REVISION OF THE NEMATODE SUBFAMILY ANGUININAE (NEMATODA, TYLENCHIDA) ON THE BASIS OF THEIR BIOLOGICAL CHARACTERISTICS

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A revision of nematodes of the subfamily Anguininae was carried out with substantiation of one new genus. The subfamily is divided into five genera: Anguina Scopoli, 1777; Paranguina Kir'yanova, 1955; Subanguina Paramonov 1967; Heteroanguina Chizhov, 1980; and Mesoanguina gen. n. Questions concerning the origin of different groups of anguinids, linked among themselves by a common trophic specialization and infective age, are discussed. Diagnoses and an identification key for the genera of the subfamily are given.

At present, there are 35 species of anguinids known in the world causing the formation of specific galls on many species of herbaceous plants. A detailed study of this group of plant nematodes with specific pathogenic effect began at the end of the 1950's; it was connected first of all with descriptions of new species and with substantiation of new genera. Paramonov (1952) while discussing the subfamily Anguininae, included three genera in it--Anguina, Nothanguina and Paranguina, but he examined this subfamily as a member of the family Tylenchidae. In 1970 after a revision of the subfamily, it already included the genera Anguina, Nothanguina and Subanguina. However, Paramonov (1970) did not include the genus Ditylenchus in the subfamily Anguininae, but retained it in the subfamily Tylenchinae. Golden (1971) proposed a subfamily Ditylenchinae with the genera Ditylenchus, Pseudhalenchus and Diptenchus, while the genera Anguina, Paranguina and Subanguina were included in the subfamily Anguininae; but he considered both these subfamilies to belong to the family Tylenchidae. However, Hooper (1978) considered the subfamily Ditylenchinae as a synonym of Anguininae. Fotedar and Handoo (1978) discussed the subfamily Nothanguininae with the genus Nothanguina and included it in the family Nothotylenchidae.

Skarbilovich (1980) included in the family Ditylenchidae the subfamily Ditylenchinae with the genera Ditylenchus and Diptenchus, and the subfamily Sychnotylenchinae with the genera Sychnotylenchus and Neoditylenchus. Siddiqi (1980) proposed a superfamily Anguinoidea with the families Nothotylenchidae (with the subfamily Nothanguininae), Anguinidae and Sychnotylenchidae. Eliava and other (1980) considered two subfamilies in the family Anguinidae--Anguininae (genera Anguina, Paranguina, Cynipanguina, Subanguina, Diptenchus, Pseudhalenchus and Ditylenchus) and Sychnotylenchinae. In the latest revision, Brzeski (1981) did not recognize the presence of subfamilies in the composition of the family Anguinidae after including in it the genera Anguina, Nothanguina, Subanguina, Ditylenchus, Diptenchus and Nothotylenchus; and he proposed two new genera, Orrina and Afrina. Sumenkova (1982) also considered the genus Ditylenchus in the subfamily Anguininae.

In the latest publication of Fortuner (1984), relating to the systematics of nematodes of the order Tylenchida, the subfamily Nothanguininae was included in the family Nothotylenchidae.

From the short history of the question it is evident that practically all authors recognize the family Anguinidae Nicoll, 1935; discrepancies only concern its composition--subfamilies and genera. We propose that only two subfamilies should be members of the family Anguinidae: Anguininae and Ditylenchinae, a matter which is sufficiently substantiated morphologically and phylogenetically. One must also accept the subfamily Nothanguininae in the family Nothotylenchidae. What also concerns the structure of the subfamily Anguininae is the fact that the need arises in connection with the description of new species and the proposal of new genera, to limit the present subfamily to the genera Anguina Scopoli, 1777; Paranguina Kir'yanova, 1955; Subanguina Paramonov, 1967; Heteroanguina Chizhov, 1980; and Mesoanguina gen. n.

