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Revision of Ordovician chitinozoan *Lagenochitina esthonica* sensu lato: morphometrics, biostratigraphy and paleobiogeography

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Abstract.—*Lagenochitina esthonica* is a globally distributed chitinozoan in Early to Middle Ordovician rocks. It is regarded as an index species for the early Floian in North America and has a stratigraphically constrained range in other regions. *Lagenochitina esthonica* is distinguished from other chitinozoans by a distinct flexure, a nearly rounded-square chamber, and a cylindrical neck with a flaring collar. However, since the first description of the species in the 1950s, it has included two varieties: a relatively short form with a test length ∼400 μm, and a slender form usually longer than 600 μm. In order to revise the taxonomy of the *L. esthonica* group, we carried out a statistical morphometric study of a large collection of well-preserved specimens from the Baltic region where the taxon was first established. Additionally, the stratigraphic and geographic distribution of both forms was analyzed based on available occurrence data. The results show that the short form occurs in the upper Tremadocian to lower Dapingian, whereas the slender form is mostly reported from the lower and middle Darriwilian. Both forms are identified on Baltica; the short form has also been reported from Laurentia and South China, whereas the other is known also from Avalonia and Gondwana. The morphological distinction, together with differences in stratigraphic and spatial ranges, suggest that the two forms represent separate species: the original stout *L. esthonica*, based on the morphology of the holotype, and the slender *L. megaesthonica* n. sp., described herein. The updated taxonomy enhances the stratigraphic and biogeographic usefulness of lagenochitinids globally.

UUID: http://zoobank.org/ec49166e-2a8d-4941-8723-f023853c5a7e.

Introduction

Chitinozoans are organic-walled microfossils common in Ordovician to Devonian marine sediments. In spite of their disputed biological origin (see Liang et al., 2020a and references therein), chitinozoans are widely used in biostratigraphy of early and middle Paleozoic rocks (e.g., Grahn and Gutiérrez, 2001; Asselin et al., 2004; Vandenbroucke, 2004; Grahn, 2005a; Steemans et al., 2009; Vandenbroucke et al., 2010, 2015; de la Puente and Rubinstein, 2013; Wang et al., 2013; Paris et al., 2015a, b; Al-Shawareb et al., 2017; De Weirdt et al., 2019; Liang et al., 2020b) since the regional and global biozonal schemes were first established around the 1990s (Achab, 1989; Paris, 1990; Nõlvak and Grahn, 1993; Verniers et al., 1995; Paris et al., 2004; Grahn, 2005b, 2006). However, alongside revised genus- and family-level systematics (Paris et al., 1999), and continuously expanding datasets from different regions in recent years, revisions of several well-known taxa are required. Sporadic discussions on index chitinozoans have been published in recent years, improving the usefulness of these taxa in biostratigraphy (Butcher, 2013; Nowak et al., 2016; Liang et al., 2017, 2019; de la Puente et al., 2020), but more work is required to further improve the chitinozoan biozonal schemes in general.

A common and distinctive key species, *Lagenochitina esthonica*, was first described by Eisenack (1955) from the Baltic Region and has since then been identified from Early and Middle Ordovician rocks from Baltica (Estonia, Sweden), Laurentia (Canada), Gondwana (western Australia, Bohemia), Avalonia (UK), and South China (full details listed in Supplemental Data 1). The diagnostic characters of *Lagenochitina esthonica* include a cylindric neck ended with a remarkable flaring collar and a distinct flexure that connects the neck with a rounded quadrate chamber. *Lagenochitina esthonica* is one of the largest representatives of the genus, with an average length of ∼500 μm based on 18 specimens from the type locality (Eisenack, 1955). Due to the distinctive morphology and wide distribution, *L. esthonica* has become one of the most characteristic species for the Early and Middle Ordovician period. In North America, it was put forward as the index taxon for the lower Floian (Achab, 1989), together with *Conochitina raymondii* Achab, 1980, just above the globally recognized *Euconochitina symmetrica* Biozone.

However, two different varieties carrying the diagnostic characters of *Lagenochitina esthonica* can be detected

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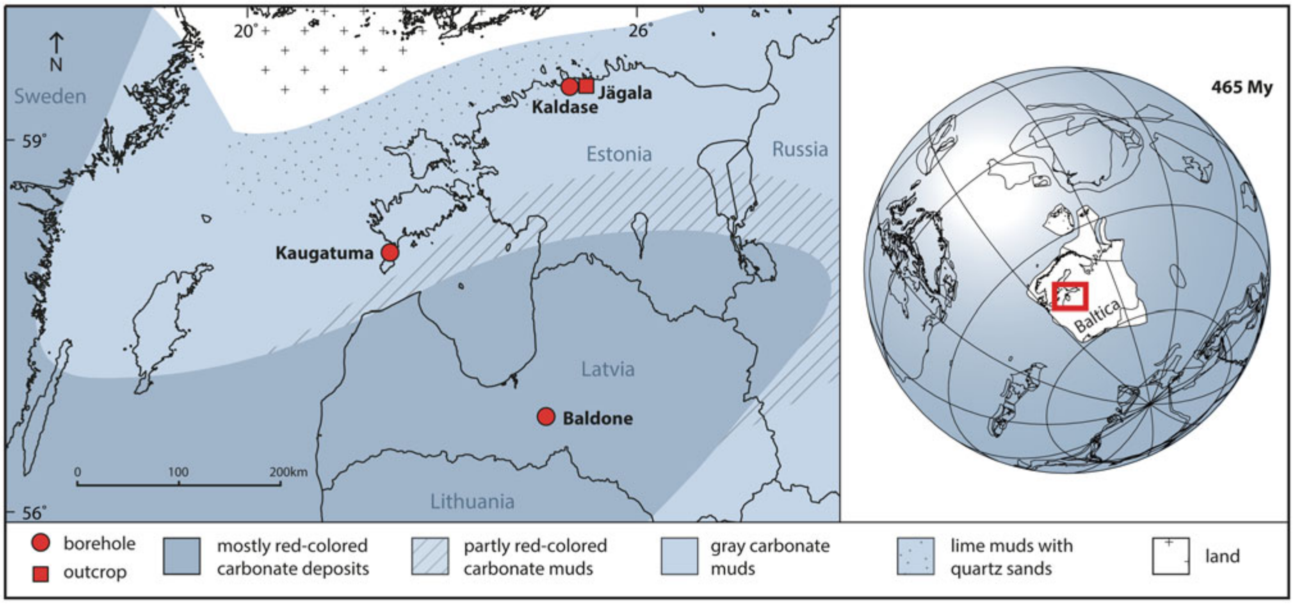

Figure 1. Paleogeographic settings of the study area. The four red marks show the localities of the four at Jägala, Kaldase, Kaugatuma, and Baldone on Baltica.

in previously published literature. One corresponds to the holotype shown in Eisenack (1955); the other developed an even larger vesicle with a much more slender outline (e.g., Jenkins, 1967, pl. 74, figs. 4, 5; Eisenack, 1968, pl. 25, fig. 25).

The morphology and taxonomy of the two forms have been discussed by previous authors. Eisenack (1968) pointed out that the short and slender forms co-occurred in the same population in the glauconite limestone in Estonia (mostly Dapingian in age), while in the "*vaginatum* limestone" and "*Expansus* limestone" in Sweden (Darriwilian), only elongated forms were recovered. Bockelie (1980) indicated that the species changed from a mixture of short and long forms in the lower Arenig to predominantly long forms in the lowermost Llanvirn. Paris (1981) denoted that the two forms are certainly related, but of different stratigraphic distributions, and suggested that a revision based on the material from the type area in Baltica may allow separating them. Paris and Mergl (1984) put forward a dividing standard that restricted typical *L. esthonica* to specimens carrying the conspicuous shoulders and flexure, as in the holotype, with a ratio of vesicle length to maximum diameter ≤4. The *L. esthonica* reported by Grahn (1980) with an inconspicuous flexure was attributed to a later-established taxon, *Lagenochitina yilingensis* Chen et al., 2009a.

The present study aims to analyze the morphology and distribution of *Lagenochitina esthonica* sensu lato in order to evaluate the similarities and differences between the short and long forms and revise the taxon accordingly. For this, we use well-preserved material from the eastern Baltic region, stratigraphically ranging from the upper Tremadocian to mid Darriwilian. The morphometrical analysis is complemented with biostratigraphical and paleobiogeographical assessment of range overlaps of the two forms of *L. esthonica* in time and space.

