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Variability of the species of the genus *Triaenophorus* Rud. (Cestoda, Pseudophyllidea)

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THE VARIABILITY OF SPECIES OF THE TRIAENOPHORUS RUD. GENUS (CESTODA, PSEUDOPHYLLIDEA)

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Tapeworms of the Triaenophorus — T. nodulosus (Pall., 1760) and T. crassus (Ford, 1868) genera are widespread among the fish of the greater part of the Holarctic Region, including the Amur transitory region. Their distribution is closely connected with the presence of their final host — the pike — whose intestines they parasitize when they are sexually mature. Numerous varieties of fresh-water fish (Perca fluviatilis, Acerina cernua, Lota lota, Esox lucius, Osmerus eperlanus, Salmo trutta, et al.), within the confines of the USSR, serve as the second intermediary host for the T. nodulosus species the plerocercoids of which in most cases inhabit the liver. The T. crassus plerocercoids settle, as a rule, inside the musculature and, rarely, inside the internal organs of fishes of the salmon, goby and pike families. According to Dubinina (1964), within the basin of the Amur river, the role of the second intermediary host is played for the T. nodulosus by the fish of the carp family, and for the T. crassus — by the eleotrids (Eleotridae family).

The related literature offers a great deal of information on the mass infection by the T. nodulosus and T. crassus plerocercoids of fishes, often resulting in their mass mortality, in the pond fish establishments of smaller bodies of water (Scheuring, 1919, 1923; Bergmann, 1924; Novikova, 1934; Petrushevskiy, 1937; Petrushevskiy and Bauer, 1948; Markevich, 1943; Izyumova, 1958). Strong invasions are suffered by the young fry of rainbow trout and perch, whereby multitudinous cysts with the T. nodulosus plerocercoids extrude mechanically the parenchyma of the liver and cause its degeneration, which often results in great mortality of the fish. The survivors lag behind in their growth and are easily afflicted by various diseases. The T. crassus plerocercoids in North America infect severely the musculature of the salmon-family fishes spoiling badly the quality of these valuable fish species and causing their mass condemnation (because of their inferior condition) (Miller, 1952).

The study of specimen of the genus Triaenophorus is of great theoretical interest to the conclusive determination of the geographical variability of the T. nodulus and T. crassus on the territory of the USSR (Dubinina, 1964). The greatest variability of these species, in relation to the parental, northern and western forms, has been detected in the basin of the Amur river, a fact which, evidently, must be attributed to their development inside the new, second intermediary hosts — fishes of the carp family for the T. nodulosus, and the bighead "gobies" (Perecottus glehni) for the T. crassus (Dubinina, 1964).

Detailed studies of the variability of specimen of the cestodes of this genus, depending on their geographical distribution and on their hosts, are bound to give us the key to the understanding of such important biological matters as the initial stages of the divergence and the formation of the species, et al. As a consequence of this, we have taken up a thorough study of the problem at hand.

This report deals with the comparison of data on the morphology and biology of both Triaenophorus species from the north-western bodies of water (Lake Ladoga) and the southern areas of the USSR (the deltas of the Dnieper, Dniester, Volga and of other rivers). In our work we made use of worms of this genus collected by us from a variety of fish caught in the southern part of the lake Ladoga, in October — November 1962, as well as in March, August, September and December 1963, and from fifteen pikes from the Volga delta. We also used praparations and fixed material from the fish population of southern bodies of water. The material from the fish of the Ukrainian and Moldavian bodies of water was kindly placed at our disposal by V.P. Koval', O.P. Kulakovskaya, N.M. Marits and R.P. Shumilo, and I am taking advantage of this opportunity to express to them my sincere gratitude.

M o r p h o l o g y. Sexually mature Triaenophorus nodulosus from the intestines of pikes caught in the lake Ladoga attain the maximum length of 280 mm and width of 5 mm. The T. crassus is longer and wider that the foregoing species (up to 410 mm in length and 8 mm in width). There is no external segmentation. The fore-part of their body has a noticeable external transverse plication which is more prominent in T. crassus. The latter differs distinctly from T. nodulosus, first of all, by its considerably

larger dimensions and by the shape of its scolex. The scolex of T. crassus looks like a truncated pyramid with a wide base and deep pseudo-bathriums; it is quite visibly separated from the body of the worm by a muscular ring. The width of the scolex at its base always exceeds its length. The scolex of T. nodulosus is elongated, narrows obtusely towards the top, and turns almost imperceptibly into a strobile. Both species have at the fore-end of their scolex a terminal disc armed with four quaint-looking hooks. The size of the scolex of worms belonging to the genus Triaenophorus from southern bodies of water is somewaht smaller than of those from northern waters, as it is shown in table 1.

