Morphological reports on two species of *Dexiotricha* (Ciliophora, Scuticociliatia), with a note on the phylogenetic position of the genus

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INTRODUCTION

Scuticociliates are free-living organisms of limnetic and marine ecosystems, and this group often draws more public attention than other ciliates, mainly because some are symbionts or opportunistic parasites of aquatic animals (Fan et al., 2011a, b; Foissner et al., 1994; Lobban et al., 2011; Pan et al., 2013). In this age of 'refinement', taking a phylogenetic view of this group with molecular analyses plays an equal role with exploring species diversity and providing standard descriptions of previously unclear species or novel species (Fan et al., 2009; Pan et al., 2011, 2013; Zhang et al., 2010, 2011).

The order Loxocephalida was proposed by Jankowski (1980) to include those genera with morphological characteristics of both scuticociliates (scutica and an apical plate) and hymenostomes (obliquely orientated oral membranelles and post-oral kineties). Based on available data, recent studies have reconsidered the phylogenetic status of the order and confirmed it as paraphyletic group, and members of the group share no analogous morphogenetic pattern (Gao et al., 2013; Li et al., 2010; Long et al., 2007; Song et al., 2005; Zhang et al., 2010, 2011). However, since the data used by these analyses were quite limited, and the inter-relationship of the order was still indeterminate, in order to characterize this order fully, more sequences are needed, along with morphological/morphogenetic descriptions of suggested members (Gao et al., 2013; Lynn, 2008; Zhang et al., 2010, 2011). *Dexiotricha*, also a candidate member of the order, has not been subjected to a molecular phylogenetic analysis. It is a confusing taxon in terms of its taxonomy, because many species were assigned to other genera, e.g. *Loxocephalus*, and several species have been confirmed to be synonyms (Foissner et al., 1994; Peck, 1974; Wilbert, 1986). Thus, a detailed morphological description and the sequences of marker genes, e.g. the small-subunit rRNA gene (SSU rDNA), will contribute not only to the taxonomy of the genus but also to the further understanding of the phylogenetic status of the order Loxocephalida.

In our study, the morphological description of two members of *Dexiotricha*, isolated from soil and freshwater, is documented based on observations of specimens *in vivo*, after protargol staining and scanning electron microscope (SEM) sample preparation. In addition, the SSU rDNA of...
the two species was sequenced for the first time, and phylogenetic analyses were performed to assess the systematic position of the genus Dexiotricha in the order Loxocephalida.

**METHODS**

**Sample collection, observation and identification.** Dexiotricha elliptica (Kahl, 1931) nov. comb. was collected from farmland at Zulfi city, north west of Riyadh, Saudi Arabia (26° 13′ 22″ N 44° 51′ 43″ E). The soil sample was taken directly, and was then processed with the non-flooded Petri dish method in the laboratory (Foissner, 1987). Dexiotricha cf. granulosa (Kahl, 1881) Foissner et al., 1994 was collected from a freshwater pond in Changfeng Park, Shanghai, China (31° 13′ 30″ N 121° 23′ 56″ E). Cells were isolated and observed in vivo using differential interference contrast microscopy. Protargol staining (Wilbert, 1975) was performed in order to reveal the infraciliature. Drawings were made with the help of a camera lucida. Measurements were made under ×100–1250 magnification. Samples for SEM were prepared as described by Gu & Ni (1993) and were observed under a Hitachi S-4800 scanning electron microscope with accelerating voltage 10.0 kV. Terminology and classification mainly follow Jankowski (1980) and Lynn (2008).

**DNA extraction and gene sequencing.** Extraction of genomic DNA was carried out according to the methods described by Gong et al. (2007). To minimize PCR amplification errors, high-fidelity TaKaRa ExTaq was used to amplify the SSU rDNA gene using universal oligonucleotide primers (forward, 5'-GAAACTGCGAATG-GCTC-3' or 5'-AATCTGGTTGATTTTGCGAGT-3'; reverse, 5'-TGATCCTTCTGCAGGTACCTAC-3') designed by Medlin et al. (1988) and Elwood et al. (1985). Cloning and sequencing were performed as reported by Zhang et al. (2011).

