Re-evaluation of the phylogenetic position of the genus *Dexiotrichides* (Protozoa, Ciliophora, Scuticociliatida) inferred from stomatogenetic and molecular information for *Dexiotrichides pangi* *

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Abstract The divisional process and systematic position of the marine scuticociliate *Dexiotrichides pangi* are studied. Based on both stomatogenetic data and 18S rDNA gene sequences, the phylogeny and morphogenetic characteristics of this taxon, and of other related genera, are analyzed and discussed. Both the divisionary events and the molecular biological data indicate that this species/genus, together with certain other genera in the *Dexiotricha*-complex, occupies an intermediate position between the tetrahymenids and the "typical" scuticociliate, which suggests that the *Dexiotricha*-like taxa should be excluded from the "true" scuticociliates. As a further contribution, the process of stomatogenesis in *D. pangi* can be summarized as follows: (1) The oral primordia in the opisthe are formed only by the proliferation of basal bodies in the scutica field, which subsequently develop into three membranelles, while the new paroral membrane seems to be generated by the sub-anterior portion of somatic kinety 1 (the 1st postoral intercalary kinety). The latter character exhibits a mode similar to *Tetrahymena*. (2) In the proter the parental membranelles are retained and remain unchanged throughout the entire division process; only the old paroral membrane is disassembled and differentiated into the anlage, which then gives rise to the new paroral membrane and the scutica of the proter. The 18S rRNA gene sequence reported here is the first one for a ciliate in the *Dexiotricha*-complex.

Keywords: marine ciliate, systematic position, stomatogenesis, 18S rRNA gene sequences, *Dexiotrichides pangi*.

In recent decades morphogenetic investigations on ciliated protozoa have been increasingly used in order to elucidate phylogenetic relationships among taxa, and separate morphologically similar taxa[1—9]. A survey of the marine scuticociliates of the north China seas has revealed much new data concerning their morphology, morphogenesis and systematics[10—12].

Until very recently, *Dexiotrichides* was a monotypic genus with *D. centralis* (Stokes, 1885) Kahl, 1931 the only known species. The morphogenesis of *D. centralis*, however, remains unknown[5, 6]. According to the redefinition made by Song et al.[13], *Dexiotrichides* is characterized as follows: body circular in cross-section and with a conspicuous apical plate; buccal cavity conspicuously depressed with cytostome located at or near the equatorial level; three transversely orientated membranelles, each comprising two to three rows of kinetosomes; paroral membrane with zigzag structure, extending to about the half length of the buccal field; multi-rowed scutica; somatic kinety 1 (SK_1) noticeably shortened at the anterior end, terminating adjacent to the posterior end of the buccal field; basal bodies in the equatorial region usually arranged in a circular pattern; in the anterior portion of somatic kinety 2 (SK_2), the basal bodies are characteristically in pairs and separated from the posterior part of SK_2; one caudal cilium.

In the same paper, a second species of *Dexiotrichides*, *D. pangi*, was also described[13]. Some morphogenetical stages of *D. pangi* were also observed, albeit incompletely, but nonetheless these observations indicated that the process of ontogeny in *Dexiotrichides* is unlike that in other scuticociliates[13]. In the present work, additional events during binary division of *D. pangi* are described. The systematic position of *Dexiotrichides* is discussed in

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the light of these observations and molecular phyogenetic analysis.

1 Material and methods

1.1 Morphogenetic observations

Cells of *Dexiotrichides pangi* used in the current studies were from a clonal culture maintained in the cell bank of the Laboratory of Protozoology, OUC. This strain was originally collected in the summer of 2002 from a water-filter-system for an aquarium of OUC.

Protargol[14] and pyridinated silver carbonate[15] impregnation methods were used to reveal the infraciliature in division stages.

Drawings of impregnated specimens were made with the help of camera lucida; measurements and most drawings were performed under 1250x magnification. Terminology and systematics are mainly according to Corliss[3].

1.2 DNA extraction and phylogenetic analyses

Extraction of 18S rDNA and PCR reaction were performed as previously described[2]. All methods used for phylogenetic analyses are as explained by Shang et al.[16]. Distance data were bootstrap resampled 1000 times. The nucleotide sequences used in this paper are available from the GenBank/EMBL databases.