Geological setting

Locality information.—The materials studied in this paper are recovered from four localities: the Jägala waterfall outcrop and Kaldase drill core from northern Estonia; Kaugatuma drill core from Saaremaa Island, western Estonia; and Baldone drill core from Latvia (Fig. 1). These sections represent the eastern part of the Baltoscandian Basin that covered large areas of Baltica during the Ordovician (Männil, 1966; Cocks and Torsvik, 2005). In this region, the Lower to lower Middle Ordovician interval is characterized by transition from siliciclastic to cool-water carbonate ramp settings (Nestor and Einasto, 1997; Dronov and Rozhnov, 2007).

Stratigraphic and geological time information.—The Jägala waterfall section exposes strata from the upper Türisalu to the Loobu formations, ranging from the Pakerort to Kunda regional stages, corresponding to the Tremadocian to lower Darriwilian (Fig. 2.1).

In the Kaldase section, strata from the lowermost Volkhov to Aseri regional stages (Fig. 2.2), corresponding to the Dapingian to middle Darriwilian, were continuously sampled for microfossil study.

In the Kaugatuma section, chitinozoan samples were collected from the upper part of the Volkhov to Lasnamägi regional stages, corresponding to the upper Dapingian to the upper Darriwilian (Fig. 2.3). The lowermost part of the Volkhov Regional Stage is characterized by reddish limestone and argillaceous limestone, which are always barren of chitinozoans.

In the Baldone section, the studied interval ranges from the Pakerort to Aseri regional stages, corresponding to the Tremadocian to lower Darriwilian (Fig. 2.4). The lower part of the section, ranging through the entire Volknov Regional Stage, is characterized by reddish sediments that are barren of organic-walled microfossils.

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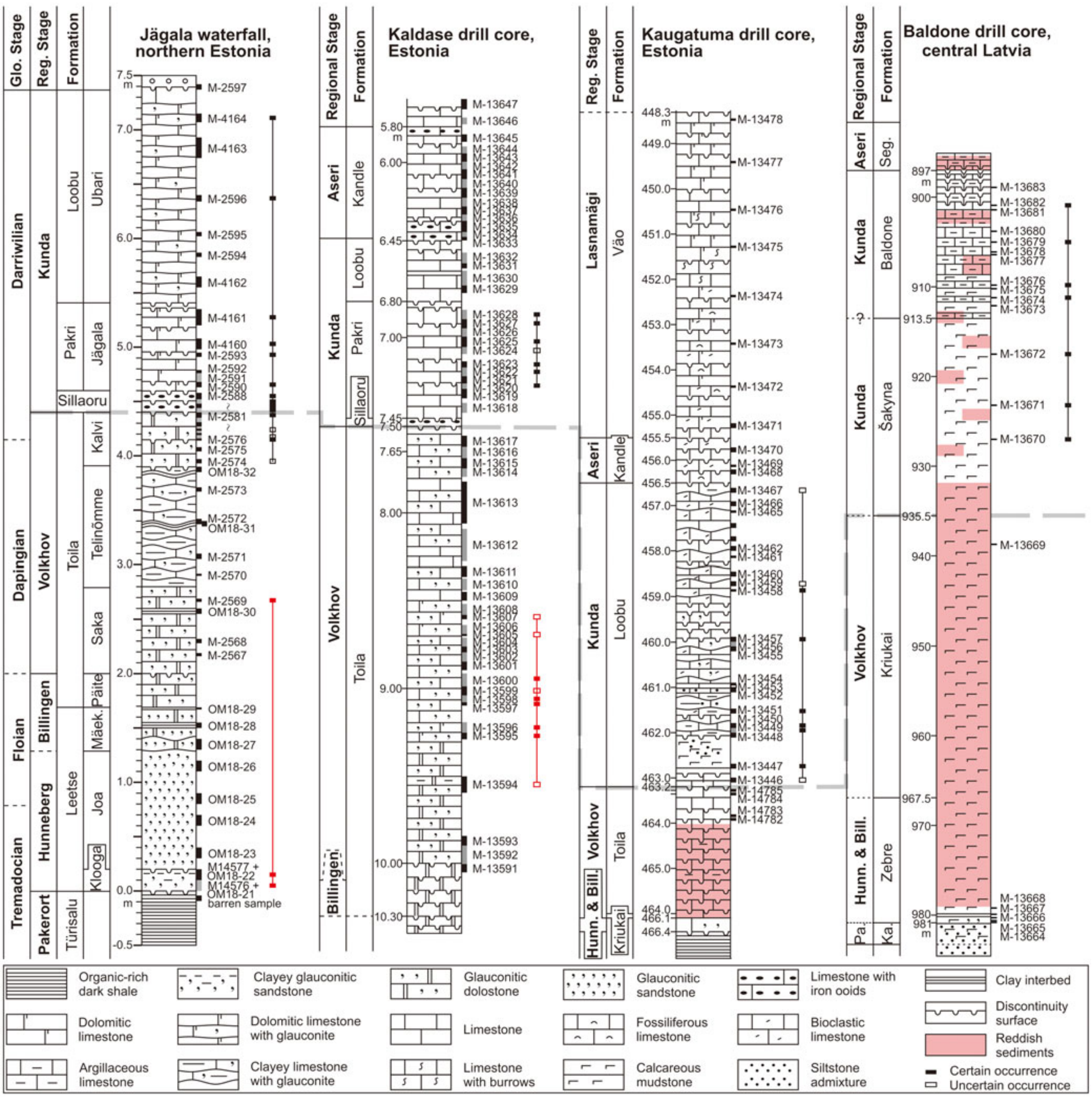

Figure 2. Lithology and biostratigraphical distribution of *Lagenochitina esthonica* at Jägala, Kaldase, Kaugatuma, and Baldone sections. Red and black range-through occurrence data represent short and slender forms of *L. esthonica,* respectively. Bill. = Billingen; Glo. = Global; Hunn. = Hunneberg; Reg. = Regional; Pa = Pakerort; Ka = Kallavere. The samples labeled with the beginning "OM" are used to distinguish those samples from those labeled with the beginning "M." OM refers to the microfossil samples re-collected by Olle Hints and his colleagues in 2018. Other samples were collected in 1969–2014 by other paleontologists.

Materials and methods

The four sections were studied for organic-walled microfossils using ∼150–300 g samples and acid extraction or disintegration techniques, following the methods described in detail by Paris (1981). Microfossils were hand-picked from the residues and stored in glycerin. Chitinozoans from the Jägala section recently have been reported by Nõlvak et al. (2019). Chitinozoan data from the other three sections have not been published previously, but the results have been used to gain general understanding of chitinozoan distribution and diversity patterns on Baltica (e.g., Nõlvak in Paris et al., 2004).

In order to obtain material for morphometric analysis, a total of 155 existing micropaleontological preparations from the four sections were studied, 35 of which contained

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Lagenochitina esthonica s.l. (Fig. 2). In total, 506 well-preserved specimens were selected for imaging, measuring, and statistical analysis. All specimens were imaged using a Leica M205A stereo microscope equipped with Leica camera system. The measurements were taken from digital images using Leica Application Suite (LAS) software. The systematic framework and terminology follow Paris et al. (1999), and the following measurements were used: vesicle length (L), chamber diameter after correction (Dp*), and the length/width ratio (L/Dp*). The correction factor of the compressed test follows Paris et al. (2015a), which is a coefficient of 0.8 for the chamber. Of the 506 specimens measured, 460 provided reliable vesicle length data and 483 reliable chamber diameter data. The results were statistically analyzed using R software (R Core Team, 2016). Material selected for scanning electron microscopy (SEM) was cleaned in distilled water and mounted on stubs using thin, water-soluble gelatin film. A Zeiss EVO MA15 SEM at TalTech was used.

Paleogeographical distribution maps were generated using the ArcGIS 10 environment. Geographic coordinates of previously reported *Lagenochitina esthonica* s.l. occurrences were estimated using Google Earth, and then transferred to paleo-GPS using PointTracker v7.0 (PaleoGIS, http://www.Paleogis.com). The paleomaps adopted in this study are from Scotese (2016).

Repository and institutional abbreviation.—Types, figured, and all the other specimens examined and studied in this paper are stored at the Department of Geology, Tallinn University of Technology (GIT), Tallinn, Estonia.

