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THE LOWER CARBONIFEROUS BRACHIOPOD GENUS
LEVITUSIA MUIR-WOOD, H. M. AND COOPER, G. A., 1960
FROM WESTERN EUROPE AND THE U. S. S. R.

BY

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(With five plates following the text)

ABSTRACT

The genus *Levitusia* MUIR-WOOD, H. M. and COOPER, G. A., 1960 is revised and details of the shell microstructure are presented enabling the shell material of Productacea and Chonetacea to be distinguished. The western European species *L. humerosa* (SOWERBY, J., 1822), the type species (with which *L. christiani* (DE KONINCK, L., 1847) is placed into synonymy), *L. sublaevis* (DE KONINCK, L., 1843) and *L. spinauris* n. sp. from Staffordshire, England, are described. Species from the U. S. S. R. are discussed, in particular *L. hyperborea* from the Urals.

RESUME

L'auteur révisé le genre *Levitusia* MUIR-WOOD, H. M. et COOPER, G. A., 1960; il donne notamment des indications sur la structure du test permettant de le distinguer de fragments de coquilles d'autres genres de Productacea et de Chonetacea. Les trois espèces suivantes de l'Europe occidentale sont revues : *L. humerosa* (SOWERBY, J., 1822), l'espèce-type, dans la synonymie de laquelle est mise *L. christiani* (DE KONINCK, L.,

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1847), *L. sublaevis* (DE KONINCK, L., 1843), *L. spinauris* n. sp. du Staffordshire, en Angleterre. Une attention particulière est accordée à *L. hyperborea* de l'Oural.

ACKNOWLEDGMENTS

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In the Dinantian limestones of Belgium the brachiopod genera *Levitusia* MUIR-WOOD, H. M. and COOPER, G. A., 1960, and *Megachonetes* SOKOLSKAJA, A. N., 1950, form important and characteristic stratigraphical marker horizons, but in fragmentary form they are not always easy to distinguish from genera like *Daviesiella* WAAGEN, W., 1884, or *Gigantoproductus* PRENTICE, J. E., 1950. G. DELÉPINE (1926) demonstrated the oblique shell fabric seen in *Daviesiella* as compared to the fabric in *Levitusia* with the crystals perpendicular to the valve surfaces. My own interest in brachiopod shell structures, especially those of chonetaceans (1972) and productaceans, stimulated the present revision of *Levitusia*, the study of its shell structure and that of similarly thick-shelled genera found in the Viséan of Belgium and Britain. A more complete report presenting the results of shell structural studies of several such genera is in preparation.

The restricted stratigraphical range of *Levitusia* species has long been recognised; K. I. LISSITZIN (1912, p. 191) mentions the importance of *Productus sublaevis* DE KONINCK, L., 1843, as an indicator of the *Caninia* Zone (C₂) in Britain. Recently W. H. C. RAMSBOTTOM (1973) lists *Levitusia humerosa* (SOWERBY, J., 1822) as a guide fossil for his second major cycle (= C₁ and lower C₂ Zones or V1a of the Belgian scheme).

During the last century the three main species names associated now within the genus *Levitusia* have been placed in synonymy with each other in a variety of combinations. This taxonomic study attempts to distinguish the species more clearly by suggesting more valid morphological

characteristics and places into synonymy with *L. humerosa*, the type species, not *L. sublaevis*, as suggested by H. M. MUIR-WOOD and G. A. COOPER (1960), but *L. christiani* (DE KONINCK, L., 1847).

I. — REDESCRIPTION OF THE GENUS

LEVITUSIA MUIR-WOOD, H. M. and COOPER, G. A., 1960

TYPE SPECIES

Productus humerosus SOWERBY, J., 1822, by original designation of H. M. MUIR-WOOD and G. A. COOPER (1960, p. 295).

SPECIES ASSIGNED TO GENUS

In addition to the type species *Levitusia* includes *L. donica* (ROTAI, A., 1931), *L. cracoviensis* (JAROSZ, J., 1917), *L. hyperborea* (NALIVKIN, D. V., ms. in ROTA, A., 1941), *L. spinauris* n. sp. and *L. sublaevis* (DE KONINCK, L., 1843).

DIAGNOSIS

Medium to large strongly concavo-convex posteriorly thickened shells with variably developed posterior rugae. Exteriors smooth or with fine radial ribbing. Major spines on ventral valve only, in rows from umbo antero-laterally in front of prominent ears and, in some, along mid-line. Ventral valve interior with deeply impressed diductor scars and conical 'brachial' cavities. Trails long and endospinous. The shell substance is laminose, pseudopunctate and, where thickened, columnar.

DESCRIPTION WITH SPECIAL EMPHASIS ON THE SHELL STRUCTURE

Medium to large strongly concavo-convex shells, widest posteriorly at their prominent ears, commonly greater than 50 mm wide. Adult trails are long, both valve fitting closely with long internal endospines especially strongly developed on the dorsal valve. Posteriorly the visceral area is irregularly rugose, but otherwise ornamentation is confined to growth lines, commonly prominent anteriorly. On the type species there is a fine radial ribbing. Major spines are characteristically confined to single or double rows from the umbo along the anterior margins of the ears and with or without a single median row situated along a gentle median ridge within a shallow depression. Some have small ventral visceral spines.

Internally the body cavity is reduced in size by considerable ventral valve shell thickening and elevated dorsal valve muscle platforms. The

ventral valve interior is especially characteristic, being known principally from internal casts, with deeply impressed diductor muscle scars and a pair of posteriorly directed conical cavities interpreted as having been filled, in life, by lophophore cones. The dorsal valve has a large, squat trifold cardinal process with deeply incised diductor myophores. The adductor muscle scars are elevated and from their anterior margins oval brachial ridges extend forwards to positions almost level with the front of the anteriorly narrow median septum.

SHELL STRUCTURE

It is commonly difficult to distinguish fragments of shell of large productacean genera, like *Levitusia*, from the large chonetacean genera, especially *Daviesiella*. G. DELÉPINE (1926, p. 379) discussed this problem very usefully in his paper on «*Productus sublaevis*». It was here that he provided drawings of sections through the shell of *Levitusia sublaevis* and *Daviesiella llangollensis* and demonstrated that the two species could be distinguished by their shell structures; that of *Levitusia sublaevis* being made of calcite prisms perpendicular to the shell surface, while that of *Daviesiella llangollensis* is formed of lamellae imbricated subparallel and at an oblique angle to the shell surface. G. DELÉPINE (1928, pl. 5, fig. 60, 61) published photographs of shell sections, at double the original size, of *D. llangollensis* and *Gigantoproductus giganteus* showing the same basic structures.

