

EARLY CAMBRIAN BUTTON-SHAPED PHOSPHATIC MICROFOSSILS FROM THE SIBERIAN PLATFORM

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ABSTRACT. Button-shaped phosphatic microfossils from the uppermost Atdabanian (Lower Cambrian) of the Siberian Platform (middle reaches of the River Lena, Yakutia, U.S.S.R.) are described as *Lenargyrion knappologicum* n. g., n. sp. The fossils have a mean diameter of about 150 μ m. One side is smooth and slightly convex, the other conical with a flat crest on which are set minute nodes. The internal structure is double-layered: the conical and nodular surfaces are formed by a dense layer capping the more porous core, which contains fine canals. No growth structures can be seen, and there is evidence of mechanical abrasion on the nodular surface. The 'buttons' were probably dermal sclerites in an animal of unknown systematic position. The possibilities of vertebrate affinities are briefly discussed, but the evidence is considered inconclusive.

PHOSPHATIC fossils have long been known to be common in Lower Cambrian rocks. Recent studies by Soviet palaeontologists, notably Missarzhevsky (1966, 1973, 1974, and in Rozanov and Missarzhevsky 1966; Rozanov *et al.* 1969) and Meshkova (1969, 1974, and in Repina *et al.* 1974), on the Upper Precambrian and Lower Cambrian carbonates of the Siberian Platform have revealed numerous such fossils, showing that in the early Cambrian a variety of animal groups developed hard parts of calcium phosphate. Most were shortlived, and their affinities are unknown, but they are often very characteristic fossils with great potential for stratigraphical work. A recent review of some of these fossils was given by Matthews and Missarzhevsky (1975).

This paper deals with a new form of early Cambrian phosphatic fossil from the Siberian Platform. The material comes from a section on the River Lena, and was collected in 1973 during an international geological excursion to the Aldan and Lena rivers, sponsored by the U.S.S.R. Academy of Sciences. At the visit to the exposure, Dr. Vladimir V. Missarzhevsky informed me of the small 'buttons' occurring at a certain level in the carbonatic sequence, and I secured a 900-g sample of the rock for investigation. The 'buttons' are described here for the first time and given the systematic name *Lenargyrion knappologicum*. They cannot yet be included confidently in any known group of organisms, but the morphology and fine structure of the sclerites give some clues to their function.

GEOLOGICAL SETTING

The sample containing *Lenargyrion* comes from a section on the River Lena at the outlet of the Achchagyj-Kyyry-Taas creek, about 200 km upstream from Yakutsk (61° 0' N., 126° 44' E.). This is locality Nr. 45 of Zhuravleva *et al.* (1969). A description of the section, together with lists of fossils, is given by Keller *et al.* (1973). The

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sample is from the middle part of the 16-m thick 2nd Member of the Transitional 'Formation' (*Perekhodnaya svita*). The rock is a light yellow, fine-grained dolomite, with voids partly or completely filled with drusy calcite. The voids are mostly in the form of winding tubes up to a few millimetres in diameter, and are probably caused by boring activities in the consolidated sediment. *Lenargyrion* occurs in the dolomitic parts of the rock.

Associated fossils. The following archaeocyathans have been reported from the 2nd Member of the Transitional 'Formation' at Achchagyj-Kyyry-Taas (Rozanov and Missarzhevsky 1966, locality 2015; see Zhuravleva *et al.* 1969, p. 84): *Archaeofungia* sp., *Compositocyathus muchattensis* Zhuravleva, Cyclocyathellidae, *Porocyathus pinus* Zhuravleva, *Lenocyathus* sp., *Coscinocyathus isointervallum* Zhuravleva. In addition to *Lenargyrion*, my sample contained *Rhombocorniculum cancellatum* (Cobbold), hyolithelminth tubes, and fragments of inarticulate brachiopods.

Stratigraphical level. The 2nd Member of the Transitional 'Formation' belongs to the youngest part of the Atdabanian Stage (archaeocyathan Zone of *Fansycyathus lermontovae*). The base of the subsequent Lenian Stage is drawn at the base of the 3rd or 4th Member (see Rozanov 1973, pp. 113–115 for discussion of this boundary).