Results

Morphology and size variation.—Results of morphometric analysis of 506 specimens of *Lagenochitina esthonica* s.l. are summarized on Figure 3. The original data of all the measurements are presented in the Supplementary Data 2. When all data are considered, the test length ranges from 268–1288 µm, with mean and median values of 675 µm and 695 µm, respectively (25^{th} and 75^{th} percentiles ∼498 µm and 817 µm, respectively; standard error 9.5). Chamber diameter ranges from 121–372 µm, with mean and median values of 219 µm and 217 µm, respectively (25^{th} and 75^{th} percentiles ∼191 µm and 246 µm, respectively; standard error 1.84). The ratio of L/Dp* ranges from 1.46–6.60, with mean and median values of 3.10 and 3.09, respectively (25^{th} and 75^{th} percentiles ∼2.46 and 3.57, respectively; standard error 0.04).

The statistical analysis shows that the three histograms of test length depicting the entire data set (Fig. 3.1), and separately the data from the Jägala (Fig. 3.4) and Kaldase sections (Fig. 3.7), are far from normal distributions. Two significant acmes can be recognized in Figure 3.1 and Figure 3.4. Values are clustered around 400 µm and a weak acme can be recognized at the interval of 800–900 µm in the Kaldase section (Fig. 3.7). The histograms of Dp* match a normal distribution when all the data are included (Fig. 3.2), while the distributions for each section individually are less perfect. Histograms of L/Dp* show a long tail at the left side, especially at the Kaldase section (Fig. 3.9).

In the Jägala section, *Lagenochitina esthonica* s.l. ranges almost through the entire section, starting from the Hunneberg Regional Stage, upper Tremadocian–Floian, and extending to the Kunda Regional Stage, lower and middle Darriwilian (Fig. 2.1). In the lower part of its range, *L. esthonica* s.l. is distinguished by a stout outline with a rounded square chamber (Nõlvak et al., 2019, fig. 6G), whereas in the upper part, starting from the upper part of the Volkhov Regional Stage, a slender form with an elongated ovoid chamber occurs (Nõlvak et al., 2019, fig. 6L, M). The vesicle length measured in the lower part ranges from 323–536 µm, with a mean value of 428 µm based on 17 specimens from samples M-14576 and M-2569. The length measured in the upper part of the section ranges from 451–1288 µm, with a mean value of 803 µm based on 42 specimens from samples M-2576 to M-4164.

In the Kaldase section, *Lagenochitina esthonica* s.l. appeared in the Volkhov and Kunda regional stages (Fig. 2.2). The histogram of test length shows that most data are grouped around 400 µm, but a low acme appeared near 800–900 µm (Fig. 3.7). The length of *L. esthonica* s.l. in the Volkhov Regional Stage ranges from 268–647 µm, with a mean value of 403 µm based on 102 specimens. Tests recovered in this interval are characterized by a rounded square chamber and a relatively short neck, which takes about one-quarter to one-third of the total length (Fig. 4.1–4.22). Specimens from the Kunda Regional Stage range from 477–1181 µm, with a mean value of 815 µm based on 18 measurements. These stratigraphically younger specimens are distinguished by a slender outline with an elongated ovoid chamber and a neck, which takes about one-third to one-half of the total length (Fig. 4.23–4.32).

In the Kaugatuma section, *Lagenochitina esthonica* s.l. occurs in the Kunda Regional Stage, from samples M-13446 to M-13459 (Fig. 2, Kaugatuma drill core, Estonia). Test length ranges from 441–963 µm, with a mean value of 689 µm based on 71 specimens. Histograms of test length, diameter of chamber, and L/Dp* show one peak (Fig. 3.10–3.12). The specimens are all preserved in full relief. Their necks may be very short (e.g., Fig. 5.5, 5.12, 5.21), about one-fifth to one-quarter of the test length. But the necks also can be very long (e.g., Fig. 5.13, 5.16, 5.18), corresponding to about two-fifths to one-half of vesicle length. The outline of the specimens is relatively slender, with an elongated chamber (Fig. 5).

In the Baldone section, *Lagenochitina esthonica* s.l. has been identified only in the Kunda Regional Stage, from samples M-13670 to M-13682 (Fig. 2, Baldone drill core, central Latvia). The histogram of test length shows a normal distribution. The length ranges from 442–1097 µm, with a mean value of 786 µm, based on 210 specimens (Fig. 3.13). Some of the compressed chambers are reminiscent of a rounded square (e.g., Fig. 6.9, 6.21–6.26). When compression is taken into consideration, the real chamber should have been less square and more elongated.

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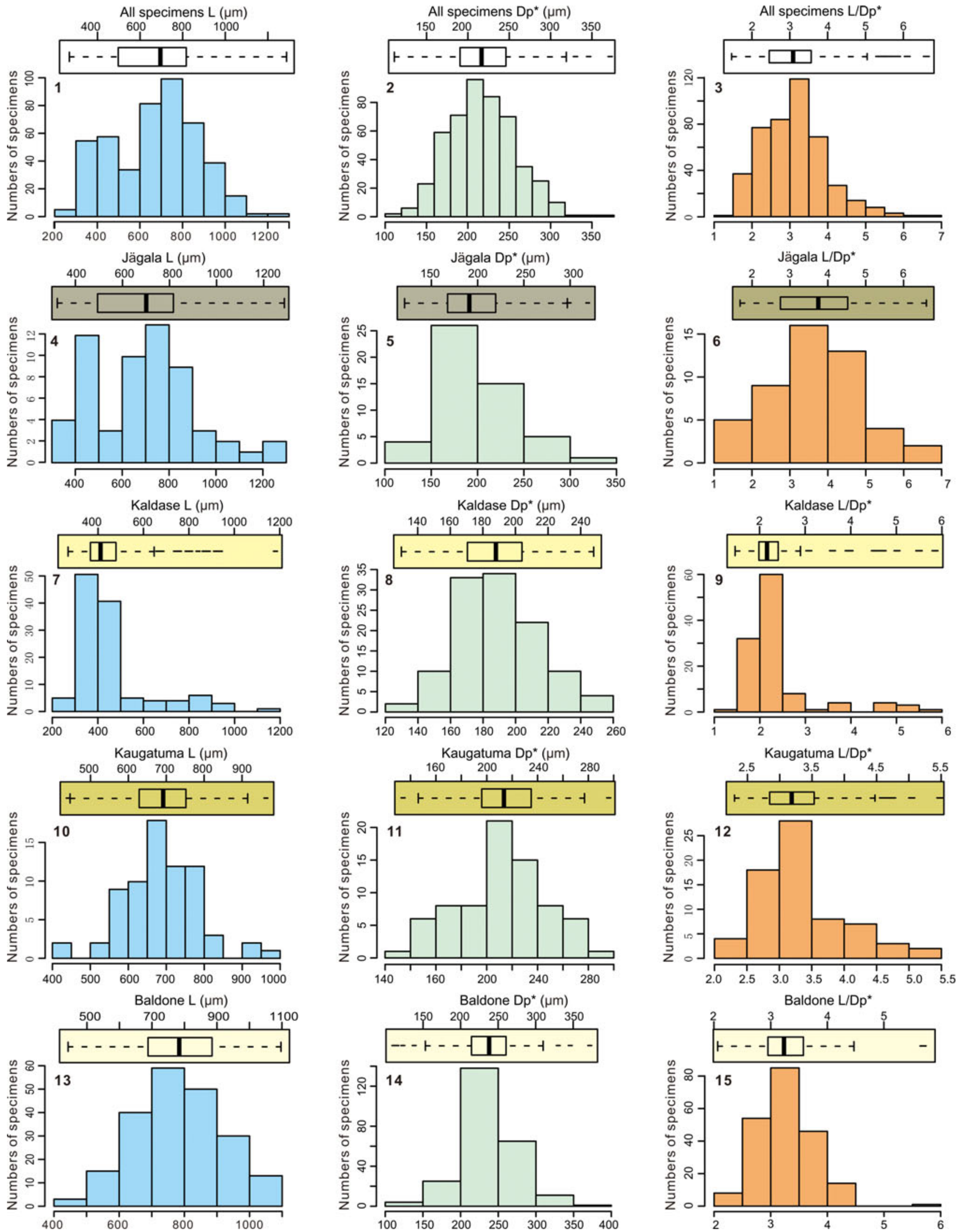

Figure 3. Histograms and box-plots of the test length (L), chamber diameter after correction (Dp*), and the ratio of L/Dp*. (**1–3**) Based on all the valid data from the studied sections; (**4–6**) based on the data from the Jägala waterfall outcrop, Estonia; (**7–9**) based on the data from Kaldase borehole, Estonia; (**10–12**) based on the data from Kaugatuma borehole, Estonia; (**13–15**) based on data from Baldone borehole, Lativa.