At the basis of practically, all classifications of nematodes of the order Tylenchida existing today lie systems built exclusively on morphological criteria. The systematics of nematodes of the family Anguinidae is no exception. Brzeski (1981) used the peculiarities of structure of the esophagus, ovary and preuterine gland as the basis of a taxonomic division of the anguinids. However, the use of only morphological characteristics does not always give an optimal result (and this is especially true for the anguinids). Already in 1970 for the first time in plant nematology Paramonov introduced into [the discussions on] the ancestral origin of the subfamily Anguininae, not morphological criteria but peculiarities of biology and ontogenesis: localization in organs of the plant-host and infective age.

The origin of the anguinids from a common ditylenchoid ancestor does not raise doubt today (Paramonov, 1970), but it is just this circumstance that determines the great commonness of morphological characteristics, while the variety of habitat environments in organs of different plant-hosts makes these characteristics greatly variable. This causes definite difficulties in the classification of a given group of obligate plant nematodes. Attempts undertaken up to now to construct a classification of the anguinids soley on the basis of morphological characteristics cannot be recognized as successes. The majority of characteristics used for this objective have not seemed sufficiently stable, and have in a series of instances been artifacts (Kir'yanova, 1955; Maggenti et al., 1973; Brzeski, 1981).

The goal of the present work is to consider and evaluate the morphological and biological characteristics of the anguinids from the point of view of their taxonomic significance, and on this basis to evaluate the phylogeny of this group of plant nematodes.

MORPHOLOGY AND ONTOGENESIS

Shape and measurements of the body. The length of the body of anguinids--from 0.8 to 5 mm--varies greatly among species, as also within a single species. Anguina klehbani is one of the smallest

species, the females being 0.8 - 1.1 mm in length; the very largest are A. agrostis, A. tritici and Paranguina agropyri--with females up to 5 mm. The intraspecific variations of body length in several species are also very significant; for example, in P. agropyri the measurements of adult individuals vary from 1.5 mm (first generation) to 5 mm in the second [generation] (Chizhov, 1978). A similar phenomenon takes place in all species with two generations in one gall. Variations of measurements of the body are observed also depending on localization. Thus, in Heteroanguina graminophila attacking the stalk the minimal measurements of adult individuals is 1.1 mm, but those attacking the leaf reach 2.5 mm (Chizhov, 1980). Measurements of the body also depend on the type of plant-host; thus, the measurements of A. agrostis infecting thin bent grass are on the average 2 times less than those infecting the purple-stem cat's tail. The sharp narrowing of the body behind the vulva is a peculiarity of several species of the anguininae (Pogosyan, 1966). Moreover, after the last molt, the adult individuals still continue to grow for some time. Apparently, the use of a character such as body length is not well-suited to the necessities of anguinid taxonomy.

The shape of the body adopted by adult individuals, after fixation at a temperature rising to 56 degrees, is a peculiarity of the anguinids which in our view is interesting. The anguinids have a vermiform body, but in many species especially as a result of a strong development of the sexual system (particularly the ovary), it at times swells so much that adult females become practically motionless. With temperature fixation, males of almost all anguinid species straighten themselves out and only individuals more than 3 mm in length are sometimes somewhat bent ventrally. The body shape of females varies depending on the species and generation (if two generations are developing in the gall) to which the female belongs. It can straighten out as do Heteroanguina graminophila, H. caricis comb. n., Subanguina radicicola, the first generation of species of the genus Mesoanguina gen. n., and Paranguina agropyri. Females of species of the genus Anguina and of the second generation of the genera Paranguina and Mesoanguina gen. n. take a C-shaped form or are spirally curled. Thus the shape of the female body with fixation by temperature rise can serve as an additional taxonomic characteristic.