In terms of the classical sequence in north-western Europe, the level with *Lenargyrion* would probably fall within the lower parts of the Lower Comley Limestones in Shropshire, i.e. the *Callavia* Sandstone, '*Eodiscus*' *bellimarginatus* Limestone, or *Strenuella* Limestone (see Rushton 1974). Matthews (1973) described a large sample of *Lapworthella dentata* Missarzhevsky from the *Strenuella* Limestone of Comley. This species was originally described from the uppermost Atdabanian of the River Lena; apart from its occurrence at the type locality at the outlet of the Sinyaya creek, about 8 km from Achchagyj-Kyyry-Taas, Missarzhevsky also reported it from the 3rd Member of the Transitional 'Formation' at Achchagyj-Kyyry-Taas (Missarzhevsky in Rozanov *et al.* 1969, p. 164; and pl. 6, fig. 9). This is just a short distance above the beds with *Lenargyrion*. The occurrence of *R. cancellatum* together with *Lenargyrion* does not help to correlate the level with the Comley sequence, since Cobbold (1921) reported the species to range from the Red *Callavia* Sandstone (Ac₂) to the *Lapworthella* Limestone (Ad), i.e. through practically all of the Lower Comley Limestones.

In Scania (south Sweden), a form very similar, if not identical, to *Lapworthella dentata* occurs in the middle and upper parts of the beds traditionally assigned to the *Holmia kjerulfi* Zone (Bengtson, unpublished). This form belongs to the species described by Wiman (1903) as *Stenotheca cornu*, but it is certainly a *Lapworthella*. The characteristically denticulated *L. cornu/dentata* are followed stratigraphically by smooth-ribbed forms in Scania (*L. bornholmiensis* (Poulsen) in the 'fragment limestone') as well as in Shropshire (*L. nigra* Cobbold in the *Lapworthella* Limestone; Cobbold 1921). It is probable that the denticulated lapworthellids mark about the same stratigraphical level in Shropshire and Scania, but a more detailed correlation of the upper Lower Cambrian sequence in Scania must await a revision of both the phosphatic faunas (revision in progress) and the calcareous faunas, particularly the trilobites. (Bergström 1973 showed that the zone-fossil *H. kjerulfi* is apparently not

even present in Scania.) It can be tentatively concluded that the level with *Lenargyrion*, in terms of Scandinavian stratigraphy, probably lies within the *H. kjerulfi* Zone.

METHODS

The phosphatic fossils were isolated through dissolution of the rock in 10% acetic acid. For optical thin sections isolated specimens were embedded in an epoxy resin and ground to a thickness of 25–30 μm . For microprobe analyses, sections of unetched specimens still embedded in the rock matrix were used. Specimens investigated under a scanning electron microscope (SEM) were coated with gold. For the study of internal structure under the SEM, fractured specimens were used, as well as sections of specimens embedded in epoxy resin and specimens still embedded in rock matrix. The polished sections were etched with 4% HCl for 5–20 seconds before coating.

SYSTEMATIC DESCRIPTION

Phylum, class, order and family unknown.

Genus *LENARGYRION* n. g.

Derivation of name. From the River Lena and the Greek *argyrion* (n.), a small coin.

Type and only species. *Lenargyrion knappologicum* n. sp.

Diagnosis. Small (observed range of diameter 50–460 μm) phosphatic sclerites in the shape of circular to oblong discs. One side smooth and slightly convex, the opposite one consisting of a conical surface with a flat crest parallel to the smooth side and capped with minute nodes. Internal structure double-layered; core of porous substance capped by denser layer forming the nodular and conical surfaces.

Lenargyrion knappologicum n. sp.

Text-figs. 1–5

Derivation of name. The science of knappology (from the Swedish *knapp*, button) was introduced by August Strindberg in his satirical work *De lycksaligas ö* (*The Island of the Blissful*, 1884). Knappology deals with classification of buttons, and thus the term is most appropriate for naming the Lena 'buttons'.