2 Results

2.1 Morphogenesis during binary fission in *Dexiotrichides pangi*

Despite thorough searching some morphogenetic stages could not be located in our impregnated specimens. We therefore describe here merely the principal process. The first stage of stomatogenesis in *Dexiotrichides pangi* is the proliferation of kinetosomes that comprise the fragment-like two- to three-rowed scutica (Fig. 1(a)). Initially, several basal bodies appear at the anterior ends of the fragments of scutica (Fig. 1(c), (d), (e), arrows), which subsequently develop into the oral primordia (OP) of the opisthe. Shortly after the formation of the OP, more kinetosomes proliferate which then align in several obliquely oriented rows (Fig. 1(f), 2(d), arrows). Somatic kinety 1 (SK_1; = 1st postoral intercalary kinety) probably does not contribute to the formation of the oral primordia, although the basal bodies in its anterior portion become re-arranged and are often composed of several dikinetids (Fig. 1(a), (c), (e)).

During the next stages, three membranelle-anlagen develop from the oral primordia, each comprising about three kinety rows (Fig. 1(f)—(h)). These then re-arrange into the membranelles for the opisthe (Fig. 1(i); 2(f), arrows).

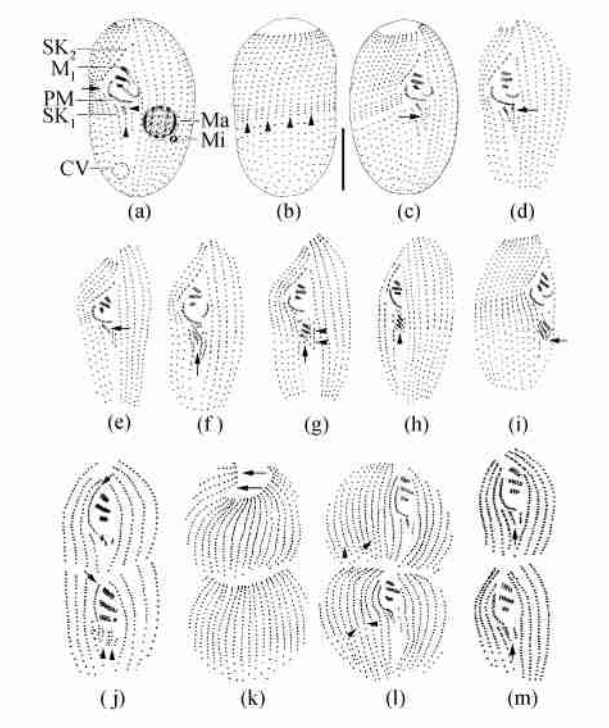

Fig. 1. Stomatogenesis of *Dexiotrichides pangi*. (a) Ventral view in a non-dividing specimen showing the buccal apparatus and ciliature, note the gap between somatic kinety 2 (SK_2) (arrow) and the scutica (arrowheads). (b) Dorsal view of the same specimen as in (a), arrowheads mark the densely ciliated area. (c)—(f) Ventral view of buccal apparatus in early stages of morphogenesis, arrows mark the proliferating kinetosomes in scutica area which are about to form the oral primordium. (g) and (h) Middle stages of division, arrowheads indicate the newly formed membranelles in the opisthe. (i) Slightly later stage than in (h), note that there are almost no "extra" basal bodies posterior to the membranelles (arrow). (j) Late divisional stage, note the newly formed paroral membrane which is derived from the old PM in the proter and the sub-anterior end of the postoral intercalary kinety (SK_1) of the opisthe (arrow). Arrowheads mark the developing scutica. (k) Dorsal view of the same stage as in (j), arrows mark the extending kineties at the apical end, note the equatorial region in both daughter cells is more densely ciliated. (l) and (m) Stage just before the cell division, arrowheads in (l) mark the densely ciliated region. CV, contractile vacuole; M_1, membranelle 1; Ma, macronucleus; Mi, micronucleus; PM, paroral membrane; $SK_{1,2}$, somatic kinety 1 and 2. Scale bar= 20 μm.

To the left of this primordial field some extra kinetosomes, often arranged in rows, are recognizable in some specimens (Fig. 1(g), arrowheads). These

appear to be resorbed during the later stages. The parental buccal apparatus remains unchanged up to this point (Fig. 1(g)—(i)). Also during this period there is a marked proliferation of basal bodies in the equatorial region of the cell, thus the kineties in this area are composed of densely arranged kinetosomes with some appearing to form dikinetids (Fig. 1(h), (i); 2(g), arrowheads).

