The Genus *Coslenchus* SIDDIQI, 1978 (Tylenchidae: Nematoda) from Japan. II. Synonymy of *Coslenchus* over *Cosaglenchus* and *Paktylenchus* based on the Phylogenic Relationships and a Key to the Species.

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Phylogeny of the genus *Coslenchus* was discussed using cladistic analysis. Transformation series of 12 major characters of the *Coslenchus* used in the analysis were evaluated through out-group comparison on the 23 genera basis. The *Coslenchus* was considered to be a sister-group of the *Aglenchus* by the synapomorphies, *i.e.* short postuterine sacs, lateral vulval flaps, and three incisures of lateral fields, and to be a monophyletic group by having longitudinal ridges of cuticle, wide body annules, and shorter tails as autapomorphies. The two lines could be recognized in the *Coslenchus* and were designated as INDICUS and COSTATUS groups after their representatives: the former had elongated postuterine sacs and tubular vaginae, the latter had swollen vaginae and short postuterine sacs. Since there was no clear gap between them, the *Coslenchus* was considered to be valid in the ordinary ranges of generic characters given by ANDRÁSSY. The *Paktylenchus* and the *Cosaglenchus* were synonymized with *Coslenchus*, since there appeared less validity in their generic characters and they were included in the COSTATUS line. A key to 31 species of the genus was given. *Jpn. J. Nematol.*, 15: 14-25 (1985).

Despite extensive supports and contributions from several authors[3,4,6,12,17], identity of the genus *Coslenchus* SIDDIQI, 1978[15] appears still obscure. In the previous paper[12] we pointed out that the *Cosaglenchus* SIDDIQUI & KHAN, 1983[18] and the *Paktylenchus* MAQBOOL, 1983[10] were doubtful genera in view of the current generic definition of the *Coslenchus*. Although they were alleged to be distinctive from the *Coslenchus* by nothing but the vaginal character-states, current definition by ANDRÁSSY[3], which was based on 20 species in stead of four in the original diagnosis[15], allowed the *Coslenchus* to accommodate different vaginal character-states as infrageneric variations. On the other hand, no one have tested a new definition of the *Coslenchus* from a view point of phylogeny. We analyzed character-states sequences on 12 major characters among the species of the genera, *Aglenchus*, *Coslenchus*, *Cosaglenchus*, and *Paktylenchus*, in order to reveal the phylogenic relationships between them.

METHODS

We adopted the cladistic analysis to find out phylogeny of the *Coslenchus*. This analysis initially requires evaluation of the transformation series (or the evolutionary sequences) of various character-states which are scattered among species of the taxon. Questions that to what extent the given character-states are *apomorphous* (derivative) or *plesiomorphous* (original) against the others should be determined at first. The *sibling species* or *sister-group* or the most related two species (groups) are recognized through *synapomorphies* (shared *apomorphous* character-states) that had been taken over from their *stem species* (common ancestor). Although every species (group) has retained any *plesiomorphies* (ancestral character-states) which had been derived from the forgoing ancestors through their *stem species*, only *synapomorphies* but *symplesiomorphies* (shared *plesiomorphous* character-states) make *monophyletic group*[8].

Which character-states are primitive in the *Coslenchus*? Table 1 shows wide range of character-states variation of 12 characters in the *Coslenchus*. Character-states on the left in Table 1 can be assumed from succeeding reasonings (indicated in figures in the parentheses) to be primitive in the *Coslenchus*. Each character of the genus has three to nine degrees of

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Table 1. Assumed transformation series of the characters

Characters (abbreviations)	character-states sequences
(1) average body length (L)	1) more than 600 μm; 2) 550±50 μm; 3) 500±50 μm; 4) 450±50 μm; 5) 400±50 μm
(2) head to body contour (H-b)	1) continuous; 2) slightly offset; 3) offset
(3) minimum head annules (Rhd)	1) 5; 2) 4; 3) 3; 4) 2; 5) 1
(4) vagina shape (Vgs)	see Fig. 1.
(5) vagina angle to body axis (Vga)	1) slightly oblique; 2) oblique; 3) much oblique; 2') right angle
(6) postuterine sac/vulval body diameter (Pus)	1) 1/4-1/3; 2) 1/3-1/2; 3) 1/2-1; 4) 1 or more; 2') 0-1/4; 3') completely absent
(7) vulval flaps length/annule width (Vfl)	1) more than 3; 2) 2-3; 3) 2; 4) 1-2; 5) 0
(8) maximum longitudinal ridges (Ldg)	1) 10-11; 2) 12-13; 3) 14-15; 4) 16-17; 5) 18-19; 6) 20-21; 7) 22-23; 8) 24-25; 9) 26-27
(9) lateral field incisure (Lfi)	1) 3; 2) 3'=narrow groove; 3) 4; 4) 6
(10) average Rex (Rex)	1) more than 60; 2) 50±5; 3) 40-50; 4) 35-40; 5) 30-35
(11) shape of tail terminus (Tt)	1) sharply pointed; 2) needle-like; 3) hair-like; 2') bluntly pointed; 3') abruptly rounded
(12) body length/tail length (c)	1) 2-3; 2) 3-4; 3) 4-5; 4) 5-6; 5) 6-7

Evolutionary degrees of characters are serially numbered from the most primitive to the most advanced.