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Figure. 4. *Lagenochitina esthonica* emend. (**1–22**) and *Lagenochitina megaesthonica* n. sp. (**23–32**) from the Kaldase section, northern Estonia. Each black scale bar on the left boundary of the figure represents 100 µm; the total length of the white background line is 2582 µm. Sample M-13596: (**1**, **6**, **9–11**, **14**, **15**, **17**, **18**, **20–22**); Sample M-13597: (**2–5**, **7**, **8**, **12**, **13**, **16**, **19**); Sample M-13622: (**24**, **26**, **32**); Sample M-13627: (**25**, **27**, **31**); Sample M-13628: (**23**, **28–30**).

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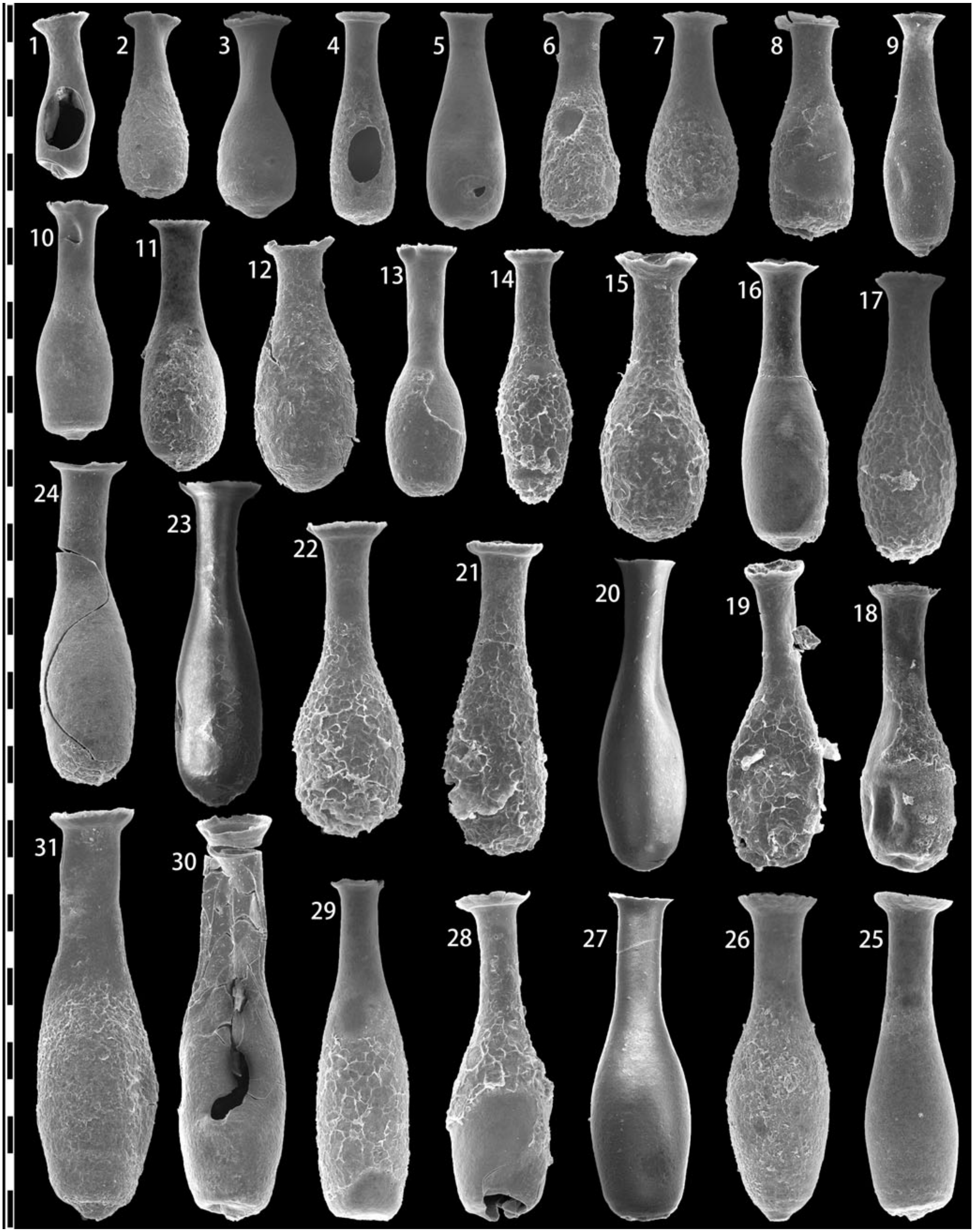

Figure 5. *Lagenochitina megaesthonica* n. sp. **(1–31)** from the Kaugatuma section, western Estonia. Each black scale bar on the left boundary of the figure represents 100 µm; the total length of the white background line is 3312 µm. All specimens are from Sample M-13458. **(23)** holotype, with a repository number of GIT 833-1. **(15)** paratype, with a repository number of GIT 833-2.

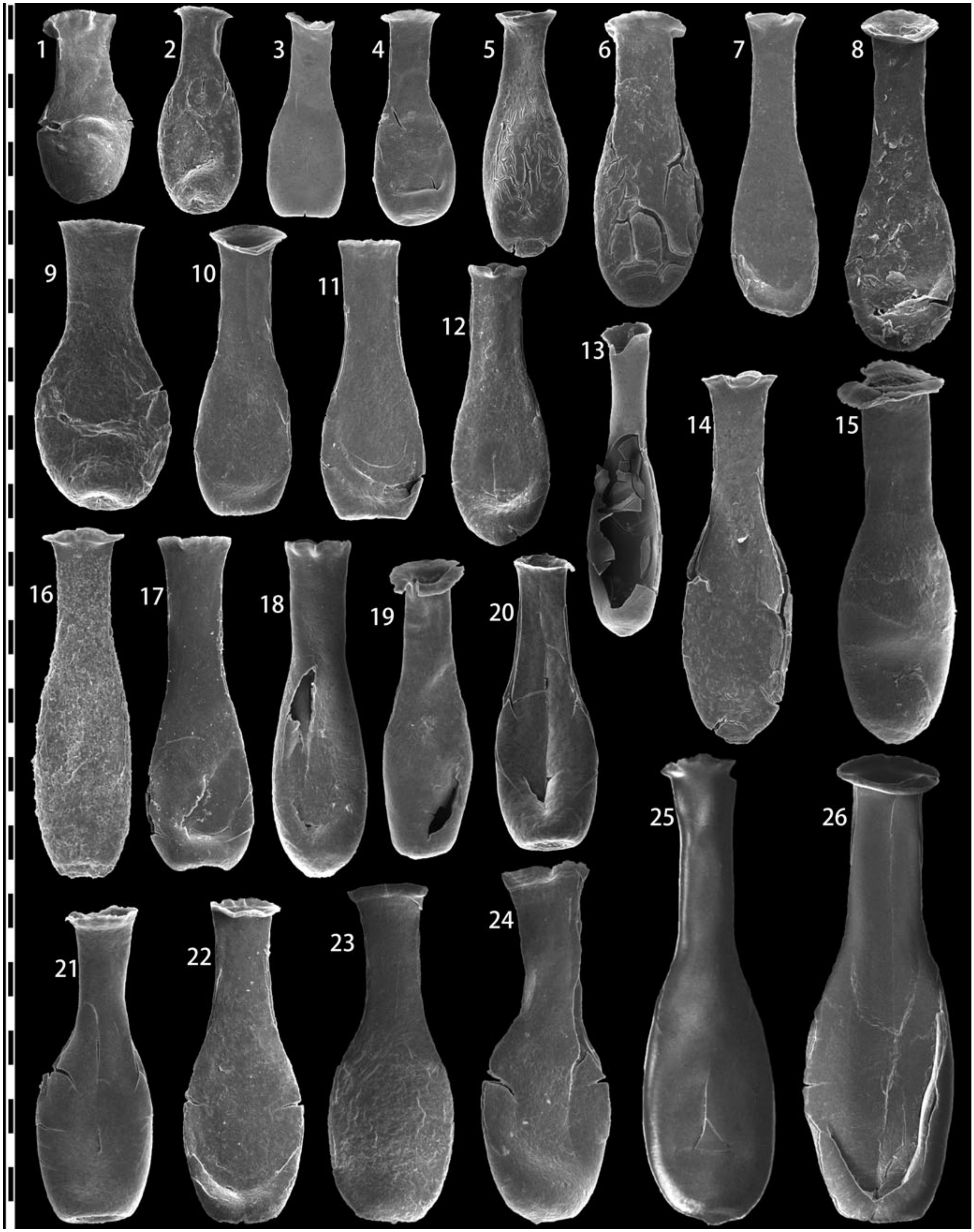

Figure 6. *Lagenochitina megaesthonica* n. sp. (**1–26**) from the Baldone section, central Latvia. Each black scale bar on the left boundary of the figure represents 100 μm; the total length of the white background line is 3584 μm. Sample M-13670: (**10–12**, **16**, **17**, **22**); M-13671: (**9**, **23**); M-13672: (**26**); M-13674: (**1**, **2**, **6**, **15**, **24**, **25**); M-13676: (**3–5**, **7**, **8**, **14**, **18**, **19**); M-13679: (**20**, **21**); M-13682: (**13**). **(23, 26)** paratypes, with repository number of GIT 833-3 and GIT 833-4, respectively.

