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Three-dimensional simulation of skeletal structure and artificial twisted appearance of Larnacillidae (Polycystina, Radiolaria)

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Abstract

The family Larnacillidae has the characteristic girdle like skeletons that are perpendicular to each other, and named as the larnacillid structure. Larnacillid individuals occasionally appear to have twisted girdles, but our rotated three-dimensional simulation model of a larnacillid individual attained "artificial" torsional state from a simple larnacillid structure. This "artificial" torsional state appears in any orientation, except in the apical, lateral, dorsal, apical-dorsal, apical-lateral and dorsal-lateral views. Overlapping wings and both sides of girdles create a false sense, with deeper focal depths in this case.

Key words: Larnacillidae

Introduction

The skeleton of the planktonic Protista group with opaline-silica test, Polycystina (Radiolaria); has a fantastic shape, having cone-like, spherical or other variable forms. Some of them have so complex skeletal structures, and such complex forms prevent us from defining a species. In the case of polycystines, the taxonomic difficulties in identifying a species are caused mainly due to two reasons. Firstly, the morphologic convergent would be well recorded in spherical and disk-shaped Polycystina, for example. Superficial features of the superfamily Actinommoidea of Order Spumellaria, are nearly identical to the family Entactinidae of Order Entactinaria; and spherical species are occasionally faced with the difficulty of deciding their phylogenetic position at the order level without the observation of internal structure (e.g. De Wever et al., 2001). Disk-shaped Polycystina also comprises of polyphyletic groups whose origins are derived from families Spongodiscidae, Larnacillidae, and other families. Taxonomic difficulties owing to morphological convergence have been solved step by step with the detailed description of the skeletal structures (e.g. Ogane, 2004; Ogane and Suzuki, 2006; Suzuki, 1998).

The other difficulty in identifying taxonomic species lies in the identification of the orientation of a specimen. Some groups of Polycystina have very complex three-dimensional structures. The family Larnacillidae is an example, and belongs to into the subsuperfamily Larnacillilae, superfamily Pylonoidea, Order Spumellaria, Polycystina by De Wever et al. (2001). The central portion for the test of this family is characterized by the presence of an ellipsoidal microsphere, and is surrounded by elliptical shells which are called as "girdles." As shown in Fig. 1, the girdle is like a single rolled ribbon-like shell and they intersect perpendicular to each other. This structure is called larnacillid structure. Two openings, called gates (Fig. 1), generally appear in the apical, lateral, and dorsal views of the larnacillid structure (De Wever et al., 2001). In the region of intersection, the wing (Fig. 1) was generally found to be well developed.

Owing to this complex structure, larnacillids have been the subject of many studies (Haeckel, 1887; Hertwig, 1879; Müller, 1858). Its structure was figured out and a new taxonomic classification was proposed based on their characteristics (Dumitrica, 1989; Kozlova, 1967; Tan and Chen, 1990). Kozlova (1967) sketched the connecting patterns of the internal skeletons of the microsphere, and defined the upper-lower dimension, and also found the principal combination amongst the perpendicular ones for the sagittal, transverse, and lateral girdles in connection with the dimensions of the microsphere. Detailed structure of larnacillid microsphere was also documented by Dumitrica (1989), who subdivided the Larnacillidae into four subfamilies with definitive characteristics of the microsphere: the Larnacillinae having an uncovered larnacillid structure, the Circodiscinae having a discoidal test