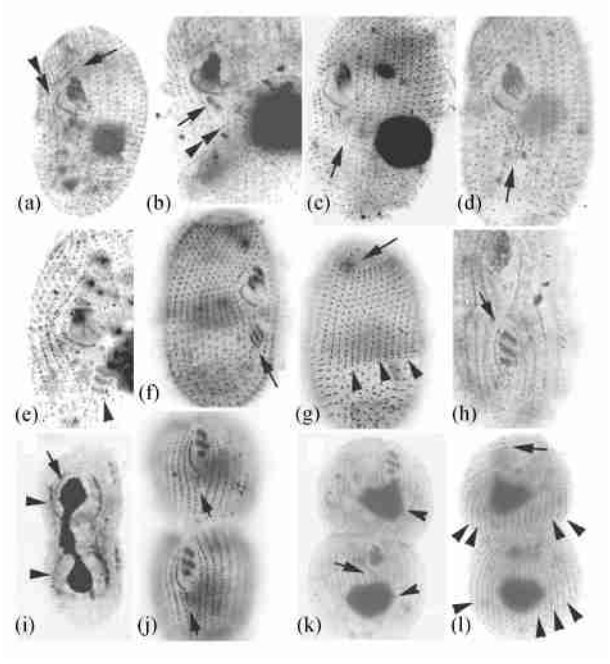

Fig. 2. Photomicrographs of stomatogenesis. (a) Ventral view of non-dividing cell, arrow marks the anterior part of somatic kinety 2 (SK_2), double arrowheads indicate the anterior end of the postoral intercalary kinety (SK_1). (b) Ventral view of non-dividing cell, arrow marks the rowed part in scutica (Sc), double-arrowheads refer the single-rowed structure of Sc. (c) and (d) Early stages of division, arrow marks the proliferation of kinetosomes in the oral primordial field. (e)—(g) Middle stage of division; (e) and (f) Ventral views, arrowhead in (e) and arrow in (f) mark the newly formed oral primordia (OP). (g) Dorsal view, arrowheads mark the densely ciliated region, arrow marks the apical plate. (h) Late dividing stage, arrow marks the paroral membrane in the opisthe. (i) To show the macronucleus in division (arrow), arrowheads mark the swollen nuclear membrane. (j) Ventral view, arrows mark the newly-built Sc in both daughter cells. (k) and (l) To show the stage just before division is completed, arrow in (k) marks the SK_1, arrow in (l) marks the extending kineties on the apical plate; arrowheads in (k) mark the divided macronuclei, arrowheads in (l) indicate the densely ciliated region of the somatic kineties.

We failed to obtain examples of the proceeding stage in the process stage, the next stage we observed being the beginning of transverse fission of the cell (Fig. 1(j); 2(h)). In this phase, the anlage for the paroral membrane (PM) in the opisthe seems to be formed by the sub-anterior portion of SK_1. The anteriormost part of SK_1 moves anteriorly and becomes the SK_1 of the proter. The newly formed PM-anlage is conspicuously longer than the PM in non-dividing cells. Some basal bodies are irregularly distributed at its posterior end (Fig. 1(j), arrowheads) and these subsequently give rise to (or join to form ?) the new scutica.

At about the same time, the parental paroral membrane de-differentiates and forms the PM-anlage of the proter. The basal bodies in this anlage become more loosely arranged, the whole structure now being single-rowed and extending the entire length of the buccal field (Fig. 1(j), arrows). Some kinetosomes are observed at the posterior end of the PM and these subsequently form the new scutica as in the opisthe.

During the subsequent stage the newly formed buccal apparatus in the opisthe continues to migrate posteriorly to reach its final position. At the same time the PM-anlage condenses into a zig-zag structure leaving some fragmentary rows of kinetosomes (the scutica) behind (Fig. 1(l), (m)). Meanwhile, the corresponding structure in the proter undergoes a similar process, the paroral membrane being re-formed with a zig-zag arrangement of basal bodies. The new scutica is also formed in the postoral area (Fig. 1(m), arrows).

As cell division nears completion all elements of the ciliary apparatus reach their final positions. The kinetosomes in the equatorial region of the somatic kineties, however, remain densely arranged after the completion of the division process. The fact that many individuals in the non-dividing stage possess this arrangement of kinetosomes indicates that this period could last for a long time.