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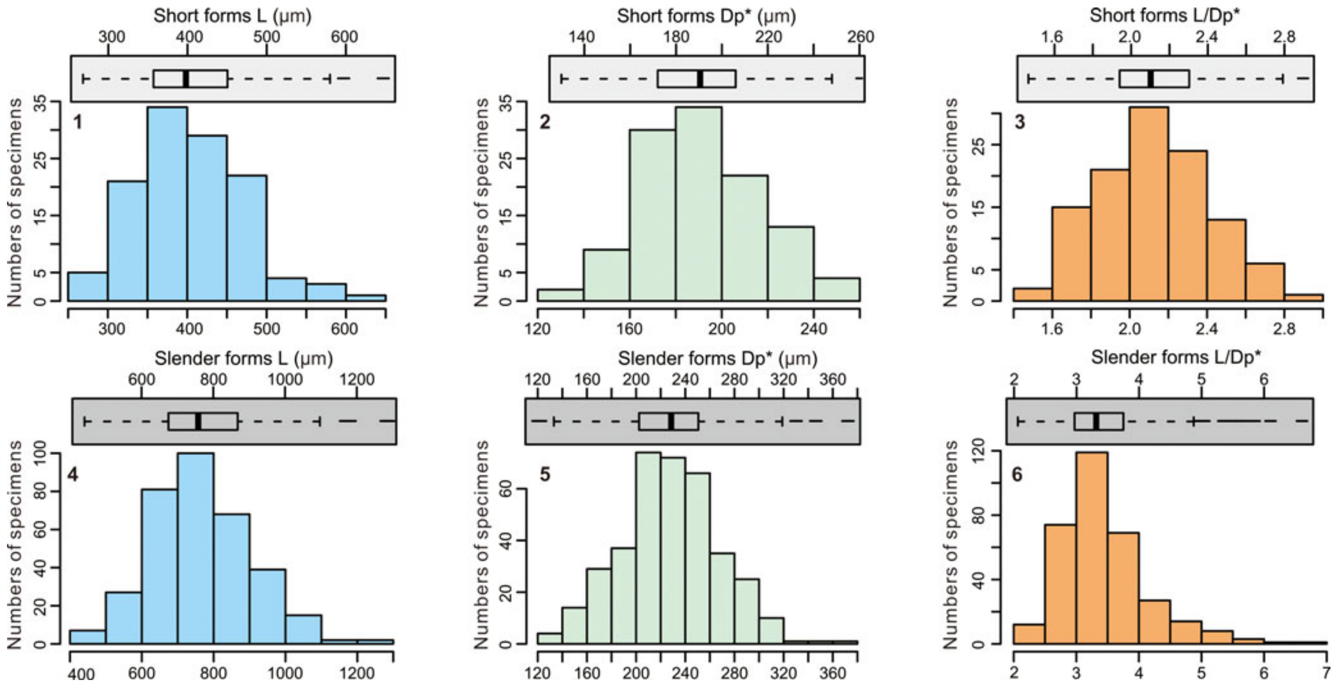

Figure 7. Histograms and box-plots of the test length (L), chamber diameter after correction (Dp*), and the ratio of L/Dp* of emended *Lagenochitina esthonica* (**1–3**), short forms and *Lagenochitina megaesthonica* n. sp. (**4–6**), slender forms.

Discussion

Morphology and size variation.—According to the statistical results presented above, two distinct groups can be recognized within the specimens previously assigned to *Lagenochitina esthonica*. Morphologically, both groups carry the diagnostic features of *L. esthonica*—large bottle-shaped chitinozoans possessing a well-differentiated neck ending with a conspicuous flaring collar and a distinct flexure with nearly parallel flanks. The main difference between the two groups is that one has a rounded square chamber, matching the morphology of the holotype of *L. esthonica*, whereas the other is much slenderer, with an elongated ovoid chamber, and a relatively longer neck.

Statistically, test length of the stout group ranges from 268–647 μm, with mean and median values of 406 μm and 398 μm, respectively (25th and 75th percentile around 357 μm and 451 μm, respectively; standard error 4.3), based on 120 specimens from the lower part of the Jägala and Kaldase sections (Fig. 7.1). Vesicle length of the slender form ranges from 441–1288 μm, with mean and median values of 769 μm and 758 μm, respectively (25th and 75th percentile around 675 μm and 868 μm, respectively; standard error 7.60), based on 341 measurements from four sections (Fig. 7.4). Generally, the length of the slender form is about twice that of the short group. The corrected diameter of the chamber of the short form ranges from 130–260 μm, about three-quarters of them range from 160–220 μm (Fig. 7.2) and the slender form ranges from 121–372 μm, nearly three-fifths range from 200–260 μm (Fig. 7.5). The L/Dp* of the slender forms is commonly ∼2.5–4 (Fig. 7.6), whereas for the short form it is a∼1.8–2.4 (Fig. 7.3). These data allow us to conclude that the two forms represent morphologically distinct assemblages with limited overlap in size and shape.

Stratigraphic distribution.—Within the four studied sections, the short form of *Lagenochitina esthonica* s.l. occurs in the Hunneberg to lower Volkhov regional stages at the Jägala outcrop and in the lower and middle parts of the Volkhov Regional Stage in the Kaldase drill core, which corresponds to the upper Tremadocian to lower Dapingian interval (Fig. 2.1, 2.2). The slender form appears in the uppermost Volkhov to Kunda regional stages at the Jägala section, and in the Kunda Regional Stage at the Kaldase, Kaugatuma, and Baldone sections, corresponding to the uppermost Dapingian to the middle part of the Darriwilian (Fig. 2). Thus, based on the distribution of *L. esthonica* s.l. in the studied sections, the stratigraphic ranges of the two groups are largely separated. Possibly, the younger, long form represents a descendant lineage of the older, shorter form.

Biogeographic distribution.—The paleobiogeographic distribution of *Lagenochitina esthonica* s.l. is wide (see Supplementary Data 1). Considering previously published data, the short form, including the holotype of *L. esthonica* in Eisenack (1955), has been reported in pre-Darriwilian strata in Estonia (Eisenack, 1955; Grahn, 1984; Hints and Nõlvak, 2006; Nõlvak et al., 2019), Russia (Obut, 1973), Norway (Bockelie, 1978, 1980), Canada (Achab, 1980, 1986), Bohemia (Paris and Mergl, 1984), and China (Chen et al., 2009a, b; Liang, 2015; Liang et al., 2017, 2018). Most of these occurrences are confined to Early Ordovician. The slender form of *L. esthonica* s.l., represented by the specimens from the Hope Shale in the UK (Jenkins, 1967), corresponding to mid Darriwilian, and has been reported in Darriwilian strata in Sweden (Eisenack, 1955, 1968, 1976a; Grahn, 1980; Grahn et al., 1996), Estonia (Eisenack, 1976b; Nõlvak et al., 2019), and France (Paris, 1981). Paleogeographically, the short form