The cuticle of the anguinids is finely annulated, and longitudinal striation is characteristic of many species. The lateral field in large females practically cannot be observed; in males it is somewhat better visible. The structure of the lateral field in the anguinids is very varied. Thus, according to Wu's data (1967), photographs of the lines of the lateral field of H. graminophila obtained under an electron microscope, showed that their number is different in different parts of the female body. A similar phenomenon takes place in Mesoanguina plantaginis comb. n. (Hirschmann, 1977). In M. picridis comb. n., the number of lines varies from 6 to 20 (Kir'yanova & Ivanova, 1968). The number and configuration of lines of the lateral field in males and females can be different (Corbett, 1966; Chit & Fisher, 1975). The lateral field can be smooth with 2 marginal lines (Kir'yanova, 1955), but the common number of lines in different species of anguinids is 4, 6, 7, 8, 10-12 and 6-20. Moreover, in descriptions of many anguinid species

information about the lateral field is generally lacking. From face view, the head is typical in ditylenchids and anguinids, and consists of 6 segments. The number or annules in the labial area in different species varies from 2 to 6, and in some species the labia are smooth. There are species in which the number of cuticular annules on the head of males (3-4) and females (4-5) is different (Kir'yanova & Shagalina, 1969). Frequently, the difference between species comes to one annule, which is impossible to consider reliable.

The structure of the tail section has definite significance, but with the exception of species with a spiked tail tip and some peculiarities in the structure and location of the bursa relative to spicules and tail tip, it (the tail section), is constructed uniformly in the anguinids.

Thus, all the characteristics enumerated above can be partially utilized for diagnoses at the species level, but their use at the genus level is practically impossible.

Esophagus. The sylet of anguinids is short and thin; its measurements in different species vary from 7 to 16 μm, and in the majority come to about 10 μm. The procorpus of anguinids is cylindrical; in large forms it plays the role of organ-accumulator for the secretion of the dorsal gland and therefore is somewhat widened in its middle part. The metacorpal bulb is oval or round with a valve. The isthmus is, as a rule, short and narrow; it can be filled from the dorsal side with the secretion of dorsal gland; it is slightly widened at the place of junction with the cardial bulb; it varies greatly in shape; and it occupies different positions in relation to the intestine. The shape and measurements [of the glands] and their position in relation to the intestine in an individual depend not only on the species, but also on the generation to which it belongs; on its age, on the conditions of its nutrition, and even on its sex. Moreover, in many anguinids the end of the ovary reaches the metacorpal bulb and is even flexed backwards at the level of the posterior bulb, which results in a great deformity of the latter and makes it impossible to determine the location in relation to the intestine.

The measurements and location of the posterior bulb depend on the generation to which the individual belongs (in species with two generations in the gall). In the smallest individuals of the first generation the posterior bulb resembles more the bulb of Ditylenchus; in the second generation it generally is trapeze-shaped and occupies a variable position. The location of the cardial bulb relative to the intestine depends on age: the older the individual, the farther behind the esophagel-intestinal valve the esophageal gland fall. Thus, in H. caricis comb. n. (Ryss & Krall', 1981; Solov'eva & Krall', 1982) the boundary between esophagus and intestine is straight in young specimens, while in old ones the glands sink so much lower than the esophageal-intestinal valve that their position is like the position of the glands in Aphelenchus. Various authors (Kir'yanova, 1955; Maggenti et al., 1973; and Siddiqi, 1980), have described in different ways the structure of the cardial bulb and the number of cells composing it. All of this reduces the taxonomic value of peculiarities of structure of the cardial bulb.

Thus, the use of peculiarities of structure of the esophagus for diagnostics both at the genus and at the species level is practically impossible.

Sexual system. In all anguinids there is a polypropagatory ovary with a transverse series of oogonia and oocytes in the germinal zone and the growth zone, and a single or multiple-row arrangement of oocytes in the zone of maturation, there is a short and narrow postovarian [oviduct]; and the spermatheca is bag-like. The preuterine gland is in the shape of a multiple-celled tube with a series of synchronous eggs, and as a rule, a short muscular anterior uterus. A very high intraspecific variability is characteristic of the anguinid sexual system, depending on the generation to which the individual belongs: on the age of the adult individual; on the point of localization; on the species of the plant-host; on its physiological condition, and so forth. So depending on the generation to which the individual belongs (in species of the genera Paranguina and Mesoanguina gen. n.), the ovary can be straight or flexed in the first generation, while the oocytes in the zone of maturation as a rule, lie in a single row; for the second generation a twice or thrice-flexed ovary is characteristic, while the oocytes in the zone of maturation are arranged in 2-5 transverse rows (Chizhov, 1978, 1980, 1984). The structure of the ovary depends to a significant degree on the age of the female: in old individuals an originally flexed ovary can be straightened, while the multiple-row arrangement of the oocytes can become single-row. The extent of flexure of the ovary also depends on the point of localization and on the species of the plant-host: in M. millefolii comb. n., in galls localized on lower quickly-wilting leaves, adult individuals are on the average smaller and the ovary is weakly-developed. In Anguina agrostis infecting the purple-stem cat's-tail, the females are on the average 2 times larger than the males from thin bent grass; the development of the ovary corresponds to the measurements of the body (Chizhov, 1980).