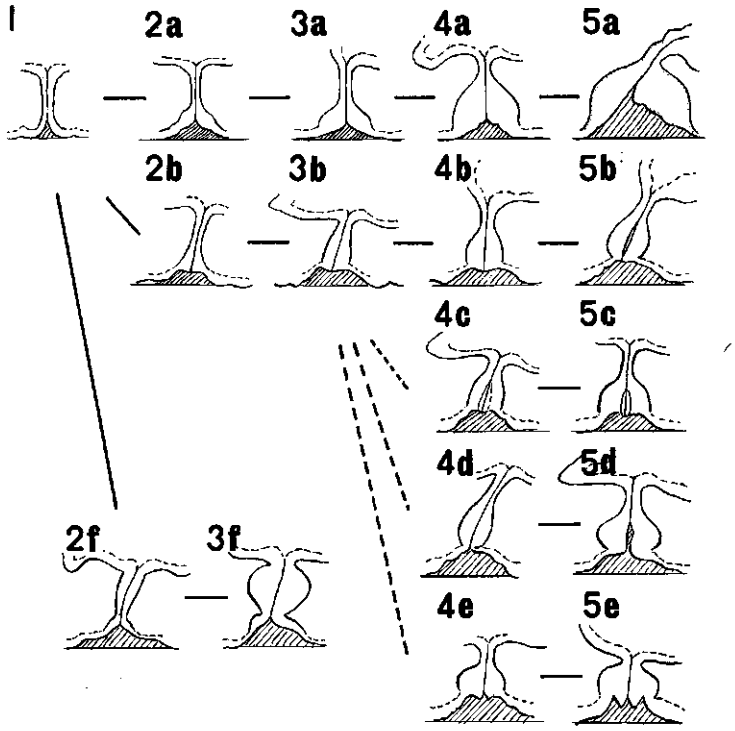

Fig.1. Assumed transformation series of female vaginae in the *Coslenchus*. Six lines are indicated alphabetically from "a" to "f", and lines are serially numbered from primitive to advanced.

evolution or transformation series, which are serially numbered from the most primitive to the most advanced. Vagina of the genus is the most specific character and we can find six different lines of transformation series of vaginae changing their shape from tubular to much swollen (Fig. 1).

According to ANDRÁSSY[1], filiform tails, inconspicuous phasmids, and short postvulval uterine branches are primitive conditions of the Tylenchidae. Although we took his view into assumption of the primitive character-states in the *Coslenchus*, without any evidence, it is impossible to compare all the character variations in regard to degree of departure from a primitive *Coslenchus* ancestor. The related genera of the genus allow us to imagine general trend of evolution of the characters and ancestral form of the *Coslenchus*. The Tylenchidae allies mentioned below in comparison cover the Tylenchidae and the Atylenchidae in the ANDRÁSSY's sense[1] referring to 23 genera: *Aerotylenchus* FOTEDAR & HANDOO, *Campbellenchus* WOUTS, *Discotylenchus* SIDDIQI, *Filenchus* (ANDRÁSSY) MEYL (including *Lelenchus*), *Irantylenchus* (KHEIRI) ANDRÁSSY, *Polenchus* ANDRÁSSY, *Tylenchus* BASTIAN, *Aglenchus* (ANDRÁSSY) MEYL, *Coslenchus* SIDDIQI, *Duosulcius* SIDDIQI, *Duotylenchus* SAHA & KHAN, *Malenchus* ANDRÁSSY, *Miculenchus* ANDRÁSSY, *Ottolenchus* (HUSAIN & KHAN) WU, *Zanenchus* SIDDIQI, *Tylodorus* MEAGHER, *Cephalenchus* (GOODEY) GOLDEN, *Gracilancea* SIDDIQI, *Imphalenchus* DHANACHAND & JAIRAJPURI, *Allotylenchus* ANDRÁSSY, *Atylenchus* COBB, *Eutylenchus* COBB, and *Pleurotylenchus* SZCZYGIEL. The *Cosaglenchus* SIDDIQUI & KHAN and the *Paktylenchus* MAQBOOL are excluded in the references.

(1) It is hard to image the initial body size of the *Coslenchus*. The existing species of the genus show no obvious peak of the species number in the range of body length. Of the Tylenchidae allies, 14 genera include species in a length of 0.7mm or more, and 12 include species in a length of 0.5 mm, while only eight genera include species 0.4 mm or less. For the *Coslenchus*, which ranges from 0.3 to 0.8 mm, the body in a length of 0.7 mm or more is tentatively considered as primitive condition of the *Coslenchus* stem ancestor.

(2) Offset head is found in 10 genera, *i.e. Filenchus-Lelenchus*, *Pleurotylenchus*, *Tylenchus*, *Aglenchus*, *Coslenchus*, *Malenchus*, *Ottolenchus*, *Cephalenchus*, *Eutylenchus*, and *Allotylenchus*, although head continuous to body contour is usual condition in the other genera. Since continuous type of head is often observed even in the above genera, offset type head may arise in parallel in the different lines. The *Coslenchus* also includes species of continuous head, and this may be initial condition of the stem ancestor.

(3) Six head annules may be symplesiomorphy in the Tylenchidae allies. Of them, *Filenchus-Lelenchus*, *Irantylenchus*, *Malenchus*, *Miculenchus*, *Pleurotylenchus*, and *Zanenchus* retained at least partially six head annulation. Although smooth heads are seen in the *Aerotylenchus*, *Discotylenchus*, *Polenchus*, *Aglenchus*, *Coslenchus*, *Duotylenchus*, *Ottolenchus*, *Tylodorus*, and *Gracilancea*, it may be due to fusion of the head annules. *Coslenchus* may initially have had at least five head annules, since some members retain this condition.

(4) Vaginae of the Tylenchidae are tubular generlly. Swollen ones in the *Coslenchus*, *Aglenchus*, *Duosulcius*, *Tylodorus*, *Gracilancea*, and *Imphalenchus* are rather rare cases. Since tubular vaginae other than various shapes of swollen ones are present in the *Coslenchus* and allied *Aglenchus*, the swollen ones may not be initial condition of the genera but may have developed later in parallel among the species of the genera.