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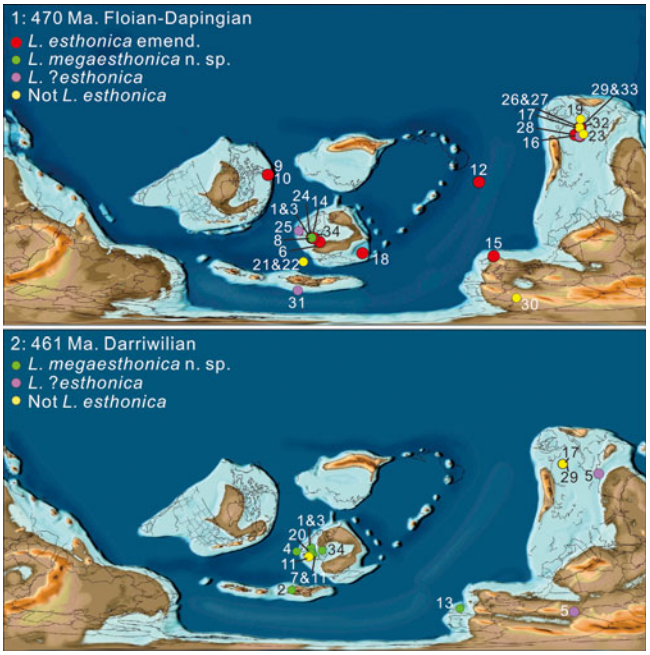

Figure 8. Paleogeographic distributions of emended *Lagenochitina esthonica* and *Lagenochitina megaesthonica* n. sp. in the interval of Floian–Dapingian (**1**) and Darriwilian (**2**). Detailed information of the occurrence data marked by numbers is presented in Supplemental Data 1. The paleomaps are according to Scotese (2016).

is distributed in Baltica, Laurentia, and South China, and the slender form occurs in Baltica, Gondwana, and Avalonia (Fig. 8). Consequently, there also seems to be biogeographic differentiation between the two forms, with only Baltica having both of them represented.

Conclusions

The above-presented results show that two groups within *Lagenochitina esthonica* s.l. can be well differentiated by both morphology and stratigraphic ranges. Statistically, two acmes can be recognized in the histograms of vesicle length, one ∼400 µm and the other in the interval of 700–800 µm. Morphologically, the short form is distinguished by a rounded square chamber with the L/Dp* ratio ∼1.4–2.9, whereas the slender form is featured by an elongated ovoid chamber with the L/Dp* ratio ∼2.0–6.6. Stratigraphically, the short form appears in the upper Tremadocian to lower Dapingian, whereas the slender form occurs mainly in the lower and middle Darriwilian. Biogeographically, the two forms co-occurred only in Baltica, further stressing the separation of the two groups. In summary, we interpret these data as indicating the presence of two rather than one species. The type specimen of *L. esthonica* (Eisenack, 1955) represents the short form, and based on that, the original species diagnosis and description are emended to include specimens carrying a rounded square chamber with a medium to large vesicle and occurring in pre-Darriwilian strata. *Lagenochitina megaesthonica* n. sp. is erected for the slender form, referring to specimens with an elongated ovoid chamber with a large to huge test, mainly restricted to the lower and middle parts of the Darriwilian. Separation of these two species provides an additional biostratigraphic marker for Baltoscandia and beyond, contributing also to an improved understanding of the biogeographic distribution of Early and early Middle Ordovician chitinozoans.

Systematic paleontology

Order Prosomatifera Eisenack, 1972
Family Conochitinidae Eisenack, 1931, emend. Paris, 1981
Subfamily Lagenochitinnae Paris, 1981
Genus *Lagenochitina* Eisenack, 1931, emend. Paris et al., 1999

Type species.—*Lagenochitina baltica* Eisenack, 1931. The holotype was recovered from the “Ostseekalk” Ordovician erratic limestone from the Baltic shore (Eisenack, 1931, p. 80–81, pl. 1, fig. 1). Because the holotype is lost, it was replaced by a neotype, also deriving from the “Ostseekalk” (Eisenack, 1959, p. 2, pl. 3, fig. 6).

Lagenochitina esthonica Eisenack, 1955, emend. Liang, Nõlvak, and Hints
Figure 4.1–4.22

1955	*Lagenochitina esthonica* Eisenack, p. 311, pl. 1, figs. 8, 9.
non 1967	*Lagenochitina esthonica*; Jenkins, p. 463, pl. 74, figs. 4, 5.
p 1968	*Lagenochitina esthonica*; Eisenack, p. 156, pl. 24, fig. 10, pl. 29, fig. 25?, text-fig. 1.
1971	*Lagenochitina esthonica*; Downie et al., p. 21, pl. 1, fig. 17.
non ?1972	*Lagenochitina esthonica*; Combaz and Peniguel, p. 145, pl. 4, figs. 1, 2, text-fig. 2.
1973	*Lagenochitina esthonica*; Obut, pl. 10, figs. 6–8.
non 1976a	*Lagenochitina esthonica*; Eisenack, p. 186, pl. 2, fig. 1; text-fig. 2.
p 1976b	*Lagenochitina esthonica*; Eisenack, fig. 6.
1978	*Lagenochitina esthonica*; Bockelie, fig. 2C, D.
1980	*Lagenochitina esthonica*; Bockelie, p. 12, pl. 2, figs 1–7, text-figs. 7C, 8.
non 1980	*Lagenochitina esthonica*; Grahn, p. 3, fig. 19 A–D.
1980	*Lagenochitina esthonica*; Achab, p. 234, pl. 3, figs. 1–6.
non 1981	*Lagenochitina esthonica*; Paris, p. 248, pl. 10, figs. 15, 20.
1984	*Lagenochitina esthonica*; Grahn, p. 22, pl. 4, figs. F, G.
1984	*Lagenochitina esthonica*; Paris and Mergl, p. 55, pl. 4, figs. 2–6.
? 1984	*Lagenochitina* cf. *esthonica*; Geng, p. 513, pl. 1, fig. 6.
non 1985	*Lagenochitina esthonica*; Zhen, p. 378, pl. 1, figs. 17–19.
non 1986	*Lagenochitina esthonica*; Gao, p. 145, pl. 3, figs 3–6, 10–15, pl. 4, figs. 1–3, 7.
1986	*Lagenochitina esthonica*; Achab, p. 693, pl. 2, figs 16–18, pl. 4, figs. 1–3.
non 1996	*Lagenochitina esthonica*; Grahn et al., pl. 3, fig. 9.

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non 2004 *Lagenochitina esthonica*; Olaru and Apostoae, p. 302, pl. 1, figs. 1–14.
non 2005 *Lagenochitina esthonica*; Olaru, pl. 3, figs. 1–14.
non 2005 *Lagenochitina esthonica*; Chen and Zhang, p. 50, pl. 1, figs. 2, 10, 17, 18, 20, 22.
non 2006 *Lagenochitina esthonica*; Hints and Nõlvak, pl. 4, fig. 27.
? 2007 *Lagenochitina esthonica*; Grahn and Nõlvak, fig. 4C.
2009a *Lagenochitina esthonica*; Chen et al., p. 324, pl. 4, figs. 4, 8, 11?.
2009b *Lagenochitina esthonica*; Chen et al., p. 159, pl. 2, fig. 7?, pl. 29, figs. 4, 8.
non 2011 *Lagenochitina esthonica*; Olaru et al., pl. 1, figs. 3, 5, 10, 18, 19, 21.
2013 *Lagenochitina esthonica*; Wang et al., p. 56, pl. 3, figs. 1–3.
2015 *Lagenochitina esthonica typical* Liang, p. 142, pl. 1, figs. 1–9.
non 2016 *Lagenochitina esthonica*; Nowak et al., fig. 7Q.
2017 *Lagenochitina esthonica*; Liang et al., pl. 1, figs. 1–5.
2018 *Lagenochitina esthonica*; Liang et al., fig. 3X.
2019 *Lagenochitina esthonica*; Nõlvak et al., fig. 6G.

Holotype.—Specimen from the lower part of the glauconitic limestone (=Toila Formation), stage B2α (=Volkhov Regional Stage), corresponding to the global Dapingian Stage, at Paldiski, Pakri Peninsula, NW Estonia (Eisenack, 1955, pl. 1, fig. 8). According to Paris (1981, p. 249), the test dimensions are L-Dp-Dc-Lp: 530-194-94-350 µm.

Diagnosis.—Medium to large *Lagenochitina* with a short cylindrical neck ended with an extraordinary flaring collar. Chamber quadrate ovoid to rounded square, usually with distinct shoulders. The test length is ~1.5–2.9 times the chamber diameter.

