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Invalidity of three Palaearctic species of *Triaenophorus* tapeworms (Cestoda: Pseudophyllidea): evidence from morphometric analysis of scolex hooks

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Abstract. A comparative study of the scolex hook morphology of five species of tapeworms of the genus *Triaenophorus* Rudolphi, 1793 (Cestoda: Pseudophyllidea), parasites of pikes (*Esox lucius* L. and *E. reichertii* Dybowski) in the Palaearctic Region, was carried out. Measurements of scolex hooks of 81 plerocercoids and 492 adults from different hosts and regions were compared using basic statistics and forward stepwise linear discriminant analysis. The shape of the scolex and that of tridental hooks were found to be suitable only for differentiation of the taxa with a similar shape of hooks, i.e. *Triaenophorus nodulosus* (Pallas, 1781) from *T. amurensis* Kuperman, 1968, and *T. crassus* Forel, 1868 from *T. meridionalis* Kuperman, 1968 and *T. orientalis* Kuperman, 1968, respectively. In contrast, discriminant analysis did not enable reliable separation of specimens of individual taxa of these two morphological groups due to high intraspecific variability and overlaps between species. This was reflected in low classification efficiencies (average 83%) of all species of the *T. crassus* group, whereas all *T. amurensis* specimens were misidentified as *T. nodulosus*. The new data also considerably enlarge (up to twofold) the size range of the species described by Kuperman in 1968, which invalidates suitability of the most important discriminant characteristic, the width of the basal plate, for delimitation of *Triaenophorus* species. Based on the present data, all Kuperman's taxa are considered to represent only distinct geographical populations of *T. nodulosus* and *T. crassus*. As a result, *T. amurensis* is synonymized with *T. nodulosus*, whereas *T. orientalis* is considered to be a synonym of *T. crassus*. Previous synonymisation of *T. meridionalis* with *T. crassus*, first proposed by Dubinina (1987), is also accepted.

Tapeworms of the genus *Triaenophorus* Rudolphi, 1793 (Cestoda: Pseudophyllidea) are frequent parasites of common pike (*Esox lucius* L.), Amur pike (*E. reichertii* Dybowski) and walleye [*Sander vitreus* (Mitchill)], distributed circumboreally (Kuperman 1973, Schmidt 1986, Bray et al. 1994). Unlike most other pseudophyllidean tapeworms, their scolex has, besides paired bothria, two pairs of well-developed, large tridental hooks. The hooks are composed of a basal plate, one central prong and two (one smaller and one larger) lateral prongs (Figs. 1–3). A most recent molecular study on the phylogeny of the Pseudophyllidea has indicated the most basal position of the genus among the "Bothriocephalidea", a more evolved group of the two, apparently unrelated clades of pseudophyllideans (Brabec et al. 2006).

The type species, *T. nodulosus* (Pallas, 1781) [syns. *Taenia rugosa* Pallas, 1760 *in part*; *Taenia piscium* Pallas, 1766 *in part*; *Taenia lucii* Müller, 1776 *in part*; *Taenia tricuspidatus* Bloch, 1779 – for other synonyms see Kuperman 1973)] and *T. crassus* Forel, 1868 (syn. *T. robustus* Olson, 1893), have been reported from a number of second (fish) intermediate hosts in Europe and Asia, including the former Soviet Union. *Triaenophorus nodulosus* also occurs in North America (Lawler and Scott 1954, Hoffman 1999). These taxa differ markedly from each other in the morphology and size of the hooks and their larvae (plerocercoids) infect different fish hosts, whereas adults may occur simultaneously in the intestine of pikes (*Esox* spp.) (Kuperman 1973, Protasova 1977).

In 1968, Kuperman erected three new species and differentiated them from *T. nodulosus* and *T. crassus* only by slight differences in the width of scolex hooks, different second intermediate hosts and zoogeographical distribution. *Triaenophorus meridionalis* Kuperman, 1968 was reported to occur only in the southeastern regions of the former Soviet Union (but without a marked boundary of its distribution in the north), whereas the distribution areas of *T. amurensis* Kuper-

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man, 1968 and *T. orientalis* Kuperman, 1968 were supposed to be limited to the Amur River basin of the Russian Far East (Kuperman 1967, 1968, 1973).

High level of intraspecific variability of *T. nodulosus* was observed by Protasova (1997), who compared scolex and strobilar characteristics of adults and plerocercoids from different regions of the ex-USSR, and Rusinek and Kuznedelov (2001), who measured *T. nodulosus* larvae and adults from fish in Baikal Lake in Russia. These data suggest that slight differences in hook measurements between *Triaenophorus* taxa reported from the Palaearctic might be accounted for by intraspecific variation of geographically distant populations of *T. crassus* and *T. nodulosus*, thus not supporting the existence of several separate species.

