

A SILURIAN CEPHALOPOD GENUS WITH A REINFORCED FRILLED SHELL

by SVEN STRIDSBERG

ABSTRACT. A new cephalopod genus, *Torquatoceras*, comprising two new species *T. undulatum* and *T. auritum*, is described from the Silurian of Gotland. *Torquatoceras* is unique in that transverse crenulated frills have been secreted during the entire growth of the shell. These frills, mainly consisting of prismatic layers, might have served as a reinforcement of the shell. In *T. undulatum* sexual dimorphism based on size variations is demonstrated. In *T. auritum* there are two vertical septa inside the body-chamber, partly separating the hyponomic sinus from the apertural opening.

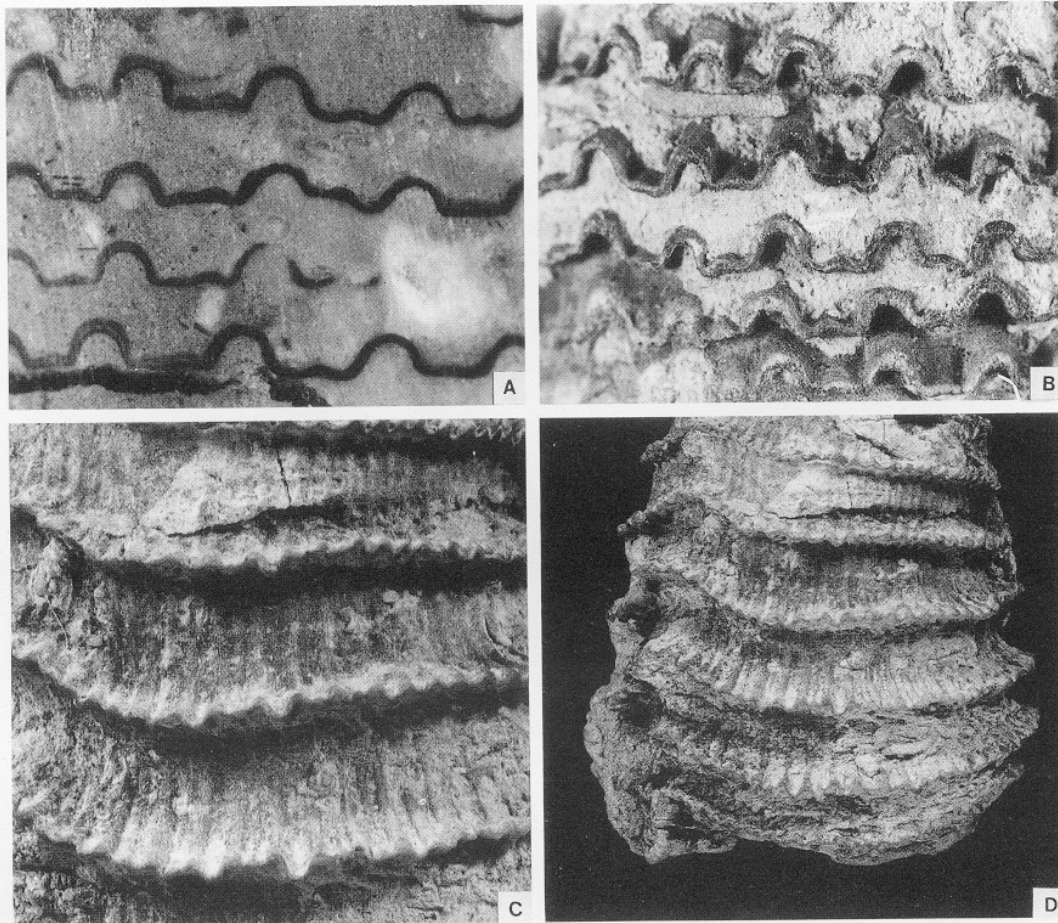
THE fossil record from the Baltic island of Gotland demonstrates very well that the Silurian cephalopod fauna in the area was rich. The shallow, tropical Silurian sea favoured the establishment of various genera and species, and thus far more than eighty species in fifteen genera have been described from the island.

Mostly the cephalopods on Gotland are found in large thanatocoenoses and the new species described herein are both collected at such a place, the Samsugns quarry in the Wenlock Slite Beds (Laufeld 1974). This quarry is moderate in size, only 75–100 m across and about 10 m deep, but is unique regarding the cephalopod fauna. No other locality on Gotland shows such a variety of species with heterogeneous shell morphology, and altogether twenty species in ten genera have been identified (Angelin and Lindström 1880, 1 species; Lindström 1890, 5 species; Hedström 1917, 8 species; Stridsberg 1985a, 4 species and herein 2 species). Still more taxa of cephalopods from Storugns have been collected and are waiting description, but in contrast to those already described they are mainly orthocones.

There are reasons for believing that all twenty species did not actually live in the Storugns area, since from their shell morphology a number of them appear to have had the same mode of life. However, the floating chambers of the cephalopod shells certainly contributed to post-mortem drifting, and obviously Samsugns was a kind of meeting place for the Silurian drifters. Similar drifting of extant *Nautilus* is well documented, especially from the south-western Pacific (Toriyama *et al.* 1965; Hamada 1964; Saunders and Spinosa 1979).