Since little attention has been paid to these important observations of G. DELÉPINE by authors of shell structural studies in the English language the subject is being fully investigated and reported elsewhere. Preliminary results of optical and scanning electron-microscope studies of shell from *Levitusia*, *Gigantoproductus*, *Daviesiella* and *Megachonetes* species support G. DELÉPINE's observations. In addition the following six general points can be made : the outer structural layer of shell material in chonetaceans and productaceans is finely laminar and within this the external morphological features such as growth lines and radial ribbing are normally developed; in relatively thin-shelled species a strongly cross-bladed laminar shell structure normally persists through to the inner surface; in heavily thickened productacean shells, like *Levitusia*, an abrupt change takes place from the outer lamellose shell to what appears, at low power magnification, to be columnar prisms approximately perpendicular to the outer valve surface. At magnifications of about 50 or more it can be seen that these prisms are formed by blocks of calcite laths, sometimes widening to curving sheets, which are somewhat fan-like in form, overgrowing adjacent laths in a spherulitic fashion. The junctions between these blocks of prisms form a microtopography of buttresses and gullies which look columnar at small magnifications; the shell of large chonetacean genera like *Megachonetes* and *Daviesiella*

(Pl. V, fig. 1, 2) normally retains its lath-like nature (C. H. C. BRUNTON, 1972) throughout the valve thickness and this structure is seen in radial sections at low magnifications as laminae dipping forward from the external surface, as indicated by G. DELÉPINE (1926); pseudopunctuation is smothered in the thick-shelled regions of *Levitusia* by the 'columnar' inner layers, but, as in chonetaceans, pseudopunctuation persists throughout the laminar thin-shelled regions and are especially strongly developed in the trail regions. Pseudopunctuation in *Gigantoproductus* (Pl. V, fig. 3-6) appears, on first evidence, to remain more persistent than in *Levitusia*, even in regions of heavily thickened shell; pseudopunctuation in the chonetacean *Daviesiella* is frequent in the laminar outer layers, especially between the ribs, and some pseudopunctae persist throughout the areas of considerable shell thickening at an angle to the shell layers. *Megachonetes* never developed such thick shell as in the above genera and many of its pseudopunctae persist throughout the shell to the inner surfaces.

DISCUSSION

In the classification of the Productidina by H. M. MUIR-WOOD (1965), *Levitusia* is the sole genus in the Levitusiinae and *Horridonia* CHAO, Y. T., 1927, the only genus assigned to the Horridoniinae. Both these subfamilies are placed in the Dictyoclostidae. This situation is somewhat unsatisfactory since by the definitions provided the two subfamilies fail to comply with one or other of the familial characteristics published. I think it is correct to group *Levitusia* and *Horridonia*, with dictyoclostids, but this being so the dictyoclostid group, currently at family level, should be recharacterised. « Brachial ridges given off horizontally » (H. M. MUIR-WOOD, 1965, p. H493) should be a characteristic of the Dictyoclostinae, not one of the whole family. A common characteristic of members of the Dictyoclostidae is that species have spines grouped or in rows from the umbo on or close to the ears. The disposition of other spines on the valves is very variable. I. M. GARAN (1975) discussed *Levitusia* and placed it, together with *Mesoplica* REED, F. R. C., 1943, *Plicatifera* CHAO, Y. T., 1927, and ? *Acanthoplecta* MUIR-WOOD, H. M. and COOPER, G. A., 1960, in the family Levitusiidae. This grouping is virtually that suggested by G. DELÉPINE (1926) for the type species of these genera, and has much to commend it morphologically. However, at present I remain unsure as to whether the morphological similarities outweigh the value of retaining a dictyoclostid grouping for these genera.

In proposing the genus *Levitusia* H. M. MUIR-WOOD and G. A. COOPER designated *Productus humerosus* SOWERBY, J., 1822, as type species and placed *P. sublaevis* DE KONINCK, L., 1843, into synonymy. The only other species assigned to the genus was *P. christiani* DE KONINCK, L., 1847a. Because of its date priorly the name *P. humerosus* has normally been quoted as a distinct species by T. DAVIDSON (1861, 1880); J. W. JACKSON

(1919), G. DELÉPINE (1926) and H. M. MUIR-WOOD and G. A. COOPER, (1960), but the relationships between *P. humerosus*, *P. sublaevis* and *P. christiani* have varied. The most usually held view is that of T. DAVIDSON (1880, p. 306) who, having seen material from Caldon Low (1) Staffordshire, collected by Mr. James ECCLES in 1870, suggested that the characteristic internal moulds from Breedon, Leicestershire, named as *P. humerosus*, belonged to the same species as the specimens from Belgium called *P. sublaevis*. J. W. JACKSON (1919, p. 508), despite his placing of *P. sublaevis* into synonymy with *P. humerosus* and his treatment of L. DE KONINCK's species as 'varietal forms', pointed out that the *P. humerosus* specimens from Breedon were possibly referable to the group of specimens he termed *P. christiani*. Then G. DELÉPINE (1926, p. 380) upheld J. W. JACKSON's view by suggesting that the J. SOWERBY internal moulds of *P. humerosus* related more closely to *P. christiani* s.s. than to *P. sublaevis*. At the same time G. DELÉPINE maintained that these 'forms', together with *P. plicatilis* SOWERBY, J. DE C., 1824, and *P. mesolobus* PHILLIPS, J., 1836, united into a distinctive group of varieties. It was in the same paper that G. DELÉPINE (1926, p. 376) illustrated sections through the shells of *P. sublaevis* and *Daviesiella llangollensis* (DAVIDSON, T., 1863) which showed important shell structural differences: that of *Productus sublaevis* had a prismatic fabric with calcite crystals perpendicular to the valve surfaces while the fabric in *Daviesiella llangollensis* was of obliquely arranged crystals. These differences are more fully discussed in the section on shell structure.