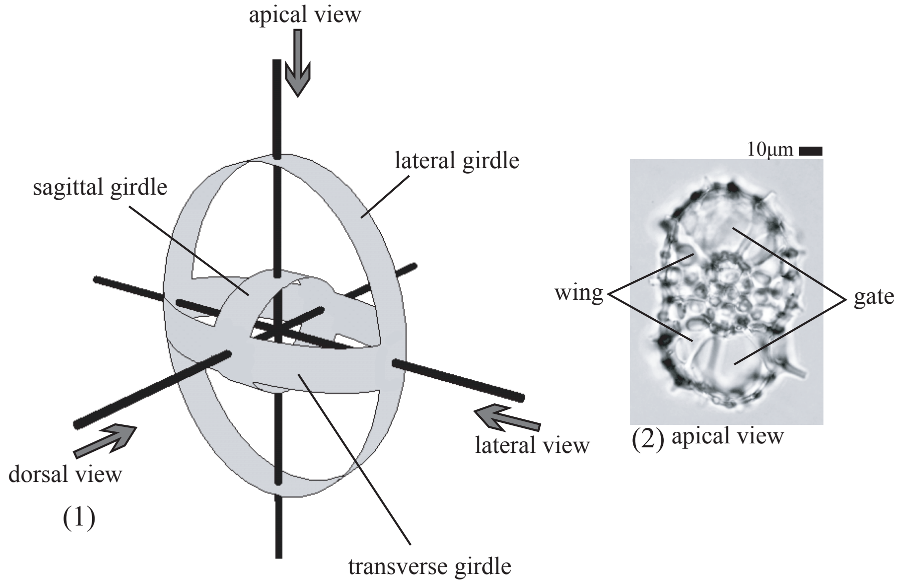

Fig. 1. The terminology of the Larnacillidae. (1) The schematic figure of girdles. (2) The apical view of a typical Larnacillidae individual. Larnacillidae, gen. et sp. indet. ODP Site 844B, Core5, Section4, (17-18cm). east equatorial Pacific, early Pliocene.

coverage over the larnacillid structure, the Cryptolarnaciinae possessing ellipsoidal or spherical test coverage over the larnacillid structure and finally, the Histiastrinae possessing a larnacillid structure covered by the cortical shell, with four chambered tubular arms. Tan and Chen (1990) depicted the differences in shape of both these gates and girdles from the apical, dorsal, and lateral views, and defined the classification at a species-level.

Despite these previous efforts, identifying the species and genus of the Larnacillidae is still very difficult, owing to the complex nature of these obliquely oriented specimens. For this reason, only few studies have dealt with the taxonomy of the Larnacillidae. In this work, we construct a three-dimensional model of a larnacillid form for simulating the changes in its appearance by making use of a commercially available morphing software.

Methods and terminology

A three-dimensional model of a larnacillid form was produced by the software - "Rokkaku-daiou, Super 5" (® Shusaku). This form is a virtual species, based on the schematic illustrations of Dumitrica (1989), Kozlova (1967), and Tan and Chen (1990). The relative size between the girdle and the gate was mainly based on the work by Tan and Chen (1990). As stressed by Dumitrica (1989), the skeletal structure of microsphere is important for the definition of the higher classification of the subfamily, but our work uses a simple ellipsoidal shape because our focus is on the changes in the appearance of the girdles. The virtual larnacillid individual was constructed finally from the inside to outside, by a simple ellipsoidal microsphere, the innermost sagittal, transverse, and lateral girdles; the next to innermost sagittal, transverse and lateral girdles, followed by the next sagittal girdle.

The morphological terminology is same to that of Tan and Chen (1990, Fig. 1) in this study, although different morphological terms are used in different studies for the same or nearly similar skeletal portions of larnacillids (Dumitrica, 1989; Kozlova, 1967; Tan and Chen, 1990).