In the varied cephalopod fauna from Samsugns there is a genus with a most unusual shell surface, consisting of crenulated transverse frills (text-fig. 1). Various kinds of shell ornamentation are well known from other cephalopod species, but this genus, *Torquatoceras* gen. nov., has an exceptional protruding system of frills around the shell. Crenulate transverse frills also occur in the Ordovician genus *Zitteloceras* Hyatt 1884, and according to Foerste (1916, p. 51) these frills, or rather lamellae, 'may have extended for a distance of about half a millimeter from the general surface of the cyrtoceracone'. The frills in *Zitteloceras* appear to be strongly similar with those on *Pentameroceras facula* Stridsberg 1985a, although the latter are not crenulated, and as discussed in the description of *Torquatoceras* herein, the frills on *P. facula* are probably not constructed in the same way as those in *Torquatoceras*.

The shell of the Bohemian species *Corbuloceras corbulatum* (Barrande 1866), is covered by crenulated frills, extending a few millimetres from the shell wall (Barrande 1867, pp. 586–587; Horný 1965, pp. 132–136, Tab. 1–2), however, *Corbuloceras* has longitudinal ribs on the shell and when crossing these ribs the frills have distinct protrusions (text-fig. 2). Similar protrusions are not preserved on any of the specimens of *Torquatoceras*.

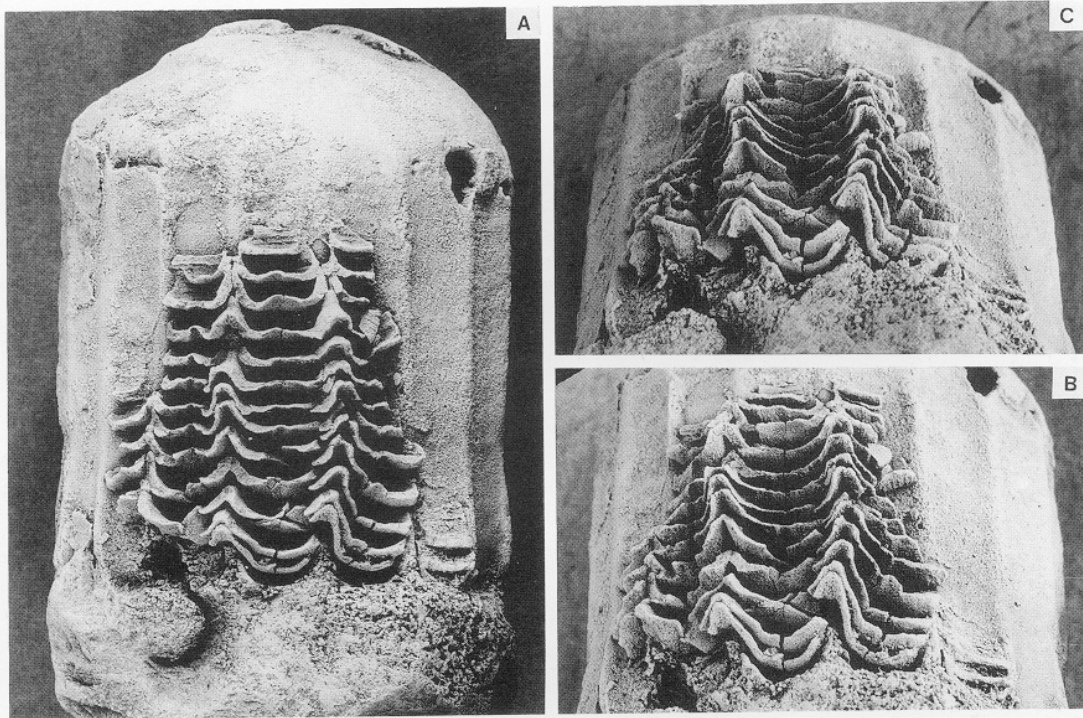


TEXT-FIG. 1. Close-up of photographs of frills in *Torquatoceras undulatum*. A and B show the rhythmic pattern found in some mature specimens with worn down (A) and well-preserved (B) shells, $\times 6.5$. C, enlarged crenulations from D, to show the outline of the frills. RM Mo 57307, $\times 4.5$ and $\times 2.2$.

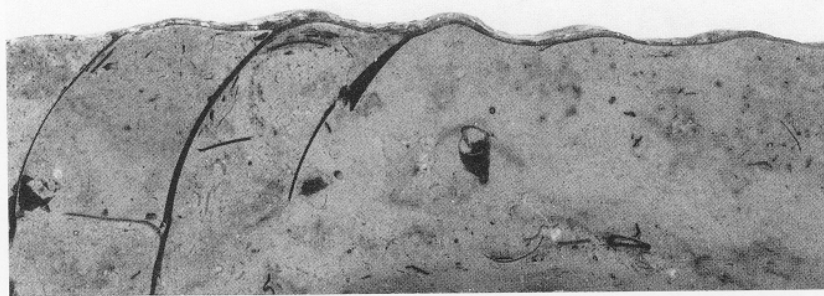
In some Silurian cephalopods, for example *Dawsonoceras*, regularly repeated bulges surround the shell. However, in these cases the bulges are the result of a repeated temporary widening of the aperture, and the thickness of the shell is thus the same in the bulges as in the adjacent parts of the shell (text-fig. 3). In *Torquatoceras*, however, the protruding frills are almost untraceable from the inside of the shell. Only slight depressions indicate occasionally where the frills are situated (text-fig. 4).