As cell division progresses, the macronucleus, which has a conspicuously swollen membrane-like nuclear envelope, divides into two parts, one going to each daughter cell before they completely separate (Fig. 2(i)). No micronucleus was observed during our investigations.

As a brief conclusion, the main stomatogenetic process can be summarized as follows:

In the proter: (1) The parental paroral membrane (PM) develops into the PM-anlage, which then gives rise to the PM and the scutica; (2) the parental membranelles 1—3 remain completely unchanged and are inherited by the proter.

In the opisthe: (1) PM-anlage probably derives from the sub-anterior portion of somatic kinety 1 which then gives rise to the new PM and possibly also a part of the scutica; (2) the oral primordia are formed by the old scutica and develop into the adoral membranelles and the new scutica (partly or completely).

2.2 Phylogenetic position of *Dexiotrichides pangi* based on 18S rDNA gene sequences

The least squares tree constructed from 18S rDNA sequences is shown in Fig. 3, which is generally extremely similar to the maximum-parsimony (Fig. 4) and maximum-likelihood (Fig. 5) trees inferred from the same sequence data. The analyses weakly support the morphological and ontogenetical data on the monophyly of the clades of scuticociliates and hymenostomatids. The scuticociliate clade, except for *Dexiotrichides pangi*, consists of 3 moderately well supported sub-groups, which possibly represent family level rank, whereas *Dexiotrichides pangi* branches at the base of this clade. The sister-taxon relationship between the Peniculina (represented by *Paramecium*) and the Hymenostomatia (represented by *Tetrahymena* and *Glauconema*) established by morphological methods[3, 17] is surprisingly weakly supported. The position of *D. pangi* is not consistently supported by maximum parsimony analysis, which groups the hymenostomes with the scuticociliates to the exclusion of the peniculines (data not shown). It is most likely that the *D. pangi* sequence is de-stabilizing the position of the hymenostomes, suggesting an intermediate position that cannot be satisfactorily resolved with currently available data.