During a research stay at the Institute of Biology of Inland Waters, Russian Academy of Sciences (RAS), in Borok, Russia and the Parasitological Institute, RAS (previously GELAN, i.e. Helminthological Laboratory of the Academy of Sciences), Moscow, Russia, in June 2004, two of the present authors (R.K. and T.S.) took the opportunity to study specimens of *Triaenophorus* described by the late B.I. Kuperman in 1968 (specimens not numbered), as well as other museum specimens (vouchers) of *T. crassus* and *T. nodulosus* from helminthological collections of the Institute of Parasitology, Biology Centre, Academy of Sciences of the Czech Republic, České Budějovice (IPCAS). In addition, the type material of Kuperman's taxa from the Zoological Institute, RAS, Saint Petersburg, Russia (ZIN) was studied. This made it possible to perform a comparative study of hook morphology and to assess the validity of all *Triaenophorus* taxa reported from freshwater fish in the Palaearctic Region.

MATERIALS AND METHODS

The following specimens of *Triaenophorus* species were studied (see Table 1 for more data on the hosts, localities and number of specimens measured):

(i) *Triaenophorus nodulosus* (IPCAS C-28 and C-40) – 219 hooks of adults and 33 hooks of plerocercoids were measured;

(ii) *T. amurensis* (ZIN 15.7.0 and 15.7.1 – probably type specimens, but not so labeled; IPCAS C-431 and C-432) – 29 + 3 hooks measured;

(iii) *T. crassus* (IPCAS C-326 and C-350) – 146 + 31 hooks measured;

(iv) *T. meridionalis* (ZIN 15.7.3 – probably type specimens, but not so labeled; IPCAS C-433) – 47 hooks of adults measured;

(v) *T. orientalis* (ZIN 15.7.4 and 15.7.6 – probably type specimens, but not so labeled; IPCAS C-434 and C-435) – 51 + 14 hooks measured.

Hooks were measured using QuickPHOTO MICRO 2.1. software (Olympus, 2004) and Olympus CX-41 and BX-51 microscopes. Four measurements of scolex hooks (1, 2 – the width and height of the basal plate; 3, 4 – lengths of two lateral prongs) were taken according to Kuperman (1968, 1973), whereas three others (5–7 – distance between lateral prongs and that between each lateral prong and median prong) were measured as obvious from Fig. 2F. Morphometric data were analysed using forward stepwise linear discriminant analyses using the software package Statistica 6.0 (1997) (StatSoft Inc., Tulsa, OK, USA) to test differences between individual taxa (Hanzelová et al. 2005, Kuchta et al. 2006). Several scoleces of *T. nodulosus* from the Czech Republic and *T. crassus* from Italy were prepared for scanning electron microscope (SEM) using the methodology outlined by Scholz et al. (1998).

RESULTS

Morphology of the scolex

The shape of scoleces of all five species studied exhibited a high intraspecific variation, apparently also due to fixation, because most specimens were compressed. Due to that, differences in the shape of the scolex between *T. nodulosus* and *T. amurensis* (Fig. 1), and *T. crassus*, *T. meridionalis* and *T. orientalis* (Fig. 2), respectively, could not be reliably recognized. Therefore, the shape of the scolex and hooks is not considered here to be suitable for species discrimination (Figs. 1–3).