W. PAECKELMANN (1931, p. 120) considered *Productus sublaevis* as synonymous with *P. humerosus* and that *P. christiani* was a variety of this species. He placed *P. humerosus* into the genus *Plicatifera*, following the relationship proposed by G. DELÉPINE (1926) and hinted at by T. DAVIDSON (1861, p. 139). In addition to the 'variety' *christiani* DE KONINCK, L., W. PAECKELMAN described two new varieties of *Productus humerosus*, namely var. *longa* and var. *plicata*.

In addition to the above mentioned taxa associated with the name *P. humerosus*, there is a new form, recognised herein, which seems to occur rarely at Caldon Low. It is a *P. sublaevis*-like shell characterised by having spines only in groups on the ears; it is more fully described below (p. 14). From the Urals another *Levitusia* species is known, *L. hyperborea*. This species is characteristic of the Upper Tournaisian, Upper Kizelov stage, of the western side of the central Urals and is recorded from Vaygach island by T. A. DEDOK (1960, p. 12). Like the western European species, *Productus hyperboreus* passed through a period of being classified as a *Plicatifera* species by A. ROTA (1941) and T. A. DE-

(1) The name Caldon Low is commonly misspelt as Cauldon Low since immediately north of the area of quarries known as Caldon Low is situated the village of Cauldon. Furthermore to the south lies the hamlet named Cauldon Lowe. These are the spellings as used on the First Series, 1:50,000 Ordnance Survey sheet number 119, and Caldon Low was the spelling used by T. DAVIDSON in his original manuscript notes.

DOK (1960). In the same year H. M. MUIR-WOOD and G. A. COOPER (1960) included *Productus hyperboreus* within their illustrations of *Acanthoplecta*, but failed to mention the species in the text description of that genus. This generic position was followed by D. V. NALIVKIN and N. N. FOTIEVA (1973) but I. M. GARAN (1975) assigned the species to *Levitusia*. I believe it is more akin to *Levitusia* than to *Acanthoplecta*, but *Levitusia hyperborea* probably represents an early evolutionary form within the genus and it may have evolved from a *Mesoplecta* or *Acanthoplecta*-like ancestor.

My own study of Belgian and British material, including the type specimens of all three principal species, leads to the conclusion that *Levitusia humerosa* is a senior synonym of *L. christiani* and that *L. sub-laevis* is a valid distinctive species.

II. — REDESCRIPTION OF THE SPECIES *LEVITUSIA HUMEROSA* (SOWERBY, J., 1822)

(Plate I, Figures 1-6; Plate II, Figures 1-5; Plate IV, Figures 1-4)

SYNONYMY (2)

- v* 1822 — *Productus humerosus* — J. SOWERBY, p. 21, fig. 322;
- v* 1847a — *Productus christiani* — L. DE KONINCK, pp. 274-276, pl. XVII, fig. 3a-e;
- v* 1847b — *Productus christiani* — L. DE KONINCK, pp. 166-167, pl. XVII, fig. 3a-e (= Pl. XVII, fig. 3a-e in L. DE KONINCK, 1847a);
- p v 1861 — *Productus humerosus*, SOW. — T. DAVIDSON, p. 147, pl. XXXVI, fig. 1, 1a, b, 2, 2a;
- p v 1861 — *Productus sub-laevis* DE KONINCK - T. DAVIDSON, p. 177, pl. XXXI, fig. 1, 1a, b, pl. XXXII, fig. 1, 1a, b (= Pl. XVII, fig. 3c-e in L. DE KONINCK, 1847a);
- 1863 — *Productus sub-laevis* — T. DAVIDSON, p. 234, pl. LI, fig. 1, 2, *cet. excl.*;
- v 1880 — *Productus humerosus*, SOW. — T. DAVIDSON, p. 306, pl. XXXVI, fig. 2;
- 1926 — *Productus christiani* DE KONINCK — G. DELÉPINE, pp. 374-375, pl. B, fig. 10, 11a, b, 12-14;
- p 1931 — *Productus (Plicatifera) humerosus* SOWERBY — W. PAECKELMANN, pp. 120-128, pl. 8, fig. 2 ?, 3, *cet. excl.*;

(2) The symbol v before the date indicates that the specimens have been checked; an * indicates that the species descriptions are regarded here as being valid; p indicates that the reference applies only in part to this species (see S. C. MATTHEWS, 1973).

- 1931 — *Productus (Plicatifea) humerosus* SOW., var. nov. *longa*. — W. PAECKELMANN, pp. 128-129, pl. 9, fig. 1a-d;
- 1931 — *Productus (Plicatifea) humerosus* SOW. var. *christiani* DE KONINCK — W. PAECKELMANN, pp. 131-133, pl. 10, fig. 1a-c, ? pl. 12, fig. 4a-c, pl. 13, fig. 1a-c;
- p 1960 — *Levitusia humerosa* (J. DE C. SOWERBY) — H. M. MUIR-WOOD and G. A. COOPER, p. 295, pl. 109, fig. 4, 5, pl. 110, fig. 3-5, *cet. excl.*;
- 1973 — *Levitusia humerosa* (J. SOWERBY, 1822) — N. N. FOTIEVA in D. V. NALIVKIN and N. N. FOTIEVA, pp. 43-44, pl. IX, fig. 4a, b, 5;
- 1973 — *Levitusia christiani uralica* FOTIEVA, subsp. nov. — N. N. FOTIEVA, in D. V. NALIVKIN and N. N. FOTIEVA, p. 44, pl. X, fig. 1a, b, 2a, b.

TYPE AND FIGURED SPECIMENS

Holotype. — BM (NH) B60959 (Pl. I, fig. 2, 3). The Holotype is that specimen figured by J. SOWERBY (1822, p. 21, fig. 322), previously figured but unnamed in his 'British Mineralogy' (1809, fig. 217), from Breedon, Leicestershire.