(5) Inclined vaginae are observed in 13 genera out of 23 considered, i.e. the *Campbellenchus*, *Filenchus-Lelenchus*, *Pleurotylenchus*, *Polenchus*, *Aglenchus*, *Coslenchus*, *Duosulcius*, *Malenchus*, *Miculenchus*, *Ottolenchus*, *Zanenchus*, *Cephalenchus*, and *Gracilancea*. Compared with the *Aglenchus*, the *Coslenchus* has less inclined vagina except for a few species. Since the slightly inclined vaginae occur generally in the *Coslenchus*, the ancestor may have had slightly inclined vagina. Similarity in the strongly inclined vagina between a few *Coslenchus* species and the *Aglenchus* may be due to convergence.

(6) ANDRÁSSY[1] characterized the Tylenchidae of his sense by the presence of short postuterine branch, although not referred to its relative length to corresponding body diameter. Of the Tylenchidae allies, we can find postuterine sac as long as vaginal body diameter or more in more than half of the members. Shorter ones being less than 1/2 times vulval body diameter

Table 2. Characters distribution in the *Coslenchus* and *Aglenchus* spp.

Species	L	H-b	Rhd	Vgs	Vga	Pus	Vfl	Ldg	Lfi	Rex	Tt	c
Genus Coslenchus	1	1	1	1	1	1	1	1	1	2	1	1
SPG SSG INDICUS	4	1	1	1	2′	2	2	1	1	2	1	3
brevis	5	1	3	1	2′	2	2	1	1	3	1	4
emelcius	4	1?3	5	1	2′	2	2	3	1	3	1	4
temparatus	5	1?2	3	1	2′	3	3	3	?	3	2′	3
indicus	4	1	3	?	?	3	1?	4	1	?	3′	4
assamensis	4	1	1	1	2′	4	2	6	3	2	1	3
tausifi	5	1	5	1	2′	3	2	2	1	3	1	4
lycus	5	1?3	5	2b	2′	4	3	3	1	3	1	4
SPG TURKEYENSIS	1	1	2	1	1	1	1	2	1	2	1	3
SSG TURKEYENSIS	2	1	2	3b	2′	2	1	2	2	3	1	3
turkeyensis	2	2	2	5d	2′	3	2	2	2	3	3	3
pastor	2	3	3	3b	2′	3	1	5	3	3	3′	4
cocophilus	4	1	2	4b	2′	2	1	3	3	3	2′	3
SSG LATERALIS	1	1	2	3b	1	1	1	5	1	2	1	3
lateralis	3	3	2	4d	2	2	1	5	4	4	3	4
polygyrus	2	3	5	4d	3	3	2	9	1	4	2	3
polonicus	1	1	2	5e	1	1	1	9	3	2	2′3′	4-5
SSG RUGOSUS	2	2	2	1	2	1	1	3	1	3	1	3
rhombus	2	3	2	2b	2	1	4	3	2	3	3	4
rugosus	2	2	2	4e	2	3	2	3	3	3	2	4
modicus	5	2	?-4	3f	2	2	1	5	1	3	2′	3
rafiqus	5	2	?-4	2f	2	3	1	5	1	3	2′	3
SPG SSG CANCELLATUS	2	1	1	1	1	1	1	3	1	4	1	2
lycopersicus	4	1	3	4a	1	3	2	7	3	4	2	4
multigyrus	2-3	2	3	2a	2′	1	2	7	3	4	3	2
cancellatus	4	2	1	2b	2	3′	1	3	3	4-5	1	3
bisexualis	5	3	3	3a	2′	2′	1	3	1	5	2′	4
tuberosus	2	3	3	5a	2	3′	1	4	1	4-5	1	3
SPG COSTATUS	2	1	2	3b	1	1	1	3	1	3	1	2
SSG AREOLATUS	3-4	1	3	4c	1	1	1	3	1	3	1	2
gracilis	3-4	1	5	5c	2	1	1	3	3	4	2-3	2
areolatus	3-4	2	3	4c	1	2	1	5	1	3-4	3′	4
SSG FRANKLINAE	3	1	4	4b	1	2′	1	3	1	3-4	1	3
japonicus	5	1	4	4b	2	3′	1	6	2	4	2′	3
franklinae	5	1	4	4b	1	2′	1	5	3	3-4	2′	4
pycnocephalus	3	1	5	4b	2	2′	1	3	1	4-5	122′	3
SSG COSTATUS	2	2	2	4b	1	2′	1	3	1	3	1	4
costatus	2-3	2	2	4b	1	2′	1	3-4	3	3-4	2-3	4
acceptus	3	2	2	4b	2′	2′	1	3	3	5	3	4
alacinatus	3	3	3	4b	1	2′	4	3	3	4	2′	4
siddiqii	2	2	3	5b	2	2′	1	7	1	3	3	4
Genus Aglenchus	2	1	5	2b	3	2′	1	0	1	1	1	1
agricola	3	1-2	5	5e	3	3′	1	0	1*	3	2	2
fragariae	3	1	5	2b	3	2′	1	0	3	1	2′	4
mardanensis	3	2	5	2b	3	3′	1	0	3	1	2′	-3
mukutii	2	2	5	2b	3	3′	1	0	1	3	2′	1

1) Figures denote evolutionary degrees of characters shown in Table 1.

2) Abbreviations indicate different subordinate categories below the genus used herein: SPG=species group; SSG=species subgroup.

3) Categories carrying the assumed charcter-states of their stem ancestors.