The preuterine gland is another part of the genital tract whose structure changes to a significant degree depending on the generation to which the adult individual belongs. In the first generation it is relatively shorter. It consists of a smaller number of cells (up to 120), and it contains 2 to 4 synchronous eggs arranged in a single row; with the second generation the preuterine gland is long (the number of eggs is up to 400, and the synchronous eggs are up to 18). The row arrangement of the preuterine gland varies in different species from 4 to 10.

Interspecific differences also take place in the structure of the sexual system of the anguinids. Thus, the single row arrangement of the oocytes in the zone of maturation of the ovary, and the relatively short preuterine gland are peculiar to the first generation of P. agropyri, and to the first generation of species of the genus Mesoanguina gen. n., but also to species of the genera Heteroanguina and Subanguina. Arrangement of the oocytes in many rows and relatively long preuterine gland are characteristic for species of the genus Anguina and the second generation of P. agropyri and Mesoanguina gen. n. A gland (organ) which reinforces the function of the preuterine gland is isolated morphologically between the spermatheca and the preuterine gland in several highly specialized

species of Anguina (A. agrostis and A. tritici) which infect the flowers of grasses, and also in the second generation of several species of the genus Mesoanguina gen. n. (Chizhov, 1980; Chizhov and others, 1981). The degree of development of the posterior uterus which has a varied structure in the anguinids, plays an important role for species diagnoses.

Inasmuch as the interspecific differences in the structure of the genital tracts of the anguinids and their intraspecific variability exceed each other to a very great degree, the use of peculiarities of structure of the genital system of the anguinids for taxonomic purposes must serve only as a secondary character. This refers in particular to such characters as the row arrangement of the oocytes in the zone of maturation of the ovary, and the number of rows of cells in the preuterine gland.

Ontogenesis. According to Paramonov (1970) the basic distinctive peculiarity of the anguinids is the specificity of their ontogeneses. This group of obligate plant nematodes has produced an original ontogenetic cycle of development, tied to a profound specialization. In contrast to the ditylenchids, the anguinids are practically incapable of independent existence outside the plant host. The originality of ontogeneses of the anguinids is often determined by the infective stage; under natural conditions there is only one infective stage peculiar to a given species in each species of anguinids. Amid all the variety of anguinids (35 species), it is possible to sort out species in which the larvae of the II stage appear infective (12 species) of the III stage (15 species), and of the IV stage (4 species); the infective stage is unknown for the remaining four species.

The level of specialization is definitely dependent on the infective stage: the higher the level of specialization of the species, the lower the infective stage of the larvae. Inasmuch as the active growth of the genital primordium in larvae of the anguininae begins from the moment of infecting a new plant host, the degree of development of the genital tract is also conditioned by the infective stage: the lower the infective stage, the more greatly developed the genital tract in mature individuals and the more intensive its function. The genital system is developed most strongly in species where the larva of stage II is infective, but also in the second generation with species having an infective larva of the II stage. This is expressed first of all in the many-row arrangement of the oocytes in the ovary's zone of maturation (S. radicicola and the first generation in species of the genus Mesoanguina gen. n. and P. agropyri constitute the exception), which in its turn determines the egg productivity of the female. If in H. graminophila (infective larva of the IV stage) the maximum productivity of the female is approximately 600 eggs, and in the second generation of M. millefolii comb. n. (infective larva of the II stage) it reaches on the average 1500, then in A. agrostis (infective second stage) it comes to 2500 eggs (Chizhov, 1980; Chizhov and others, 1981).