Table 1

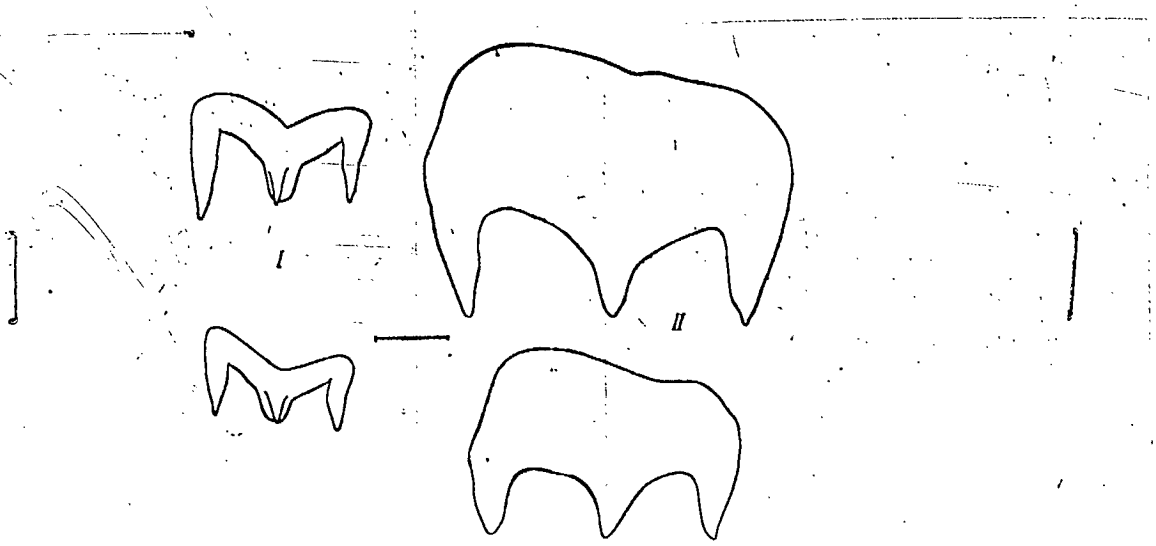
DIMENSIONS OF THE SCOLEX OF TRIAENOPHORUS NODULOSUS AND T. CRASSUS FROM DIFFERENT BODIES OF WATER (IN MM)

Species and body of water	Length	Width of terminal disc	Width of tail end	Source
T. nodulosus				
Lake Ladoga	0.44—0.88	0.31—0.49	0.38—0.77	Our own data.
Dnieper delta	0.28—0.55	0.24—0.37	0.28—0.50	
North American bodies of water	0.55—0.92	0.35—0.42	0.26—0.64	Cooper, 1918.
Canadian bodies of water	0.44—0.62	0.30—0.35	0.53—0.72	Miller, 1945.
T. crassus				
Lake Ladoga	0.88—1.32	0.68—1.05	0.88—1.65	Our own data.
Dnieper delta	0.62—0.99	0.61—1.0	0.61—1.43	
Volga delta	0.66—1.10	0.66—1.0	1.16—1.49	
North American bodies of water	0.92—1.29	0.67—0.92	0.92—1.38	Hjortland, 1928.
North American bodies of water	0.98—1.12	0.77—0.84	1.05—1.30	Cooper, 1918.

The T. nodulosus plerocercoids from the liver of smelts (Osmerus eperlanus n. ladogensis) attain the length of 220 mm, but more often their length ranges between 40 and 105 mm. The length of plerocercoids from the liver of burbots (Lota lota) in the lake Ladoga ranges from 70 to 340 mm. It is interesting that the initial stages of the formation of gonads in the form of an accumulation of cells were observed in the plerocercoids from the liver of burbots, but no fully formed genital complexes were ever discovered in them. The T. crassus plerocercoids from the musculature of the vendace (Coregonus albula) attain the length of 420 mm.

All plerocercoids are long and non-segmental, with fully developed hooks but without any formed genital complexes. The major part of the worm's body consists of a "tail" with underdeveloped muscles, filled with friable parenchyma..The size of hooks of sexually mature worms is the same as that of the plerocercoids.

The T. nodulosus and T. crassus differ distinctly from each other by the shape and size of their hooks; those of the latter species being considerably larger and more massive.. The hooks of T. nodulosus have a curved V-shaped basal lamina the top end of which is stretched out towards the back. Two side teeth and one middle tooth, all strongly curved, protrude from the basal lamina. The basal lamina of T. crassus is wider and has but slightly curved two side and one middle tooth. The hooked basal lamina rests within the musculature on the corners of the terminal disc in such a way that the curved ends of side hooks jut out from the surface of the scolex. The hooks of both species are asymmetrical because the side tooth, nearest to the bothrium, is always longer than the second side tooth located at the edge of the scolex (see figure).