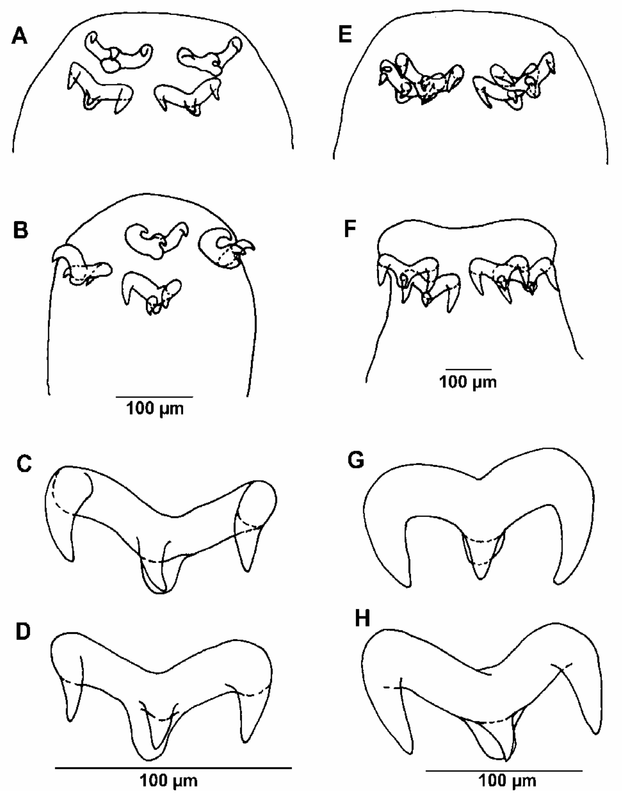

Fig. 1. Scoleces and scolex hooks of *Triaenophorus amurensis* Kuperman, 1968 (A–D) and *T. nodulosus* (Pallas, 1781) (E–H). **A**, **C**, **D** – adults from the intestine of *Esox reichertii*, Amur River, Russia; **B** – plerocercoid from the liver of *E. reichertii*, Amur River, Russia; **E**, **F** – adults from the intestine of *Esox lucius*, Mácha Lake, Czech Republic; **G**, **H** – plerocercoids from the liver of *Perca fluviatilis*, Mácha Lake, Czech Republic.

Table 1. Survey of *Triaenophorus* specimens studied.

Species	Host	Locality	Number of hooks examined	
			Plerocercoid	Adult
T. nodulosus		RUSSIA		
	Coregonus albula	Rybinsk reservoir, Yaroslavl	2	–
	Esox lucius	Segozero Lake, Karelia	–	5
		SLOVAKIA		
	Lepomis gibbosus	Eastern Slovakia	3	–
		CZECH REPUBLIC		
	Perca fluviatilis	Mácha Lake – Břehyně	28	–
	Esox lucius	Mácha Lake – Břehyně		188
		ITALY		
	Esox lucius	Bracciano Lake	–	1
		Vico Lake	–	2
		MACEDONIA		
	Esox lucius	Prespansk Lake	–	15
		NORWAY		
	Esox lucius	Gjende Lake	–	8
		Total	252	
T. amurensis		RUSSIA		
	Esox reichertii	Amur River	3	–
		Amur River	–	11
		Lake Bolon	–	18
		Total	32	
T. crassus		ITALY		
	Coregonus albula	San Valentino Lake	17	–
	Esox lucius	San Valentino Lake	–	114
		NORWAY		
	Coregonus albula	Locality unknown	2	–
		RUSSIA		
	Coregonus albula	Rybinsk reservoir, Yaroslavl	12	–
	Esox lucius	Delta of Yenisey River	–	7
		Kolyma River	–	2
		Ob River	–	15
		Penzhina River	–	5
		Rybinsk reservoir, Yaroslavl	–	2
		Segozero Lake, Karelia	–	1
		Total	177	
T. meridionalis		RUSSIA		
	Esox lucius	Delta of Volga River, Astrakhan	–	30
		Kuban River	–	4
		Volga River	–	12
		Locality unknown	–	1
		Total	47	
T. orientalis		RUSSIA		
	Perccottus glenii	Amur River	3	–
		Bolon Lake	11	–
	Esox reichertii	Amur River	–	2
		Bolon Lake	–	7
		Delta of Toma River	–	8
		Sheyetyanka Lake	–	7
		Ul River	–	1
		Yelabuga River	–	6
		Zeya River	–	20
		Total	65	

Scolex hook measurements

Measurements of scolex hooks are summarized in Table 2. Hook characters of plerocercoids and adults were compared by *t*-test, but no significant differences were found (data not shown). Since most measurements overlapped between the species, it was not possible to distinguish hooks of all specimens of individual taxa on the basis of any single character only. In addition, most dimensions markedly differed in their range, especially their maximum limits, from those used by Kuperman (1968, 1973) to differentiate *T. amurensis* from *T. nodulosus*, and *T. meridionalis*, *T. orientalis* from *T. crassus*. For example, the maximum value of the most important discriminative characteristic, i.e. the width of the basal plate, was reported by Kuperman (1968, 1973) to reach 165 µm in *T. orientalis*, but the plate can be in fact as much as 330 µm wide (Table 2). Thus the present data considerably enlarge the size range of hook measure-