Syntypes. — MNHN 1942-1, 276 (Pl. I, fig. 6 = Pl. XXXII, fig. 1b in T. DAVIDSON, 1861), UPS D812 (Pl. II, fig. 1-4 = Pl. XXXII, fig. 1, in T. DAVIDSON, 1861) of *Productus christiani* are two original specimens figured by L. DE KONINCK (1847a, Pl. XVII, fig. 3a-e; 1847b, Pl. XVII, fig. 3a-e). One, in the Paris « Muséum National d'Histoire Naturelle », registered as 1942-1, 276, is principally an external mould of the dorsal valve on which a few shelly fragments remain and was illustrated on plate XVII, figures 3d, e. The second specimen is in the E. DE VERNEUIL collection at the « Université de Paris-Sud », Orsay, registered as D812, and was figured by L. DE KONINCK on plate XVII, figures 3a-c. This is an almost complete ventral valve exterior, well preserved and is here selected as Lectotype; a replica is housed in the British Museum (Nat. Hist.), BB. 61636. The type locality of this specimen is in question since L. DE KONINCK (1847b, p. 167) states England, while the board with the specimen mentions Wales. The lithology and appearance of the specimen are, however, very similar to those of specimens from Caldron Low, Staffordshire.

Figured specimen. — BM (NH) 97699 (Pl. I, fig. 1 = Pl. XXXI, fig. 1a in T. DAVIDSON, 1861, under the name *Productus sublaevis*, DE KONINCK) in T. DAVIDSON's Collection, from the Carboniferous Limestone near Leek, north Staffordshire (T. DAVIDSON's plate explanation suggesting that the specimen probably came from Clitheroe, Lancashire, is an error); BM (NH) B55766 (Pl. I, fig. 4), internal cast

from the Breedon dolomites, Leicestershire; BM (NH) BB13612, BB13613 (Pl. I, fig. 4, 5 = Pl. 110, fig. 4, 5 in H. M. MUIR-WOOD and G. A. COOPER, 1960), the Carboniferous Limestone of Caldon Low, Staffordshire; BM (NH) BB61648 (Pl. IV, fig. 1-4), collected by Mr. C. CHAMPION from Low Viséan limestones of Caldon Low, Staffordshire; Manchester Museum L3614 (Pl. II, fig. 5). Labelled by J. W. JACKSON « *Levitusia* cf. *christiani* ». From Caldon Low, Staffordshire.

Replicas of all complete figured specimens are in the collections of the « Institut royal des Sciences naturelles de Belgique » under the number I. G. 26056.

MATERIAL

Other specimens studied, but not figured herein, include : three specimens from Visé, Belgium, from the DE RYCKHOLT Collection, I. G. 3440a-c; several specimens from Caldon Low, Staffordshire, three from the Manchester Museum L 4953A, L 11532, L 11533, and several incomplete specimens from the Mr. C. CHAMPION Collection.

TYPE LOCALITY AND AGE

J. SOWERBY (1822, p. 21) noted that his figured specimen came from « Breden, near Derby, by favour of the lamented S. Tennant, Esq. ... as an example of Magnesian Limestone ». According to G. H. MITCHELL and C. J. STUBBLEFIELD (1941) the Breedon, Leicestershire locality is likely to have been Breedon Hill rather than Breedon Cloud. The age of these dolomitic limestones is upper C₁ to lower C₂ Zones of the lower Viséan.

DIAGNOSIS

Large, broad *Levitusia* commonly with slight ventral median ridge, within median depression, bearing single row of spines. Flanking spines in single to double row at 55° to 60° from mid-line, just anterior of ears. Delicate radial ribbing of 4 to 5 per one mm width; strongly developed endospines on trails and deep brachial cavities in adult ventral valves.

DESCRIPTION

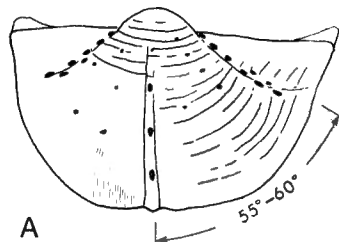
T. DAVIDSON (1861) gives quite a full description of the species in its original form of internal casts. He gave no description of exteriors since he treated *Productus sublaevis* and *P. christiani* as synonymous with each other, but distinct from *P. humerosus*. T. DAVIDSON (1880) placed *P. sublaevis* in synonymy with *P. humerosus*, having studied specimens described and lent to him by J. ECCLES (1870) and collected from Caldon Low,

Staffordshire, but he provided no additional description. Internal casts of *Levitusia humerosa* commonly display only the ventral valve surface, but when the impression of the dorsal valve is also preserved it can be seen that the cavities of the posterior visceral region and 'cone' regions of the brachial cavity were deep, even when the shell was closed. The impressions of endospines, at the start of the trails, are usually visible and their V-shaped arrangement on the ventral valve can be seen on the Holotype (Pl. I, fig. 2 = middle illustration pl. 322 in J. SOWERBY, 1822). The rare casts of dorsal surfaces show the impressions of a large, squat, strongly lobate cardinal process, and a pair of anteriorly elevated and divided adductor muscle scars from between the anterior ends of which a narrow, low median septum reaches anteriorly across the relatively flat visceral area to the start of the endospinous region. In the past the hinge-line has been described as narrow because shell thickening in the ventral valve had reduced the visceral cavity to such an extent that little or no internal cast space remained lateral to the ventral diductor muscle scars. Complete shell specimens, originally called *Productus christiani*, have been described by L. DE KONINCK (1847a, b), G. DELÉPINE (1926) and, in part, by H. M. MUIR-WOOD and G. A. COOPER (1960) when they described *Levitusia* for the first time. Such specimens display the full width of the wide hinge line.

The posterior rugation is distinctive, although not always regularly or consistently developed. There may be up to twenty of these ridges. The fine radial ribbing is relatively evenly distributed over the valve surfaces with a mean value of 4 to 5 per one mm width of shell. However, posteriorly and in the mid-valve region the ribbing may reach 6 per one mm (Text-figure). This ribbing is present on the two dorsal interiors figured by H. M. MUIR-WOOD and G. A. COOPER (1960, Pl. 110, fig. 5). Fine growth lines intersect the ribbing and may be prominent anteriorly where they are commonly deflected ventrally in the position of the shallow median sulcus. Both the median sulcus and low spinose ridge, commonly present within it, vary in their degree of development. The spine bases along the mid line occur at intervals of from 7 to 10 mm on the ridge. In addition the normal *Levitusia* umbonal and ear spines occur at widening intervals from the umbo at 55° to 60° from the mid-line.