CONSTRUCTION OF FRILLS

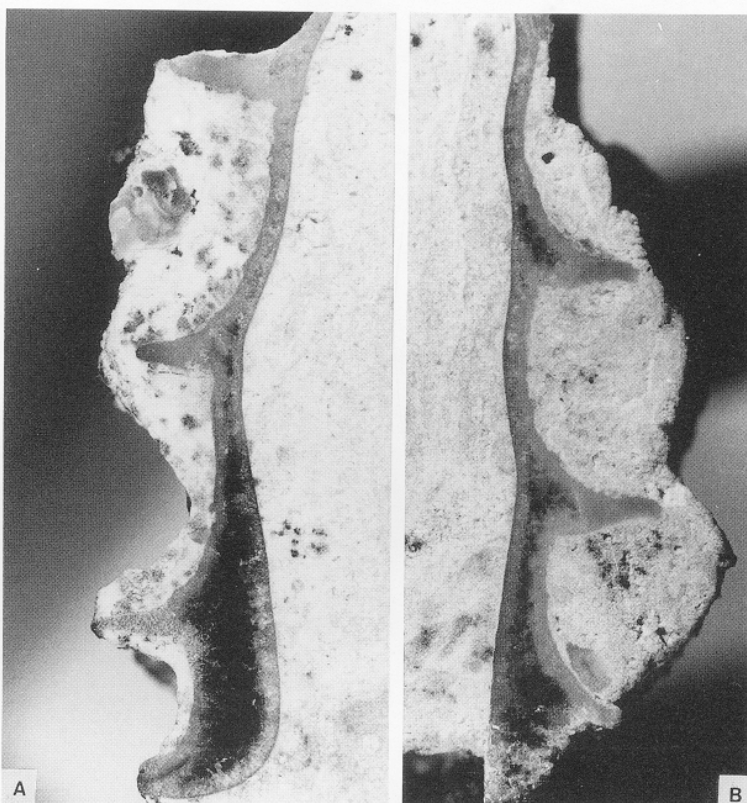
The presence of frills on the shell surface of *Torquatoceras*, makes the cephalopod resemble a rugose coral. In some rugose corals rhythmic shell growth is very common and frills similar to those of *Torquatoceras* are found in various species. The shell growth, however, is far from similar



TEXT-FIG. 2. Three views (A-C) from various angles of the same area of *Corbuloceras corbulatum* (Barrande 1866), specimen L 6561, Narodní Muzeum, Prague. $\times 1.75$. A, lateral view with apical end upwards. B, view towards the apical end showing the protruding parts of the frills on top of the longitudinal ribs. In C it is evident that the protrusions are more striking than the ribs, and thus not just a reflection of the underlying surface.



TEXT-FIG. 3. Cross-section of a specimen of *Dawsonoceras*, illustrating the regularly repeated bulges surrounding the shell. The dark thin lines are the three last septa. $\times 2.5$.



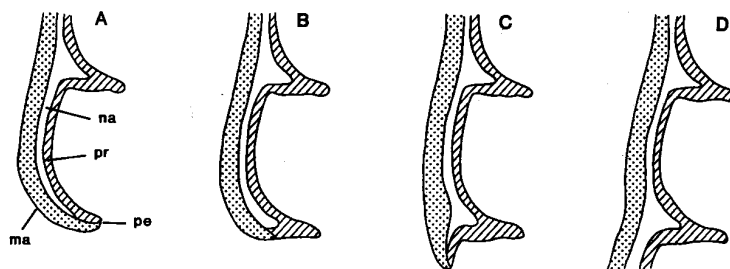
TEXT-FIG. 4. Cross-sections of the outermost part of the shell in *Torquaticeras undulatum*, RM Mo 57245. In A the reinforcement in the apertural area is clearly visible. In B the beginning of the reinforcement can be seen on the lowermost part of the shell. $\times 15$.

as the frills on corals are interpreted as having been built up during extreme stretching out of the secreting ectoderm. Such stretchings are supposed to have taken place when the polyps were extended to release the planula larvae when the Moon was in a specific position. Similar rhythmic shell growth has been suggested for the cephalopods (Kahn and Pompea 1978) but as explained by Saunders and Ward (1979), comparisons can not be made.

In molluscs the mantle would hardly act in the same way as the ectoderm in the corals, and furthermore, the frills on *Torquaticeras* are present from the most juvenile stage to the fully adult specimen.

The construction of the frills in *Torquaticeras* is a procedure which is unusual among nautiloids, as the mantle growth must have frequently changed directions. Instead of continuing shell secretion along the apertural edge, the mantle must have turned round to secrete the apertural side of the frill after the secreting of the apical side of each frill (text-fig. 5A-B). After the deposition of a frill the shell-secreting epithelium inside the frill must have reduced its length, and during this phase shell deposits eventually filled up the interior of the frill with nacreous layers (text-fig. 5C-D).

After the completing of a frill the shell-secreting epithelial cells from the interior of the frill must have been reduced, as the inside of the body-chamber has a smooth surface (text-figs. 4 and 5).



TEXT-FIG. 5. Four hypothetical phases (A-D) in the secretion of a frill in *Torquatoceras*, drawn from the frills in text-fig. 4B. A, the secretion of the shell wall between two frills and the apical side of a partly secreted frill. B, the mantle has turned round and secretes the apertural side of the new frill. C, the frill is completed and the mantle continues the secretion of the phragmocone wall. D, the intermediate space inside the frill is 'filled up' with, most probably, nacreous layer and the mantle follows the phragmocone shell wall. Abbreviations: ma = mantle; pe = periostracum; pr = outer prismatic layer; na = nacreous layer.

Cross-sections of the shell do not show any space for extensions of the mantle into the frills (text-fig. 4), and thus any damage on the frills could not be repaired after the withdrawal of the mantle.