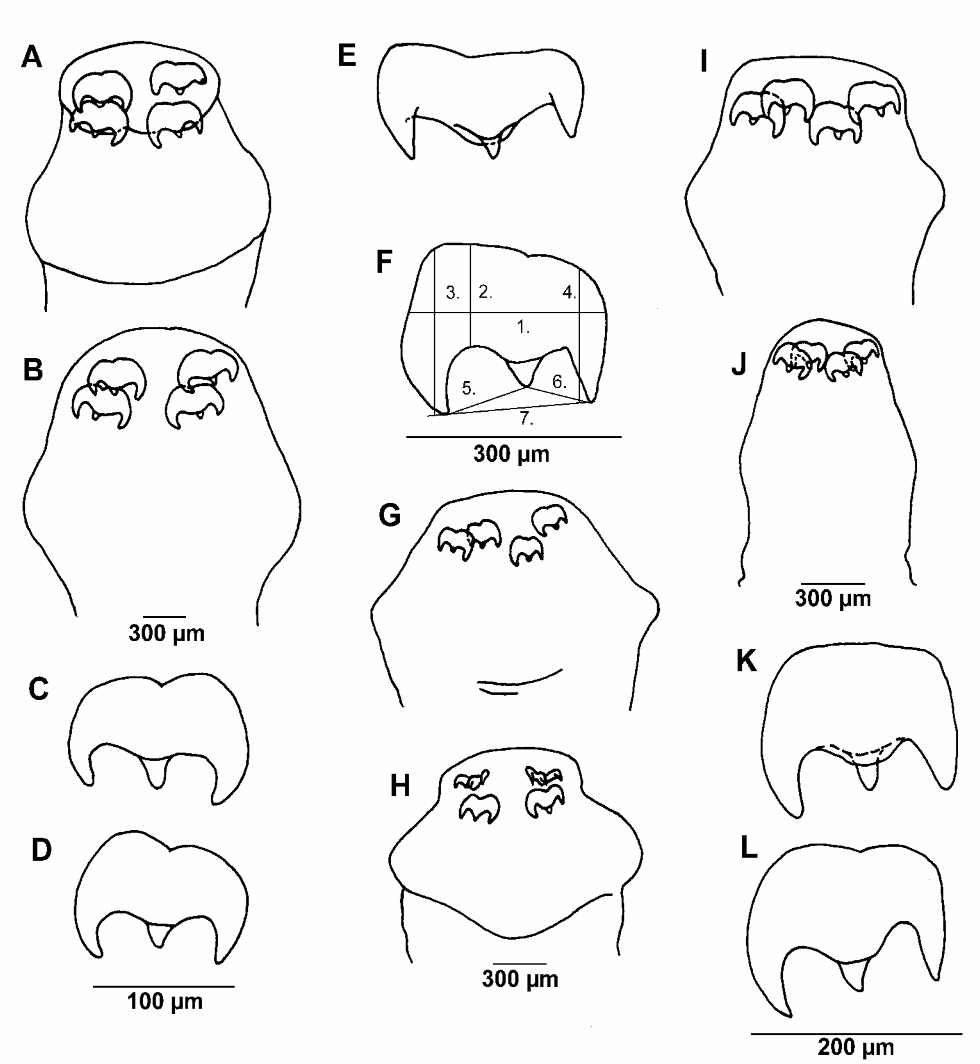

Fig. 2. Scoleces and scolex hooks of *Triaenophorus crassus* Forel, 1868 (A–D), *T. meridionalis* Kuperman, 1968 (E–H), and *T. orientalis* Kuperman, 1968 (I–L). Measurements of hooks compared in this study are indicated in F. **A** – adult from the intestine of *Esox lucius*, Penzhina River; **B**–**D** – plerocercoids from the musculature of *Coregonus albula*, Rybinsk reservoir; **E**–**H** – adults from the intestine of *E. lucius*, Volga River delta; **I** – adult from the intestine of *Esox reichertii*, Bolon Lake; **J** – plerocercoid from the liver of *E. reichertii*, Bolon Lake; **K** – adult from the intestine of *E. reichertii*, Zeya River; **L** – plerocercoid from the musculature of *Perccottus glenii*, Bolon Lake. All localities in Russia.

ments of all species under study, which actually much more resemble each other. This overlap in the size of scolex hooks invalidates discriminative characteristics used by Kuperman (1968, 1973) to differentiate individual *Triaenophorus* taxa.

Discriminant analysis

Results of a forward stepwise linear discriminant analysis, with all seven variables used by the model to separate and discriminate five species of *Triaenophorus*, are presented in Table 3 and Fig. 4. It is apparent that the measurements of the scolex hooks of *T. amurensis* overlap those of *T. nodulosus*; similarly, the size of the hooks of *T. meridionalis*, *T. orientalis* and *T. crassus* also overlap (Fig. 4). Using Wilk's Lambda parameter, the height of the basal plate was found to be the most suitable distinguishing characteristic. The first two roots of the model based on the measurements accounted for 99.6% of the total variation among samples. However, the model provided overall correct classification efficiency of 83% only, with the high efficiency obtained only for *T. nodulosus* specimens (100%). Correct classification of taxa of the *T. crassus* morphological group, i.e. *T. crassus*, *T. meridionalis* and *T. orientalis*, was very low (23% only for *T. meridionalis* and 77% for *T. orientalis*) and all samples of *T. amurensis* were misclassified as *T. nodulosus* (Table 4).