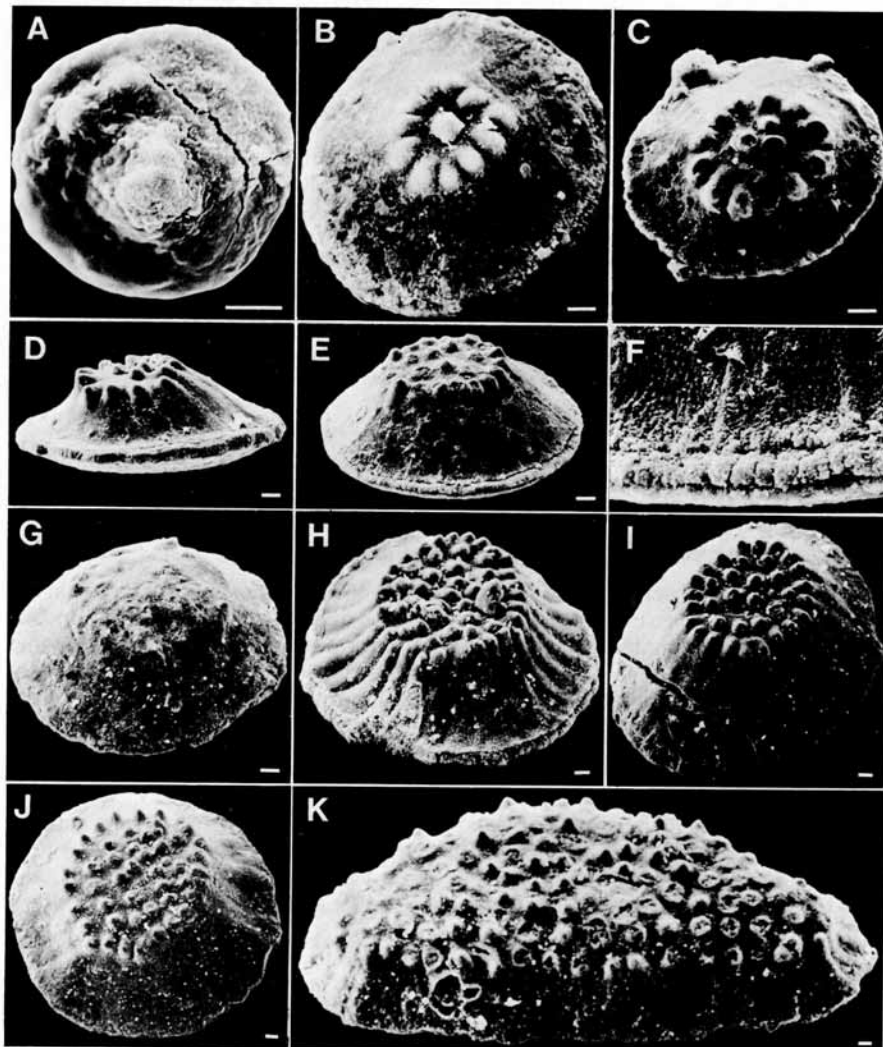
Holotype. Swedish Museum of Natural History, Stockholm No. X 1543.

Diagnosis. As for the genus.

Material. Around 800 investigated specimens. Using the SEM, 236 specimens were studied; optical thin sections were made of 14 specimens in different orientations; polished and etched sections for SEM study were made of 7 specimens.

Distribution. The species is known so far only from the type locality at Achchagyj-Kyyry-Taas.

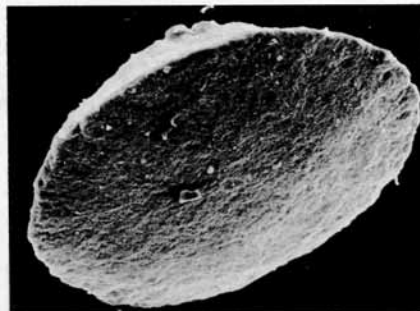
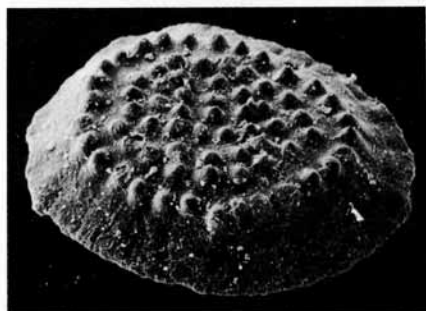
Morphology. Text-figs. 1–5 give a representative picture of the variations in size and morphology. The discs are circular to oblong in outline. The observed size range



TEXT-FIG. 1. Sclerites of *Lenargyrion knappologicum* n. sp. SEM photographs. Scale bar in lower-right corners is 10 μ m. A, Swedish Museum of Natural History, Stockholm (SMNH) No. X 1533; \times 900. B, X 1534; \times 450. C, X 1535; \times 450. D, X 1536; \times 300. E, X 1537; \times 300. F, detail of E; \times 1200. G, X 1538; \times 300. H, X 1539; \times 250. I, X 1540; \times 250. J, X 1541; \times 200. K, X 1542; \times 200.

(length of longest diameter) is 50–460 μm , most specimens falling between 100 and 220 μm . In one exceptionally large specimen (text-fig. 1K) with a long diameter of 460 μm , the ratio between the long and short diameter is as high as 1.8:1, but in no other case does this ratio exceed 1.5:1 (the second largest specimen found has a long diameter of 300 μm). There is no clear correlation between size and roundness. The thickness of the discs is fairly constant between 65 and 85 μm , except for the smallest specimens (below *c.* 100 μm in diameter).

One side of the disc is smooth and slightly convex (text-figs. 1D, 3–5), while on the opposite side is a surface capped with minute nodes (text-figs. 1, 2, 4, and 5). This *nodular face* is smaller in diameter than the *smooth face*, and consequently there is an approximately conical surface, here called the *girdle*, which connects them (text-figs. 1, 2, 4, and 5). The size relationship between the smooth and nodular faces varies considerably, but typically it is about 2:1 in linear dimensions.