Results

The framework for the seven girdles and corresponding realistic illustrations are shown in Figs. 2 and 3, respectively. Figure 3 also demonstrates that a larnacillid structure can show variable appearances in different oblique views. It is noteworthy that many twisted structures appeared in certain directions. The most typical and principle views of a larnacillid structure are shown in Figs. 3.1, 3.21, and 3.25; i.e., the apical, dorsal, and lateral views, respectively. Similarly, Figs. 2.1, 2.21, and 2.25 show the apical, dorsal, and lateral views of the girdle frameworks. A column starting from Fig. 2.1 and 3.1 through Fig. 2.5 and 3.5 forms the specimen which was rotated at an interval of 22.5 degrees along the transverse girdle, showing a change in the apical view. A vertical column from Figs. 2.1, 2.6, 2.11, 2.16, 2.21, 3.1, 3.6, 3.11, 3.16, to 3.21, shows the specimens being rotated at intervals of 22.5 degrees along the sagittal girdle, where appearance changes from an apical (Figs. 2.1, 3.1) to a dorsal view (Figs. 2.21, 3.21). Similarly, a column Figs. 2.5, 2.10, 2.15, 2.20, 2.25, 3.5, 3.10, 3.15, 3.20 and 3.25 shows the rotated specimen at an interval of 22.5 degrees along the axis of the lateral girdle, wherein the appearance change from an apical (Figs. 2.5, 3.5) to a lateral view (Figs. 2.25, 3.25). Likewise, a column Figs. 2.21, 2.22, 2.23, 2.24, 2.25, 3.21, 3.22, 3.23, 3.24, and 3.25 shows the appearance changing from a dorsal (Figs. 2.21, 3.21) to a lateral view (Figs. 2.25, 3.25), at an interval of 22.5 degrees. The remaining figures (Figs. 2.7, 2.8, 2.9, 2.12, 2.13, 2.14, 2.17, 2.18, 2.19, 3.7, 3.8, 3.9, 3.12, 3.13, 3.14, 3.17, 3.18, and 3.19) depict the oblique view.

1. Apical views (Figs. 2.1-2.5, 3.1-3.5)

Precise recognition of the larnacillid structure in the apical view is based up on correct recognition of the orientation of the sagittal and lateral girdles. Figs. 2.1 and 3.1 show a vertical sagittal girdle while Figs. 2.5 and 3.5 show a vertically oriented lateral girdle. In the apical view, the sagittal girdle passes over the transverse girdle showing elliptical aspect. The lateral girdle is oriented vertical to the page (Fig. 3) and overlap with the sagittal girdle, so that it cannot be differentiated from other girdles. It can only be recognized on the connecting portion between the lateral girdle and the upper portion of the sagittal ring in Figs. 3.1, 3.2, 3.3, 3.4, and 3.5. Gates appear almost circular, and open vertically to the page (Fig. 3). The inner transverse girdle is observable through the outer lateral and sagittal girdles.

2. Apical-dorsal and dorsal views
(Figs. 2.6, 2.11, 2.16, 2.21, 3.6, 3.11, 3.16, 3.21)

Difficulties in the recognition of the larnacillid structure in the apical view are probably related to the unrecognized oblique appearances (Figs. 2.6, 2.11, 2.16, 3.6, 3.11, 3.16) between the apical (Figs. 2.1, 3.1) and dorsal views (Figs. 2.21, 3.21). The dorsal view is definitively different from the apical view. The outline of the dorsal view corresponds to the shape of the lateral girdle. In Fig. 3.21, the lateral girdle is crossed with the sagittal girdle. Twin distorted elliptical gates open vertically to the page (Fig. 3). On rotating the specimen from the apical to the dorsal side by 45 degrees, the gates that were observable in the apical view (Figs. 3.1 and 3.6) were hidden, as shown in Fig. 3.11. On further rotation up to 67.5 degrees from the apical to the dorsal view (Fig. 3.16), the twin gates appear in the lateral view.

3. Apical-lateral and lateral views
(Fig. 2.10, 2.15, 2.20, 2.25, 3.10, 3.15, 3.20, 3.25)

The appearance between the apical (Figs. 2.5, 3.5) and lateral views (Figs. 2.25, 3.25), can be seen to have changed dramatically as shown in Figs. 3.10, 3.15, 3.20, and 3.25. The lateral view comprises of a large elliptical sagittal girdle and intersects the transverse girdle. The inner sagittal girdle can be seen through the outermost lateral girdle in Fig. 3.25. The 3D-model was rotated at 22.5 degrees from the apical to the lateral view and lies a little to the side (Fig. 3.10), but the 3D-model that undergoes a similar rotation by 45 degrees from the apical to the lateral view dramatically changes in appearance with the twin gates on the transverse girdle (Fig. 3.15). On the other hand, the individual rotated by 22.5 degrees from the lateral to the apical (Fig. 3.20) is very similar in appearance to the lateral view (Fig. 3.25).