Due to the recrystallization of the shell material, no details of the various shell layers can be observed on any of the specimens examined. If, however, the shell of *Torquatoceras* was constructed in the same way as the shell of *Nautilus* (Mutvei 1964), it can be assumed that the frills did not have any semi-prismatic layer inside the nacreous layer, as the secretion of this semi-prismatic layer took place long after the 'closing' of the frills when the epithelial cells turned to 'muscle-cells'. Only the periostracum the outer prismatic layer and the nacreous layer can have been represented in the crenulated frills.

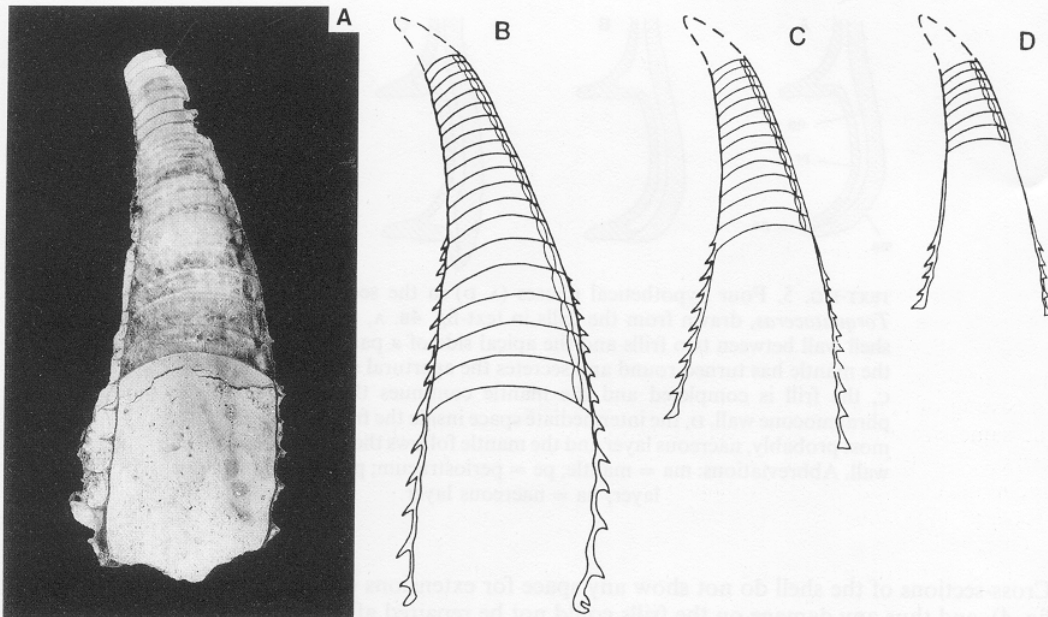
REGULARITY OF FRILL GROWTH

As septa and frills in *Torquatoceras* were constructed at intervals, there is reason to ask if secretion of frills was in any way correlated with the secretion of septa. Frills, as well as septa, are very closely spaced in the juvenile part of the phragmocone and considerably more widely spaced in the mature part. During the final growth stage, however, the frills were more closely spaced again but this was caused by the shape of the aperture. The area around the hyponomic sinus has very limited space between the last frills, while on the other hand, the frills on the ventrolateral lobes are fairly widely spaced.

Due to the apical end of the phragmocone always being missing, it is not possible to compare the total number of septa and frills in a complete shell. However, by counting septa and frills backwards, from the aperture towards the apical end, it is possible to make an hypothetical reconstruction of various growth stages. If the growth of septum and frills were synchronized the various reconstructed growth stages must show a shell with roughly the same proportions of body-chamber and the chambered section of the phragmocone as in a mature specimen.

A specimen with an unusually large number of preserved septa has been used for reconstructions of three different growth stages (text-fig. 6). In each case, the same number of frills and septa have been removed, and the proportions of body-chamber and chambered part of the shell can be compared. Due to the difficulties in observing the frills in the juvenile part of the shell, reconstructions in this part of the shell have been omitted.

The comparisons of the reconstructed growth stages, including specimens not illustrated, show



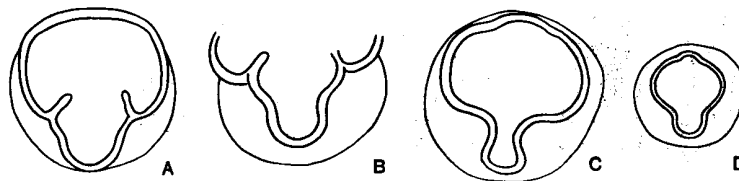
TEXT-FIG. 6. A photograph and three drawings of a cut shell of *Torquatoceras undulatum*, RM Mo 56353, showing different growth stages. A, the cut shell, $\times 2$. B, the mature shell as shown in A. C, the same shell as in B but with six frills and six septa removed. D, the same shell as in B but with twelve frills and twelve septa removed. The missing apical end of the shell is reconstructed.

that the hypothesis of a synchronized secretion of septa and frills is realistic, although the body-chamber proportionally decreases in relative volume from the juvenile reconstructions to the adult specimens. This might be explained by the fact that the adult specimen has many more developed frills, proportionally thicker as well as wider than those on the juvenile shells, and thus needed more floating capacity. Furthermore, the possible negative buoyancy on the juvenile shell can also be explained by an hypothesis that the juvenile *Torquatoceras* was benthic.

If the number of frills and of septa are the same in *Torquatoceras*, the secretion of these items must have been parallel. Whether or not secretion was simultaneous is impossible to decide on shell studies alone. Most probably, however, the apertural shell growth, and thus the frills, continued all the time, and were not influenced by the repeated movements of the soft parts when the mantle reorganized for secretion of a new septum.