TEXT-FIG. 2 (left). Holotype of *Lenargyrion knappologicum* n. sp. SMNH No. X 1543. SEM photograph; $\times 250$

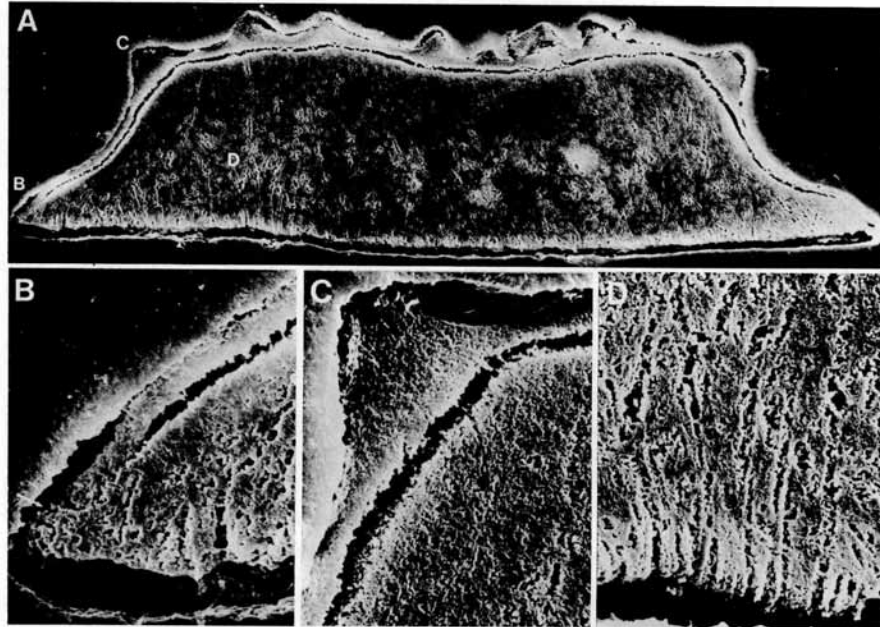
TEXT-FIG. 3 (right). Sclerite of *Lenargyrion knappologicum* n. sp. SMNH No. X 1544. SEM photograph, showing smooth face; $\times 300$.

The nodes have a diameter of about 10–15 μm and a density of about 50 per 0.01 mm^2 . The outermost ones are arranged in a ring, but this regular order decreases progressively towards the centre of the face. Exceptionally, a node may occur on the girdle outside the otherwise well-defined face (text-fig. 1J, upper left). Specimens may have some or all of the nodes effaced. In most cases, the missing nodes are represented by fracture surfaces, whereas neighbouring nodes are unaffected. This can be seen in text-fig. 1E and K. In a few cases, as represented by the specimen in text-fig. 1G, the whole nodular face is almost smooth, although the nodular pattern may still be faintly visible. Commonly, the sharp brim of a sclerite appears unaffected by any kind of abrasion, even when part or all of the nodes are thus missing.

The profile of the girdle is concave to straight, rarely convex. Commonly it has radiating patterns which are directly related to the outermost ring of nodes. This is very pronounced in text-fig. 1H, but can also be seen in text-figs. 1D, E, I–K, and 2. Also, a finer radiating pattern may be present (text-fig. 1F). The girdle ends in a circumferential demarcation line (e.g. text-fig. 1D–F) which is related to the internal structure (see below and text-figs. 4 and 5). The brim of the disc often bears fine transverse

striations (text-fig. 1D, E, F, H, I), and this surface sometimes passes directly into the smooth face, or sometimes meets further circumferential lines (e.g. text-fig. 1F).

The surface of the slightly convex smooth face is in fact somewhat rougher than that of the girdle and nodular face (cf. text-fig. 3 and text-figs. 1, 2), but bears no regular structures.



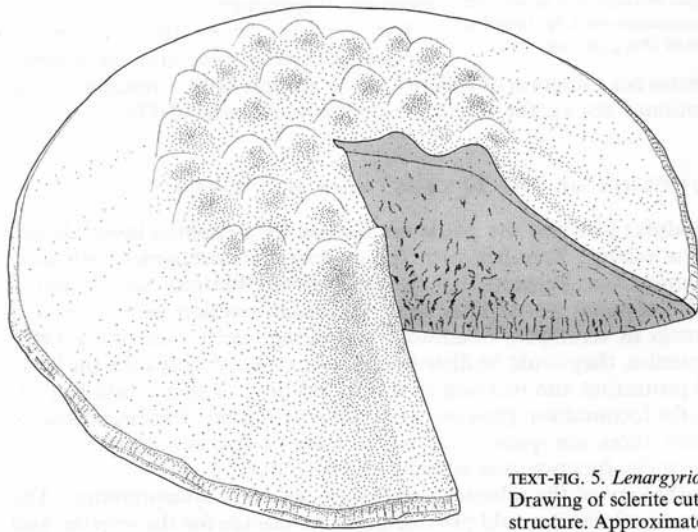
TEXT-FIG. 4. Polished and etched section through sclerite of *Lenargyrion knappologicum* n. sp. SMNH No. X 1545. A, over-all view of section, showing distinct histological differentiation into capping (top), forming nodular face and girdle, and core. Positions of B-D indicated; $\times 530$. B-D, details of A; $\times 2120$. Note external boundary between capping and core in B (white arrow).