4. Dorsal-lateral views
(Figs. 2.22-2.25, 3.22-3.25)

The appearance changes from the dorsal (Figs. 2.21, 3.21) to the lateral view (Figs. 2.25, 3.25) as shown in Figs. 3.22, 3.23, and 3.24. The 3D-model was rotated by 22.5 degrees from the dorsal to the lateral view (Fig. 3.22), and is similar to the dorsal view showing the twin gates. The 3D-model that undergoes a rotation by 45 degrees changes dramatically in appearance from the dorsal to the lateral view (Fig. 3.23). In Fig. 3.23, the gates in the dorsal view are partly hidden, whereas they can partly be seen in the lateral view. In Fig. 3.24, the 3D-model was rotated by 22.5 degrees from the lateral to the dorsal view, showing similar an image to that of the lateral view.

5. Oblique views
(Fig. 2.7-2.9, 2.12-2.14, 2.17-2.19, 3.7-3.9, 3.12-3.14, 3.17-3.19)

The modeled larnacillid structure comprises of girdles perpendicular to each other, and did not have any twisted girdles. However, in any oblique view of the same, apart from apical, lateral, dorsal, apical-dorsal, apical-lateral, and dorsal-lateral views, it shows more or less torsional views. The series of Figs. 2.7, 2.12, 2.17, 3.7, 3.12, and 3.17 were rotated lengthwise by intervals of 22.5 degrees from the position of Figs. 2.2 and 3.2. One cannot differentiate Fig. 3.7 from Fig. 3.2. However, the gates are barely visible in Figs. 3.12 and 3.17, and the transverse girdle of Figs. 3.12 look twisted. The front side of the left portion of the transverse girdle and the back side of the right portion of the transverse girdle appears to be joined in Fig. 3.12, and they looks one S-curved twisted girdle (Fig. 4.1). The series of Figs. 2.8, 2.13, 2.18, 3.8, 3.13, and 3.18 were rotated lengthwise by intervals of 22.5 degrees from the position of Fig. 3.3. As before, we cannot distinguish between Fig. 3.8 and Fig. 3.3, like in Fig. 3.7, but Figs. 3.13 and 3.18 look quite different when compared to Fig. 3.3. In Fig. 3.13, the gates are invisible, while transverse and lateral girdles look twisted like Fig. 3.12(Fig. 4.2). However, in Fig. 3.18, gates from the lateral view become visible and transverse and lateral girdles look twisted as well. The series of Figs. 2.9, 2.14, 2.19, 3.9, 3.14, and 3.19 were rotated lengthwise by intervals of 22.5 degrees from the position of Fig. 3.4. It can be seen that Fig. 3.9 makes a little difference from Figs. 3.7 and 3.8. In Fig. 3.14, the gates on the sagittal girdle become visible. These gates can be seen clearly in Fig. 3.19, which is similar