* Using SEM, RASKI & MAGGENTI[14] showed three incisures in this species.

are rare but present in the *Discotylenchus*, *Filenchus-Lelenchus*, *Aglenchus*, *Coslenchus*, *Duosulcius*, *Gracilancea*, and probably in *Allotylenchus*. As synapomorphy speculate we upon the long postuterine branch as long as body diameter for Tylenchidae allies, the moderate one being about 1/2 times body diameter for some genera of the Tylenchinae (sensu ANDRÁSSY[1]), and further shorter one being 1/4 to 1/3 times body diameter or slightly longer for *Coslenchus-Aglenchus* sister-group. Postvulval uterine sacs of the *Aglenchus* are vestigial in one species and completely absent in the remained three species (Table 2). Those of the *Coslenchus* are generally short as well. Longer ones in the *Coslenchus* extending over 1/2 times body diameter might have been developed secondarily. As ANDRÁSSY[1] assumed that paired gonad was derived from unpaired one and maintained that "any clear perception is further hampered by the circumstance that the paired genital organ become secondarily unpaired", we may suppose the similar relation in the postuterine sac length in regard to degree of departure from ancestors of the different species subgroups in the *Coslenchus*.

(7) The vulval lateral flaps are common in the *Coslenchus* and observed in the *Aglenchus*, *Cephalenchus*, and *Imphalenchus* but not in the most other genera, so that this is an evident apomorphous character-state in the Tylenchinae allies and may be synapomorphy of the *Coslenchus-Aglenchus* sister-group. Naturally the vulval lateral flaps of the *Coslenchus*, as being descended from the ancestor, should be regarded as plesiomorphous character for the *Coslenchus*.

(8) Longitudinal ridges around the body is an obvious apomorphous character in the Tylenchinae allies. There are five genera having this character, *i.e.* *Campbellenchus*, *Pleurotylenchus*, *Coslenchus*, *Atylenchus*, and *Eutylenchus*. Although there is no strict relation between the *Coslenchus* and other four genera, and evolutionary sequence of occurrence of the ridges in number is, therefore, not sufficiently determined, we can recognize common tendency that about 10 ridges excluding lateral fields is the lowest number in the four genera with exception of the *Campbellenchus* having 21 and 26 ridges. We may take the lowest number being 10 as initial condition of the character of the *Coslenchus*.

(9) Various number of lateral incisures are recognized in the Tylenchidae allies. Two and four incisures are common. Three and six incisures are rare. Three lateral incisures are observed rarely in the *Filenchus-Lelenchus* (mostly four) and *Aglenchus* (two of the four species), and often in the *Coslenchus*, while the *Campbellenchus*, a species of *Coslenchus*, *Tylodorus*, and *Cephalenchus* have six incisures. Presumably, two incisures are most primitive in the Tylenchidae allies and three incisures may be intervened between two and four incisures in the evolution of the character. It should be further noted that the four incisures in the *Coslenchus* and the *Aglenchus* show somewhat difference from those of other genera such as *Tylenchus*, because the lateral fields in the cross section show three longitudinal bands in the latter, while two longitudinal bands leaving middle space or groove between them in the former two which give an impression to have four particularly when the middle space is wide. Thus there are two different types of four incisures in the Tylenchidae allies. Six incisures might have been derived from four incisures of *Coslenchus-Aglenchus* type.

(10) Tylenchidae generally has fine and large number of body annules. Wide body annule being about 2 μm wide at mid-body in the moderate-sized genera, *i.e.* *Tylenchus*, *Coslenchus*, *Aglenchus* (rarely in two species), *Malenchus*, *Ottolenchus*, *Cephalenchus*, and *Imphalenchus* might have developed through the fusion of some neighboring annules. Although the *Coslenchus* always has wide body annules being 2 μm or wider, the closely related *Aglenchus* has relatively narrow body annules. It is even as fine as 0.8 μm apart in one species of the latter. The ancestor of the *Coslenchus* as well as the *Aglenchus* may have had fairly narrow and large number of body annules.

(11) The descriptive adjectives focused exclusively on the very terminus of the tail are hardly applicable in evaluating the evolution of tail terminus. For extreme example, the

adjective "pointed" is commonly applied to both those fine terminus that abruptly tapers from thick subterminal region and that evenly tapers from very narrow subterminal region. The customary adjectives are also applied here with necessary definition as: a. "hair-like (HL)" for the tip at the end of filament subterminal region; b. "needle-like (NL)" for fine tip evenly tapered from very narrow subterminal region; c. "sharply pointed (SPT)" for the fine tip evenly tapered from somewhat thick subterminal region; d. "bluntly pointed (BPT)" for the fine one abruptly tapered from relatively thick subterminal region; e. "abruptly rounded (AR)" for abruptly or bluntly rounded tip tapered from thick subterminal region. The "finely rounded" condition is, in most cases, not constant condition within the species but closely associated with both SPT and BPT conditions. It is interesting to observe that SPT and BPT conditions are most frequent in the Tylenchidae allies considered. Of the 23 genera, 17 show this condition, while the HL and NL conditions occur in 12 genera and AR condition in six genera. Thus we may assume that ancestor of Tylenchidae allies as a whole has had relatively thick tail with pointed apex, not hair-like nor abruptly rounded. In the *Coslenchus*, the highest frequency in species number is located at the SPT condition. Also in *Aglenchus* the "finely rounded" condition tapered from somewhat thick subterminal region occur in two of four species. HL condition has not been observed so far but NL and BP are the other conditions of the *Aglenchus*. Accordingly, we considered the SPT condition to be ancestral (plesiomorphous) of the two genera.