Hooks of the Triaenophorus nodulosus (I) and T. crassus (II) found inside fishes from two different bodies of water: from the Ladoga lake (top row); from the Dnieper delta (bottom row).

The size and shape of their hooks are the most characteristic and distinguishing features of the genus Triaenophorus.

Within each of the species the size of hooks varies subject to certain limitations. In order to learn more about the size and the shape of hooks of both Triaenophorus species found in the fish of the Ladoga lake and of the southern bodies of water, measurements had to be taken of of the width and height of the basal lamina, as well as of the length of the larger and the smaller teeth.

Measurements were taken of one hundred hooks of each species from the Ladoga lake, of ninety hooks of the T. nodulosus, and one hundred seventy-five hooks of the T. crassus from the Dnieper and Volga deltas, from the Dniester and Pruth rivers, as well as from other bodies of water in the Ukraine. All measurements were processed by the generally accepted methods of variable statistics with the calculation of the true average size (M) and of the average error (m). The comparison results of the measuring of hooks of both Triaenophorus species from the northern and the southern bodies of water are presented in tables 2 and 3.

In making an anlysis of these tables, one's attention is drawn by the constant and steady decline in the size of hooks, indicated by all four features, in both species from southern bodies of water in relation to those from the north. Besides, the hooks in T. nodulosus from southern bodies of water, as compared with those from the north, lost from 25 to 27% in size, with the exception of the length of the smaller side teeth which diminished by 20.8%. In T. crassus the height of the basal lamina and the length of the ~~the~~ side teeth diminish gradually and evenly from the north towards the south by 45 — 47%, while the width of the basal lamina becomes narrower by 36.2%.

It must be pointed out that the size of hooks in the T. crassus diminishes from north to south remarkably more that in the T. nodulosus. As a matter of fact, the difference in the variability of the T. crassus exceeds that of the T. nodulosus in regard to the width of the basal lamina by 10.5%, to its height — by 20.8%, to the length of the larger side tooth — by 18.4%, and of the smaller side tooth — by 24.7%. Moreover, the extreme variants of all four distiguishing features of the T. nodulosus from southern bodies of water constantly transgress the lower limit of the very same species from the north, whereas in the T. crassus such transitions, if they occur at all, are very insignificant.

Table 2

DIMENSIONS OF THE HOOKS OF TRIAENOPHORUS NODULOSUS FOUND IN THE FISH FROM DIFFERENT BODIES OF WATER (IN MICRONS)

	From lake Ladoga (north)		From southern bodies of water		Size ratio of separate features of northern to those of the southern forms, in %%	Authenticity index of the difference (+)
	Limits	M ± m	Limits	M ± m		
Width of the basal lamina	118—165	139.8±0.9	78—132	110.9±1.1	125.7	21
Height of the basal lamina	22—38	30.8±0.3	17—32	24.4±0.3	126.9	14
Length of the larger side tooth	55—110	80.7±1.1	33—80	63.3±1.0	127.2	12
Length of the smaller side tooth	44—88	68.4±0.2	33—77	55.8±1.0	120.8	12

Table 3

DIMENSIONS OF THE HOOKS OF TRIAENOPHORUS CRASSUS FOUND IN THE FISH FROM DIFFERENT BODIES OF WATER (IN MICRONS)

	From lake Ladoga (north)		From southern bodies of water		Size ratio of separate features of northern to those of the southern forms in %%	Authenticity index of the difference (+)
	Limits	M ± m	Limits	M ± m		
Width of the basal lamina	253—308	278.9±1.0	165—231	204.4±1.0	136.2	52
Height of the basal lamina	121—165	145.2±0.7	66—132	97.7±1.0	147.8	39
Length of the larger side tooth	187—253	224.9±1.2	116—198	153.8±1.5	145.6	36
Length of the smaller side tooth	154—220	177.6±1.3	72—165	121.4±1.5	145.5	28

B i o l o g y and e c o l o g y. Both Triaenophorus species are widely disseminated throughout the lake Ladoga. Information on the extent of infection among the fish of this body of water is contained in the works of Jääskeläinen (1921), of Barysheva and Bauer (1957), of Bauer and Nikol'skiy (1957), and in the special research studies of the T. nodulosus in smelts carried out by Lopukhina (1963). In comparing our own