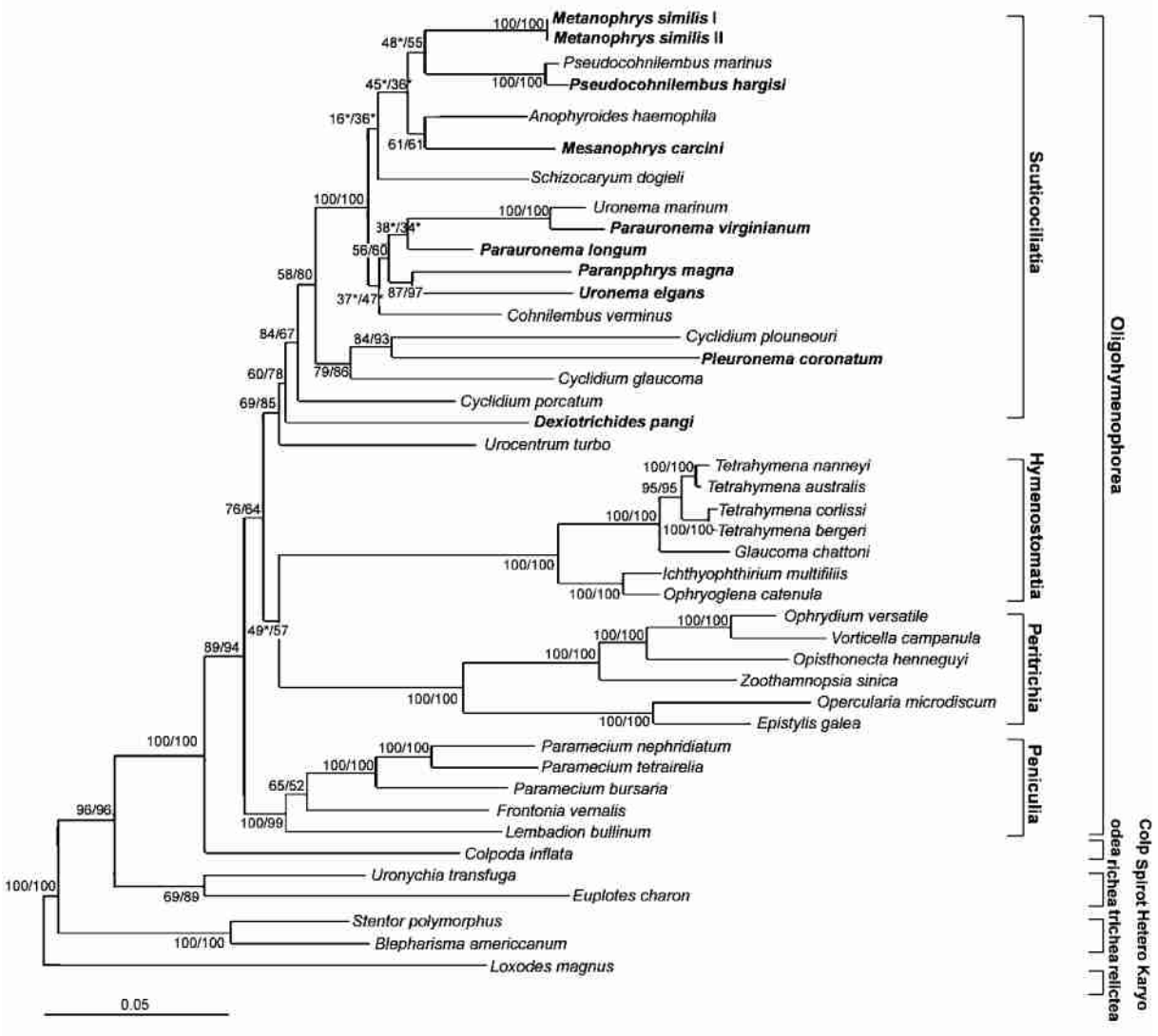

Fig. 3. An SS rDNA tree derived from evolutionary distances. The consensus tree of 1000 bootstrap resamplings of the data set was constructed using the least-squares (LS) method. Evolutionary distance is represented by the horizontal component separating species. The scale bar corresponds to 10 substitutions per 100 positions. The sequences determined presently appear in boldface.