(12) ANDRÁSSY[1] stated that a long tail is a primitive character of the Tylenchida. Tails are also slender and elongate in the Tylenchidae allies. For example, fairly longer tails being nearly 30% of body length (c≒3.3) are often found in nine genera, *i.e.* *Filenchus-Lelenchus*, *Polenchus*, *Aglenchus*, *Coslenchus*, *Malenchus*, *Ottolenchus*, *Cephalenchus*, *Imphalenchus*, and *Allotylenchus*, while those longer than 20% of body length (c<5) are found in three genera, *i.e.* *Campbellenchus*, *Gracilancea*, and *Discotylenchus*. Very short tails being about 10% of body length (c≒10) are observed only in the *Tylenchus*. We can not determine of what percentage were the tail in the primitive Tylenchidae allies but can assume, in the primitive Tylenchinae, that the tail had occupied more than 30% of body length. The most elongated tail may be a primitive condition of the *Coslenchus*, since the allied *Aglenchus* has elongate and slender tail as common as *Coslenchus*.

RESULTS AND DISCUSSION

A. MONOPHYLY of the *Coslenchus*

The *Aglenchus* shows the closest affinity to the *Coslenchus*. We can assume the ancestor of the *Aglenchus* applying common transformation series of the characters with the *Coslenchus*. Assumed ancestor of the *Aglenchus* (Table 2) may have had long body achieving 0.8 mm or so; head hardly offset without striae; tubular vagina directing strongly anteriorly; very short postuterine sac; large vulval lateral membrane; three incisures on lateral fields; very narrow (0.8 μm or less) body annule in a large number; long tail being 1/2.5 times body length or longer than two times vulva-anus distance with sharply pointed terminus; body without longitudinal ridges around. Further, we can assume ancestral condition of the *Coslenchus-Aglenchus* sister-group as the following: larger body (0.8 mm or so); head continuous to body contour with five or six fine annules; tubular and little anteriorly directed vagina; short postvulval uterine sac (1/4 to 1/3 times vulval body diameter); developed lateral vulval flaps; three incisures on lateral fields; narrow (0.8 μm or less) body annule in a large number; long filiform tail being 1/2.5 times body length with sharply pointed terminus; and body without longitudinal ridges around.

The character-states of the *Aglenchus*, then, can be arranged as a) synapomorphy with the *Coslenchus*: very short postuterine sac, presence of lateral vulval flaps, three incisures on lateral fields; b) symplesiomorphy with the same: tubular vagina, continuous head, long filiform tail being 1/2.5 times body length with sharply pointed terminus; and c) autapomorphy of itself:

smooth head, much inclined vagina.

Presence of longitudinal ridges around body (numbering 10 at least in initiator), wide (about 2 μm) and prominent body annule, and shorter tail being 1/3.4 or more times body length indicate an autapomorphy of the *Coslenchus*. The primitive *Coslenchus* may have had five or six head annules, and slightly anteriorly directing vagina: they are accountable as plesiomorphous character-states that derived from the Tylenchidae ancestor through the *Coslenchus-Aglenchus* stem ancestor. Accordingly, the *Coslenchus* is evidently a sister-group of the *Aglenchus*.

B. GROUPING OF THE SPECIES.

An analysis of the phylogeny[6] based on the transformation series of the characters provides four phyletic lines of the *Coslenchus* designated as:

1) "Indicus" species group (7 spp.)—*indicus*, *assamensis*, *lycus*, *temparatus*, *brevis*, *emelcius*, and *tausifi*.

2) "Turkeyensis" species group (10 spp.)—*turkeyensis*, *pastor*, *cocophilus*, *lateralis*, *polygyrus*, *polonicus*, *modicus*, *rugosus*, *rafiqus*, and *rhombus*.

3) "Cancellatus" species group (5 spp.)—*lycopersicus*, *multigyrus*, *cancellatus*, *bisexualis*, and *tuberosus*.

4) "Costatus" species group (9 spp.)—*costatus*, *acceptus*, *alacinatus*, *siddiqii*, *pycnocephalus*, *japonicus*, *franklinae*, *areolatus*, and *gracilis*.

These species groups (see Table 2) can be arranged further into two lines with sibling relationship: the first line comprising a single species group of "Indicus" is designated as Indicus group; the second line including "Turkeyensis", "Cancellatus", and "Costatus" species groups is designated as the Costatus group (Table 3). There seem to be some gaps in the character-states between the two, although we can confirm that the *Coslenchus* is an integrated genus.

Table 3. Characters distribution among the stem of subordinate categories

Categories	L	H-b	Rhd	Vgs	Vga	Pus	Vfl	Ldg	Lfi	Rex	Tt	c
GR SPG SSG INDICUS	4	1	1	1	2′	2	2	1	1	2	1	3
GR COSTATUS	1	1	1	1	1	1	1	2	1	2	1	2
SPG TURKEYENSIS	1	1	2	1	1	1	1	2	1	2	1	3
SSG TURKEYENSIS	2	1	2	3b	2′	2	1	2	2	3	1	3
SSG LATERALIS	1	1	2	3b	1	1	1	5	1	2	1	3
SSG RUGOSUS	2	2	2	1	2a	1	1	3	1	3	1	3
SPG SSG CANCELLATUS	2	1	1	1	1	1	1	3	1	4	1	2
SPG COSTATUS	2	1	2	3b	1	1	1	3	1	3	1	2
SSG AREOLATUS	3-4	1	2	4c	1	1	1	3	1	3	1	2
SSG COSTATUS	2	2	3	4b	1	2′	1	3	1	3	1	4
SSG FRANKLINAE	3	1	4	4b	1	2′	1	3	1	3-4	1	3
Gen. Coslenchus	1	1	1	1	1	1	1	1	1	2	1	1
Gen. Aglenchus	2	1	5	2b	3a	2′	1	0	1	1	1	1

1) Figures denote evolutionary degrees of characters shown in Table 1.