The size variability of individual taxa is markedly lower in the group of *T. nodulosus* (the coefficient of variability of the height of the basal plate 18.6%) than in *T. crassus* and related species, i.e. *T. orientalis* and *T. meridionalis*, which is very high (CV = 32.8%) (Fig. 4).

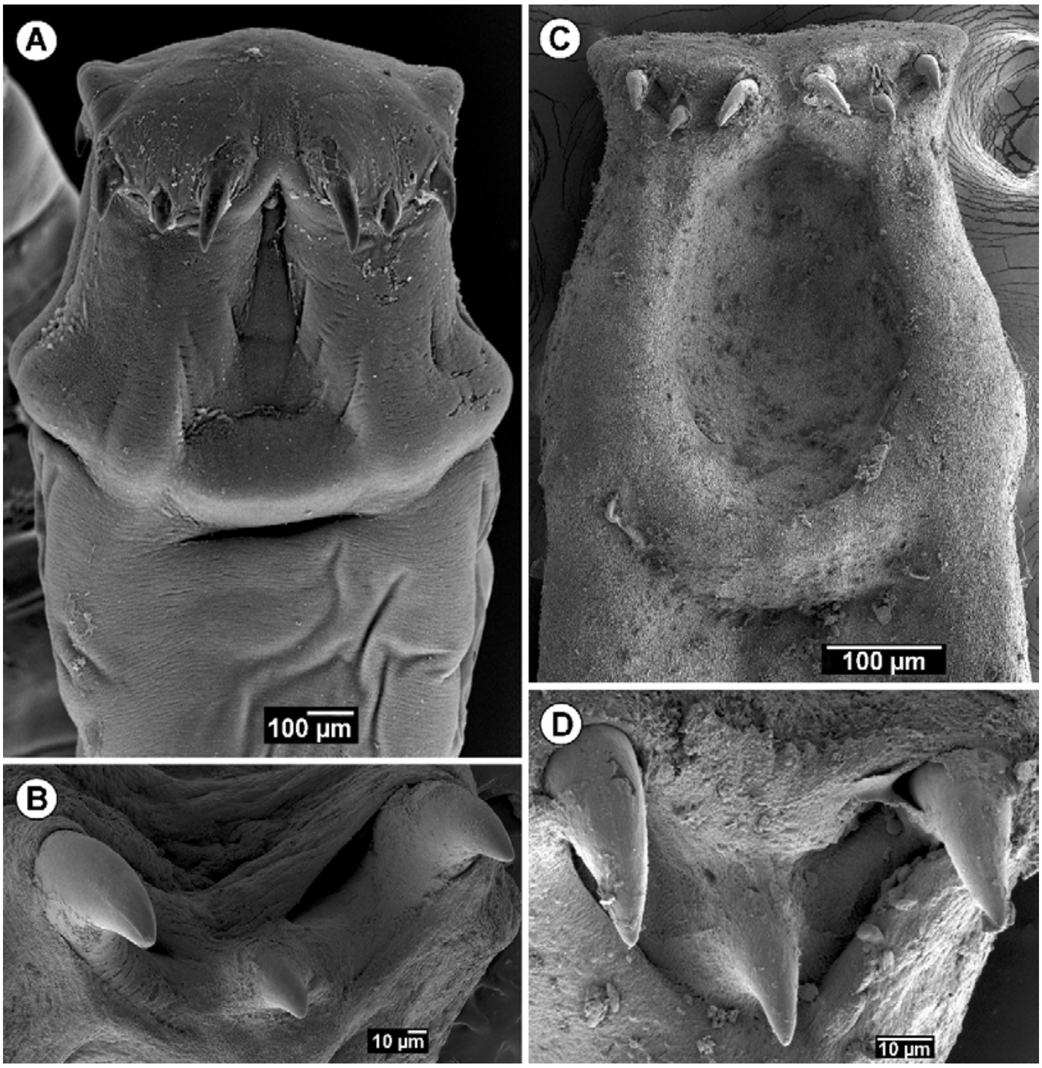

Fig. 3. Scanning electron micrographs of scoleces (A, C) and scolex hooks (B, D). **A**, **B** – adults of *Triaenophorus crassus* Forel, 1868 from the intestine of *Esox lucius*, San Valentino, Italy; **C**, **D** – adults of *T. nodulosus* (Pallas, 1781) from the intestine of *E. lucius*, Mácha Lake, Czech Republic.