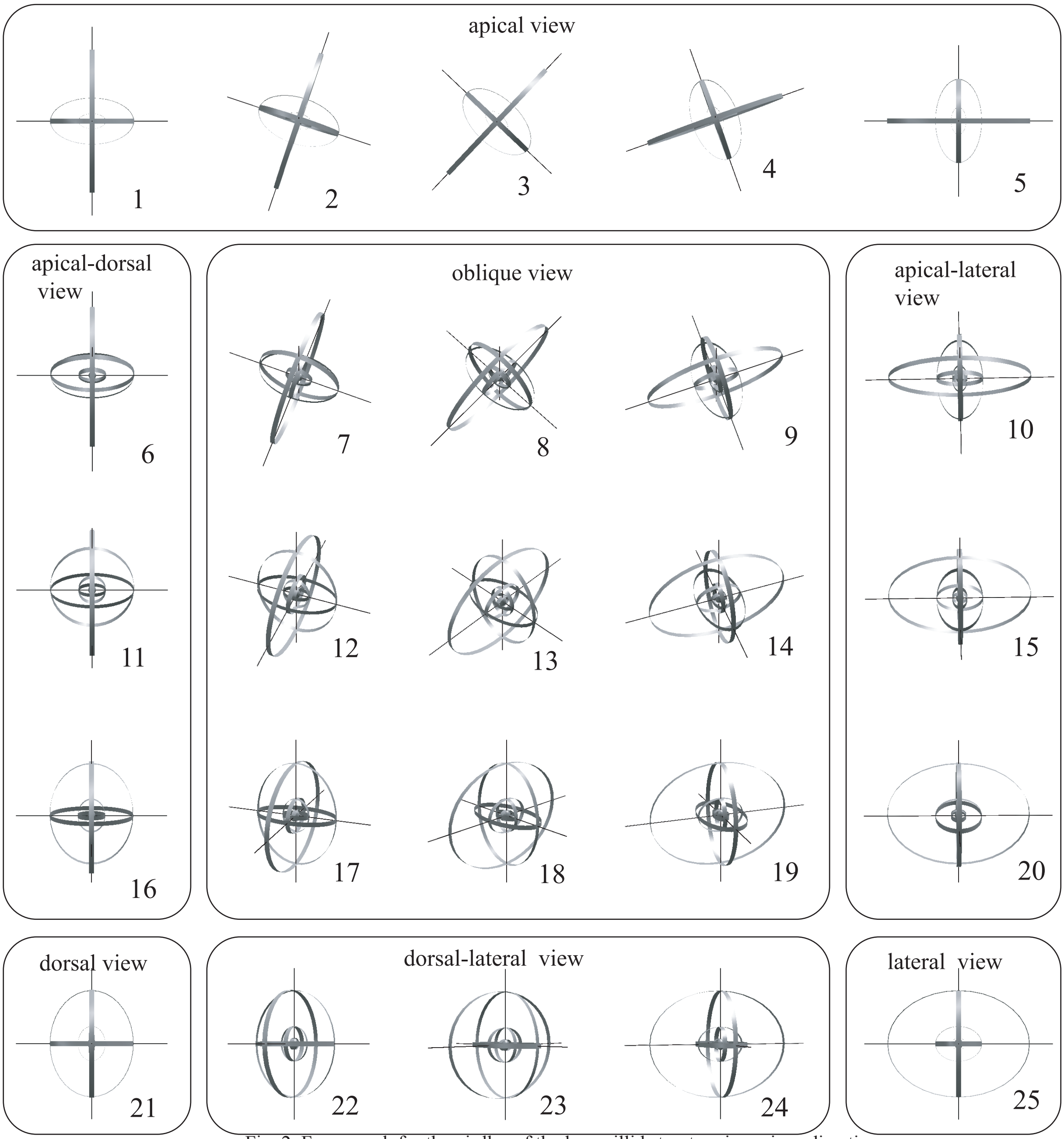

Fig. 2. Framework for the girdles of the larnacillid structure in various directions.

to the dorsal view (Fig. 3.25), but the transverse and lateral girdles are twisted as in Fig. 3.19 like Fig. 3.12 (Fig. 4.3).

Discussion

Using three-dimensional modeling of the larnacillid structure, we attempt to explain the appearance of the larnacillid specimen, at different angles of rotation. In particular, this modeling study provides a solution for the difficulties associated with the recognition of real structures and the "artificial" torsional view.