Table 4

THE EXTENT OF INFECTION AMONG THE FISH IN THE SOUTHERN PART OF THE LAKE LADOGA BY THE SPECIES OF THE GENUS TRIAENOPHORUS

Вид рыб Fish species	(1) Количество исследованных рыб	Локализация паразита Localization of parasites	*T. nodulosus* (2) наши данные: (4) процент заражения	*T. nodulosus* (2) наши данные: (5) интенсивность заражения	*T. nodulosus* (3) по: Барышева и Бауэр, 1957: (4) процент заражения	*T. nodulosus* (3) по: Барышева и Бауэр, 1957: (5) интенсивность заражения	*T. crassus* (2) наши данные: (4) процент заражения	*T. crassus* (2) наши данные: (5) интенсивность заражения	*T. crassus* (3) по: Барышева и Бауэр, 1957: (4) процент заражения	*T. crassus* (3) по: Барышева и Бауэр, 1957: (5) интенсивность заражения
Esox lucius	90	Intestine	63.3	20	80	86	86.7	82	60	15
Lota lota	15	Liver	100	26	87	37	0	0	0	0
Perca fluviatilis	20	Intestine	22	4	7	8	5	1	0	0
		Liver								
Leuciscus idus	5	Body cavity, intestine	0	0	27	7	0	0	0	0
Silurus glanis	—	Intestine	—	—	33	47	—	—	0	0
Acerina cernua	—	Body cavity	—	—	20	3	—	—	0	0
Anguilla anguilla	—	Intestine	—	—	15	7	—	—	0	0
Osmerus eperlanus n. *Ladogensis*	30	Liver, internal organs	55.2	2	93	5	0	0	7	1
Coregonus albula	15	Musculature	0	0	0	0	60	4	0	0
Salmo trutta	1	Internal organs	0	0	27	4	0	0	0	0
Salmo salar sebago	—	Liver, body cavity	—	—	60	6	—	—	0	0
Thymallus thymallus	—	Body cavity	—	—	+	2	—	—	0	0
Acipenser sturio	—	Intestine	—	—	+	20	—	—	0	0

LEGEND: (1) - Quantities of investigated fishes.
(2) - Our own data.
(3) - According to Barysheva and Bauer, 1957.
(4) - Percentage of infection.
(5) - Intensity of infection.

data on the extent of infection by plerocercoids and by fully grown worms of this genus among the fish in the southern part of the lake Ladoga with the material collected by Barysheva in 1938—1940 (Barysheva and Bauer, 1957), a clear understanding may be gained of the vital importance of all the variations in the extent of infection which have occurred in the course of the last twenty-five years (see table 4). Barysheva and Bauer (1957) point out with special emphasis

that the percentage and intensity of infection of the pike by T. nodulosus are always higher than by T. crassus (T. nodulosus — 80% in the southern and 100% in the northern part of the lake with maximum intensity of 86 (worms); T. crassus — 60% in the southern and 33% in the northern, with maximum intensity of 15). According to our own data, on the contrary, the extent of infection of the pike by T. crassus in the southern part of the lake Ladoga exceeds considerably that by T. nodulosus (T. crassus — 86.7% with the intensity of infection up to 82, and T. nodulosus — 63.3% with the intensity up to 20).

It can be seen from table 4 that the infection of the smelt, according to Barysheva and Bauer (1957), by the plerocercoid of T. nodulosus declines from 93% to 55% (as per our own data).

No plerocercoids of T. crassus were discovered by Barysheva and Bauer inside the vendace in the southern part of the lake, while in the northern part a few of them were infected very slightly (7%). High intensiveness of infection of the vendace by T. crassus (60% with the intensity of infection up to 4) is recorded in our collections of material. Petrushevskiy (1940) also remarks upon the high percentage (59%) of infection by the parasite among the vendace in the lake Onega. According to information supplied by Rumyantsev (1963), the extensiveness of infection by T. crassus among the vendace in the Karelian lakes amounts to 36.8 — 73.3% (Middle Kuyto and Kopati). Intense infection of the vendace by plerocercoids of T. crassus is prevalent in the lakes of Canada (Miller, 1945).

In order to obtain a clear picture of the regularity in the dissemination of both species of the genus Triaenophorus throughout the lake Ladoga, we shall carry out an analysis of the ecological interdependence and the nutritional connections between the first and the second intermediary hosts, as well as between the second and the final hosts, of these cestodes.

According to data supplied by Sokolova (1956), the zooplankton of the lake Ladoga attains in the most productive areas, on the average, from 34 to 64 thousand units per cubic metre. In respect of the quantity of organisms, the Copepoda are predominant in all areas of the lake,

the cyclopes and the nauplius larvae being in the majority and amounting in most cases to 70 — 80% of all planktonic organisms. The most characteristic forms of plankton are: Cyclops vicinus, Mesocyclops oithonoides, M. leucarti, Eucyclops serrulatus, Macrocyclops albidus and Diaptomus gracilis (Skorikov, 1910; Sokolova, 1956). Among these are many species that can serve as the first intermediary hosts for both species of the genus Triaenophorus (Michajlow, 1962). Judging by the distribution of planktonic organisms during the spring period throughout the entire lake, within the 0—2-metre horizon, the Copepoda and Cladocera are always predominant. Consequently, the abundance of cyclopes in the shore-line zone during the spring season is conducive to the dissemination of both Triaenophorus species among their first intermediary hosts.