2) Abbreviations indicate the different categories used herein: Gen.=genus; GR=group; SPG=species group; and SSG=species subgroup.

3) Categories carrying the assumed character-states of their stem ancestors.

Indicus group is somewhat distinct from the Costatus group. Autapomorphy of its stem ancestor appears to be shorter body length (500 μm or less), vagina being right angle to body axis, longer postuterine sac which is 1/3 or more times corresponding body diameter, relatively

reduced vulval lateral flaps, and shorter tail with c value being at least four. Presently characters of the existing species of this group may approach those of some species of the Costatus groups through the parallel evolution, so that differences in the certain characters between them become obscure. We can generalize the member of the group by the smaller body being 500 μm or less, not offset head with at most three annule or completely smooth contour, tubular vagina being right angle to body axis, prominent postvulval uterine sac being 1/3 to 1 or more times corresponding body diameter, small number of longitudinal ridges around body seldom exceeding 16, lateral field with three incisures, body annules narrow in a comparatively large number, tail terminus sharply or bluntly pointed or rounded never hair-like, and short tail never exceeding 1/5 times body length.

Although Costatus group including wide range of different species groups is not easily characterized as in Indicus group, stem ancestor of the group might have shown large number of plesiomorphous characters. These characters become obscure due to parallel evolution in the descendants. The synapomorphy of the group is obscure as well but its stem ancestor might have at least a larger number of longitudinal ridges of cuticle as an autapomorphy than stem ancestor of Indicus group did. Although members of this group are generally characterized by the different modes of swollen and inclined vaginae, it should be better regarded as a result of recent parallel evolution and not as autapomorphy.

Under the Costatus group, we can recognize three species groups. The "Costatus" species group (including AREOLATUS, FRANKLINAE, and COSTATUS species subgroups) may be a sister-group of the "Cancellatus" species group (having a single species subgroup), and these combined species group may be further in the sibling relationship with the "Turkeyensis" species group (including LATERALIS, TURKEYENSIS, and RUGOSUS species subgroups). The "Turkeyensis" species group has its autapomorphy in the head with three or four annules, short tail being 1/4 times body length. Members of this group are greatly differentiated but generally characterized by the prominent postvulval uterine sac being 1/4 to 1/2 or more times corresponding body diameter, the pear-shaped long vagina with somewhat spaced inner wall or the bell-shaped one (this type is different from the former because of its hardly offset ventral contour) with its aperture slightly pointed and protruded, and tail about 1/5 times body length. This species group shows variable vaginae from much oblique to right angle to body axis as well as various number of longitudinal ridges of cuticle from 12 to 27.

The stem ancestor of "Cancellatus"+"Costatus" sister-group has its autapomorphy in the slightly shorter body less than 600 μm, large number of longitudinal ridges of cuticle being 14 or more, fewer and wider body annules. Generally the members of this sister-group are characterized by the bell-shaped vagina with deeply separated or closed aperture, or with double inner wall, and vagina never strongly oblique. The differences in the characters between "Cancellatus" and "Costatus" species groups become obscure. Wide annules being 2.2 to 3.5 μm, and fewer annules (40 or less) between head and excretory pore are regarded to be autapomorphy of the stem ancestor of the "Cancellatus" species group. The members as such are characterized generally by the bell-shaped vagina with deeply notched aperture and, reduced or no postuterine sac. The bell-shaped short vagina with closed aperture or with double inner wall is thought to be autapomorphy of the stem ancestor of the "Costatus" species group. Generally this group is characterized by the continuous or slightly offset head, bell-shaped short vagina rarely with double inner wall, only slightly produced postvulval uterine sac being shorter than 1/4 times body diameter.

C. POSITIONING OF *Cosaglenchus* AND *Paktylenchus* IN RELATION TO *Coslenchus*

The *Cosaglenchus*[18] was founded solely on the inclined vagina being considered to be distinct from the *Coslenchus* the vagina of which was given as at right angle to body axis[15]; and the *Paktylenchus* was said to be distinguishable from the *Coslenchus* in the "strongly cuticularized vagina oblique to body axis and prominent sunken vulva with vulval flaps[10] ".

Anteriorly directed vagina is certainly apomorphous character-state, but this occurs in the different species groups of the *Coslenchus* + *Cosaglenchus* + *Paktylenchus* (presently called *Coslenchus* complex) without coincidence of any other characters. When we admit the *Cosaglenchus* on the basis of the inclined vagina, the genus comes polyphyletic group. Inevitably, the remainder of the *Coslenchus* complex come polyphyletic as well.

An extraordinarily ample vagina of the *Paktylenchus tuberosus* is indeed an obvious apomorphous character-state, yet the genus *Paktylenchus* has a few difficulties in acceptance. First, the claimed autapomorphy of the genus is nothing but a vaginal shape, and it seems not to have a sufficient long history to distinguish the independent genus but to have developed recently within the *Coslenchus* complex. Vaginal shape is variable in the *Coslenchus* complex and allied *Aglenchus* and we can safely place it at the terminalia of the series of vaginal transformation with deeply notched aperture (Fig. 1, line 1-5a). Many taxonomists agree that closely related taxa have sufficient gaps of characters which can be traced back to the early period of the separation of the taxa. Accordingly, we suspect that present ranking of *Paktylenchus* to the generic status is over estimation for the species *P. tuberosus*: it will represent only a branch in the *Coslenchus* complex. Secondly, if the *Coslenchus* should be as old as *Paktylenchus* proposed, it must have some autapomorphy to characterize itself. Our analysis, for the present, does not offer such autapomorphy to the *Coslenchus* when the *Paktylenchus* is excluded. Therefore, we can conclude that the *Cosaglenchus* and *Paktylenchus* represent variations merely in the specific level, not the generic one, and the two genera should be synonymized with the *Coslenchus*.