**Phylogenetic analyses.** Other than the SSU rDNA sequences of the two species, sequences used in the present analyses were obtained from the NCBI GenBank database. Sequences were first aligned using the GUIDANCE algorithm (Penn et al., 2010a) with default parameters in the GUIDANCE web server (Penn et al., 2010b). Ambiguous columns in the alignment below the confidence score of 0.6 calculated by GUIDANCE were removed. The final alignment including 1720 sites and 74 taxa was used to reconstruct phylogenetic trees using the methods described below. Coleps nolandi, Tiarina fusa and Prorodon teres were chosen as the outgroup taxa. The most appropriate model for phylogenetic analyses was selected by both Modeltest version 3.4 (Posada & Crandall, 1998) and MrModeltest version 2.2 (Nylander, 2004). Maximum-likelihood (ML) analyses were carried out using RAxML-HPC2 version 7.2.8 (Stamatakis et al., 2008) on the CIPRES Science Gateway (Miller et al., 2010) using the GTR + G model as the selected option. Support came from a majority rule consensus tree of 1000 bootstrap replicates. Bayesian inference (BI) analysis was performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) on the CIPRES Science Gateway using the GTR + I + G model as selected by MrModeltest version 2.2 according to the Akaike information criterion. Markov chain Monte Carlo simulations were run with two sets of four chains for 4000000 generations with a sample frequency of 100 generations, and the first 10000 trees were discarded as burn-in. All remaining trees were used to calculate posterior probabilities using a majority rule consensus.

**RESULTS**

**Family Loxocephalidae Jankowski, 1964**

**Genus Dexiotricha Stokes, 1885**

**Dexiotricha elliptica** (Kahl, 1931) nov. comb. (Figs 1 and 2; Table 1)


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**Fig. 1.** D. elliptica (Kahl, 1931) nov. comb. from life (a, c) and after protargol staining (b, d, e). (a) Ventral-lateral view (from present work); arrow marks the caudal cilia. (b) D. media sensu Small & Lynn, 1985. (c) Ventral views of L. elliptica sensu Kahl, 1931 (from Kahl, 1931). (d, e) Ventral (d) and dorsal (e) views of infraciliature; arrowhead in (d) marks the densely arranged basal bodies in the anterior part of SK1 and the arrow depicts the anteriorly shortened SKn. The arrowhead in (e) marks the two dikinetids in each somatic kinety. CVP, Contractile vacuole pore; M1-3, membranelles 1–3; Ma, macronucleus; Mi, micronucleus; PK, post-oral kineties; PM, paroral membrane; Sc, scutica; SK1, n, somatic kinety 1, n. Bars, 25 μm.
Detailed study and a description have never been given for this species; thus, an improved diagnosis is supplied here.


**Deposition of voucher specimens.** One voucher slide with protargol specimens is deposited in the Laboratory of Protozoology, East China Normal University, with registration number FXP-2012-10-7-1.

**Description.** Cells 45–55 × 20–25 μm *in vivo*, with length : width about 2 : 1. Body shape long ellipsoidal, with ventral side straight, dorsal side gently curved (Figs 1a and 2c). Buccal cavity is small with inconspicuous buccal cilia (Figs 1a and 2a, b). Cytoplasm colourless and containing numerous granules of about equal size (Figs 1a and 2d, g). Food vacuoles approx. 5 μm in diameter present when well fed (Fig. 2a, b). Pellicle non-concave, with inconspicuous ridges along cilia rows (Fig. 2f). Extrusomes uneasy to detect, about 4 μm long (Figs 1a and 2d). Contractile vacuole located posteriorly near left of meridian, approx. 6 μm in diameter; contracting interval about 10 s (Figs 1a