As a result of the rising summer temperatures within the shallow, thoroughly warmed through, stretches of water, the lake's eastern and Volkhov areas become the most productive ones as far as the zooplankton is concerned. This, more than anything else, explains the most noteworthy accumulation of the vendace (the second intermediary host of T. crassus) during the spawning period along the north-eastern shores of the Ladoga lake. The run of the vendace, who feed in summer exclusively on zooplankton, aimed at this area, coincides with the maximum development of zooplankton towards the end of June, continues into July, and comes to an end in August. In the event of an early spring, the vendace can be expected to appear in these areas even in the first half of June (Pokrovskiy, 1956).

At the very same time, due to the rising temperature within the shore-line stretches of water, the smelt goes over from the bottom to the pelagic feeding, a factor which leads to the aggravation of competition between the vendace and the smelt, because the bulk of their nourishment consists of the cyclopes and bosmins (Saldau, 1956).

The young fry of whitefish and perch inhabits, more often than anywhere else, the Volkhov and the Schlüsselburg inlets and feeds on the very same zooplankton species (Saldau, 1956).

Pike, i.e. the final host of both Triaenophorus species, is spread widely all over the Ladoga lake. The exit of sexually mature

Triaenophorus strobiles from the pike's intestine and the development of coracidiums in their eggs occur in the second half of April and in May, thus coinciding with the pike's spawning activities. The latter take place within the shore-line zone at the depth of not over 1.5 m and in water temperatures ranging from 2.3 to 10.6°C (1959—1961). After spawning, the pike disperses throughout the entire lake (Gavrilova, 1962).

Thus, the mass development of the Triaenophorus' coracediums occurs in May and coincides with the intensive development and the scattering within the shore-line zone of cyclopes, thus creating conditions highly conducive to the latter's infection. The coracediums degluted inside the cyclopes develop into procercoids and remain in them for the duration of one month (Michajlow, 1962). The infection by Triaenophorus of the smelt, the vendace, the young fry of whitefish and perch, as well as of other fish species, takes place in June and early in July when they feed ravenously on zooplankton, particularly on the Copepoda. Procercoids develop inside these fishes into plerocercoids. The plerocercoids of T. nodulosus make themselves at home inside the internal organs, more often in the liver, of the smelt, burbot, perch and others, while those of T. crassus settle down inside the musculature of the vendace, of the young fry of whitefish, et al.

In summer time, pikes disperse throughout the entire lake, occupy the same ecological niche as the smelt and the Salmonidae, and feed on these intensively. Often, when we cut open a pike, we find inside from 2 to 4 vendaces and smelts.

Bearing in mind the high degree of infection among the smelts by the plerocercoids of T. nodulosus and among the vendaces by the plerocercoids of T. crassus, it can be considered that the principal, second intermediary host for the T. nodulosus in the Ladoga lake is the smelt, while for the T. crassus it is the vendace.

Evidently, in the Ladoga lake, the perch does not play a vital role in the dissemination of T. nodulosus, although in many other bodies of water this species serves as the principal, second intermediary host for these cestodes (Scheuring, 1923; Izyumova, 1958, et al.).

According to data supplied by Barysheva and Bauer (1957), the infectivity of the burbot by T. nodulosus amounts to only 7%, but according to our own data — to 22%, albeit we found them in the burbot's intestine only.

Regardless of the high extensiveness of the infectivity of the burbot by the plerocercoids of T. nodulosus (100%), its value as the second intermediary host is rather low. In the opinion of Bauer (1959), strong infection of older burbots occurs in consequence of serving as a host for the second time to the plerocercoids of T. nodulosus obtained from the swallowed fish. Large burbots, among those examined by us, could not have possibly served as nourishment to pikes. Consequently, the plerocercoids of T. nodulosus were simply accumulated inside the internal organs of burbots without taking any part in the subsequent continuation of the cycle of life.

The cases of T. nodulosus infecting the fish of the carp family are very rare in the European part of the USSR (Petrushevskiy, Mosevich and Shchupakov, 1948). In the southern part of the Ladoga lake such infection was discovered by Barysheva inside the internal organs and intestines of 27% of the golden orfes (Leuciscus idus) examined by her. (Barysheva and Bauer, 1957). No T. nodulosus were ever found by us inside the golden orfe. Evidently, the presence of T. nodulosus inside the golden orfe can be blamed only on the latter's rapacity. As far as the lake whitefish (Coregonus lavaretus) is concerned, its role as the second intermediary host is insignificant. At the age of 1 to 3 years, whitefish are only lightly (from 7 to 13%) infected by the plerocercoids of T. crassus (Bauer and Nikol'skaya, 1957).