Previous studies described the skeletal structure of larnacillids in detail, but it has been hard to correlate that part of a larnacillid individual that would actually correspond with the schematic and probably simplified, illustrations. Fig. 2 shown in this study is an advanced version of the schematic illustrations that are based on Dumitrica (1989) and Kozlova (1967). Such studies have shown only three girdles, whereas our interpretation is based on seven girdles for the identification of real individuals, and can be useful. For the comparison with actual larnacillid individuals, the 3-D models in Fig. 3 can be more effective. It differs from the framework laid down in Fig. 2, in the sense that the girdles in the inner portion are hidden by the outer girdles, and the intersection between the girdles develops "wing" instead of a square intersection as in Fig. 2. Such differences can generate quite different impressions of actual individual and the schematic framework.

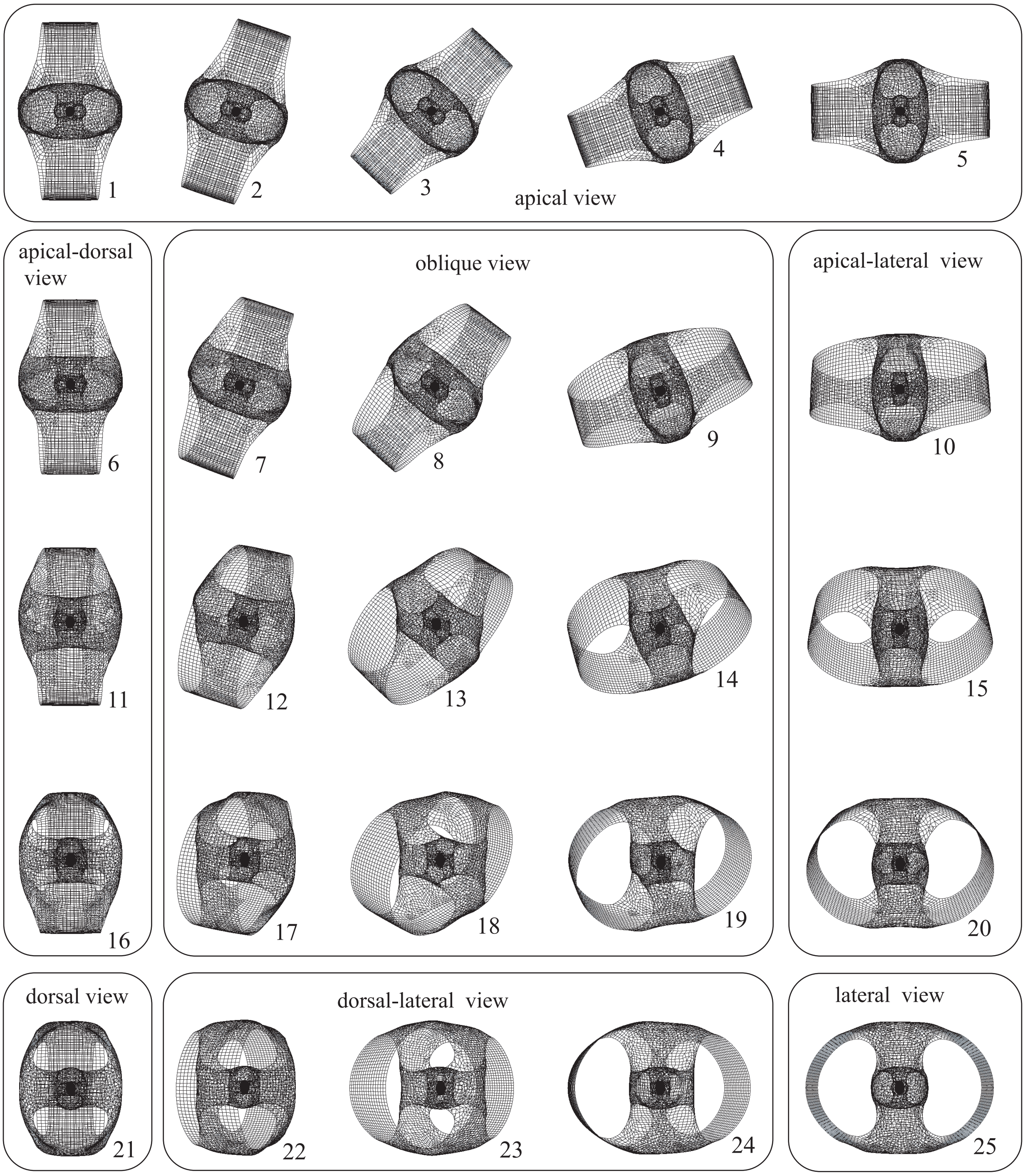

Fig. 3. Realistic illustrations of the larnacillid structure in various directions.

As mentioned before, the twisted structure can be problematic. Normal strewn slides for the polycystine assemblages are fixed with respect to the individuals with mounting media such as Canada Balsam, so that we have to identify obliquely oriented larnacillid individuals. For example, several larnacillid species with twisted structure were illustrated by Haeckel (1887) (Fig. 4.4). Kozlova (1967) also made illustrations and schematic figure of a torsional girdles (Fig. 4.5). However, some of the species with torsional girdles are considered