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**Fig. 2.** *D. elliptica* (Kahl, 1931) nov. comb. from life (a–h) and after protargol staining (i–l). (a, e) Lateral-ventral views of slightly compressed individuals; the arrow in (a) indicates the buccal field and the arrow in (e) refers to the contractile vacuole. (b) Anterior portion, showing the buccal cavity (arrow) and the food vacuoles (arrowheads). (c, d) Individual in free swimming (c) and slightly compressed (d); the arrow marks the caudal cilium, and arrowheads indicate the extrusomes. (f) Surface of the cell, to show the kinety rows (arrowheads). (g) Posterior portion, showing the small granules in the cytoplasm (arrowheads). (h) Dorsal view to show the somatic cilia. (i) Ventral view of infraciliature; the arrowhead shows the anteriorly shorted SKn and the arrow marks the contractile vacuole pore. (j) Showing the buccal apparatus and part of the somatic kineties; the arrowhead marks the densely arranged kinetids in the anterior part of SK1 and the arrow indicates the posterior end of SK2. (k) Showing the buccal argyrome (arrow). (l) Dorsal view of infraciliature. See legend to Fig. 1 for abbreviations. Bars, 25 μm.
Table 1. Morphometric characterization of *D. elliptica* (Kahl, 1931) nov. comb. (first line) and *D. cf. granulosa* (second line)

Data are based on protargol-impregnated specimens. —, Not detected.

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and 2e). Single macronucleus, located near mid-body, about 11 × 10 μm in size (Figs 1a, e and 2i). Length of somatic cilia about 8 μm (Figs 1a and 2h). Caudal cilium flexible and extremely long, 20–40 μm (Figs 1a and 2d).

Infraciliature as shown in Figs 1(d, e) and 2(i–l). Constantly 16 somatic kineties, which mostly consist of monokinets extending along the entire length of the cell. SK2 to SKn-1 consist of two pairs of dikinetids in their anterior end (Figs 1d and 2i, l). Anterior six or seven kineties of SK1 densely arranged, SKn anteriorly shorter and starting at level of membranelle 1, consisting only of monokinets (Figs 1d and 2i, j). Three post-oral kineties (PK), each consisting of one pair of dikinetids in its anterior end. PK1 starting anteriorly below posterior end of paroral membrane, nearly extending to the end of the cell, PK3 shorter, starting anteriorly near cytostome, extending over half of body, PK2 very short, comprising only four kineties, anteriorly near scutica (Figs 1d and 2i, j). SK2 posteriorly shorter and ending near contractile vacuole pore (Figs 1d and 2j). Buccal apparatus consists of three transversely positioned oral membranelles (M) as follows. M1 extends obliquely toward posterior from right to left, consisting of three parallel rows and a curved row around anterior end of three rows. First row is two kineties shorter than the other two. M2 forms a 30° intersection angle with M1 and consists of two rows of five to seven kineties, and some additional kineties on its right side. M3 is parallel to M2, smaller than M1 and M2. Paroral membrane is slightly curved, located on right margin of buccal cavity, terminating anteriorly from level of M1 and M2. Scutica composed of three pairs of dikinetids located near posterior end of paroral membrane (Figs 1d and 2j). About nine oral ribs converge towards cytostome (Fig. 2k). Contractile vacuole pore detectable after protargol staining, located near the end of SK2 (Figs 1a and 2i).

**Dexiotricha cf. granulosa** (Kent, 1881) Foissner et al., 1994 (Figs 3 and 4; Table 1)

**Description.** Cells measure 50–70 × 15–25 μm in vivo, oval shaped with anterior end narrowed and posterior end broadly rounded (Figs 3a and 4a). Cytoplasm contains numerous granules, distinctly ring-like and with a regular size of about 1–2 μm (Figs 3a and 4a, b). Food vacuoles present in well-fed individuals (Figs 3a and 4b). Contractile vacuole located near caudal end about 6 μm in diameter, with single excretory pore (Figs 3a and 4a, e, g, h); buccal membranelles inserted in inner wall of buccal cavity, about 6 μm long (Figs 3a and 4f). Somatic cilia and caudal cilium about 8 and 15–20 μm long, respectively (Figs 3a and 4a, e, g).