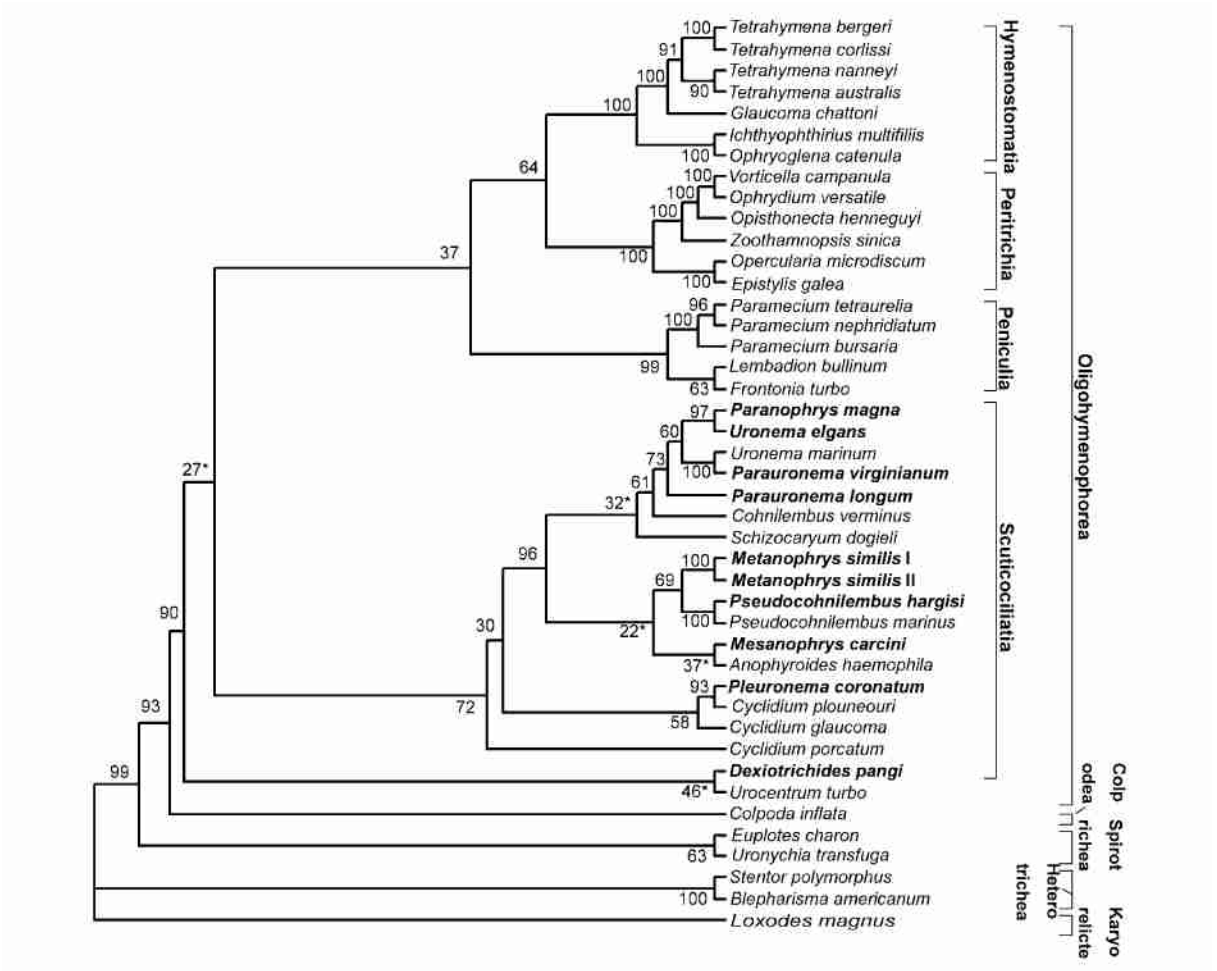

Fig. 4. A maximum-parsimony tree inferred from 18S rDNA gene sequences using a bootstrap resampling of the data set. The numbers at the nodes represent the bootstrap values. Asterisks indicate bootstrap values of less than 50%. The sequences determined presently appear in boldface.

Though some contradictions are present, e.g. the genera *Uronema* and *Cyclidium* are paraphyletic and *Cohnilembus* groups with *Uronema-Parauronema-Paranophrys*-cluster, viz. usually near *Pseudocohnilembus* as revealed recently[16], all these cases are associated with only moderate bootstrap support and are not better resolved by maximum parsimony analysis. The results obtained in the present work do, however, consistently locate *Dexiotrichides pangi* outside the "true" scuticociliates and between the Scuticociliatia and Hymenostomatia. This position, taken with the morphological evidence, could be simply explained by considering the "true" scuticociliates to be a clade within the hymenostomes, rather than as sister taxa.

3 Discussion

Over the past 50 years various studies have demonstrated that the scuticociliates and hymenostomes are closely related, notwithstanding the fact that their divisional processes are of fundamentally different patterns[3,6,17—19].

Morphologically, *Dexiotrichides pangi* resembles the "true" scuticociliates especially with respect to the infraciliature and silverline system, e.g. the presence of apical plate, the caudal cilium and the scutica, having a *Cyclidium*-like silverline pattern[5,13]. Unlike most other scuticociliates, however, *D. pangi* has a postoral intercalary kinety (=SK1), a feature typical of the tetrahymenids (Table 1) and its somatic basal bodies are predominantly monokinetid rather than dikinetid. According to the redefinition by Foissner[6], stomatogenesis in most scuticociliates belongs to the "scuticobuccokinetal" type which is characterized by the opisthe's oral primordia deriving either from: (1) the paroral membrane and from a separate set of basal bodies (scutica) located either posterior to (or adjacent to) the paroral membrane, or (2) solely from the paroral membrane[6]. In both the proter and the opisthe the