to be artificial because the “artificial” torsional girdles were produced in our simulations in some orientations except in the apical, lateral, dorsal, apical-dorsal, apical-lateral, and dorsal-lateral views. Overlapping images with wings and both sides of the girdle create the illusion of torsional structure (Fig. 4.1-3). It is hoped that our modeling study would provide an important insight into the classification of this group.

Those having twin gates with an ellipsoidal test which is visible in a particular orientation can easily be identified as a member of the family Larnacillidae. On the other hand, those with torsional appearance under an oblique view were

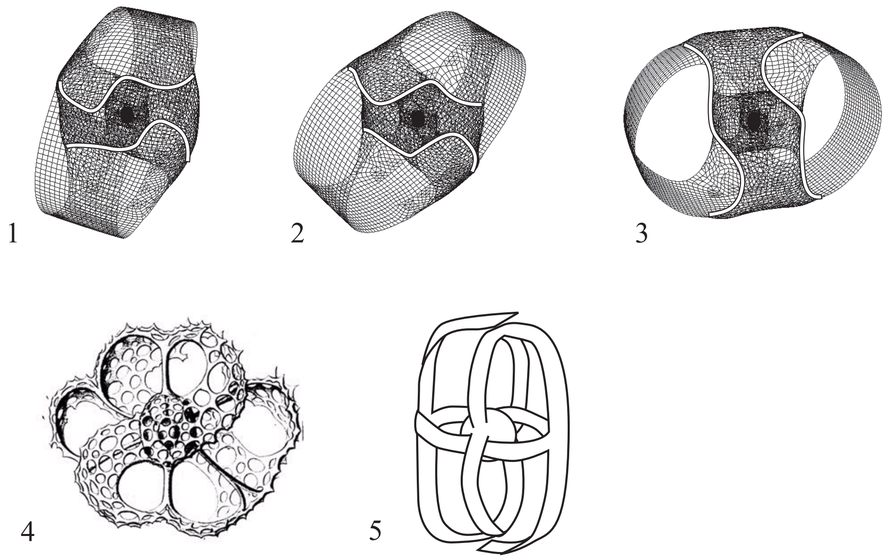

Fig. 4. (1)-(3) The oblique views of illustrations of the larnacillid structure. The white line represents the "artificial" torsional girdle. (4) The larnacillid structure with torsional girdle illustrated in Haeckel (1887). (5) The schematic figure of larnacillid structure with torsional girdle based on Kozlova (1967).

occasionally indistinguishable from other polycystine groups like lithelids. Lazarus et al. (2005), already pointed out that particular larnacillids with thick superficial cover and pylome are difficult to be identified from lithelids. This is partly due to the nearly opaque thick superficial cover, and may also be related to the orientation of its internal structure, even if such structure is observable in these morphotypes. A very shallow focus depth for observation of larnacillids is essential to recognize the orientation of the larnacillid structures.

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