Internal structure. Both in optical thin sections and in polished and etched sections studied by SEM microscopy, the discs are clearly seen to be built up of two components (text-fig. 4). The surfaces of the nodular face and girdle are formed by a continuous layer which is $2\ \mu\text{m}$ thick at the girdle and somewhat thicker at the nodular face. The nodes are formed entirely by this layer, which may reach a thickness of around $15\ \mu\text{m}$ at a node. This layer is here called the *capping*; it terminates just short of the brim of the disc, and the boundary can be seen externally as the demarcation line mentioned above (text-fig. 4B, arrow). The remainder of the disc is made up of a slightly more porous substance, here called the *core*. The porosity as observed has probably been exaggerated by the etching processes, but there can be no doubt that the core is less dense than the capping. The primary porosity is probably the main reason why *Lenargyrion* sclerites are easily corroded, even in weak acids.

The porosity is generally greater near the smooth face, although this too may be a result of the acid preparation, which is likely to have stronger effects where the substance is not protected by the capping. Very often, particularly near the smooth face, the porosity can be seen to consist of fine canals with a direction roughly parallel to the axis of the disc (text-fig. 4D). This may be compared to the striation of the brim (text-fig. 1F). In a few specimens there are suggestions of a layering close to and parallel to the smooth face. This may reflect the same structure as the external circumferential growth lines seen in some specimens (e.g. text-fig. 1F, bottom) outside the capping-core demarcation line.

The wide space between capping and core seen in text-fig. 4A-C seems to be an artefact due to shrinkage of the epoxy resin or to the etching being facilitated in the zone of contact between the two layers. It is less prominent on not so deeply etched specimens, and has not been observed in fresh fracture surfaces.

No discrete apatite crystallites have been identified with certainty, although the granulated pattern seen in the specimen in text-fig. 4 suggests more or less isodiametric crystallites with an approximate size of $0.2-0.3 \mu\text{m}$. As observed under a polarizing microscope, the crystallographic c axes in the core are generally aligned parallel to the axis of the disc and, in the peripheral parts, parallel to the surface of the girdle. This direction corresponds well to that of the canals in text-fig. 4, and the extinction between crossed nicols usually brings out a pattern which appears to conform to the direction of the canals. Often there is a layer of particularly strong extinction along the smooth face. The extinction in the capping is usually weak, but at least in one section the orientation of c axes has been observed to be perpendicular to the inner surface, both in the girdle and in the nodular face.



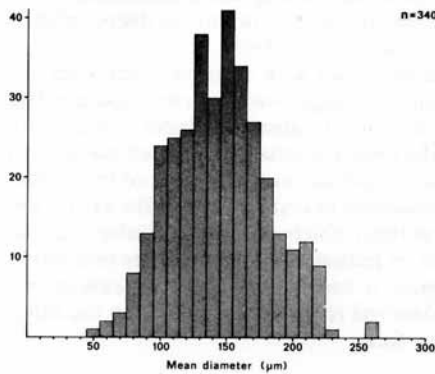
TEXT-FIG. 5. *Lenargyrion knappologicum* n. sp.
Drawing of sclerite cut open to show internal structure. Approximately $\times 500$.

Investigations with a microprobe revealed no difference in chemical composition between core and capping. Both have a composition corresponding to that of fluorite apatite.

When dissolved in acid such as HCl some, but not all, sclerites leave a shrivelled 'ghost' of presumably organic matter.

There is no internal evidence of periodic growth of the sclerites. Once the capping had been formed, they could not have grown at all unless the growth was coupled with periodical resorption of at least the capping.