Infraciliature as shown in Figs 3(b, c) and 4(c, d, i, j). Twenty-eight to thirty somatic kineties, mostly comprising monokinets extending along the whole body (Fig. 3b, c). Somatic kineties near buccal field curved along shape of paroral membrane (Fig. 4c). About eight kineties in anterior part of SK1 densely arranged (Figs 3b and 4i). SKn anteriorly shorter than others and having just monokinets (Fig. 3b). From left side of SKn, about 12 kineties contain only one dikinetid in the anterior end, while the remaining somatic kineties contain two pairs of dikinetids in the anterior end; on the left of SKn, 12 kineties (Fig. 3b, c). Two to four post-oral kineties: PK1, the rightmost one, comprises one dikinetid in the anterior end and monokinets in the remaining part; PK2 contains only three to five monokinets. The number of post-oral kineties on the right of PK2 varies from zero to two (Figs 3b and 4c, e). Buccal apparatus consists of three transversely positioned oral membranelles: M1 and M2 three-rowed, M3 two-rowed (Figs 3b and 4i). Paroral membrane distinctly curved in mid-portion, starting anteriorly from level between M1 and M2 and curving posteriorly around M2 and M3 (Figs 3b and 4i). About 11 oral ribs subvert the buccal area (Fig. 4g). Scutica located near posterior end of PM, possibly comprising three pairs of dikinetids (Fig. 3b, j).

**SSU rDNA sequences and phylogenetic analyses**

The SSU rDNA sequences of the two species have been deposited in GenBank with the length, DNA G+C content and accession number as follows: *Dexiotricha elliptica*, 1683 bp, 44.83 mol%, KF878932; D. cf. *granulosa*, 1769 bp, 46.30 mol%, KF878931. Pairwise comparison reveals that *D. elliptica* and *D. cf. granulosa* differ from each other in 96 positions, with 94.32% sequence identity. They differ from the former *Dexiotricha* sp. MD-2012 (GenBank accession no. JQ723963) in 105 and 15 positions (sequence identity of 93.70 and 99.13%), respectively.

The resulting topologies generated using two algorithms (BI and ML) are generally concordant; therefore, a single topology is presented with support values from both
algorithms indicated on the branches (Fig. 5). In the phylogenetic trees, Loxocephalida is not monophyletic, with most of its members forming a sister clade to the core scuticociliates (25% ML, 0.90 BI), while Cinetochilum and Dexiotrichides group in other subclasses. All three Dexiotricha species form a monophyletic group with full

**Fig. 3.** *D. cf. granulosa* (Kent, 1881) Foissner et al., 1994 from life (a) and after protargol staining (b, c). (a) Ventral-lateral view of a typical individual; the arrow marks the contractile vacuole, and the arrowhead indicates the caudal cilia. (b) Ventral side of the infraciliature; the arrowhead indicates the somatic kineties on the left of SKn, which comprise only one dikinetid. (b) Dorsal side of infraciliature; the arrow marks the bare anterior end. See legend to Fig. 1 for abbreviations. Bars, 25 μm.