FUNCTION OF FRILLS

The advantage of the frills, decorating *Torquatoceras*, is difficult to understand, and only speculations can be made about their function. The presence of this ornamentation must add extra weight to the shell, although the frills, as well as the shell, are rather thin. This conclusion was reached after comparisons with other cephalopods of the same size from the same locality, but unfortunately recrystallization precludes an exact comparison. On average cephalopods with no frills had 50–60% thicker shells. Since the shell was thinner in *Torquatoceras* than in other comparable shells, the function of the frills might have been to reinforce the shell. For cephalopods, at least those swimming forms, it is a question of priorities if the shell must be strong but heavy or light but fragile. The combination light and strong is difficult to accomplish with the



TEXT-FIG. 7. A, B, drawings of the apertural opening in the two specimens of *Torquatoceras auritum*, illustrating the vertical walls in the body-chamber. See also Plate 64, figs. 2 and 5. C, D, illustrate the size difference between the two morphs of *T. undulatum*. See also Plate 63, figs. 2 and 10.

usual mode of shell construction, as an increase in thickness of the shell to achieve strength, necessarily causes an increase in weight. However, a thin shell supported by an external framework, consisting of crenulated frills, can achieve considerably better strength than an ordinary shell of the same size and the same weight, especially as the frills are always perpendicular to the shell surface. Furthermore, the crenulations of the shell between the frills contribute further to a strong and light construction. In the diagnosis of *C. corbulatum*, another species with a frilled shell, Horný (1965, p. 136) stated that the shell wall was rather thin.

Other qualities in *Torquatoceras*, favouring the hypothesis of a thin but reinforced shell, are the reinforced apertural edge and the vertical septa in *T. auritum* (text-fig. 7 and Pl. 64). The reinforced apertural edge is by no means a peculiarity of *Torquatoceras*, as this is common in almost all oncocerid cephalopods from Gotland (Stridsberg 1985a). Presumably this is an advantage for most brevicones as they very often have a complex apertural opening with lobes and sinuses. Vertical septa, however, have thus far only been observed in *T. auritum*. As discussed in the taxonomic part herein, our knowledge is very limited about the outlines of these septa, but naturally any kind of extra shell construction must support the total strength of the shell. Possibly, the vertical septa not only strengthened the shell, but also assisted in protecting the soft parts from external danger. The lateral view shows clearly that the outer parts of the vertical septa protrude outside the apertural opening (Pl. 64, fig. 3).

If the hypothesis that the crenulated frills served to strengthen the shell is correct, then there must be a reason for a reinforced shell. Above all, the function of the shell was to protect the inhabitant from any kind of danger. Mostly this danger comes from predators, but occasionally from the energy of the environment. Regarding *Torquatoceras*, the only known predators capable of destroying such a strong shell, were the eurypterids. These animals are well known from Gotland and in the Högklint Beds, lower Sheinwoodian, where the occurrence of eurypterids resulted in the *Pterygotus* beds.

The possibility that a reinforced shell developed to withstand physical damage in a turbulent reef environment, might explain the presence of the frills. One must keep in mind that the Palaeozoic reef fauna probably consisted considerably more of shell carrying organisms than is the case today. Not only the cephalopods but also all the fishes and many gastropods have abandoned external skeletons or shells, and at least the two first groups rely on speed in favour of armour, while some gastropods are bad tasting or poisonous. The use of a reinforced shell like that of *Torquatoceras*, might have been an attempt to survive in a tough environment.

SYSTEMATIC PALAEOONTOLOGY

Order ONCOCERIDA Flower, 1950
 Family TRIMROCERATIDAE Hyatt, 1900
 Genus *Torquatoceras* gen. nov.

Derivation of name. Latin *torquatus*, adorned with a collar.

Type species. Torquatoceras undulatum sp. nov.

Diagnosis. Circular, exogastric (convex ventral side) brevicone. Contracted aperture with two ventrolateral lobes on each side of the hyponomic sinus. Shell surface covered with transverse undulating frills, which on the ventral side are V-shaped due to the growth of the hyponomic sinus. Slender empty siphuncle.

Discussion. The genus *Torquatoceras* is placed in the family Trimeroceratidae due to the outline of the aperture and the slender empty siphuncle. Furthermore, *Torquatoceras* appears to be closely related to *Pentameroceras facula*, another species of the Trimeroceratidae.

Species. T. undulatum sp. nov. and *T. auritum* sp. nov.

Torquatoceras undulatum sp. nov.

Plate 63, figs. 1-10; text-figs. 6 and 7C, D

Derivation of name. Latin *undulatus*, undulating, referring to the undulating frills.

Holotype. RM Mo 56365.

Type stratum. Slite Beds, unit g, upper Sheinwoodian.

Type locality. Samsugns 1, Gotland, Sweden.

Material. Eleven macroconchs and forty to fifty more or less well-preserved microconchs from Gotland, Sweden. Macroconchs RM Mo 56274-56275, 56842-56845, 57305, 57307, 155957-155960. Microconchs RM Mo 56353, 56356, 56358, 56365-56366, 56368-56369, 56373-56374, 56377, 56379, 56383, 56392, 57244-57249, 152776, 157719 and twenty to thirty less well-preserved specimens, all at Naturhistoriska Riksmuseet, Stockholm, Sweden. All well-preserved specimens are mature.

Diagnosis. A species of *Torquatoceras* with a circular exogastric brevicone, having crenulate transverse frills. In mature specimens a contracted aperture with two ventrolateral lobes.