DISCUSSION

Species of *Triaenophorus* occurring in the Palaearctic Region form two distinct groups, separated from each other by a different shape and size of the scolex and its tridental hooks (Kuperman 1973; this study – Figs. 1–3). The present study, based on morphological and biometrical evaluation of extensive material of all five species considered by Kuperman (1968, 1973), Protasova (1977) and Schmidt (1986) to be valid, also demonstrated that *T. nodulosus* and *T. amurensis* can be easily distinguished from the remaining taxa, namely *T. crassus*, *T. meridionalis* and *T. orientalis* (Figs. 1, 2). However, the shape of the scolex and that of its hooks appeared to be unsuitable for discrimination of species within these two species groups, because no species-specific differences were found in any of the taxa studied (Figs. 1–3).

Measurements of scolex hooks of the species studied markedly differed from those provided in the literature (Kuperman 1968, 1973, Dubinina 1987), because the minimum and maximum size limits observed in the present study considerably exceed those listed by the above-mentioned authors. This is also valid for the width of the basal plate, which was the crucial characteristic used by Kuperman (1968, 1973) to separate three new taxa from *T. nodulosus* and *T. crassus*. The size range of this character is in fact much higher than that reported by Kuperman (1968, 1973), the actual maximum width of the plate being up to 30% higher in *T. amurensis*, 60% in *T. meridionalis* and 100% (i.e. twice as large as reported by Kuperman 1973) in *T. orientalis* (Table 2). In contrast, the minimum values of all characters measured correspond more or less to those

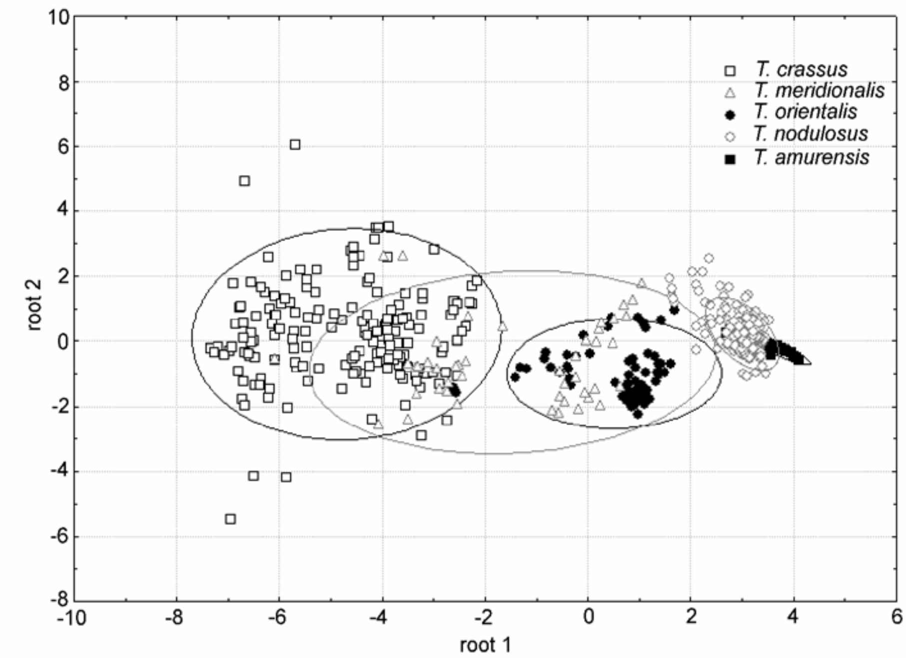

Fig. 4. Forward stepwise linear discriminant analysis plot of seven morphometric variables of scolex hooks of *Triaenophorus* species. The data are presented in the first two planes (Root 1 vs. Root 2). Ellipses represent 90% confidence intervals about the means.

Table 2. Measurements (in µm) of scolex hooks of *Triaenophorus* species. Kuperman (1968, 1973) and present data.

	1[#]		2		3	
	Kuperman	This study	Kuperman	This study	Kuperman	This study
T. nodulosus	99–176* (127.6 ± 1.8)	86–179 (112.1 ± 1.0)	22–33 (25.3 ± 0.5)	18–45 (27.0 ± 0.3)	55–110 (73.8 ± 0.9)	43–114 (68.9 ± 0.7)
T. amurensis	66–88 (81.4 ± 09)	70–112 (90.4 ± 2.4)	14–44 (17.9 ± 0.4)	14–34 (21.4 ± 0.8)	33–55 (43.9 ± 0.5)	32–65 (47.8 ± 1.7)
T. crassus	253–341 (300.9 ± 1.2)	103–428 (305.8 ± 6.9)	121–176 (148.6 ± 0.6)	110–254 (157.1 ± 2.1)	187–275 (238.5 ± 1.4)	104–342 (257.3 ± 3.3)
T. meridionalis	165–231 (211.9 ± 0.7)	159–362 (235.1 ± 7.7)	66–132 (98.6 ± 0.7)	57–182 (110.3 ± 4.5)	116–198 (159.6 ± 1.6)	103–315 (175.4 ± 7.2)
T. orientalis	121–165 (146.9 ± 1.0)	130–330 (174.8 ± 5.5)	55–88 (73.0 ± 0.6)	49–133 (76.7 ± 2.0)	88–143 (123.1 ± 0.9)	98–210 (130.1 ± 3.2)