D. Identity of the *Coslenchus*

The most significant characteristics of the *Coslenchus* are presence of longitudinal ridges, coarse annulation as wide as 2 μm or more, well developed vulval flaps, lateral fields with narrow middle grooves. With Andrássy[3], we can accommodate the generic definition with the tubular to swollen vagina and various degree of oblique vagina considering them to be specific variation.

Two lines in the *Coslenchus* are proposed, but we do not consider that they should be ranked as the subgenera. Phylogeny of the *Coslenchus* became complicated probably because of the convergence of the characters and recovery of the ancestral characters (adavism). The latter is likely to occur in the actual phylogeny of the genus, although we disregarded with some exceptions so as to simplify the situation. Presently we are unable to give clear picture (especially to the Costatus group) by the obvious apomorphous character-states, even by the number of longitudinal ridges, postuterine sac length, shape of vagina, and so on. We regard the lines having comparatively short history and species still under the active adaptive radiation, and these may explain the complicated situation in the *Coslenchus*.

Finally, we note some deviations of character-states in the species recognized after or without relation to Andrássy's definition[3]. *C. polygyrus*[4] and *C. polonicus*[6] bearing 26 or 27 longitudinal ridges around the body. Further, *C. polonicus* largely deviates from the definition by the longer body achieving 0.8 mm, larger number of body annules being 75 in oesophageal region and from 48 to 58 in vulva-anus region. *C. lycus*[17], *C. modicus*[18] comb. n., *C. temparatus*[17], *C. tuberosus*[10] comb. n., and *C. polonicus* have longer spear reaching 14 or 15 μm. It is desirable that they should be taken into account for the future revised definition of the genus.

Key to the species of *Coslenchus*

1. Vagina almost tubular or club-shaped (obpyriform) 2
— Vagina slightly to much swollen ventrally 12
2. Postuterine sac longer than half a vulval body diameter 3
— Postuterine sac half or less a vulval body diameter 7
3. Mid-body cuticle with at most 15 longitudinal ridges 4

— Mid-body cuticle with at least 16 longitudinal ridges 6
4. Head with three annules; about 40 annules from head to excretory pore; V value less than 67 ..... *temparatus* SIDDIQUI & KHAN, 1983[17]
— Head unstriated; cuticle with at least 40 annules from head to excretory pore; V value 67 or more 5
5. Postuterine sac shorter than vulval body diameter; lateral fields 1/4 times body diameter ..... *tausifi* SIDDIQUI & KHAN, 1983[17]
— Postuterine sac longer than vulval body diameter; lateral fields 1/3 times body diameter ..... *lycus* SIDDIQUI & KHAN, 1983[17]
6. Postuterine sac longer than vulval body diameter; cuticle with 18 to 20 longitudinal ridges; lateral fields with four incisures; basal oesophageal bulb slightly lobed posteriorly ..... *assamensis* (PHUKAN & SANWAL, 1980)[13]
— Postuterine sac shorter than vulval body diameter; cuticle with 16 longitudinal ridges; lateral fields with three incisures; basal oesophageal bulb with rounded posterior margin ..... *indicus* (KHAN, CHAWLA, & PRASAD, 1969)[3]
7. Postuterine sac shorter than 1/3 vulval body diameter; lateral fields with four incisures; excretory pore less than 41 annules separated from head 8
— Postuterine sac longer than 1/3 vulval body diameter; lateral fields with three incisures; excretory pore more than 39 annules separated from head 9
8. Vagina oblique; postuterine sac completely absent; head with five annules; cuticle with 14 longitudinal ridges ..... *cancellatus* (COBB, 1925)[3]
— Vagina at right angle to body axis; postuterine sac 1/4 to 1/3 times vulval body diameter; head with three annules; cuticle with 22 longitudinal ridges ..... *multigyrus* SIDDIQI, 1981[3,16]
9. Vagina at right angle to body axis; head continuous to body contour 10
— Vagina oblique; head offset or slightly offset 11
10. Cuticle with 10 longitudinal ridges; head with at least three annules; tail terminus pointed ..... *brevis* SIDDIQUI & KHAN, 1983[17]
— Cuticle with 14 longitudinal ridges; head smooth; tail terminus rounded ..... *emelcius* SIDDIQUI & KHAN, 1983[17]
11. Body shorter than 500 μm; cuticle with 18 longitudinal ridges; spear knobs near the seventh body annule ..... *rafiqus* (SIDDIQUI & KHAN, 1983) *comb. n.* =*Cosaglenchus rafiqus* SIDDIQUI & KHAN, 1983[18]
— Body longer than 500 μm; cuticle with 14 longitudinal ridges; spear knobs near the fifth body annule ..... *rhombus* ANDRÁSSY, 1982[3]
12. Postuterine sac longer than 1/4 times vulval body diameter 13
— Postuterine sac rudimentary, 1/4 or less times vulval body diameter 22
13. Cuticle with 10 to 15 longitudinal ridges 14
— Cuticle with 16 to 27 longitudinal ridges 17
14. Postuterine sac about 1/2 times vulval body diameter; spear knobs at the sixth or seventh body annule; head slightly offset 15
— Postuterine sac 1/3 or less times vulval body diameter; spear knobs at the eighth or ninth body annule; head continuous with body contour 16
15. Vagina at right angle to body axis; cuticle with 12 longitudinal ridges; lateral fields with very narrow middle grooves; tail terminus hair-like; advulval ventral cuticle normally annulated ..... *turkeyensis* SIDDIQI, 1981[16]
— Vagina oblique; cuticle with 14 longitudinal ridges; lateral fields with separated middle grooves; advulval ventral cuticle irregularly divided into small annules; tail terminus finely pointed ..... *rugosus* ANDRÁSSY, 1982[3]
16. Vagina at right angle to body axis, with double inner wall ventrally; head unstriated; tail terminus hair-like ..... *gracilis* ANDRÁSSY, 1982[3]
— Vagina oblique, with simple but slightly spaced inner wall; head with four annules; tail terminus rounded ..... *cocophilus* ANDRÁSSY, 1982[3]
17. Cuticle with at least 22 longitudinal ridges 18
— Cuticle with at most 20 longitudinal ridges 19
18. Postuterine sac 1/3 to 1/2 times vulval body diameter; vagina slightly oblique; cuticle with 22