Occurrence.—If the synonymy list of the present study is adopted, the valid *Lagenochitina esthonica* occurrences are mainly from Baltica, Laurentia, and South China (Fig. 8), including the lower glauconitic limestone (Toila Formation, Dapingian) (Eisenack, 1955, 1968, 1976b), the Vääna limestone (Dapingian) (Grahn, 1984), and the Leetse Formation (Floian) (Hints and Nõlvak, 2006; Nõlvak et al., 2019) in Estonia; Arenig strata (Floian) of the Pestovo borehole, Moscow Basin in central Baltica (Obut, 1973); the Valhallfonna Formation (Floian) in Spitsbergen, Norway (Bockelie, 1978, 1980); the lower part of the Lévis Formation (Floian) in Quebec (Achab, 1980, 1986); the Klabava Formation (Floian–Dapingian) in the Prague Basin, Bohemia (Paris and Mergl, 1984); the Hunghuayuan, lower part of the Dawan, Ningkuo, and Tungtzu formation (upper Tremadocian–Floian) in South China (Chen et al., 2009a, b; Wang et al., 2013; Liang, 2015; Liang et al., 2017, 2018). In the present study, *Lagenochitina esthonica* occurs in the Hunneberg to lower Volkhov stages at the Jägala section, and in the lower and middle parts of the Volkhov Regional Stage in the Kaldase core, corresponding to the upper Tremadocian to lower Dapingian, Early to early Middle Ordovician.

Description.—Test medium to large, ranging from 268–647 µm (average 406 µm) in length. Neck clearly differentiated and cylindrical, taking ~15–40% of the test length, ended with an extraordinary flaring collar (e.g., Fig. 4.7, 4.8). Chamber quadrate ovoid to rounded square, usually with distinct shoulders. The maximum diameter is located at the middle part of the chamber, which is 1/3 to 2/3 times the test length after correction. Flexure distinct, flanks nearly parallel to slightly swollen, base flat or slightly convex, base margin rounded. Mucron usually present, but with various shapes and size: it can be short and narrow (e.g., Fig. 4.8, 4.13) or short and wide (e.g., Fig. 4.11, 4.22); sometimes it is prolonged and became narrow in the aboral side (e.g., Fig. 4.5, 4.21); sometimes the test lacks a mucron, which is replaced by a rounded scar (e.g., Fig. 4.20). Test surface can be smooth, but consists of minute granules (e.g., Fig. 4.11, 4.15); it can also have a rugose to spongy surface (e.g., Fig. 4.17, 4.21).

Materials.—Seventeen specimens were recovered from samples M-14576 and M-2569 from the Jägala waterfall section (Nõlvak et al., 2019), and 103 specimens from samples M-13595 to M-13600 from the Kaldase drill core, Estonia (Fig. 2).

Dimension.—Dimensions (Table 1) are based on 120 specimens, 12 of which are compressed and others are preserved three-dimensionally.

Remarks.—The emended *Lagenochitina esthonica* is restricted to specimens with a relatively short test, which is represented by the holotype of the species established by Eisenack (1955). The slender forms with a larger and slender test, represented by the specimens reported by Jenkins (1967), are excluded, as are the slender forms reported elsewhere (Eisenack, 1968, 1976a, b; Grahn, 1980; Paris, 1981; Grahn et al., 1996; Hints and Nõlvak, 2006; Nõlvak et al., 2019). The short forms recovered in the Jägala (Nõlvak et al., 2019, fig. 6G) and Kaldase (Fig. 4.1–4.22) sections share the same morphology, similar test size, and were recovered from the same strata in the same area as the holotype. The two specimens recovered in the Canning Basin, Australia (Combaz and Peniguel, 1972) have a relatively large test size, with lengths of 600 µm and 670 µm, and a stout chamber; however, the distinctive flaring collar cannot be observed. The classification of those two specimens requires further study because no valid *esthonica*

Table 1. Dimensions of *Lagenochitina esthonica* emend. L = test length, Ldp = chamber length, Dp = chamber diameter, Dp* = corrected chamber diameter, Dn = neck diameter, Dn* = corrected neck diameter, Dc = collar diameter, Dc* = corrected collar diameter, L/Dp* = the ratio of the test length to corrected chamber diameter, Dp*/Dn* = corrected chamber diameter to neck diameter, and Ln/L = neck length to test length. The correction factors of 0.7 and 0.8 are adopted for the compressed neck and chamber, respectively, following Paris et al. (2015a). Raw data of all the measurements are presented in Supplemental Data 2.

	L	Ldp	Dp	Dp*	Dn	Dn*	Dc	L/Dp*	Dp*/Dn*	Ln/L
	µm									
Minimum	268	183	130	130	50	50	75	1.46	1.71	0.15
Maximum	647	454	325	260	177	177	197	2.90	3.20	0.39
Average	406	288	195	191	88	85	125	2.12	2.27	0.29
Valid number	119	117	114	114	114	114	91	113	111	116

data have been reported in this time interval in the area. The specimen reported by Geng (1984) from the Hunghuayuan Formation at Yichang resembles the general outline of *L. esthonica*, but lacks the distinctive flaring collar. The specimens recovered in the upper Meitan Formation (Zhen, 1985) share similar outline with the slender form of *L. esthonica*, but with a significantly smaller size. The specimens reported from the Hungshihyen Formation (Gao, 1986) have been re-identified as *Lagenochitina obeligis* Paris, 1981, by Liang et al. (2020b). The data reported from the Tulghes Group in Romania (Olaru and Apostoae, 2004; Olaru, 2005; Olaru et al., 2011) are pieces and hard to classify based on the images presented. The specimens lacking a distinct flexure with a short neck, such as figure 19B–D in Grahn (1980), have been revised as *Lagenochitina yilingensis* by Chen et al. (2009a). The small specimens recovered from the Hunghuayuan and Meitan formations (Chen and Zhang, 2005) later were emended as *Lagenochitina chongqingensis* by Chen in Chen et al., 2009b. The specimens reported from the Ningkuo Formation at Yiyang, South China (Wang et al., 2013) have the smallest size of *L. esthonica*, with test lengths that range from 170–224 µm. The image shown in Nowak et al. (2016) features a less-flaring collar and ovoid chamber that closely resembles *Lagenochitina* cf. *L. longiformis* Obut, 1995, recovered in the Leetse Formation in northern Estonia by Hints and Nõlvak (2006).

Lagenochitina megaesthonica new species, Liang, Nõlvak, and Hints
Figures 4.23–4.32, 5, 6

- 1967 *Lagenochitina esthonica*; Jenkins, p. 463, pl. 74, figs. 4, 5.
- 1968 *Lagenochitina esthonica*; Eisenack, p. 156, pl. 29, fig. 25, text-fig. 1.
- 1971 *Lagenochitina esthonica*; Downie et al., p. 21, pl. 1, fig. 17.
- 1976a *Lagenochitina esthonica*; Eisenack, p. 186, pl. 2, fig. 1, text-fig. 2.
- p 1976b *Lagenochitina esthonica*; Eisenack, figs. 22, 23.
- 1980 *Lagenochitina esthonica*; Grahn, p. 32, fig. 19A.
- 1981 *Lagenochitina esthonica*; Paris, p. 248, pl. 10, figs. 15, 20.
- 1996 *Lagenochitina esthonica*; Grahn et al., pl. 3, fig. 9.
- ? 2015 *Lagenochitina esthonica elongata* Liang, p. 145, pl. 11, figs. 10–12.
- ? 2018 *Lagenochitina* aff. *esthonica*; Liang et al., fig. 4W.
- 2019 *Lagenochitina esthonica*; Nõlvak et al., pl. 4, fig. 6L, M.

Holotype.—Specimen (GIT 833-1, Fig. 5.23) from sample M-13458 (Kunda Regional Stage, middle Darriwilian; Fig. 2), Kaugatuma drill core, western Estonia, with L-Dp-Dc-Lp dimensions of 867-229-116-574 µm.

Paratypes.—Figure 5.15 (GIT 833-2) from sample M-13458, Kaugatuma drill core, western Estonia, with L-Dp-Dc-Lp dimensions of 772-288-120-494 µm; Figure 6.23 (GIT 833-3) from sample M-13671, Baldone drill core, Latvia, with L-Dp*-Dc*-Lp dimensions of 964-291-112-598 µm; and Figure 6.26 (GIT 833-4) from sample M-13672, Baldone drill core, Latvia, with L-Dp*-Dc*-Lp dimensions of 1348-365-147-844 µm.

Diagnosis.—Large to huge *Lagenochitina* (441–1288 µm, Fig. 9) with a relatively long cylindrical neck (~18–55% of the test length) ended with extraordinary flaring collar. Chamber elongated ovoid with almost parallel flanks, shoulders not distinct. The length is ~2–6.6 times the chamber diameter.