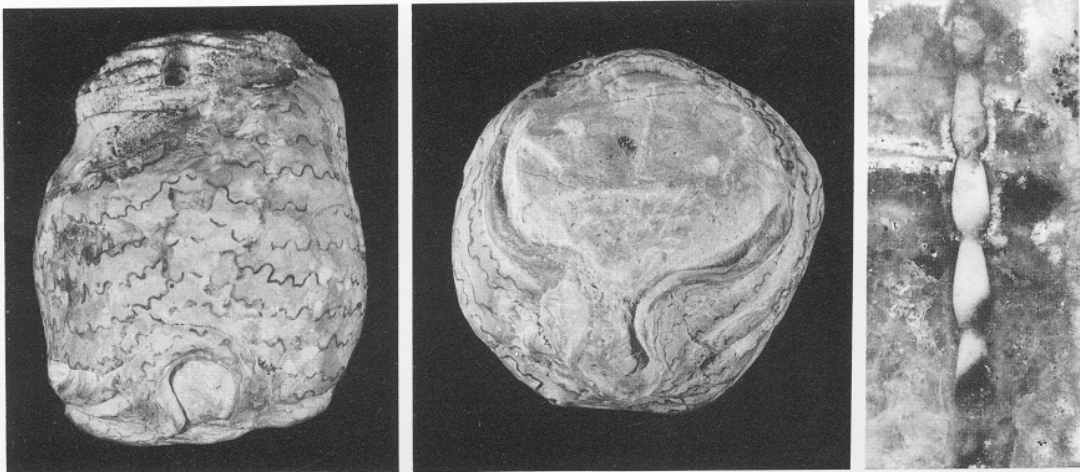
Description. Slightly exogastric, circular phragmocone with a straight body-chamber. The shell surface consists of crenulate transverse frills, 1.5-2.5 mm wide, perpendicular to the shell wall. The crenulation on the frills continues on the shell surface between the frills. In some of the bigger specimens the crenulation shows a specific rhythm (text-fig. 1), which is repeated on all frills. The distance between the frills increases during growth to reach a maximum at about mid body-chamber. Close to the aperture the distance between the frills decreases and the last frills can only be observed on the ventrolateral lobes. On the ventral side of the phragmocone the frills are V-shaped, due to the position of the hyponomic sinus during the shell growth.

Because of a distinct size dimorphism the distance between the frills varies considerably. As an average the maximum distance on macroconchs is 5 mm and on microconchs 2 mm. The slender empty siphuncle, located close to the ventral shell wall, has an average thickness of about 2 mm in macroconchs and about 1 mm in microconchs (Pl. 63, fig. 3). The ratio of the length and width of the body-chamber is 3 to 2. Inside the apertural rim the shell is reinforced (text-fig. 4) and this reinforcement is further developed by the crowding of the last frills around the apertural opening. Altogether this shell growth forms a ridge along the edge of the aperture.

Dimorphism. The material is divided into two very distinct size groups, the macroconchs being about twice the length and width of the microconchs, and this size dimorphism is interpreted as sexual dimorphism (text-fig. 7C, D; Pl. 63, figs. 2 and 10). Dimorphism is fairly common among Silurian oncocerid cephalopods

EXPLANATION OF PLATE 63

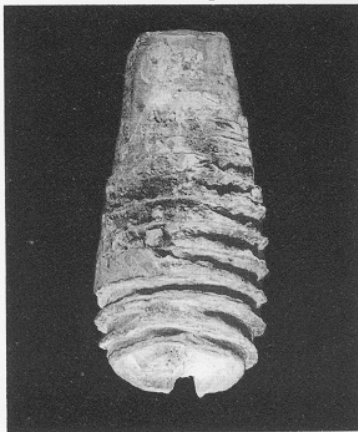
Figs. 1-10. *Torquatoceras undulatum* sp. nov. Slite beds, unit g. Samsugns 1. 1 and 2, ventral and apertural views of RM Mo 56842 with worn down frills, $\times 1.5$. 3, an enlargement of the siphuncle of the holotype RM Mo 56365, $\times 6$. 4-7, dorsal, lateral, ventral, and apertural views of the holotype RM Mo 56365, $\times 1.5$. 8-10, dorsal, lateral, and apertural views of RM Mo 152776, $\times 1.5$.



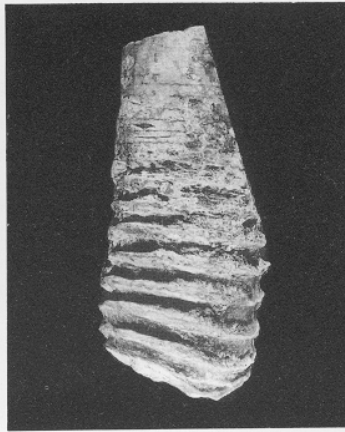
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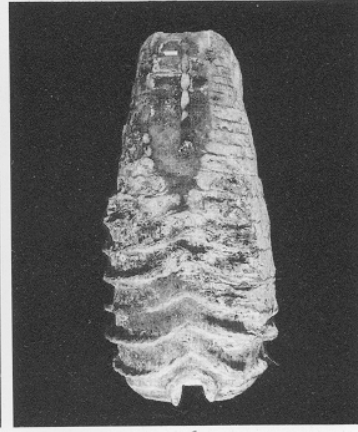
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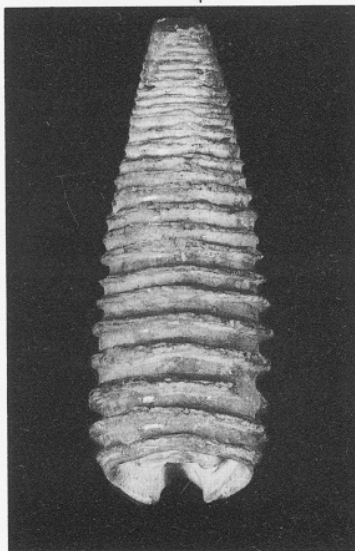
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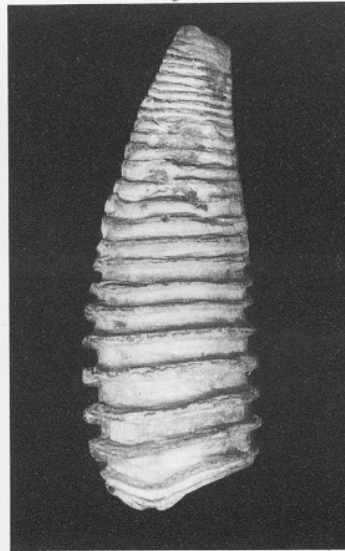
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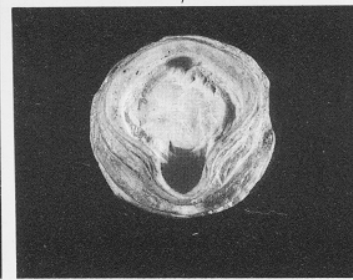
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STRIDSBERG, *Torquatoceras*