Diagrams showing the principal exterior diagnostic features of *Levitusia humerosa* (SOWERBY, J., 1822) (A), *L. spinauris* n.sp. (B), *L. sublaevis* (DE KONINCK, L.G., 1843) (C). In addition to outlines, the typical dispositions of spines, rugae and radial ribbing are depicted. Additional notes on the external ornamentation of these three species are provided. The rib counts have been taken from several places on the same specimen as well as from different specimens: Of the twenty four rib counts made in which there are four ribs per one mm width on *L. humerosa*, eight were within 10 mm of the mid-line and sixteen from the more lateral areas on the shell. Similarly of these twenty-four counts three came from the posterior visceral area while twenty one came from the more anterior and trail regions. In general the rib counts display a slight increase in the number of ribs per one mm width of shell medianly and posteriorly on both species having ribs.

EXTERNAL ORNAMENTATION

L. humerosa

A

Spines

Single to double row of umbonal-flanking spines at anterior margin of ears; about 55° to 60° from mid-line.

Single row of median spines to anterior margin.
Few scattered small body spines.

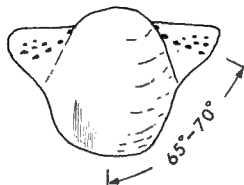
Rugae

Prominent & persistent over venter & visceral region.
Up to about 23 medianly.

Growth lines prominent anteriorly.

Ribbing
(radial ribs per 1mm width)

No. of ribs	3	4	5	6	7
Mid region	0	8	10	5	0
Flanks	1	16	11	1	0
Posterior	0	3	15	6	0
Anterior	1	21	6	0	0

L. spinauris

B

Single to multi-rows of umbonal-flanking spines on ears at about 65° to 70° from mid-line.

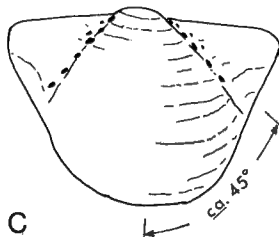
No median or body spines.

No rugae.

Growth lines over complete shell.

Mid region	0	0	1	2	1
Flanks	0	0	8	1	0
Posterior	0	0	2	2	1
Anterior	0	0	7	1	0

Less well developed than on L. humerosa.

L. sublaevis

C

Double to single row of umbonal-flanking spines on umbonal slopes at about 45° from mid-line.

No median or body spines.

Impersistent, tending to fade medianly and confined posteriorly.

Growth lines especially posteriorly

None.

On each side of the umbo these spines form a single row which, within about 10 mm, became double and extended around the antero-median borders of each ear. The visceral spines mentioned by H. M. MUIR-WOOD and G. A. COOPER (1960, p. 295), and figured by L. DE KONINCK (1847b, Pl. 17, fig. 3c), are only distinguishable on very well preserved shells. They occur on rugae of the visceral region in an apparently random fashion; they are smaller in diameter than the ear or median spines and on the specimen figured by L. DE KONINCK total about fifteen in number.

Two superbly preserved dorsal valve interiors from Caldon Low have been illustrated by H. M. MUIR-WOOD and G. A. COOPER (1960), one of which is refigured here together with a portion of its original ventral valve (Pl. I, fig. 5). The relationship between this portion of ventral valve, which is clearly conspecific with L. DE KONINCK's concept of *L. christiani*, and an internal cast of *L. humerosa* is illustrated in plate I, figure 4.

When *Levitusia* shells were closed the trails fitted closely together and, in life, would have been sealed by the mantle tissue, despite the strongly developed marginally directed endospines (Pl. I, fig. 2, 5). These endospines leave a distinctive pattern on internal casts of *L. humerosa* (Pl. I, fig. 2). In adult specimens the shell material of ventral valves is very thick posteriorly, reaching over 15 mm in thickness, while that of dorsal valves remained thin, other than for the muscle platforms. It is because the shell of dorsal valves is thin that their internal surfaces are seldom preserved on internal casts of *L. humerosa*, as originally described by J. SOWERBY.

The principal characteristics allowing the synonymy of *Productus christiani* within *P. humerosa* are as follows: the relationship of deep brachial cavities in the ventral valve of *P. christiani* with the cones of *P. humerus* and of the deeply impressed ventral diductor muscle scars; the median sulcation; the relative width of the specimens; the convergence to the mid-line of the internal and external ornamentations of the ventral trails in both groups of specimens, and the presence of both groups of specimens as the most common *Levitusia* species in the Caldon Low area of Staffordshire. I suspect that the Lectotype of *L. christiani* also came from this locality.

III. — REDESCRIPTION OF THE SPECIES *LEVITUSIA SUBLAEVIS* (DE KONINCK, L., 1843) (Plate III, Figures 1-9; Plate IV, Figures 5, 6)

- p v* 1843 — *Productus sublaevis* — L. DE KONINCK, pp. 157-158,
pl. X, fig. 1c-e, *cet. excl.*;
p 1847b — *Productus sublaevis* — L. DE KONINCK, pp. 75-77,
pl. VII, fig. ? 1a, b-d, *cet. excl.*;

- p 1861 — *Productus sub-laevis*, DE KONINCK — T. DAVIDSON, pp. 177-178, not figured.
 1919 — *P. aff. sublaevis*, DE KON. — J. W. JACKSON, p. 507, p. 509;
 1919 — *P. sublaevis*, — J. W. JACKSON, p. 508, p. 509;
 1926 — *Productus sublaevis* DE KONINCK — G. DELÉPINE, pp. 373-374, pl. A, ? fig. 1a, b, 2-9, fig. 1-4 *in textu* p. 376;
 p 1931 — *Productus (Plicatifera) humerosus* SOWERBY — W. PAECKELMANN, pp. 120-128, pl. 6, ? fig. 5a-c, pl. 11, ? fig. 1a-d, *cet. excl.*;
 p 1960 — *Levitusia humerosa* (J. DE C. SOWERBY) — H. M. MUIR-WOOD and G. A. COOPER, p. 416, pl. 109, fig. 2, 3, pl. 110, fig. 1, 2, *cet. excl.*

TYPE AND FIGURED SPECIMENS

Lectotype. — MNHN 1942-1, 584b (Pl. III, fig. 1-3 = pl. 10, fig. 1e *in* L. DE KONINCK, 1843) here selected, Paris « Muséum National d'Histoire Naturelle ». A replica has kindly been supplied to the British Museum (Nat. Hist.) by Mademoiselle J. DROT and is registered BB61640.

