter than proboscis. Proboscis receptacle single-walled sac with cerebral ganglion at its posterior end, anterior part of proboscis receptacle enclosed by massive neck ring. Lemnisci digitiform, large, posteriorly narrowing dramatically, slightly unequal, much longer than proboscis receptacle, reaching to posterior half of anterior testis in males. Shorter lemniscus with 1 giant nucleus, larger lemniscus about 10 % longer, with 2 giant nuclei.

Male. Based on 6 mature individuals. Reproductive system in posterior two thirds of body. Testes large, elongate oval, tandem, contacting or slightly overlapping each other. Anterior testis longer than posterior one. Syncytial cement gland elongate pyriform, with 8 giant nuclei, contiguous to posterior testis by its anterior end. Rounded cement gland reservoir entering 2 cement ducts. Sperm ducts on ventral side of testis swelling posteriorly, then constricting to form common sperm duct at level of cement reservoir. Saefftigen's pouch dorsal, elongate, at level of common sperm reservoir. Genital pore terminal.

Female. Based on 7 mature specimens. Female genital system occupying 5–8 % of trunk length. Uterine bell about as long as vagina and uterus together. Uterus with composite uterine complex between uterus and uterine bell. Genital pore subterminal. Ripe eggs elliptical, with polar prolongations of fertilization membrane.

Taxonomic summary

Synonym. *Neoechinorhynchus agilis* (Rudolphi, 1819) sensu Yamaguti (1935).
Type host. *Mugil cephalus* L.
Other hosts. *Liza haematocheila.*
Type locality. Ariake Sea, Inland Sea, Suruga Bay.
Other localities. Japan Sea: Kiyevka Bay, Razdol'naya Delta.
Site of infection. Intestine.
Type material. MPM 22471 (SY 7562, SY 7563), 22472 (SY 75–64), 22473 (SY 75–65), 22474 (SY 75–66).
Etymology. The new species is named after the eminent helminthologist Satyu Yamaguti.

Remarks

N. (*H.*) *yamagutii* sp. n. is distinguished from all other species of the genus by the following combination of the characters: i) all hooks are equal in size in each row, hooks decrease progressively in length posteriorly, all hooks are rooted; ii) a thick neck ring is present; iii) the neck is relatively short; iv) six dorsal and two ventral giant hypodermal nuclei are present; v) lemnisci are slightly unequal, reaching to the posterior half of the anterior testis; vi) the male reproductive system occupies two posterior thirds of the body.

According to Amin (2002), the egg structure is a character of subgeneric importance. In the view of the current evidence only 11 species of the genus are in the subgenus *Hebesoma*: *N.* (*H.*) *carinatus* Buckner et Buckner, 1993; *N.* (*H.*) *chrysemydis* Cable et Hopp, 1954; *N.* (*H.*) *didelphis* Amin, 2001; *N.* (*H.*) *doryphorus* Van Cleave et Bangham, 1949; *N.* (*H.*) *idahoensis* Amin et Heckmann, 1992; *N.* (*H.*) *lingulatus* Nickol et Ernst, 1987; *N.* (*H.*) *manasbalensis* Kaw, 1951; *N.* (*H.*) *pungitius* Dechtiar, 1971; *N.* (*H.*) *rostratus* Amin et Bullock, 1998 (emend.); *N.* (*H.*) *tenellus* Amin et Muzzall, 2009; *N.* (*H.*) *violentus* (Van Cleave, 1928) Salgado Maldonado, 1978 (emend.) according to Amin, 2002, Amin and Muzzall, 2009.

N. (*H.*) *yamagutii* sp. n. differs from *N.* (*H.*) *violentus, N.* (*H.*) *manasbalensis* and *N.* (*H.*) *pungitius* in the cylindrical-shaped trunk (rather than spindle-shaped in

N. (*H.*) *violentus* and fusiform in *N.* (*H.*) *manasbalensis* and *N.* (*H.*) *pungitius*); from the *N.* (*H.*) *violentus* by the presence of the giant hypodermal nuclei (rather than giant hypodermal nuclei not marked); from *N.* (*H.*) *carinatus, N.* (*H.*) *chrysemydis, N.* (*H.*) *doryphorus* and *N.* (*H.*) *tenellus* by having equal proboscis hooks in each row (rather than lateral anterior proboscis hooks longer than other hooks in same row); from *N.* (*H.*) *idahoensis* by hooks decreasing in size posteriorly (rather than anterior proboscis hooks similar in length to middle hooks); from *N.* (*H.*) *tenellus* by the absence of sensory pits on the proboscis (rather than 2 sensory pits present at the level of the middle hooks); from *N.* (*H.*) *rostratus* by having all hooks of the proboscis rooted (rather than only anterior proboscis hooks rooted); from *N.* (*H.*) *carinatus* and *N.* (*H.*) *idahoensis* by having subequal lemnisci (rather than lemnisci markedly unequal); from *N.* (*H.*) *chrysemydis* by the absence of papilla at the posterior end of female (rather than small knob-like papilla present); from *N.* (*H.*) *didelphis* by having a single uterine bell in the female (rather than two uterine bells present in the latter species).