**Fig. 4.** *D. cf. granulosa* (Kent, 1881) Foissner et al., 1994 from life (a, b), after protargol staining (c, d, i, j) and after SEM preparation (e–h). (a) Lateral-ventral view of a typical individual; the arrowhead marks the caudal cilium, and the arrow indicates the contractile vacuole. (b) Showing the ring-like granules in the cytoplasm. (c, d) Ventral (c) and dorsal (d) view of the infraciliature; arrowheads mark the post-oral kineties and the arrow refers to the two dikinetids anterior of each somatic kinety. (e) Ventral view; arrow indicates the shortened post-oral kinety which is composed of only three kinetids, the arrowhead marks the anteriorly shorted SKn and the double arrowhead shows the contractile vacuole pore. (f) Details of buccal field; arrowhead marks the oral fibres. (g) Detail of contractile vacuole pore. (h) Right-lateral view; the arrow indicates the dikinetids in the anterior part and the arrowhead refers to the contractile vacuole. (i, j) Infraciliature of buccal field; arrowhead marks the single kinetids in the anterior of somatic kineties at the left side of buccal cavity and the arrow indicates the scutica. See legend to Fig. 1 for abbreviations. Bars, 25 μm.
support, though the relationships within loxocephalids are unsolved due to low support.

**DISCUSSION**

Remarks on *Dexiotricha elliptica*

Kahl (1931) reported the species *Loxocephalus ellipticus* from a freshwater habitat. According to his description on two populations, cells of *L. ellipticus* measured about 40–55 μm in *vivo*, with eight or nine somatic kineties on one side and coarse granules in the cytoplasm; moreover, the contractile vacuole was located near the posterior end (Fig. 1c). The abovementioned description corresponds well with our organism, especially for the subcaudally located contractile vacuole. Thus, we believe our population is conspecific with *Loxocephalus ellipticus* Kahl, 1931. However, both the original description and the present description showed that this organism has no similarities with *Loxocephalus* species. Consequently, a new combination *Dexiotricha elliptica* nov. comb. is proposed. Due to the feminine gender of the genus, the species name must be changed accordingly.

Small & Lynn (1985) reported a population of *D. media* and illustrated the infraciliature without description (Fig. 1b). However, *D. media sensu* Peck, 1974 apparently has more somatic kineties than the population of Small & Lynn (1985) (31–34 compared with about 16, counted from the figure). Moreover, Foissner et al. (1994) had synonymized *D. media* Peck, 1974 with *D. granulosa*. According to the great similarities in terms of the details of the infraciliature and the subcaudally located contractile vacuole, we believe that *D. media sensu* Small & Lynn, 1985 is conspecific with *D. elliptica*.

The genus *Dexiotricha* comprises only six species after Foissner et al. (1994) synonymized *D. media* and *Dexiotricha plagia* with *D. granulosa*. Considering the location of the contractile vacuole and its excretory pore, *D. elliptica* is most

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**Fig. 5.** ML tree inferred from SSU rDNA sequences, showing the position of *D. elliptica* and *D. cf. granulosa*. Nodal support for branches in the ML/BI trees is indicated; ‘–’ indicates bootstrap value disagreement between the ML tree and the reference BI tree at a given node. Bar, 5 substitutions per 100 nucleotide positions. *Coleps nolandi*, *Tiarina fusa* and *Prorodon teres* are the outgroup taxa.
similar to *Dexiotricha colpidiopsis*, but differs by having fewer somatic kineties (16 vs 24–28) (Fig. 6e, f; Table 2).

*D. elliptica* differs from *D. granulosa*, the type of the genus, in having fewer somatic kineties (16 vs 30–38) and a posteriorly located contractile vacuole and in the absence of ring-like granules (Foissner et al., 1994; Fig. 6g–j; Table 2).

According to Jankowski (1964), *D. elliptica* differs from *D. granulosa*, the type of the genus, in having fewer somatic kineties (16 vs 30–38) and a posteriorly located contractile vacuole and in the absence of ring-like granules (Foissner et al., 1994; Fig. 6g–j; Table 2).

*Dexiotricha tranquilla* differs from *D. elliptica* in having more kineties (20–24 vs 16) and two post-oral kineties/fragments (Fig. 6a–c; Table 2).