Figured specimens. — BM (NH) 64690 (Pl. III, fig. 4-6). L. DE KONINCK Collection from the Visé region of Belgium; BM (NH) B5798 (Pl. III, fig. 7-9). T. DAVIDSON Collection from near Clitheroe, Lancashire; BM (NH) BB61647 (Pl. IV, fig. 5, 6) from the V1a of Ocquier, Belgium.

Replicas of all complete figured specimens are in the collections of the « Institut royal des Sciences naturelles de Belgique » under the number I. G. 26056.

MATERIAL

Other specimens studied, but not figured herein, include : one specimen from Visé, Belgium, from the exhibit collection of the « Institut royal des Sciences naturelles de Belgique »; eight specimens from Visé, Belgium, from the DE RYCKHOLT Collection, I. G. 3440.

TYPE LOCALITY AND AGE

L. DE KONINCK (1843, p. 158) gives the locality of this species as Visé, from the « calcaire anthraxifère supérieur ». Some rocks in this area are now known to be of basal Viséan age (V1).

DIAGNOSIS

Strongly convex *Levitusia* with weak posterior rugation, no radial ribbing and with spines limited to double rows on each side of umbo reduced to single row on each flank at about 45° from mid-line. Ventral median sulcus weak or lacking.

DESCRIPTION

Specimens of this species most commonly came from the Visé region of Belgium and sometimes have suffered slight distortion, resulting in uncertainty as to their original shapes. In both longitudinal and transverse sections the profiles are strongly convex, although a variably developed shallow ventral median sulcus may affect the transverse profile. The ears form the widest part of the shell, but in some specimens spreading and flattening of the trails may widen the anterior end of the shell to equal that of the ears. The median sulcus, when present, has neither a ridge nor a row of spines. External ornamentation consists of irregularly developed rugae posteriorly, extending for about 25 mm from the umbo; growth lines, especially marginally; and a row, occasionally double, of up to eight spines on either side of the umbo between the flanks and ears at about 45° from the mid-line. There is no radial ribbing even on well-preserved shells, but growth beyond points of damage commonly resulted in a pathological pseudoplication. In addition, when shells are deeply exfoliated radially aligned pseudopunctae within the shell substance may produce the effect of an irregular radial striation.

The internal morphology of *L. sublaevis* is virtually unknown through a lack of suitable material. However it is clear that the shell substance of the visceral region of the ventral valve is thick whilst the trails are thin-shelled and moderately endospinose.

IV. — DESCRIPTION OF *LEVITUSIA SPINAURIS* n. sp.

(Plate II, Figures 6-8)

DERIVATIO NOMINIS

The characteristic presence of spine bases on the ears of this species is recorded in the specific name : *spina* (latin, féminin) = spine or thorn; *auris* (latin, féminin) = ear.

TYPE SPECIMEN

H o l o t y p e . — BM (NH) B5799 (Pl. II, fig. 6-8), T. DAVIDSON Collection, given to him by Mr. J. WARDLE in July 1862 and labelled by T. DAVIDSON as *Productus sublaevis*.

A replica is in the collections of the « Institut royal des Sciences naturelles de Belgique » under the number I. G. 26056.

MATERIAL

Other specimens studied, but not figured herein, include : one specimen from Caldon Low, Staffordshire, from the Manchester Museum, L 4953B; one specimen from the C2 of Dove Dale, Derbyshire, from the Mr. C. CHAMPION's Collection, 263.

TYPE LOCALITY AND AGE

T. DAVIDSON's manuscript label on the holotype states that the specimen came from « the Carb. Limestone of Caldon Low quarries Staffordshire ». These quarries are about 1.5 km south of Waterhouses on the A523 between Ashbourne and Leek, Low Viséan, V1 in age.

DIAGNOSIS

Small to medium *Levitusia*, similar in shape to *L. sublaevis*, but with prominent, wide ears, a very fine radial ribbing of 5 to 6 ribs per 1 mm width and spine bases increasing in number laterally onto each ear at 65° to 70° from mid-line.

DESCRIPTION

The strong convexity of the ventral valve in transverse profile resemble that of *L. sublaevis* and the umbonal and visceral regions are more strongly differentiated from the ears than in *L. humerosa*. As in *L. humerosa* the radial external ornamentation remains fairly constant in frequency over the complete shell; in this species, however, the ribbing is less clearly developed than in *L. humerosa* and is slightly finer with 5+ ribs per one mm width, as compared to a usual count of 4 on the type species.

There are neither median nor 'body' spines on the ventral valve but the flanking spines are characteristic in being at the high angle of 65° to 70° from the mid-line, a position which confines them to the ears, rather than being in the depression between the ears and flanks as in the other two species. During ontogeny the numbers of spines increased laterally so that adult valves have clusters of spine bases on each ear.

Broken specimens show that the ventral valve was heavily thickened, as in all species assigned to *Levitusia*. The trails are endospinous and the ventral diductor scars are radially ribbed, but otherwise internal morphology has not been seen.

LOCALITIES

At present the species is known from only five reasonably complete specimens in addition to the type specimen. All but one, which came from the north slope of Thorp Cloud, Dove Dale, Derbyshire, are from Caldon Low, north Staffordshire. These localities are about 8 km from one another and the specimens came from rocks of C_2 ($= V_{1a}$) age, at the base of the Viséan, in areas from where « reef » facies have been described.

DISCUSSION

It is fairly certain from his note upon *Productus humerosus* in Dove Dale that J. W. JACKSON (1919, p. 507, p. 508) saw this species, but it is not clear into which of the four « varieties » he recognised he would have assigned these shells. This is because he did not include radial ribbing as a characteristic, so making it difficult to distinguish between *Levitusia spinauris* and *L. sublaevis* without well preserved material showing the flanking spines. In his third « variety », « *Productus* aff. *christiani*, DE KON. » J. W. JACKSON included 'narrow and broad forms', and the new species most likely fits into the 'narrow' part of this grouping.

It is the intermediate nature of the characteristics of *Levitusia spinauris* which makes it necessary to consider not only the outline shapes of *Levitusia* species, in order to distinguish them, but also highlights the importance of considering the exact disposition of spines on the ventral valve and the nature of the external ornamentation. Thus the shape of *L. spinauris* is similar to that of *L. sublaevis* while the radial ribbing resembles that of *L. humerosa*; the disposition of the rows of umbonal flanking spines differs from those of the other two species. Visceral spines, such as those scattered on *L. humerosa*, do not occur on *L. sublaevis* or the new species (Text-figure).