As we analyze the data on the dissemination of the Triaenophorus species among the fish of the Ladoga lake and on the degree of their infection, we arrive at the conclusion that the ecological factors play a decisive role in it. This opinion is shared by Lawler and Scott (1954).

Of indubitable interest is the examination of interrelations between the T. nodulosus and T. crassus when they inhabit simultaneously the intestine of the pike. In the opinion of Scheuring (1929), a strong invasion by T. crassus is possible only in the absence of T. nodulosus. The ratio of T. nodulosus to T. crassus inside the fish specimen invaded

by both parasites is the following: 27 : 61; 11 : 131; 3 : 133. In this connection, Scheuring points out that T. crassus is found in large pikes taken from large lakes. According to the data of Michajlow (1932), in the event of a joint invasion, quite to the contrary, the T. nodulosus prevail over the T. crassus at the ratio of 142 : 5 and 27 : 7.

Out of 30 pikes taken from the Ladoga Lake and investigated by us for the purpose of determining the interrelation between both Triaenophorus species, joint invasion by both parasites was found in 16, i.e. in 53.3% of them; 3 pikes (10%) were infected by T. nodulosus, and 10 (33.3%) — by T. crassus alone. In all cases of joint invasions by these parasites of the pike's intestines the T. crassus were predominant, and the proportional ratios of T. nodulosus to T. crassus were 2 : 82; 14 : 77; 3 : 29; 3 : 53; 4 : 42; 1 : 34; etc. The size of the investigated pikes ranged from 45 to 75 cm.

As a rule, both parasites were located in the fore-part of the mid-intestine, confined within a limited area. In possession of more powerful hooks and of deep pseudo-bothriums, the T. crassus can penetrate deeper that T. nodulosus into the intestine wall and fasten themselves more securely to it. The intestine wall acquires much additional thickness at the spot taken up by T. crassus, so that the lumen of the intestine sometimes becomes quite small. Its mucous membrane becomes hyperemic, and in the spring this may lead to the hemorrhagic inflammation. At the point of T. crassus's attachment a crateriform ulcer is formed with a canal into which the scolex of the parasite gets embedded. Connecting tissues proliferate around the ulcer and form tubercles. In the event of a strong invasion, these tubercles become so numerous that the zone of the parasites' attachment reminds one of a grater. The reaction of the host's tissues to the invasion of these parasites is dealt with in detail in the works of Cooper (1918) and Scheuring (1923 and 1929). In cases of very strong infection, T. nodulosus become embedded not in the fore-part only but throughout the entire mid-intestine without causing any particularly strong irritation of tissues accompanied by the formation of ulcers and tubercles.

The reason for the predominance of T. crassus over T. nodulosus

in a joint invasion of the pike's intestine is to be found, we suppose, in the ecological factors, specifically, in the nutritional ties between the final and the second intermediary hosts. Fairly important role is played in this respect by the powerful attachment apparatus of T. crassus worms which enables them to fasten themselves securely in the usual place of localization of both species, i.e. in the fore-part of the mid-intestine.

Thus it follows that the strong invasion by T. crassus of the pike in the Ladoga lake via the vendace and the possession by the parasite of a powerful attachment apparatus result in the constant predominance inside the pike's intestines of T. crassus over T. nodulosus. The matter of interrelations between both species when they inhabit simultaneously the pike's intestines calls for further studies and for an experimental verification.

According to the findings of Michajlow (1962), no sexually mature T. nodulosus worms were ever observed in Poland before January, during the 1951—1959 period. According to our own observations on the Ladoga lake, the laying of gonads of both Triaenophorus species took place at the end of October and early in November, 1962, when water temperature was 7°C. By that time the genital complexes were fully developed, but eggs were found in a few odd worms only. Ripe eggs appear in some of the strobiles of both Triaenophorus species in December. It is interesting to cite the fact of finding eggs in T. nodulosus, on the 13th of October, 1963, from a pike caught in the Beloye lake in the vicinity of Leningrad.

Some authors are of the opinion that the phenological factor is the principal factor which governs the maturation time of the genus Triaenophorus. (Lawler and Scott, 1954).