Thus, a correlation is observed between the infective stage and the intensification of function of the female genital tract (basically the ovary and the preuterine gland). As regards the preuterine gland, not only its structure but also its length in relation to the general length

of the genital tract can serve as an index of the level of specialization of different species of the anguininae. So, if in percentage, the ovary in the anguinids and Ditylenchus dipsaci constitutes 69-73% on the average (the absolute lengths are very different--D. dipsaci is 0.9 mm, but A. agrostis is 2.3 mm), then the preuterine gland in D. dipsaci is 8% (abosolute length is 100 /um), in M. millefolli comb. n., and H. graminophila is 15% (absolute length is 300 /um), while in A. agrostis it is 20% (absolute length is 650 /um) of the overall length of the genital tract (Chizhov and others, 1981). Thus, the infective stage of the anguinids, which determines in many of them the level of their specialization is a reflection of the phylogenesis of this group, and in our view can be used as an important taxonomic criterion.

TROPHIC SPECIALIZATION

Of 35 species of anguinids 17 species are parasites of monocotyledons (16 of them have hosts from the cereal family and 1 from the sedge family), and 18 infect dicotyledons (the hosts of 12 of them are species of the family Compositae). One species each goes to borage, umbellifer, plantain, nightshade, knotgrass and primrose.

According to present-day thinking, the cereals and the Compositae are two of the most advanced families in respect to the evolution and two with the greatest numbers in species composition (Bush, 1959; Tachtadzhyan, 1966). 80 percent of the species of anguinids known to the present day go in these two families; it is characteristic that the largest number of species of plants from these two families are hosts to D. dipsaci (Kir'yanova & Krall', 1971; Dekker, 1972; Goodey, 1933).

A peculiarity of the trophic specialization of the anguinids which are parasitizing monocotyledons (genera Anguina, Paranguina and Subanguina) is the fact that the majority of them have a heterogeneous spectrum of plant-hosts. Thus, S. radicicola is distinguished by a wide spectrum of about 20 genera (more than 25 species) and A. agrostis, by 14 genera (more than 30 species). In other species of anguinids which are parasitizing monocotyledons, the number of plant-hosts is somewhat less (from 4 to 16 species) and only for a few of them is it known that they infect a single species of plant-host. For this group of species the galls are characterized by an oval shape with clearly expressed internal cavity. In species which infect above-ground organs of monocotyledons, the galls are stained, as a rule. As hypertrophy takes place in the pathological process, so also does hyperplasy of the infected tissue. One generation of parasite is developing in the gall (with the exception of P. agropyri). The infective larva is of the II stage. Evidently, species of this group carry their lineage from ancestral root forms of the type S. radicicola which is characterized by a heterogeneous spectrum of plant-hosts and in infective larva of the II stage.

A peculiarity of trophic specialization of the anguinids which parasitize dicotyledons consists of the fact that they are characterized by a narrow spectrum of plant-hosts. For most of the species (12) only one species of plant-host is known; a small number (4) have two to four species of

plant-host from one genus; and for M. millefolii comb. n., eight species of plant-host are known; seven of them of the genus Achillea. Only unstained, often very downy galls with a clearly expressed internal cavity are characteristic of species of the genus Mesoanguina gen. n. As hypertrophy takes place in the pathological process, so also does hyperplasia of the infected tissue. Two morphologically different generations are developing in the gall. The infective larva is of the II stage.

The origin of the narrow trophic specialization of the anguinids which parasitize on dicotyledons probably is connected with the fact that they carry their lineage from ancestral forms of stalk ditylenchids which were already profoundly enough adapted to their plant-host.