V. — OBSERVATIONS ON OTHER *LEVITUSIA* SPECIES

Specimens collected mainly by D. V. NALIVKIN from Fergana and described by M. YANISHEVSKY (1918, p. 129) as *Productus humerosus* var. *lata* should mostly be considered as true *Levitusia humerosa*, since they resemble closely the exteriors described as *Productus christiani* by L. DE KONINCK. At least one specimen figured by YANISHEVSKY was included by W. PAECKELMANN (1931) in his *Productus (Plicatifera) humerosus* var. *longa* which again is probably a true *Levitusia humerosa*. The *Levitusia* specimens described by J. JAROSZ (1917) from the Krakow area seem to belong to *L. humerosa* although his new species *L. cracoviensis* may be valid.

Other taxa described in Russian literature are *Productus hyperboreus*, *P. sublaevis* var. *donica* and *Levitusia christiani uralica* FOTIEVA, N. N., 1973. I. M. GARAN's (1975) paper, which arrived during the completion of this script, deals with the taxonomy and evolution of *Levitusia* in the Soviet Union and thus is complemented by this work. In her paper the unsatisfactory situation of authorship and date of *L. hyperborea* is explained, although not resolved; D. V. NALIVKIN (1939) wrote up his description of southern Ural productaceans but the work remained unpublished until, in modified form, it appeared under joint authorship with N. N. FOTIEVA (1973). However, in the meantime several authors had used the name *Productus hyperboreus* in their own publications, always attributing it to D. V. NALIVKIN, but without a date. This is the current practice in Russia despite the fact that the name was first published and the species first illustrated by A. ROTAI (1941) as «*Productus (Plicatifer) hyperboreus* NALIVKIN sp. nov. (in Litt.)». According, therefore, to the International Rules of Zoological Nomenclature the authorship of *P. hyperboreus* should be A. ROTAI, 1941. Such a change would be both confusing, since for over thirty-five years the name has been attributed to D. V. NALIVKIN, as well as unfortunate since it was he who did the work in 1939 upon which subsequent authors have stood. This question of authorship and reference is one which should be dealt with by Russian palaeontologists in possession of all the facts and for the present I refer the species *P. hyperboreus* to D. V. NALIVKIN ms. in A. ROTAI, 1941.

Levitusia hyperborea is represented in the collections of the British Museum (Nat. Hist.) by three specimens (B57100-02) from the type locality of Mount Ivanova on the western side of the central Urals, from rocks of upper Tournaisian age. The morphology of these specimens agrees with the recently published redescrptions given for *L. hyperborea* by D. V. NALIVKIN and N. N. FOTIEVA (1973) and by I. M. GARAN (1975) in most respects save for the spine arrangements. *L. hyperborea* is a relatively small shell, normally less than 50 mm wide at the hinge, with a highly convex profile and long flaring trails; it has well defined ears, lacks any radial ribbing and in the disposition of its umbonal flanking spines it resembles *L. sublaevis*. It contrasts with *L. sublaevis* in having a well developed median row of spines in a shallow sulcus, similar to those of *L. humerosa*. The British Museum (Nat. Hist.) representatives, kindly sent from Leningrad in 1930, only display these three distinct rows of spines whereas the redescription by D. V. NALIVKIN and N. N. FOTIEVA (1973), where the species is assigned to the genus *Acanthoplecta*, notes the presence of additional spines close to the hinge line and others scattered on the rugae of the visceral region. Unfortunately their published illustrations do not show these spines so the true nature of spine disposition remains in some doubt on specimens assigned to *Levitusia hyperborea*.

L. sublaevis var. *donica* was elevated to an independent species by D. V. NALIVKIN and N. N. FOTIEVA (1973) and redescrbed by I. M. GARAN

(1975). It came from Low Viséan (CV_{1a}) rocks in the Kalmius region of the Donbass basin of southwestern Russia, and is also recorded from the upper Kosvin horizon of the southern Urals. *L. donica* appears to be similar to *L. humerosa* in shape, size and in having a fine radial ornamentation. Posterior rugation is prominent and there seem to be no median spines.

Levitusia christiani uralica also came from the Kosvin (lower Viséan) of the southern Urals and since it seems closely similar to *L. humerosa* the placing of it into synonymy with that species by I. M. GARAN (1975) appears justified. I. M. GARAN's somewhat overbroad view of *L. humerosa* included both L. DE KONINCK's taxa, *Productus christiani* and *P. sublaevis*, with the result that some differentiation of species within Russian *Levitusia* may be obscured.

A species name which might be associated with the genus *Levitusia* is *Productus personatus* SOWERBY, J., 1822, illustrated in three views on his plate 321. The specimen (B60980) from the Carboniferous limestone (probably Viséan) of the Kendal district, Cumbria, is an internal mould and is well illustrated by J. SOWERBY. T. DAVIDSON (1861, Pl. 36, fig. 3) refigured the specimen but typically accentuated the muscle fields and 'brachial' bulges; the figure is also reversed. T. DAVIDSON published no description of this species and, other than the plate description, its only mention (1861, p. 143) is in the discussion of *P. giganteus* SOWERBY, J., 1822, where he wrote «...believed by some to be the internal cast of a circular example of *P. giganteus*, but of which I am not yet perfectly satisfied». In volume eleven of the original T. DAVIDSON drawings, at the British Museum (Nat. Hist.), against his drawing of *P. personatus* he notes «Having had the original example for some time with me I have been able to convince myself that it is the same species as *P. humerosus* ...». Then in a later pencil note he added: 'it might belong to *P. hemisphaericus* !?». The one clear thing to emerge is that T. DAVIDSON remained uncertain as to the relationship of *P. personatus*. The name does not seem to have been used since and in view of these problems of affinity it seems wisest to suppress the use of the name.

The ventral valve internal morphology of the original specimen indicates to me a position within *Gigantoproductus* and it is somewhat similar to the *Producta aurita* of J. PHILLIPS (1836).