Occurrence.—The reported data are mainly from Baltica, Avalonia, and North Gondwana (Fig. 8), including the "*Expansus* Limestone" (Kunda Regional Stage, lower to middle Darriwilian) of Fjäcka, Dalarna, Sweden (Eisenack, 1955); the Hope Shale (middle Darriwilian) in Shropshire, England (Jenkins, 1967); the Vaginatum Limestone (Kunda Regional Stage) in Öland, Sweden (Eisenack, 1976a); strata of upper Langevoja to lower Valaste and upper Aluoja regional substages (ca. lower and middle Darriwilian) in Öland, Sweden (Grahn, 1980); the middle part of the Domfront Pissot Formation (ca. middle Darriwilian) in Brittany, France (Paris, 1981); strata above the Granby Event in the Kunda Regional Stage in the Granby crater, Sweden (Grahn et al., 1996); and the Sillaoru and Pakri formations (lower Darriwilian) at Jägala, Estonia (Nõlvak et al., 2019). The data from South China (Liang et al., 2018) require further investigation. In the present study, *Lagenochitina megaesthonica* n. sp. appears in the uppermost Volkhov to Kunda regional stages at Jägala, and Kunda Reginal Stage at the Kaldase, Kaugatuma, and Baldone sections, corresponding to the upper part of the Dapingian to lower and middle parts of the Darriwilian, Middle Ordovician.

Description.—Test large to huge, ranging from 441–1288 µm with an average value of 769 µm in length. Neck clearly differentiated and cylindrical, occupying ~18–55% of the test length, ended with an extraordinary flaring collar. Chamber elongated ovoid to sub-cylindric. The maximum diameter is located at the middle part of the chamber, which is 15–50% of the test length after correction. Flexure broad and shoulders inconspicuous, flanks nearly parallel to slightly swollen, base flat or slightly convex, base margin rounded. Mucron usually present, but with various shapes and size, as in *Lagenochitina esthonica* emend. Test surface can be smooth or covered by rugose to spongy structures (e.g., Fig. 5.21, 5.22). The rugose and smooth surface can co-occur in one specimen (e.g., Fig. 5.28, 5.29).

Etymology.—Referring to the large size and the name *Lagenochitina esthonica*, under which specimens of the new species previously have been assigned.

Materials.—Forty-four specimens were recovered from samples M-2576 and M-4164 from the Jägala section, Estonia; 18 specimens were recovered from samples M-13622 and M-13628 from the Kaldase drill core, Estonia; 75 specimens were recovered from samples M-13447 to M-13458 from the

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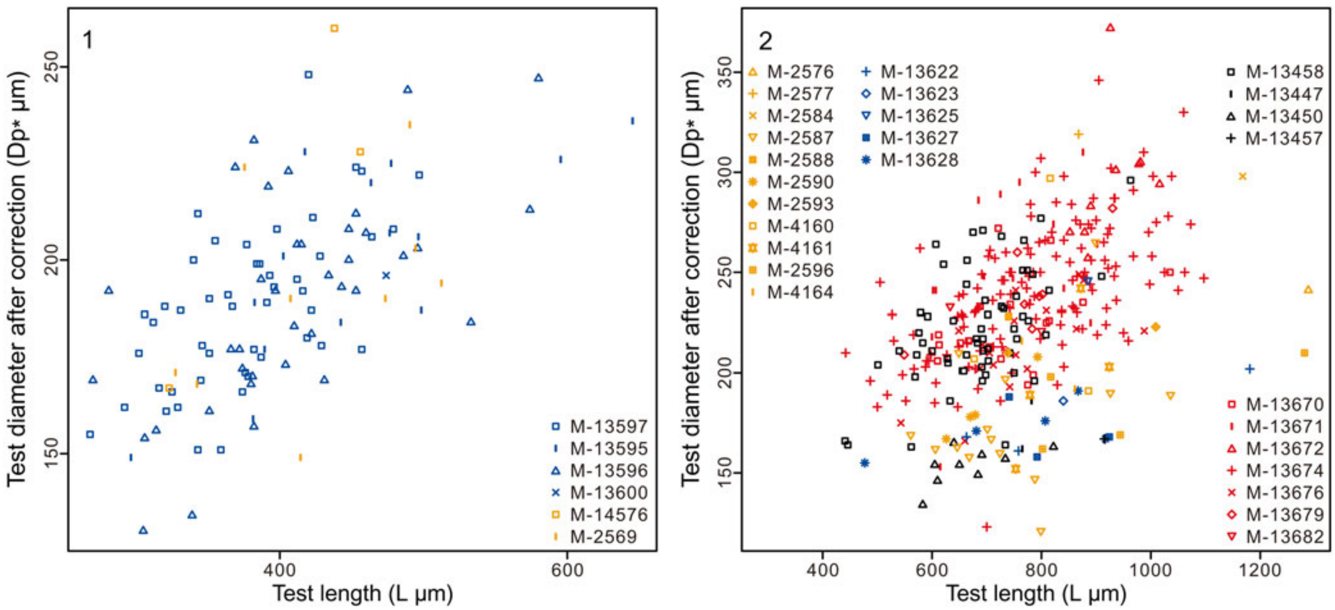

Figure 9. Cross plot of the test length and chamber diameter after correction of *Lagenochitina esthonica* emend. (**1**) and *Lagenochitina megaesthonica* n. sp. (**2**). The red, blue, black, and orange symbols represent data from Baldone, Kaldase, Kaugatuma, and Jägala sections, respectively. Different shapes represent data from different samples.

Kaugatuma drill core, Estonia; and 249 specimens were recovered from samples M-13670 and M-13682 from the Baldone drill core, Latvia (Fig. 2).

Dimension.—Dimensions (Table 2) are based on 386 specimens, 244 of which are compressed and others are preserved three-dimensionally.

Remarks.—Large and slender forms of previously reported *Lagenochitina esthonica* (Eisenack, 1968, 1976a, b; Grahn, 1980; Paris, 1981; Grahn et al., 1996; Hints and Nõlvak, 2006; Nõlvak et al., 2019). *Lagenochitina megaesthonica* n. sp. is distinguished by its large test with a flaring collar in all *Lagenochitina* species. It differs from *L. esthonica* emend. in its large and slender test (Fig. 9) with a less-distinctive flexure and weak shoulder. The test outline of *L. megaesthonica* n. sp. resembles *Lagenochitina boja* Bockelie, 1980, in slender form with a flaring collar, but differs from the latter in having a more distinct flexure and larger test. Some specimens possessing a very short neck (e.g. Fig. 5.5, 5.6, 5.12) resemble *Lagenochitina yilingensis* in test morphology. However, considering the small number of such specimens, they are taken to represent intraspecific variation within *L. megaesthonica* n. sp. in this study. *Lagenochitina esthonica elongata* and *Lagenochitina* aff. *L. esthonica* are adopted for the same material recovered in the uppermost Meitan Formation at Tongzi, Guizhou, South China (Liang, 2015; Liang et al., 2018). These specimens also share a slender outline and a flaring collar resembling *L. megaesthonica* n. sp.; however, their test length is shorter, ranging from 434–592 µm, and the collar is less flaring than in typical *L. megaesthonica* n. sp. Considering that only three specimens have been recovered, a question mark is added in the synonymy list at the present.

Table 2. Dimensions of *Lagenochitina megaesthonica* n. sp. L = test length, Ldp = chamber length, Dp = chamber diameter, Dp* = corrected chamber diameter, Dn = neck diameter, Dn* = corrected neck diameter, Dc = collar diameter, Dc* = corrected collar diameter, L/Dp* = the ratio of the test length to corrected chamber diameter, Dp*/Dn* = corrected chamber diameter to neck diameter, and Ln/L = neck length to test length.. The correction factors of 0.7 and 0.8 are adopted for the compressed neck and chamber, respectively, following Paris et al. (2015a). Raw data of all the measurements are presented in Supplemental Data 2.

	L	Ldp	Dp	Dp*	Dn	Dn*	Dc	L/Dp*	Dp*/Dn*	Ln/L
	µm									
Minimum	441	248	121	121	68	68	91	2.06	1.42	0.18
Maximum	1288	824	413	372	212	172	284	6.6	3.42	0.55
Average	769	490	260	228	140	108	183	3.45	2.14	0.36
Valid number	341	358	369	369	353	353	223	328	345	320

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Data availability statement

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.vmcvdncsx.

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