The third, most narrowly specialized group of anguinids (Heteroanguina) is close in accordance with morphology and biology to contemporary phytopathogenic ditylenchids. Both monocotyledons (cereals and sedges) and dicotyledons (umbellifers and knotgrasses) are plant-hosts of nematodes of this genus. They cause the formation of partially or fully stained galls of different shapes, without a clearly expressed internal cavity. The pathological process is characterized by hypertrophy of the infected tissue. A single generation develops in the gall. The infective larva is of the IV stage. Evidently, nematodes of this genus originate from ancestors common to contemporary ditylenchids, and occupy an intermediate position between pathogenic ditylenchids and anguinids.

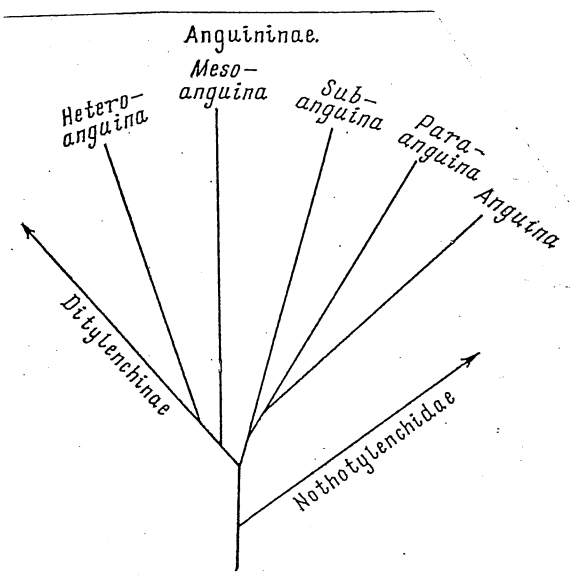

Diagram of possible phylogenetic relationships among genera of the subfamily Anguininae.

IDENTIFICATION KEY OF SUBFAMILIES OF THE FAMILY ANGUINIDAE NICOLL, 1935

1(2). Body slender, not more than 2 mm. Cardial bulb pear-shaped. Ovary oligo--or mezopropagatory; oocytes in the zone of maturation in a single row. Preuterine gland regular, with 4 rows with 4-7 cells per row; not longer than the spermatheca. All stages of development are infective. Several species are plant nematodes of specific pathogenic effect; the majority are microphagous .... subfamily Ditylenchinae.

2(1). Body slender or enlarged posteriorly to the end of the esophagus, up to 5 mm long. Cardial bulb hypertrophic. Ovary polypropagatory; oocytes in the zone of maturation in a single row or in 2-5 transverse rows. Preuterine gland irregular, in the shape of a multicellular tube, with 32 to 400 cells arranged in 4-10 rows; far longer than the spermatheca. Each species has an infective larva of only one definite stage (II, III or IV). They cause the formation of specific galls on many species of flowering plants ... . subfamily Anguininae.

1(6). Parasites of monocotyledons (cereal family); infective larva of the II stage.

2(5). Cause formation of unstained galls on the roots and on the base of the stalk of cereals.

3(4). Multicellular hook-shaped galls on roots. One generation develops in the gall ..... Subanguina.

4(3). 1, very rarely 2 galls on the base of the stalk. 2 morphologically different generations ..... Paranguina.

5(2). Cause formation of usually stained galls on above-soil organs of cereals. A number of species form only seminal galls .... Anguina.

6(1). Parasites of dicotyledons or monocotyledons. Infective larva of the III or IV stage.

7(8). Parasites of dicotyledons. Form unstained, often downy galls with a clearly expressed internal cavity. 2 morphologically different generations develop in the gall. The infective larva is of the III stage ..... Mesoanguina gen. n.

8(7). Parasites of dicotyledons or monocotyledons. The galls are without a clearly expressed internal cavity and are partially or completely stained. One generation develops in the galls. The infective larva is of the IV stage ..... Heteroanguina.

DIAGNOSIS AND COMPOSITION OF THE SUBFAMILY ANGUININAE NICOLL, 1935

Relatively large forms, up to 5 mm in length. With thermal fixation, the males straighten out and the females, depending on the species, straighten out, take C-shaped form or twist into a spiral. Cuticle finely annulated, and a longitudinal striation is observed in many species. Cephalic capsule closed and generally annulated. Stylet 7-16 µm long. Esophagus tylenchoid, and often with a powerfully developed cardial bulb.