Though no report of its infraciliature is available, *Dexiotricha polystyla* can be easily distinguished from *D. elliptica* in having multiple caudal cilia (Fig. 6d; Table 2).

**Remarks on *Dexiotricha cf. granulosa***

The species *D. granulosa* has been numerously reported under several synonyms, and Foissner et al. (1994) synonymized *D. plagia* and *D. media* (Fig. 6g–j; Table 2). Considering the great similarities in body size, distinct ring-like granules, the location of the contractile vacuole and the infraciliature, the present study supports the synonymy of the three species. Our population also corresponds well with previous reports on the general infraciliature and most characters from living cells. The prominent difference is the location of the contractile vacuole: in all previous reports, the contractile vacuole of *D. granulosa* is located equatorially, while, in our population, it is located subcaudally (five individuals *in vivo*), and the contractile vacuole pore revealed by SEM is also located near the posterior 1/5 (three individuals). Moreover, the number of somatic kineties is fewer than in previous reports (28–30 vs 30–38). The location of the contractile vacuole or excretory pore is considered to be a stable feature and a very important character to distinguish species, and the number of somatic kineties has also been taken into consideration for classification (Fan et al., 2009, 2011a, b; Foissner et al., 1994). However, in this case, considering the similarities of all other characters, especially the general infraciliature and ring-like granules, we are inclined to designate our organism as *D. cf. granulosa* for the time being. More information based on multiple populations along with sequences of the SSU rDNA are obviously needed.

**Phylogenetic analysis of the genus *Dexiotricha***

The order Loxocephalida is not monophyletic, since *Cinetochilum* clusters with Apostomatia and *Dexiotrichides* clusters with the clade comprising Hymenostomatia and Peritrichia, which corresponds well with previous reports (Gao et al., 2013; Zhang et al., 2010, 2011). Three *Dexiotricha* species/populations form a monophyletic group with
full support, which then clusters with Cardiostomatella and Paratetrahymena, suggests the validity of assigning Dexiotricha to Loxocephalida based on their morphological characters, e.g., having oblique oral membranelles, post-oral kinetics and scutica (Li et al., 2006; Lynn, 2008). However, the node supports are quite low, which indicates that phylogenetic relationships within this order are still indeterminate. Dexiotricha, Paratetrahymena, Cardiostomatella and Dexiotrichides belong to the family Loxocephalidae (Lynn, 2008), but such an assignment is not well supported by phylogenetic analyses, since Dexiotrichides is outside the clade that contains the other three genera. Moreover, previous morphogenesis studies rejected the familial assignment, because there is not much similarity among the morphogenesis of the three genera (data for Cardiostomatella are not available): Paratetrahymena was reported to have a ‘monoparakinetal’ pattern, quite like a hymenostome (Li et al., 2010); Dexiotricha was defined to have a ‘scuticobuccokinetal’ pattern, but the parental paroral membrane was not involved in the formation of the opisthe’s oral primordial (Song et al., 2005); in contrast, Peck (1974) reported that, in D. media, the parental paroral membrane took part in the formation of the opisthe’s oral primordia. Thus, greater taxonomic sampling as well as more molecular evidence is needed in order to investigate further the systematic relationships of the order Loxocephalida and relationships among its members.

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REFERENCES


Table 2. Comparison of Dexiotricha species

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<tr>
<td>D. polystyla</td>
<td>50–70 long (v)</td>
<td>NA</td>
<td>NA</td>
<td>Mid-body Multiple</td>
<td>Foissner (1987)</td>
<td></td>
</tr>
<tr>
<td>D. elliptica</td>
<td>45–55 × 20–25 (v)</td>
<td>16</td>
<td>2–4</td>
<td>Subcaudal</td>
<td>1</td>
<td>This study</td>
</tr>
</tbody>
</table>

*Data from: ch, Chatton–Lwoff-prepared specimen; p, protargol-prepared specimen; v, specimen observed in vivo.