(Stridsberg 1985a, b). The apertural shape in combination with the shell morphology in the macroconchs as well as in the microconchs, indicates a specific mode of life, and it is most unlikely that two species with the same mode of life lived in the same place. Although after the death of the animals the empty shells are known to drift around in the ocean, and perhaps become concentrated in some places, it must be pointed out that all specimens of *T. undulatum* are found in one locality only, macroconchs as well as microconchs.

Discussion. The condition of the preserved material varies widely and the most complete specimens are the microconchs. Some of these have a well-preserved apertural region and an almost complete phragmocone, although the apical end is always broken off. The crenulations, however, are best observed on some of the macroconchs, and here the rhythmic pattern can easily be followed from frill to frill (text-fig. 1A, B). These patterns are not so well pronounced on the microconchs but the state of preservation of these does not permit any accurate measurements.

A similar rhythmic pattern is also found in *C. corbulatum* (text-fig. 2) but in this species the frills regularly protrude. On worn-down specimens, however, the pattern is very similar to that of *Torquatoceras*.

Comparison. The outline of *T. undulatum* is very close to that of *T. auritum*, and the only known difference between the two species is the presence of two ventrolateral vertical septa, partly enclosing the hyponomic sinus, in *T. auritum*. The size of the two species is almost the same, as is the configuration of the frills. Due to the very limited material of *T. auritum*, only two incomplete specimens, further comparison is not possible.

In *P. facula* Stridsberg 1985a the shell surface has transverse surficial annulations, although they are not crenulated as in *Torquatoceras*. Furthermore, the annulations of *P. facula* do not seem to be constructed in the same way as in *T. undulatum*, in which the frills were secreted during an extraordinary position of the mantle. The apertural constrictions on *P. facula* and *T. undulatum* are totally different in regard to the lobes and sinuses, although both species have a distinct hyponomic sinus and very pronounced ventrolateral lobes. Probably the apertural shape in the two species is the result of convergent evolution. The size of *P. facula* is about the same as the microconchs of *T. undulatum*.

Torquatoceras auritum sp. nov.

Plate 64, figs. 1-9; text-fig. 7A, B

Derivation of name. Latin *auritum*, referring to something with ears.

Holotype. RM Mo 56284.

Type stratum. Slite beds, unit g, upper Sheinwoodian.

Type locality. Samsugns 1, Gotland, Sweden.

Material. Two specimens from Gotland; RM Mo 56277 and RM Mo 56284 in the Naturhistoriska Riksmuseet, Stockholm, Sweden. Both specimens are mature.

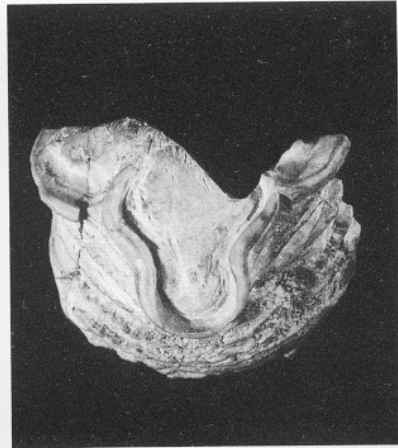
Diagnosis. A species of *Torquatoceras* with a circular, probably exogastric breviconic phragmocone, having crenulate transverse frills. In mature specimens a contracted aperture with two ventrolateral lobes, each with a vertical septum partly enclosing the hyponomic sinus.

EXPLANATION OF PLATE 64

Figs. 1-9. *Torquatoceras auritum* sp. nov. Slite beds, unit g, Samsugns 1. 1-3, ventral, apertural, and lateral views of RM Mo 56277. In the lateral view (3) the protrusion of the vertical septa outside the apertural opening is shown, $\times 1.5$. 4, 5, 7, 8, dorsal, apertural, ventral, and lateral views of the holotype RM Mo 56284 with worn down frills, $\times 1.5$. 6, enlarged detail of the apertural area of specimen RM Mo 56277, $\times 4.5$. 9, enlarged detail of the apertural area of the specimen RM Mo 56284, $\times 4.5$.