It is also necessary to indicate the differences between *N.* (*H.*) *yamagutii* sp. n., *N.* (*N.*) *agilis*, *N.* (*H.*) *personatus* and *N.* (*N.*) *tylosuri*, because all occur in *M. cephalus*. According to the current evidence, the form described by Yamaguti (1935) from *M. cephalus* as *N. agilis* actually represent *N.* (*H.*) *yamagutii* sp n. The present study shows that *N.* (*H.*) *yamagutii* sp. n. differs from *N.* (*H.*) *personatus* sp. n. and *N.* (*N.*) *tylosuri* by the presence of the thick neck ring (rather than the neck ring absent) and distinct ranges of proboscis hooks length (anterior 82.5–115, middle 45–60, posterior 36–56 in males, 78–105, 36–58, 34–55 in females vs. 122.5–155, 72.5–97.5, 63–85 in males, 120–157, 74–100, 60–83 in females in *N.* (*H.*) *personatus* sp. n. and 60–69, 30, 30–35 in males, 75, 35, 35 in females in *N.* (*N.*) *tylosuri*, respectively), from *N.* (*N.*) *agilis* and *N.* (*N.*) *tylosuri* by the subequal in length lemnisci reaching the anterior testis in males (rather than unequal in length lemnisci, not reaching the anterior testis on males), from *N.* (*N.*) *agilis* by absence of the caudal papilla (rather than a medium-sized caudal papilla disposed terminally to the genital pore), from *N.* (*N.*) *agilis* and *N.* (*N.*) *tylosuri* by eggs with concentric membranes (rather than polar prolongations of the fertilization membrane present in fully ripe eggs) (comparative data from Amin, 2002).

Due to excellent state of voucher specimens provided by Yamaguti (1935) and the long term usage of the description based on those we propose the specimens studied herein from MPM as the type specimens of *N.* (*N.*) *yamagutii* sp. n. However, examined slides MPM 22473 SY 75–65 contained mixed set of specimens including both *N.* (*N.*) *yamagutii* sp. n. and *N. tylosuri* (Yamaguti, 1939). The latter was described only several years later. This explains a wide range of metric characteristics provided for *N. agilis* in Yamaguti's (1935) redescription.

Discussion

The present study reveals that *N. agilis,* so far regarded as a single form with a wide geographical distribution and multiple host range, represents at least three species, separated by geographic and host barrier. About a hundred years ago Van Cleave (1921) stated the absence of *N. agilis* in American freshwater hosts, explaining earlier erroneous identifications of acanthocephalans, by morphological similarity among the species *Neoechinorhynchus*, as well as the marked tendency to ascribe collected forms to already known European species. A good example of misidentification was recently provided by Amin et al. (2001), who described *N.* (*N.*) *iraqensis* from *L. abu* in freshwater localities of Iraq, putting upon doubts more than 25 papers with records of *N. agilis.*

C. labrosus occurs in Eastern Atlantic and Mediterranean were the only recorded host of *N.* (*N.*) *agilis* according to this study. This acanthocephalan has been traditionally considered as a parasite of *M. cephalus*. However, we consider that this is due to poor understanding of the taxonomy of Mugilidae when the original description of *N. agilis*

was published (Rudolphi, 1819). So it is impossible to define the type host for this worm. *C. labrosus* probably is a single typical host of *N.* (*N.*) *agilis*.

M. cephalus is one of the few coastal marine species of fish considered to have worldwide distribution in tropical, subtropical and temperate zones (Thomson, 1990). Nevertheless, it has been shown that *M. cephalus* showed significant genetic heterogeneity (Crosetti et al., 1993; Huang et al., 2001). Recent studies indicate that it may represent a species complex that includes at least 14 species (Durand et al., 2012; Whitfield et al., 2012). Parasite host specificity may vary even if species is close in ecology and genetics. Parasites are usually considered to be good biological markers of their host evolution and diversity (Euzet et al., 1989; Thomas et al., 1996). The current knowledge of the diversity and distribution of *Neoechinorhynchus* spp. in mullets support this hypothesis. At the same time species diversity of this genus can be the result of allopatric or alloxenic speciation.

Samples of acanthocephalan parasites from *M. cephalus* in the northeast Atlantic and the northwest Pacific revealed the presence of two new species of acanthocephalans. One of those is *N.* (*H.*) *personatus* sp. n. from the Azov-Black Sea region and the Mediterranean, other, *N.* (*H.*) *yamagutii* sp. n., from the Japan coastal waters. Both of them occurred in other mullet hosts with respect to their geographic distribution. *N.* (*H.*) *personatus* sp. n. was registered in *L. aurata* and *L. haematocheila*, and *N.* (*H.*) *yamagutii* sp. n. in *L. haematocheila*.

The natural range of *L. haematocheila* is the Amur River estuary and the Sea of Japan. It has been introduced in the Azov-Black Sea in order to replace two sympatric species of mullets that had undergone severe reductions in population. Now it is fully acclimated and widely exploited by fishermen in Ukrainian, Russian and Turkish waters (Starushenko, Kazanski, 1996). The absence of *N.* (*H.*) *yamagutii* sp. n. in the new area indicates that this parasite was not introduced together with its host. We suppose that might happen due to this parasite was not transferred to the region of introduction or did not find suitable conditions for the life cycle.

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