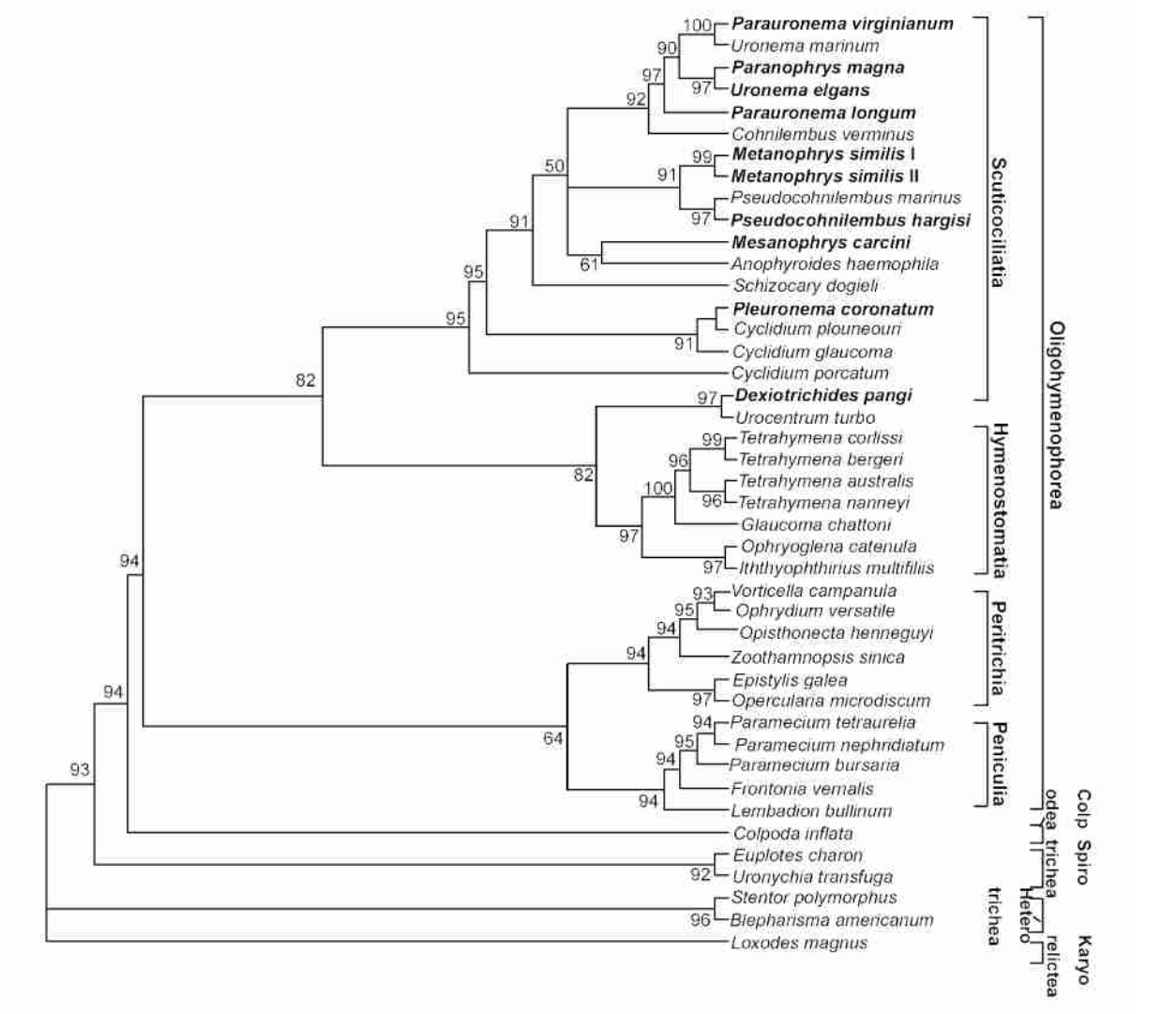

Fig. 5. A maximum-likelihood tree inferred from 18S rDNA gene sequences using a bootstrap resampling of the data set. The numbers at the nodes represent the bootstrap values. The sequences determined presently appear in boldface.

scutica derives from the posterior end of the paroral membrane anlage[20—23].

On the contrary, the typical mode of divisional process in tetrahymenids is "monoparakinetal", which belongs to the teloparakinetal pattern[6]. In this mode, only one postoral kinety is involved in the formation of the oral anlagen and initially the proliferation of the kinetosomes occurs *de novo* and alongside, rather than within, the parental structure. All membranelles in the opisthe derive from these oral anlagens and no scutica is formed[6, 8, 9].

Based on the morphogenetic processes, *Dexiotrichides pangi* is possibly more similar to tetrahymenids, particularly during the early stages of stomatogenesis. The formation of the paroral membrane in the opisthe and the origin of the oral primordia, which involves a single field of basal bodies generated from the kinetosomes of the scutica rather than "*de novo*" as in tetrahymenids, for example, are very similar to those in the tetrahymenids (Table 1). By contrast in typical scuticociliates, most parts of OP in the opisthe are formed by the anlagen derived from the parental paroral membrane[22]. Another morphogenetic event in *D. pangi* resembling that of "true" scuticociliates is the mode of development of the paroral membrane in the proter, which is by a process of de-differentiation of the parental structure followed by re-formation of the new membrane and the scutica (vs. no changes in tetrahymenids). Like the hymenostomes, the paroral membrane shows no indication comprising 3 segments in *D. pangi* (Fig. 1) as is characteristic of scuticociliates[17].