Procorpus and isthmus are accumulating organs for the secretion of the dorsal gland. Ovary polypropagatory, the germinal zone varies from straight to three times flexed; oocytes in the zone of maturation of the ovary arranged in 1 row or in 2-5 transverse rows. Spermatheca cylindrical or sac-like. Preuterine gland irregular, and in the shape of a multicellular tube of 32 to 400 cells, arranged in 4-10 rows. From 2 to 18 synchronous eggs can be found in it at the same time. Form specific galls on the roots (1 species) and the above-soil organs of flowering plants. They have only one (II, III or IV) infective stage. The plant nematodes are of specific pathogenic effect, and there are no mycetophagous.

Type genus: Anguina Scopoli, 1777. Other genera: Paranguina Kir'yanova, 1955; Subanguina Paramonov, 1967; Heteroanguina Chizhov, 1980; and Mesoanguina gen. n.

Anguina Scopoli, 1777. With thermal fixation, females take a C-shaped form or twist into a spiral. Ovary flexed twice or three times, the oocytes in the maturation zone lie in 2-5 transverse rows. Preuterine gland irregular, in the shape of a multicellular tube, and up to 18 sychronous eggs can be found in it. In species which cause seminal galls, the structure (organ) which reinforces the function of the preuterine gland is morphologically separated between the spermatheca and the preuterine gland. Forms galls on leaves, stalks, panicles and flowers of many species of cereal grasses (but A. microlaenae--only on the rhizomes). One generation develops in the gall, and generally only one per season. Galls with a clearly expressed internal cavity stained in many species. As hypertrophy takes place in the pathological process, so also does hyperplasia of the infected tissue. The infective larva is of the II stage.

Type species: Anguina tritici (Steinbuch, 1799) Filip'ev, 1936. Other species: A. agropironifloris Norton, 1965; A. agrostis (Steinbuch, 1799) Filip'ev, 1936; A. australis Steiner, 1940; A. danthoniae (Maggenti et al., 1973) Brzeski, 1981; A. graminis (Hardy, 1850) Filip'ev, 1936; A. hyparrheniae Corbett, 1966; A. microlaenae (Fawcett, 1938) Steiner, 1940; and A. poophila Kir'yanova, 1952.

Paranguina Kir'yanova, 1955. Forms one gall, rarely two galls, on the base of the stalk of twitch (crouch) grass (Agropyron repens) in cereal cultures (except oats). Two morphologically different generations develop in the gall. The second generation is on the average 2 times larger than

the first. Adult individuals of the first generation and males of the second generation straighten out with thermal fixation and females of the second generation take a C-shaped form. In the first generation, ovary straight or flexed, oocytes in the zone of maturation lie in a single row, and preuterine gland relatively short (up to 5 synchronous eggs). The ovary of the second generation is twice or three times flexed, the oocytes are in 2-3 rows, and the preuterine gland is very long (up to 12 synchronous eggs). As hypertrophy takes place in the pathological process, so also does hyperplasy of the infected tissue. The galls havs a clearly marked internal cavity. The infective larva is of the II stage.

The type and only species is Paranguina agropyri Kir'yanova, 1955.

Subanguina Paramonov, 1967. Adult individuals straighten out with thermal fixation. The ovary, depending on the measurements of the female, varies from straight to twice flexed; the oocytes in the zone of maturation lie in a single row. Preuterine gland irregular, with 48-60 (52) cells and up to 4 synchronous eggs. Infects the root system of cereal grasses, causing hook-shaped galls. In the pathological process, there is an hypertrophy of the parenchymal tissues of the root with formation of an inner cavity. One generation develops in the gall (two to three per season). It is the only species in which not only infective larvae, but also the eggs and sexually mature and sexually immature adult individuals winter in the galls. The infective larva is of the II stage.