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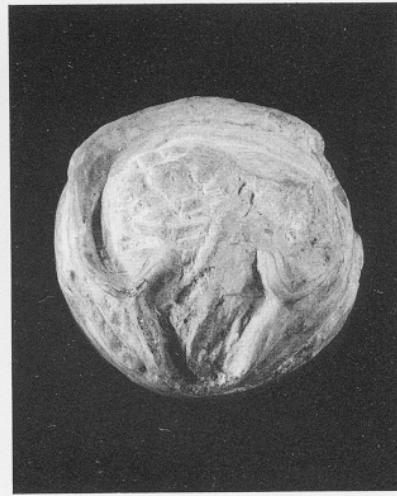
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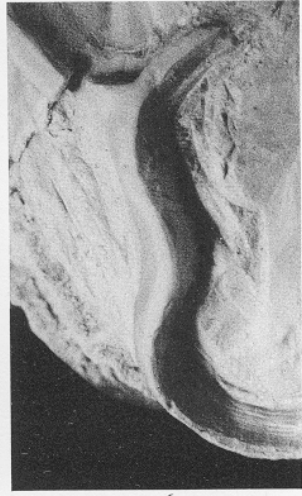
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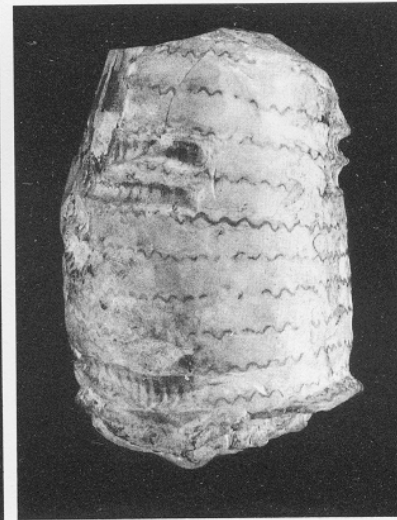
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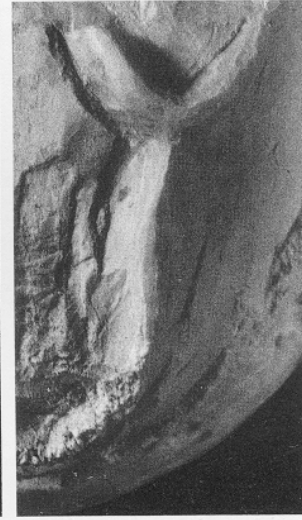
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STRIDSBERG, *Torquatoceras*

Description. Circular straight body-chamber on a probably exogastric phragmocone. The shell surface consists of crenulate transverse frills, which reach about 1.5 mm perpendicularly out from the shell surface. Between the frills the crenulations can be followed on the shell surface as longitudinal furrows (Pl. 64, figs. 4 and 7). The distance between the frills on the body-chamber (the only preserved part of the shells) varies between 2.5–3.5 mm. In the apertural ridge, however, the frills are piled up on each other, forming an edge about 2.0 mm wide. A few of the frills in the apertural ridge are exposed on the ventrolateral lobes, situated on both sides of the hyponomic sinus (Pl. 64, fig. 2).

From the ventrolateral lobes, two vertical septa protrude almost 5 mm towards the centre of the apertural opening. The pronounced shape of the hyponomic sinus can be followed on all older frills by a V-shaped bend towards the apical end of the shell (Pl. 64, fig. 7). The empty slender siphuncle is almost 2 mm wide in the last chambers. The ratio of the length and width of the body-chamber is estimated to be 3 to 2.

Discussion. As the only known specimens of *T. auritum* are both incomplete, knowledge of the phragmocone is very limited. However, the shape of the body-chamber of the holotype indicates an exogastric curvature, as is also the case with *T. undulatum*. The two vertical septa, one from each ventrolateral lobe, are well developed in the apertural area and are firmly connected to the apertural rim. Since the specimens are recrystallized, as is the sediment in the body-chamber, it is not possible to document the extensions of the vertical septa along the inside of the body-chamber. Sections made inside the body-chamber in specimen RM Mo 56277 (Pl. 64, figs. 1–3), show no details at all of the continuation of the vertical septa. Due to the recrystallization it is not known if the two protrusions really are the outer part of two septa or not, and naturally they might as well have been two spines, secreted during the build-up of the apertural rim. Anyhow, the exposed remains of the construction favour the interpretation of two minor septa, perhaps ending a few millimetres behind the apertural edge.

The function of the vertical septa is hard to understand, primarily because we have incomplete knowledge of their shape, but presumably they supported the hyponome in one way or another. The area left for the hyponome, restricted by the apertural rim and the two vertical septa, would still allow a fairly flexible hyponome. As the only likely means of navigation was to alter the direction of the hyponome this was essential for any kind of swimming. Naturally any distension of soft parts must influence the swimming direction but as this would produce a notable drag for the animal, this method is unlikely.

Comparison. *T. auritum* is in many ways identical with *T. undulatum*, and actually the two vertical septa are the only distinguishing characteristics of *T. auritum*. The size of the macroconchs of *T. undulatum* is the same as the conchs of *T. auritum*. Due to these facts it could be questioned whether the two morphs are one species or not, and in case they were the same species, the vertical septa could be some kind of sexual dimorphism. However, in *T. undulatum* there is a most distinct size dimorphism and there are strong reasons to believe that a specific type of aperture would favour a specific mode of life. It must be assumed that the identity of the apertural shape in the two size groups of *T. undulatum* is a better argument for sexual dimorphism, than the external similarities with *T. auritum*. The apertural shape of the latter might possess other qualities and thus another mode of life. The apertural rim is notably thicker on *T. auritum* than on *T. undulatum*, but due to the limited material of *T. auritum* the thick ridge might as well be the result of better preserved specimens of this species.

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