Table 1. Comparison of stomatogenetic events, patterns of structure-formation and morphological characterization in *Dexiotrichides pangi*, tetrahymenids and typical scuticociliates.

Character	*Dexiotrichides pangi*	Most other typical scuticociliates	Tetrahymenids
Postoral intercalary kineties	Single	Absent	2 or more
Silverline system	No intermediate line	No intermediate line	With intermediate line
Scutica in non-divisional stage	Present	Present	Absent
Apical plate	Present	Present	Absent
Caudal-cilium-complex[a)]	Present	Present	Absent
Buccal cavity	Inconspicuous	Inconspicuous	Conspicuous
Formation of paroral membrane in the proter	Newly formed	Newly formed	Retained from old structure
Formation of three membranelles in the opisthe	Completely from OP Formed by old Sc	Partly from Sc, Partly from OP[b)]	Completely from OP Formed by old Sc
Type of stomatogenesis[c)]	Monoparakinetal[d)]	Scuticobuccokinetal	Monoparakinetal
Origin of paroral membrane in the opisthe	From sub-anterior part of postoral intercalary kinety[e)]	From splitting of the parental PM	From sub-anterior end of postoral intercalary kinety

a) This structure consists of a basal-body-complex with one caudal cilium and a specialized silverline circle which extends around the caudal pole; b) seen in most groups of scuticociliates; c) according to definitions in ref.[7]; d) atypical; the basal bodies in the OP do not occur *de novo* like in tetrahymenids, rather they develop from the proliferation of basal bodies in the scutica; e) not completely clear, but very possibly the PM is formed from the sub-anterior part (not extreme "anterior end") of the postoral intercalary kinety, while the anteriormost part takes part in the formation of the postoral intercalary kinety in the proter. (Abbreviations: OP, oral primordia; Sc, scutica)

At least 13 nominal genera of scuticociliates possess a *Dexiotricha*-like ciliary pattern in the sense that they have: obliquely oriented *Tetrahymena*-like membranelles; a deeply excavate buccal cavity; an evenly curved paroral membrane; a postoral intercalary kinety (in most cases); a short fragment with densely packed dikinetids at the anterior end of SK_1. These are: *Dexiotricha*, *Dexiotrichides*, *Platynematum*, *Cardiostomatella*, *Cinetochilum*, *Balanonema*, *Pseudoplatynematum*, *Cristigera*, *Paratetrahymena*, *Pseudocinetochilum*, *Loxocephalus*, *Sphenostomella* (= *Sathrophilus*) and *Paradexiotricha*[5,7,17,24]. According Corliss[3] and Lynn & Small[17], these are assigned to 5 or 3 different families respectively. Nevertheless, only four of these taxa mentioned above have been studied morphogenetically, albeit insufficiently in some cases, i.e. *Sphenostomella* (*Sathrophilus*), *Loxocephalus*, *Dexiotricha* and now *Dexiotrichides*[4,6,7,19]. Of these, *Sphenostomella* (*Sathrophilus*) and *Loxocephalus* seem to have similar modes of morphogenesis to that of *Dexiotrichides*[4,7], while *Dexiotricha* exhibits a mixed pattern, i.e. the oral primordia in the opisthe are apparently formed by kinetosomes both from the scutica area and from a kinety derived from the parental paroral membrane. The stomatogenetic process of the latter is hence also partly similar to that in most other 'typical' scuticociliates, i.e. the parental paroral membrane splits at a very early stage of division, part of which then gives rise to the formation of the oral primordia.

In conclusion, we suggest that, based on the morphological, morphogenetical and molecular data, those ciliates with *Dexiotricha*-like ciliary pattern, which form, morphologically and very likely also morphogenetically, a clearly outlined group belonging to an assemblage between the typical Scuticociliatia and Hymenostomatia. They represent hence an intermediate taxon (i.e. at about order level) and should be excluded from the true scuticociliates. Furthermore, these ciliates might be divided into at least two sub-groups (likely at the family level) according to the stomatogenetic patterns: those with a *Dexiotrichides*-type pattern and those with a *Dexiotricha*-type.

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