Frequency. Text-fig. 6 is a size-frequency histogram for all specimens (340) found in the unsifted residue of 39.6 g of rock. The curve is unimodal and approaches normal



TEXT-FIG. 6. Size-frequency histogram of all sclerites (340) of *Lenargyrion knappologicum* n. sp. found in etching residue of 39.6 g of rock.

distribution. However, the etching of this sample also revealed that some *Lenargyrion* sclerites dissolve even in the 10% acetic acid used and, although factors other than size (e.g. degree of porosity) also appear to be important for the preservation, small specimens are generally more likely to have been destroyed than larger ones. Another factor, which might also have caused a loss of small specimens in this count, is that these were more likely to be overlooked among the bulk of remaining dolomite grains of approximately the same size. It is thus likely that a true size-frequency curve would include more small specimens.

Extrapolating from the number of specimens found in this count, the number of *Lenargyrion* sclerites per kilogram of rock would be around 8500. Considering the possible losses mentioned above, the true value probably exceeds 10 000.

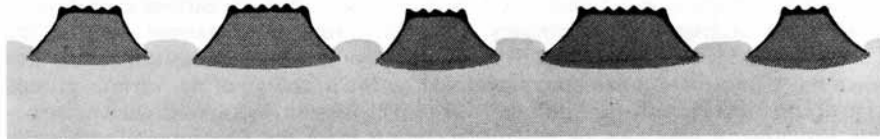
FUNCTION OF THE *LENARGYRION* SCLERITES

The fact that the nodular face and the girdle are formed by a capping layer, denser than the core of the sclerite, together with the evidence of mechanical abrasion restricted to the nodular face, suggests that the *Lenargyrion* 'buttons' were external dermal sclerites. The capping would thus serve the same function as enamel and enamel-like substances in vertebrate odontodes (= 'dermal teeth'; see Ørvig 1967, p. 47). As dermal sclerites, they could be distributed more or less evenly over the body surface for general protection and increase of surface friction, or they could be concentrated in organs for locomotion, grasping, or dealing with food. The circumstance that abraded nodular faces are quite common, in spite of the minute size of the sclerites, suggests that the function was not merely protective.

The general morphology of the sclerites agrees well with this interpretation. The broad base (i.e. the smooth face) would provide good anchorage for the sclerite, and

the nodes would serve to increase the friction. The fact that the thickness is roughly equal (c. 65–85 μm) in sclerites of all sizes except those smaller than 100 μm in diameter would reflect the demand that the nodular faces of neighbouring sclerites be in the same plane. This would also mean that the sclerites were situated fairly close to each other, although the regular curve of the brim shows that they were not in contact.

Text-fig. 7 shows a reconstruction of the outer part of the body wall of *Lenargyrion*, based on the above interpretation, with the sclerites shown in their assumed functional position. The picture gives no indication as to whether they were also formed in this position, or within or below the epithelial tissue. However, the fact that there is no evidence of successive growth of sclerites, in spite of the large variation (almost by a factor of ten) in their individual diameters, indicates that they were unable to grow once they had assumed their shape and functional position. If the animal increased its skeletal mass during growth, it probably did so by adding new sclerites rather than increasing the size of the old ones. Whether the latter were retained, resorbed, or shed is not possible to determine. This inability of the sclerites to grow suggests that they were not formed in the position shown in text-fig. 7, but rather were secreted by tissue below the body surface, through which they afterwards erupted. However, the evidence for this is not conclusive.



TEXT-FIG. 7. Hypothetical reconstruction of outer part of body wall of *Lenargyrion knappologicum* n. sp., showing inferred position of sclerites (capping black, core dark grey) relative to soft tissue (light grey). Approximately $\times 130$.

One possible alternative interpretation is that the sclerites were opercula of tube-dwelling animals. This view stems from the fact that the conical shape of the girdle would make them fit snugly (smooth face outwards) against the aperture of such a tube, as well as from the presence of phosphatic tubes (although very rare compared to the 'buttons') with comparable diameter in the same sample. The lack of growth structures could be explained by the assumption that the animal continually shed its opercula during growth, and the presence of a capping layer could represent a modification of the surface of attachment with the secreting epithelium. However, the evidence for selective abrasion of the nodular face would remain unexplained by this model, and for this reason it is considered less probable.

AFFINITIES OF *LENARGYRION*

Very little can be said about the *Lenargyrion* animal itself, except that it was probably equipped with dermal sclerites, in general structure superficially similar to odontodes of, e.g. thelodonts or sharks. It is tempting to take this general similarity as an indication of deeper homology, since an apatitic sclerite consisting of a porous core

with fine canals and a capping of denser material would agree quite well with a simple unit of the dermal skeleton that might be expected to occur in the earliest vertebrates of the hypothetical primary micromeric stage of skeletal development (Ørvig 1968, p. 381), i.e. the initial stage in which the dermal skeleton supposedly consisted of isolated, minute scales. However, *Lenargyrion* sclerites show no conclusive vertebrate characteristics such as cavities after odontoblast processes (dentinal tubules) or osteoblasts, and the rare examples of acellular bone tissue in vertebrates (e.g. aspidin in heterostracans) seem to offer no striking points of comparison. Consequently, any such suggestion of homology between skeletal tissues of *Lenargyrion* and vertebrates is highly speculative.