	4		5	6	7
	Kuperman	This study	This study	This study	This study
T. nodulosus	44–90 (64.5 ± 1.1)	32–96 (58.4 ± 0.7)	25–76 (45.4 ± 0.5)	26–69 (41.4 ± 0.5)	52–144 (84.9 ± 0.9)
T. amurensis	32–49 (39.3 ± 0.7)	25–59 (39.6 ± 1.5)	28–54 (39.2 ± 1.3)	23–46 (35.0 ± 1.0)	51–96 (71.9 ± 2.0)
T. crassus	154–231 (189.7 ± 1.5)	117–327 (210.3 ± 3.7)	82–309 (149.9 ± 2.5)	87–302 (146.3 ± 3.3)	134–364 (257.0 ± 3.4)
T. meridionalis	72–165 (131.5 ± 1.4)	77–228 (134.4 ± 6.0)	65–159 (97.6 ± 3.2)	58–149 (89.7 ± 3.5)	129–298 (185.6 ± 6.3)
T. orientalis	66–121 (104.2 ± 1.0)	72–169 (103.8 ± 2.5)	42–104 (66.7 ± 2.1)	46–109 (63.7 ± 1.6)	99–207 (129.0 ± 3.3)

[#]**1** – width of basal plate, **2** – height of basal plate, **3** – length of longer lateral prong, **4** – length of shorter lateral prong, **5** – distance between longer lateral and median prongs, **6** – distance between shorter lateral and median prongs, **7** – distance between both lateral prongs; *minimum to maximum (mean ± standard error).

Table 3. Summary of the linear discriminant analysis of seven variables of the scolex hooks of five *Triaenophorus* species.

	Wilk's Lambda	Partial Lambda	F-remove	p-level	Tolerance	1-Tolerance
2. Height of basal plate	0.080640	0.784299	38.640900	0.000000	0.375445	0.624555
5. Distance between longer lateral and median prongs	0.065969	0.958724	6.048970	0.000090	0.508834	0.491166
3. Length of longer lateral prong	0.065789	0.961341	5.650030	0.000183	0.258090	0.741910
7. Distance between both lateral prongs	0.065477	0.965921	4.957010	0.000621	0.263938	0.736062
6. Distance between shorter lateral and median prongs	0.065437	0.966511	4.868170	0.000725	0.475476	0.524524
4. Length of shorter lateral prong	0.064200	0.985132	2.120450	0.076933	0.460462	0.539538
1. Width of basal plate	0.064080	0.986982	1.853220	0.117235	0.325745	0.674255

Table 4. Classification efficiency (%) of five species of *Triaenophorus* based on seven morphometric characteristics of hooks.

	% correct identification	TN	TA	TC	TM	TO
T. nodulosus (TN)	100	**252***	0	0	0	0
T. amurensis (TA)	0	32	**0**	0	0	0
T. crassus (TC)	93	0	0	**165**	12	0
T. meridionalis (TM)	23	4	0	14	**11**	18
T. orientalis (TO)	77	8	0	0	7	**50**
Total	83	296	0	179	30	68

*Correctly identified specimens (in bold).

of Kuperman (1968, 1973; Table 2). This indicates that this author did not measure the largest specimens of *T. amurensis*, *T. meridionalis* and *T. orientalis*, although they were available in his collection.

The discriminative value of seven hook measurements obtained in this study was low, with average correct identification being 83% only. Only *T. nodulosus* was correctly identified in all cases, apparently because it has by far the largest distribution area and the widest spectrum of fish intermediate hosts (Lawler and Scott 1954, Kuperman 1973, Protasova 1977, 1997, Hoffman 1999, Rusinek and Kuznedelov 2001). On the contrary, none of *T. amurensis* specimens was correctly identified, all being misidentified as *T. nodulosus* (Table 4).