The type and only species is Subanguina radicicola (Greeff, 1872) Paramonov, 1967.

Heteroanguina Chizhov, 1980. Adult individuals straighten out with thermal fixation. Ovary from straight to three times flexed. The arrangement of the oocytes in the zone of maturation of the ovary is, as a rule, in a single row. Preuterine gland relatively long--up to 6 synchronous eggs.

Form leaf and stalk galls on species of the of cereal, umbellifer, sedge and knotweed families. The galls are partially or fully stained. They cause hypertrophy of the infected tissue, without a clearly expressed internal cavity. One generation develops in the gall; one or two per season. The infective larva is of the IV stage.

Type species: Heteroanguina graminophila (Goodey, 1933) Chizhov, 1980. Other species: H. caricis (Solov'eva & Krall', 1982) comb. n.; H. ferulae (Ivanova, 1977) comb. n.; and H. polygoni (Pogosyan, 1966) comb. n.

Mesoanguina Chizhov et Subbotin, gen. n.

Two morphologically different generations develop in the gall. Adult individuals of the first generation are of smaller dimensions; they straighten out with thermal fixation. Individuals of the second generation are significantly larger; with thermal fixation, females take a C-shaped form or twist spirally, and males straighten out. Ovary of

first generation females straight or flexed, oocytes in the zone of maturation usually arranged in a single row, preuterine gland short, and with up to 4 synchronous eggs. Ovary of the second generation females twice of three times flexed; its tip can reach the metacorpal bulb. The oocytes in the zone of maturation lie transversely in two to four rows. Preuterine gland relatvely longer; with up to 16 synchronous eggs. Form unstained, smooth or downy galls. On the whole they are parasites of Compositae. Five species infect the same number of families of dicotyledons. In the pathological process both hypertropy and hyperplasy of the infected tissue take place with formation of a cavity inside the gall.

Type species: Mesoanguina millefolii (Low, 1874) comb. n. Other species: M. amsinckia (Steiner & Scott, 1935) comb. n.; M. balsamophila (Thorne, 1926) comb. n.; M. centaureae (Kir'yanova & Ivanova, 1968) comb. n. M. chartolepidis (Pogosyan, 1966) comb. n.; M. cousininae (Kir'yanova & Ivanova, 1968) comb. n.; M. kopetdaghica (Kir'yanova & Shagalina, 1969) comb. n.; M. mobilis (Chit & Fisher, 1975) comb. n.; M. montana (Kir'yanova & Ivanova, 1968) comb. n.; M. moxae (Yokoo & Choi, 1968) comb. n. M. pharangii (Chizhov, 1984) comb. n.; M. picridis (Kir'yanova, 1944) comb. n.; M. plantaginis (Hirschmann, 1977) comb. n.; and M. varsobica (Kir'yanova & Ivanova, 1968) comb. n.

Four more species enter into the composition of the subfamily Anguininae: Anguina pustulicola (Thorne, 1934) Goodey, 1951; A. spermophaga Steiner, 1937; A. tumefaciens (Cobb, 1932) Filip'ev & Schuurmans Stekhoven, 1941 (parasites of three species of herbaceous plants of the cereal family) and A. klebahni Goffart, 1942 (it infects Primula flaridae Ward., from the Primulaceae family). However, because of the absence of sufficiently detailed information on their morphology and biology, the membership of these species in one or another genus remains unclear.

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REVISION OF THE SUBFAMILY ANGUININAE (NEMATODA, TYLENCHIDA) BASED ON THEIR BIOLOGICAL PECULIARITIES

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Summary

The subfamily Anguininae has been revised and a new genus has been described. The subfamily is divided in five genera: *Anguina* Scopoli, 1777; *Paranguina* Kirjanova, 1955; *Subanguina* Paramonov, 1967; *Hetcroanguina* Chizhov, 1980; *Mesoanguina* gen. n. The origin of different groups interrelated by a common trophic specialization and invasion age is discussed. Diagnoses and a key are provided for the genera of the subfamily Anguininae.