longitudinal ridges; lateral fields with four incisures; head with three annules ..... *lycopersicus* (HUSAIN & KHAN, 1976)[3,9]

— Postuterine sac one to half as long as vulval body diameter; vagina much oblique; cuticle with 26 to 27 longitudinal ridges; lateral fields with three incisures; head unstriated ..... *polygyrus* BAJAJ & BHATTI, 1983[4]

19. Lateral fields with six incisures; tail terminus hair-like ..... *lateralis* ANDRÁSSY, 1982[3]

— Lateral fields with three or four incisures; tail terminus rounded or pointed 20

20. Body 560 to 600 μm long; head offset; lateral vulval flaps three annule long or longer; lateral fields with four incisures ..... *pastor* ANDRÁSSY, 1982[3]

— Body 380 to 560 μm long; head slightly offset; lateral vulval flaps one or two annule long; lateral fields with three incisures 21

21. Vagina at right angle to body axis; spear 10 to 11 μm long ..... *areolatus* (EGUNJOBI, 1967)[3,5,7]

— Vagina oblique; spear 13 to 15 μm long *modicus* ..... *modicus* (SIDDIQUI & KHAN, 1983) *comb. n*
=*Cosaglenchus modicus* SIDDIQUI & KHAN, 1983[18]

22. Cuticle with at least 22 longitudinal ridges 23

— Cuticle with 14 to 21 longitudinal ridges 24

23. Cuticle with 22 to 26 longitudinal ridges; body 680 to 790 μm long; knobs of spear at the 13th body annule ..... *polonicus* BRZESKI, 1982[6]

— Cuticle with 22 longitudinal ridges; body 540 to 560 μm long; spear knobs at the sixth body annule ..... *siddiqii* ANDRÁSSY, 1982[3]

24. Lateral fields with three incisures (middle grooves very narrow) 25

— Lateral fields with four incisures (middle grooves more spaced) 27

25. Vagina bell-shaped, much swollen, occupying three body annules ventrally; cuticle with 16 longitudinal ridges ..... *tuberosus* (MAQBOOL, 1983) *comb. n.*
=*Paktylenchus tuberosus* MAQBOOL, 1983[13]

— Vagina pyriform or moderately expanded ventrally; cuticle with 14 longitudinal ridges 26

26. Vagina oblique; head smooth and continuous with body contour ..... *pycnocephalus* SIDDIQI, 1981[16]

— Vagina at right angle to body axis; head offset, with three annules ..... *bisexualis* SIDDIQI, 1981[16]

27. Body small, never exceeding 500 μm ; head with two or three annles continuous to body contour 28

— Body longer than 450 μm ; head offset, or slightly offset with three or four annules 29

28. Cuticle with 16 to 18 longitudinal ridges; annules from head to anus 163 to 186; rectum longer than one anal body diameter; tail 1.0 to 1.4 times vulva-anus distance ..... *franklinae* SIDDIQI, 1981[16]

— Cuticle with 18 to 21 longitudinal ridges; annules from head to anus 148 to 163; rectum shorter, about 3/4 times anal body diameter; tail 1.3 to 1.6 times vulva-anus distance ..... *japonicus* MIZUKUBO & MINAGAWA, 1984[12]

29. Lateral vulval flaps absent; lateral fields 1/4 times body diameter; head with three annules; tail terminus pointed ..... *alacinatus* SIDDIQI, 1981[16]

— Lateral vulval flaps distinct; lateral fields 1/4 to 1/3 times body diameter; head with four annules; tail terminus pointed or hair-like 30

30. Annules wide, 3.0 to 3.6 μm in mid-body region; basal oesophageal bulb small, half as long as isthmus; lateral fields originating shortly before median bulb ..... *acceptus* ANDRÁSSY, 1982[3]

— Annules narrower, 2.2 to 3.3 μm in mid-body region; basal oesophageal bulb 2/3 times isthmus or longer; lateral fields originating just behind head. ..... *costatus* (DE MAN, 1921)[3]

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和文摘要

邦産*Coslenchus*属線虫の分類
Ⅱ. *Coslenchus*属の新参シノニム2属と種の検索表

水久保隆之・皆川　望

*Coslenchus*属には広い形質変異が認められるため、その属性について系統発生の観点から検討した。主要12形質の形質転換系列に基づき推定した祖先状態を比較し、その結果、本属を*Aglenchus*属と姉妹群関係を持つ単系統群であると結論した。また種の系統発生を分析した結果、本属に2系列にまとめられる4種群を認めたが、系列間に明確なギャップがないため本属は従来の範囲で有効であると考えた。さらに，本属に近似した*Paktylenchus*属及び*Cosaglenchus*属を定義している，陰門あるいは膣の形質を検討した。その結果，それらの形質は本属の1種群の形質転換系列の末端に位置付けられるごく新しく派生した形質及び種群間で，平行的に派生した形質と考えられた。このことから上記2属を*Coslenchus*属のシノニムにし、新しいコンビネーションを含めて種の検索表を付した。