The data available from the relevant literature, as well as our own, on the worms of the genus Triaenophorus found in the fish of southern bodies of water enable us to define the limits of their southward expansion, to learn more about the circle of their hosts, and to solve other related problems. Information on the dissemination of plerocercoids and of adult T. nodulosus and T. crassus worms among their hosts in

southern regions is presented in table 5. That table shows that both species are fairly wide-spread all over the south but, curiously enough, the T. crassus worms, as a rule, are predominant merely in the river d deltas, where there is a high degree of infection (Dniester delta — 80%, Volga delta — 46.6%, the southern Bug — 86.6%). Dogel and Bykhovskiy (1939) found in the Volga delta no T. crassus worms inside the pike's intestines, whereas, at the present time, its infection by this parasite in that region has reached the 46.6% mark with maximum intensity of 30 (worms). The wide dissemination and the high degree of infection of the fish by T. crassus worms in the deltas of large rivers of the south are caused by the presence there of a large quantity of gobies, i.e. of the second intermediary hosts of this species in southern bodies of water. The role of the pike as the second intermediary host of worms of the genus Triaenophorus is more prominent in the southern than in the northern bodies of water.

This, of course, gives a start to the question of principal importance: should the T. crassus worms be regarded as a northern or a southern form? The opinions of various authors in this respect differ greatly.

Fuhrmann (1909) is inclined to regard this species as a northern form. Bauer (1959) also considers the T. crassus to belong exclusively to the northern form common, in the main, to the northern areas of the Holarctic Region and, particularly, characteristic of the circumpolar phylum. The southern limits of dissemination of this species in Siberia run along the polar circle, or slightly south of it. Bauer insists that in the Baltic provinces T. crassus worms may be found in the Onega and Ladoga lakes only, but do not appear farther south.

Markevich (1934) adheres to an opposite point of view by insisting that in the European part of the USSR the T. crassus species constitutes primarily the southern form and gets replaced progressively more and more by the T. nodulosus towards the north.

Dogel and Bykhovskiy (1939) believe that the southern limits of the habitat of the T. crassus species is definitely and rapidly moving towards the south.

Table 5

THE EXTENT OF INFECTION AMONG THE FISH IN SOUTHERN BODIES OF WATER OF THE USSR BY THE SPECIES OF THE GENUS TRIAENOPHORUS

Водоем / Body of water	Исследованные рыбы / Investigated fish species	Локализация паразита / Localization of parasites	*T. nodulosus* (1) процент заражения	*T. nodulosus* (2) интенсивность заражения	*T. crassus* (1) процент заражения	*T. crassus* (2) интенсивность заражения
Middle Dnieper near Kanev (Markevich, 1949)	*Esox lucius.*	Intestine	12	2—3	16	1—4
		Liver	4	2	0	0
	Perca fluviatilis.	"	16	2—8	0	0
	Lota lota.	"	24	1—6	0	0
Lower Dnieper (Malevitskaya and Lopukhina, 1955)	*Esox lucius.*	Intestine	20	—	20	—
		Liver	—	—	—	—
	Perca fluviatilis.	"	—	—	—	—
Dnieper delta (Koval', 1962)	*Esox lucius.*	Intestine & liver	6.6	—	80	—
	Perca fluviatilis.	Liver	13.3	—	0	0
	Mesogobius batrachocephalus.	"	6.6	—	0	0
Southern Bug (Koval' & Piryanik, 1957)	*Esox lucius.*	Intestine	0	0	86.6	3—29
	Mesogobius batrachocephalus.	Musculature	0	0	7.6	8
Dniester (Shumilo, 1953)	*Esox lucius.*	Intestine	—	—	25	—
	Silurus glanis.	"	—	—	33	—
Pruth flood plains (Marits, 1957)	*Esox lucius.*	Intestine	26	2—10	23	1—5
		Liver	—	7	0	0
	Perca fluviatilis.	Intestine	11.7	2—10	0	0
Volga delta Dogel' & Bykhovsky, 1939)	*Esox lucius.*	Intestine	8	1	—	—
		Liver	12	1	0	0
	Neogobius kessleri.	Musculature	0	0	+	1
Volga delta (our data, 1963)	*Esox lucius.*	Intestine	6.6	5	46.6	3—30

LEGEND: (1) - Percentage of infection.
(2) - Intensity of infection.

In our opinion, the northern origin of the T. crassus, so closely connected with the second intermediary hosts, i.e. the Salmonidae which inhabit the north, is beyond any doubt. The wide dissemination of the T. crassus throughout the northern bodies of water (the Ladoga and Onega lakes, the Karelian lakes, et al.), richly populated by the Salmonidae — the principal, second intermediary hosts of this species — and the severe infection by it of the fish there testify to the fact that this species originate from the northern areas. This is in agreement with the point of view expressed by Bauer (1959). But the expansion of the T. crassus must not be presumed to be limited to the northern areas of the Holarctic Region only.

Its ability to adapt itself to the development inside new, second intermediary hosts (Gobiidae and Esocidae), instead of the Salmonidae, in the north made it possible for this species to penetrate far into the south and to become disseminated fairly widely there.