Dubinina (1987) doubted the validity of Kuperman's taxa, synonymizing *T. meridionalis* with *T. crassus* and considering *T. amurensis* and *T. orientalis* to represent only geographical races (subspecies) of *T. nodulosus* and *T. crassus*, respectively. However, she also provided the key of Kuperman (1973), which made her synonymy somewhat hidden in the text. Similarly, Protasova (1997), evaluating measurements of the scolex and strobila of numerous samples of *T. nodulosus*, did not use her extensive data, which confirm extremely high range of intraspecific variability of *T. nodulosus*, to synonymize *T. amurensis*.

Unlike *T. amurensis* and *T. orientalis*, which were considered to be limited in their distribution to the Far East, where neither *T. nodulosus* nor *T. crassus* allegedly occur, *T. meridionalis* is not in fact geographically isolated from the latter taxon, because their distribution overlaps in the southwestern part of Russia (Protasova 1997). The measurements of *T. meridionalis* (width of the basal plate 159–362 µm) fall well into the size range of *T. crassus* (103–428 µm) (Table 2).

All available specimens of the three taxa erected by Kuperman (1968) are represented by permanent mounts and no material suitable for DNA analysis could be obtained to support taxonomic conclusions proposed here, i.e. invalidation of these species (see below). However, results of statistical analysis of extensive material of all Palaearctic taxa provide sufficient evidence for the following conclusions: (i) *T. amurensis* is not recognized as a separate subspecies of *T. nodulosus*, as considered by Dubinina (1987), but it is synonymized with *T. nodulosus* because of the absence of any species-specific differences between these two taxa; (ii) the synonymy of *T. meridionalis* with *T. crassus*, first proposed by Dubinina (1987), is accepted here because there are no marked morphological or biometrical differences between these two species, the former taxon apparently representing only a southernmost population of the widely distributed *T. crassus*; (iii) *T. orientalis* is also invalidated, becoming a junior synonym of *T. crassus*, because the size of scolex hooks overlaps between these two taxa and their reliable differentiation is not possible.

Somewhat smaller measurements of hooks of *T. orientalis* compared to those of many, but by far not all *T.*

crassus specimens, are considered to reflect the occurrence in different fish intermediate and definitive hosts at the extreme margin of the distribution area of *T. crassus*. Similar host- and geographically-related size differences have been observed in several fish parasites, including pseudophyllidean cestodes from freshwater fish (Molnár 1977, Pool and Chubb 1985, Pool 1987).

It seems that Kuperman (1965, 1968, 1969, 1973) overestimated slight morphological differences between populations of the polymorphic taxa *T. nodulosus* and *T. crassus*, which occur in a large distribution area and exhibit high intraspecific variability, as documented for *T. nodulosus* from the former Soviet Union by Protasova (1997) and Rusinek and Kuznedelov (2001). In addition, the present data demonstrate the incorrectness of the metrical data used to separate these taxa, because measurements in the original descriptions did not cover the whole range of size variability of individual species (Table 2).

Discriminant analysis of measurements taken from 573 hooks of five European taxa also showed the height of the basal plate to be the most important diagnostic character. In the *T. nodulosus* group (including *T. amurensis*), the basal plate is 14–45 µm high, whereas it measures from 49 to 254 µm in the *T. crassus* group (*T. orientalis* and *T. meridionalis* included). The width of the basal plate is easier to measure, but it is less suitable to discriminate individual taxa and may overlap, ranging from 66 to 179 µm in the former group and from 103 to 428 µm in the latter (Tables 2, 3). Other hook measurements may also overlap between the species, which implies that metrical data should be used for species differentiation with caution.

Both taxa considered to be valid can easily be differentiated by a markedly different shape of the hooks (Figs. 1, 2). A distinct shape (usually trapeziform in *T. crassus* – Fig. 2, versus spherical or almost rectangular, with blunt anterior end in *T. nodulosus* – Fig. 1) and size of the scolex (larger in *T. crassus*) can also be used for separation of these taxa, provided the worms are properly fixed, i.e. not flattened by compression as did most researchers in the 1960–1980's.

Besides the five *Triaenophorus* taxa dealt with above, another species, *Triaenophorus procerus* Özcelik, 1979 was established only on the basis of the shape and size of scolex hooks of two plerocercoids from the liver of perch, *Perca fluviatilis*, from the Upper Lake Constance, Germany (Özcelik 1979), but Dubinina (1987) synonymized this species with *T. nodulosus*. Brinker and Hamers (2000) provided convincing arguments that plerocercoids of *T. nodulosus* with incompletely developed scolex hooks were incorrectly considered by Özcelik (1979) to represent a separate species. It is evident that *T. procerus* is an invalid taxon and its synonymy with *T. nodulosus*, first proposed by Dubinina (1987), is considered to be correct.

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