The question of affinities of *Lenargyrion* is thus better left open at present. Whereas the sclerites appear to show some agreement with the structure and function of a primitive vertebrate dermal skeleton, the evidence for vertebrate affinity is far from convincing, and there remains a strong possibility that these Cambrian sclerites originated in an unknown group of invertebrates, unrelated to the vertebrate stock. The earliest presumed vertebrate of which there is a published record, *Anatolepis*, is of Arenigian age and carried a continuous, very thin armour, set with minute elliptical to rhomboidal plates (Bockelie and Fortey 1976). In addition, Winder (1976) gives a reference to an unpublished record (by N. E. Cygan 1962) of presumed fish remains in the Upper Cambrian. It is not unlikely that the earliest evolution of mineralized skeletons in vertebrates occurred during a substantial part of the Cambrian, and it may be possible to arrive at a conception of Cambrian vertebrates when more information has been assembled on the histology of the various groups of problematical phosphatic fossils that occur in Cambrian rocks. With such information available, it may also be possible to find a place for *Lenargyrion* within the zoological system.

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Note added in proof. In a recent report on Cambrian to Triassic conodont stratigraphy of the Taurus Range in Turkey, Gedik (1977) briefly described and illustrated fossils similar to *Lenargyrion knappologicum*. They were referred to the new genus and species *Hadimopanella oezgueli*. Judging from Gedik's illustrations, *H. oezgueli* differs from *L. knappologicum* in that the capping terminates shortly outside the nodular face, so that most of the width of the girdle shows the exposed surface of the core. Also, the nodes are coarser (about 20 μm in diameter as compared to 10–15 μm in *L. knappologicum*) and their density is correspondingly smaller (about 15 per 0.01 mm^2 as compared to about 50 per 0.01 mm^2 in *L. knappologicum*). Thus the two species are clearly distinguished from each other; whether or not the generic name *Lenargyrion* should be considered a junior subjective synonym of *Hadimopanella* is better judged when more forms of this little-known group have been described.

Gedik's material comes from reddish nodular limestones stated to belong to the Upper Cambrian. However, the additional fossils he reported from these beds, *Prooneotodus tenuis* (Müller) and *Hertzina? bisulcata* Müller, do not prove a late Cambrian age. Both species are known from the Middle Cambrian as well, and this is true also for the third conodont-like form, *Furnishina furnishi* Müller, which Gedik (1977, p. 36) reported from approximately equivalent beds in the same area.