Frequently recorded observations of the T. crassus in southern bodies of water, accompanied by the high infectivity of the fish in river deltas, has motivated Markevich (1934) to consider this species as belonging to the southern form.

In our opinion, the T. crassus constitutes a form of northern origin which has penetrated far into the south along the larger rivers and became disseminated widely there thanks to its ability to adapt itself to the development inside new, second intermediary hosts, instead of inside the Salmonidae in the north.

As it was pointed out previously, the comparative morphological analysis of both Triaenophorus species from both the northern and the southern bodies of water shows that the size of hooks in the forms from southern waters diminishes noticeably by comparison with those from northern waters (see tables 2 and 3). Evidently, this is bound up with the influence of the climatic factor on the morphology of these parasites and, specifically, with much earlier development of cestodes and faster formation of hooks at higher temperatures.

It is characteristic that the dimensions of hooks in the T. crassus diminish from north to south to a much greater extent than those in the T. nodulosus (see tables 2 and 3). In southern latitudes, the special morphological features of the T. crassus are affected not only by the modification in the ecological conditions, but also by the replacement of the second intermediary hosts, i.e., instead of the Salmonidae in the north, the Gobiidae and Esocidae in the south. This is bound to have an effect on the morphology of hooks, the germination of which occurs at the plerocercoidal phase, as it was pointed out by Dubinina (1964) in respect of both Triaenophorus species from the fish of the Amur river basin. The size of hooks of the European Triaenophorus forms is almost twice the size of those of the Amur forms. The T. nodulosus retains in southern bodies of water the same second inter-

mediary hosts as in the north (Perca fluviatilis, Lota lota, et al.); subject to changes are the ecological conditions only. In view of this, by comparison with the T. crassus, the size of hooks of the T. nodulosus species changes considerably less from north to south.

This being the case, the alterations observed in the species of the genus Triaenophorus from southern bodies of water are more prominent whenever the change in their ecological conditions is linked with the ability of these parasites to adapt themselves to the development inside new intermediary hosts.

C O N C L U S I O N S

1. The investigation of worms belonging to the genus Triaenophorus in the Ladoga lake provides valid reasons to consider that the ecological factors (nutritional ties between the first and second, the second and final hosts; habituation of these hosts to the identical ecological niches at a specific time; the phenological system of the body of water) exercise a vital influence on the dissemination and the degree of infection among the various fish species, and also determine the circle of hosts of these parasites.

2. The predominance of the T. crassus over the T. nodulosus in a joint invasion of the intestines of the lake Ladoga's pikes is the result of close nutritional ties between the final host — the pike (Esox lucius) — and the second intermediary host of the T. crassus — the vendace (Coregonus albula) — and also of the possession by the parasite of a powerful attachment apparatus which enables it to fasten itself securely at the habitual place of localization of both species, i.e. in the fore-part of the mid-intestine.

3. The comparative studies of the T. nodulosus and the T. crassus from the fish of the Ladoga lake (north) and from some of the southern bodies of water in the USSR (Dnieper delta, Dniester, Pruth, Pripet, Volga delta, et al.) have resulted in the establishment of the morphological variability of these species which is reflected in the size of their hooks — their most characteristic systematic symptom..

4. A marked reduction in the size of hooks of both Triaenophorus species is in evidence from the north towards the south, whereby the size of hooks in the T. crassus gets smaller considerably more than of those in the T. nodulosus.

5. The morphological variability of the hooks of worms of the genus Triaenophorus is, evidently, bound up directly with the modification in climatic conditions, in particular, with the rise of temperature in southern bodies of water which contributes to the more rapid development of cestodes and speeds up the formation of their hooks.

Besides, a vital influence is exercised on the morphological peculiarities of the attachment apparatus by the replacement of the second intermediary hosts, because it is exactly inside of these that the full formation of the hooks occurs during the plerocercoidal phase.

Therefore, a particularly drastic change in the size of hooks takes place in the T. crassus for whom the altered climatic conditions in the south are combined with the replacement of the second intermediary hosts (instead of Salmonidae — Coregonus — in the north, Gobiidae — Neogobius kessleri, Mesogobius batrachocephalus — and the pike itself in the south). The T. nodulosus retain in southern bodies of water the same second intermediary hosts as in the north (Perca fluviatilis, Lota lota, et al.); there are changes in the climatic conditions only, and the size of hooks of this species diminishes, therefore, in the south much less than that of the T. crassus.

6. The T. crassus is a species of northern origin which has penetrated far into the south along the larger rivers later than the T. nodulosus but became widely disseminated there due to its ability to adapt itself to the development inside the new second intermediary hosts (Gobiidae and Esocidae).

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