REFERENCES

- BERGSTRÖM, J. 1973. Classification of olenellid trilobites and some Balto-Scandian species. *Norsk geol. Tidsskr.* **53**, 283-314.
- BOCKELIE, T. and FORTEY, R. A. 1976. An early Ordovician vertebrate. *Nature*, **260** (5546), 36-38.
- COBBOLD, E. S. 1921. The Cambrian horizons of Comley (Shropshire) and their Brachiopoda, Pteropoda, Gasteropoda, etc. *Q. Jl geol. Soc. Lond.* **76**, 325-386.
- GEDİK, I. 1977. Orta Toroslar'da konodont biyostratigrafisi. [Conodont biostratigraphy of the Middle Taurus.] *Türk. Jeol. Kurumu Bil.* **20**, 35-48. [In Turkish, with an English summary.]
- KELLER, B. M. et al. 1973. Putevoditel' ehkskursii po rekam Aldanu i Lene. *Mezhdunarodnaya ehkskursiya po probleme granitsy kembriya i dokembriya*. [Excursion guide to the Aldan and Lena Rivers. International excursion on the problem of the Precambrian-Cambrian boundary.] 118 pp. Moscow, Yakutsk. [In Russian and English.]
- MATTHEWS, S. C. 1973. Lapworthellids from the Lower Cambrian *Strenuella* limestone at Comley, Shropshire. *Palaeontology*, **16**, 139-148.
- and MISSARZHEVSKY, V. V. 1975. Small shelly fossils of late Precambrian and early Cambrian age: a review of recent work. *Jl geol. Soc. Lond.* **131**, 289-304.
- MESHKOVA, N. P. 1969. K voprosu o paleontologicheskoy kharakteristike nizhne-kembrijskikh otlozhenij Sibirskoj platformy. [To the question of the palaeontological characteristics of the Lower Cambrian deposits of the Siberian Platform.] In ZHURAVLEVA, I. T. (ed.). *Biostratigrafiya i paleontologiya nizhnego kembriya Sibiri i Dal'nego vostoka*, 158-174. Izd. 'Nauka', Moscow. [In Russian.]
- 1974. Cambroscleritida incertae sedis—novyj otryad kembrijskikh iskopaemykh. [Cambroscleritida incertae sedis—a new order of Cambrian fossils.] In ZHURAVLEVA, I. T. and ROZANOV, A. YU. (eds.). *Biostratigrafiya i paleontologiya nizhnego kembriya Evropy i severnoj Azii*, 190-193. Izd. 'Nauka', Moscow. [In Russian.]
- MISSARZHEVSKY, V. V. 1966. Pervye nakhodki *Lapworthella* v nizhnem kembrii Sibirskoj platformy. [The first finds of *Lapworthella* in the Lower Cambrian of the Siberian Platform.] *Paleont. Zh.* **1966** (2), 13-18. [In Russian.]
- 1973. Konodontoobraznye organizmy iz pogranychnykh sloev kembriya i dokembriya Sibirskoj platformy i Kazakhstana. [Conodont-shaped organisms from the Precambrian-Cambrian boundary strata of the Siberian Platform and Kazakhstan.] In ZHURAVLEVA, I. T. (ed.). *Problemy paleologii i biostratigrafii nizhnego kembriya Sibiri i Dal'nego vostoka*, 53-57. Izd. 'Nauka', Moscow. [In Russian.]
- 1974. Novye dannye o drevnejshikh okamenelostyakh rannego kembriya Sibirskoj platformy. [New data on the oldest Cambrian fossils of the Siberian platform.] In ZHURAVLEVA, I. T. and ROZANOV, A. YU. (eds.). *Biostratigrafiya i paleontologiya nizhnego kembriya Evropy i severnoj Azii*, 179-189. Izd. 'Nauka', Moscow. [In Russian.]
- ØRVIG, T. 1967. Phylogeny of tooth tissues: evolution of some calcified tissues in early vertebrates. In MILES, A. E. W. (ed.). *Structural and Chemical Organization of Teeth*, **1**, 45-110. Academic Press, New York.
- 1968. The dermal skeleton; general considerations. In ØRVIG, T. (ed.). *Current Problems of Lower Vertebrate Phylogeny*, 373-397. Almqvist & Wiksell, Stockholm.
- REPINA, L. N. et al. 1974. *Biostratigrafiya i fauna nizhnego kembriya Kharaulakha (khr. Tuora-Sis)*. 299 pp. Izd. 'Nauka', Moskva. [In Russian.]
- ROZANOV, A. YU. 1973. Zakonomernosti morfologicheskoy ehvolyutsii arkehotsiat i voprosy yarusnogo raschleneniya nizhnego kembriya. [Regularities in the morphological evolution of archaeocyathans and questions regarding the stage division of the Lower Cambrian.] *Trudy geol. Inst. Akad. Nauk SSSR*, **241**, 164 pp. [In Russian.]

- ROZANOV, A. YU. and MISSARZHEVSKY, V. V. 1966. Biostratigrafiya i fauna nizhnikh gorizontov kembriya. [Biostratigraphy and fauna of the lower beds of the Cambrian.] *Trudy geol. Inst. Acad. Nauk SSSR*, **148**, 126 pp. [In Russian.]
- *et al.* 1969. Tommotskij yarus i problema nizhnej granitsy kembriya. [The Tommotian Stage and the problem of the Cambrian lower boundary.] *Ibid.* **206**, 380 pp. [In Russian.]
- RUSHTON, A. W. A. 1974. The Cambrian of Wales and England. In HOLLAND, C. H. (ed.). *Cambrian of the British Isles, Norden, and Spitsbergen*, 43-121. John Wiley & Sons, London, New York, Sydney, Toronto.
- WIMAN, C. 1903. Studien über das Nordbaltische Silurgebiet. I. Olenellussandstein, Obolussandstein und Ceratopygeschiefer. *Bull. geol. Instn Univ. Upps.* **6**, 12-76.
- WINDER, C. G. 1976. Enigmatic objects in North American Ordovician carbonates. In BASSETT, M. G. (ed.). *The Ordovician System: proceedings of a Palaeontological Association symposium, Birmingham, September 1974*, 645-657. University of Wales Press and National Museum of Wales, Cardiff.
- ZHURAVLEVA, I. T., MESHKOVA, N. P. and LUCHININA, V. A. 1969. *Geologicheskij profil' cherez rajon stratotipicheskogo razreza nizhnego kembriya v srednem techenii r. Lena.* [A geological profile through the region of the Lower Cambrian stratotypical section in the middle reaches of the River Lena.] 176 pp. Izd. 'Nauka', Novosibirsk. [In Russian.]

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