VI. — CONCLUSIONS

The type species of *Levitusia*, *L. humerosa* includes those specimens described as *Productus christiani* by L. DE KONINCK. The other Belgian species, *L. sublaevis* and *L. spinauris* n. sp., occur within the same stratigraphical interval as *L. humerosa*, within the basal strata of the Viséan (V1a). Closely related forms of *Levitusia* have been described from

Poland by J. JAROSZ (1917) and on into the Donetz (K. I. LISSITZIN, 1912) and Donbass (I. M. GARAN, 1975) basins. Russian literature has described low Viséan *Levitusia* species from the southern Urals and M. YANISHEVSKY (1918) described specimens from Fergana, southeast of Tashkent. From upper Tournaisian rocks of the central Urals and from Vaygach island, between the Urals and Novaya Zemlya, I. M. GARAN (1975) has described specimens which could have been ancestral to *L. humerosa*. This distribution of *Levitusia* species is confined to the European palaeogeographical plate of A. G. SMITH, J. C. BRIDEN and G. E. DREWRY (1972), with the possible exception of the Fergana records which occur in a poorly known region, so far as the margins of crustal plates are concerned.

The well known western European species are found in or closely associated with dolomites, oolites or 'knoll-reef' facies, as described by J. W. JACKSON (1941). These rocks commonly indicate regressive sedimentary regimes and in some localities evidence of earth movements closely follow the rocks containing *Levitusia*. In other areas there is evidence of marginal marine environments, all of which are suggestive of shallow marine living conditions in areas having well oxygenated seas. The heavy shells, strong spines and long endospinous trails may be adaptations to cope with such ecological conditions.

The observations of G. DELÉPINE (1926) differentiating the shell of *Levitusia* from that of the chonetacean *Daviesiella* are supported and preliminary further observations upon the shell fabrics of these genera are recorded. In recognising small pieces of thick shell from one or other of these genera the loss of pseudopunctae in the columnar fabric of *Levitusia* is important whereas within the oblique fabric of *Daviesiella* some pseudopunctae persist.

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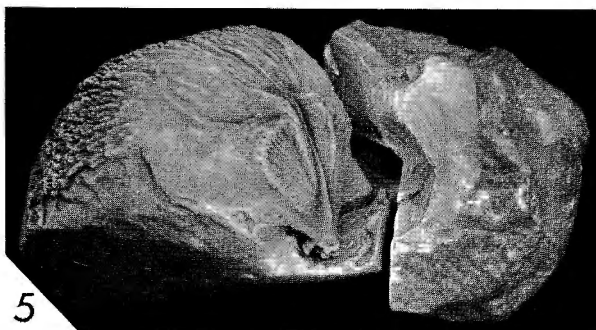
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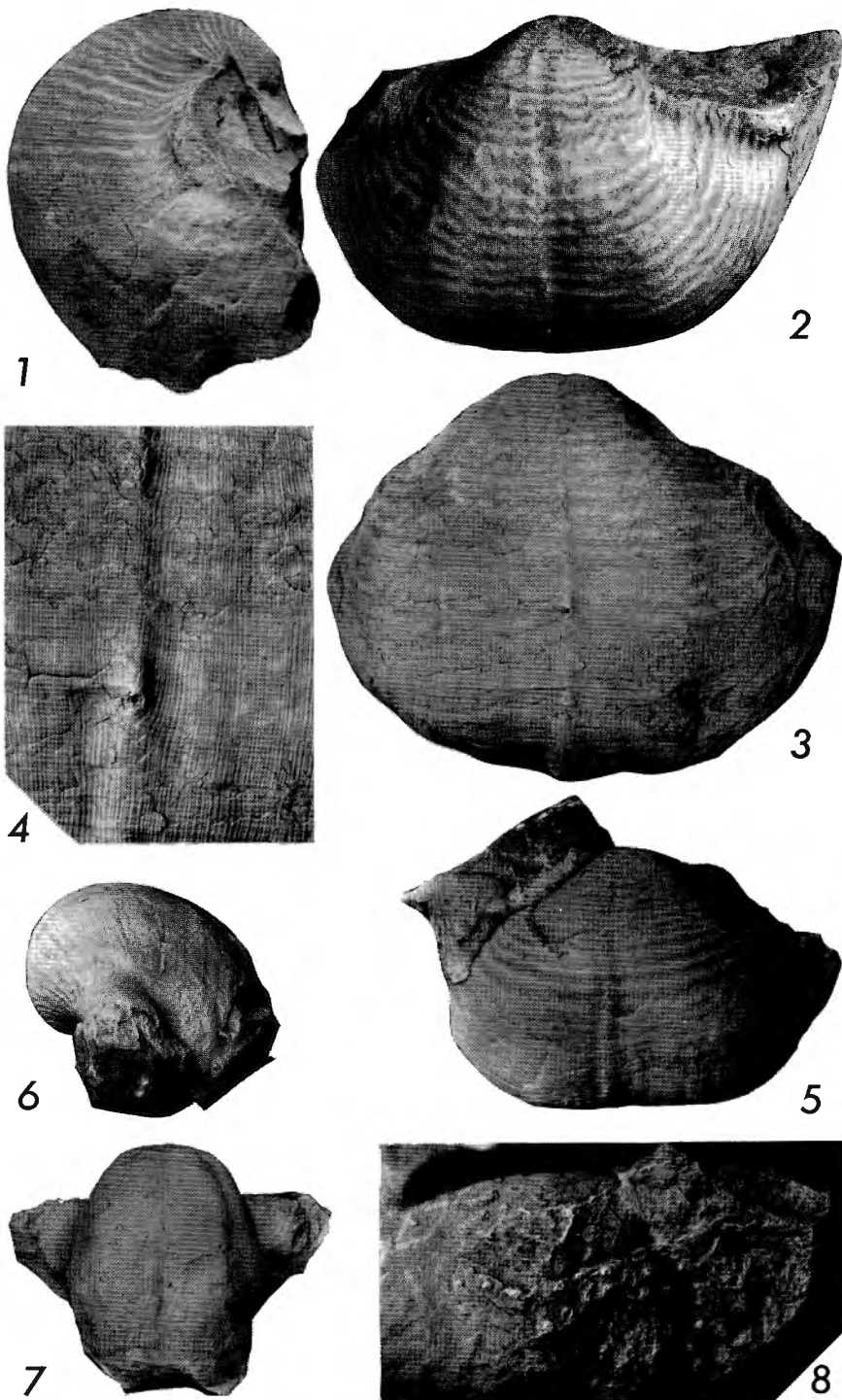


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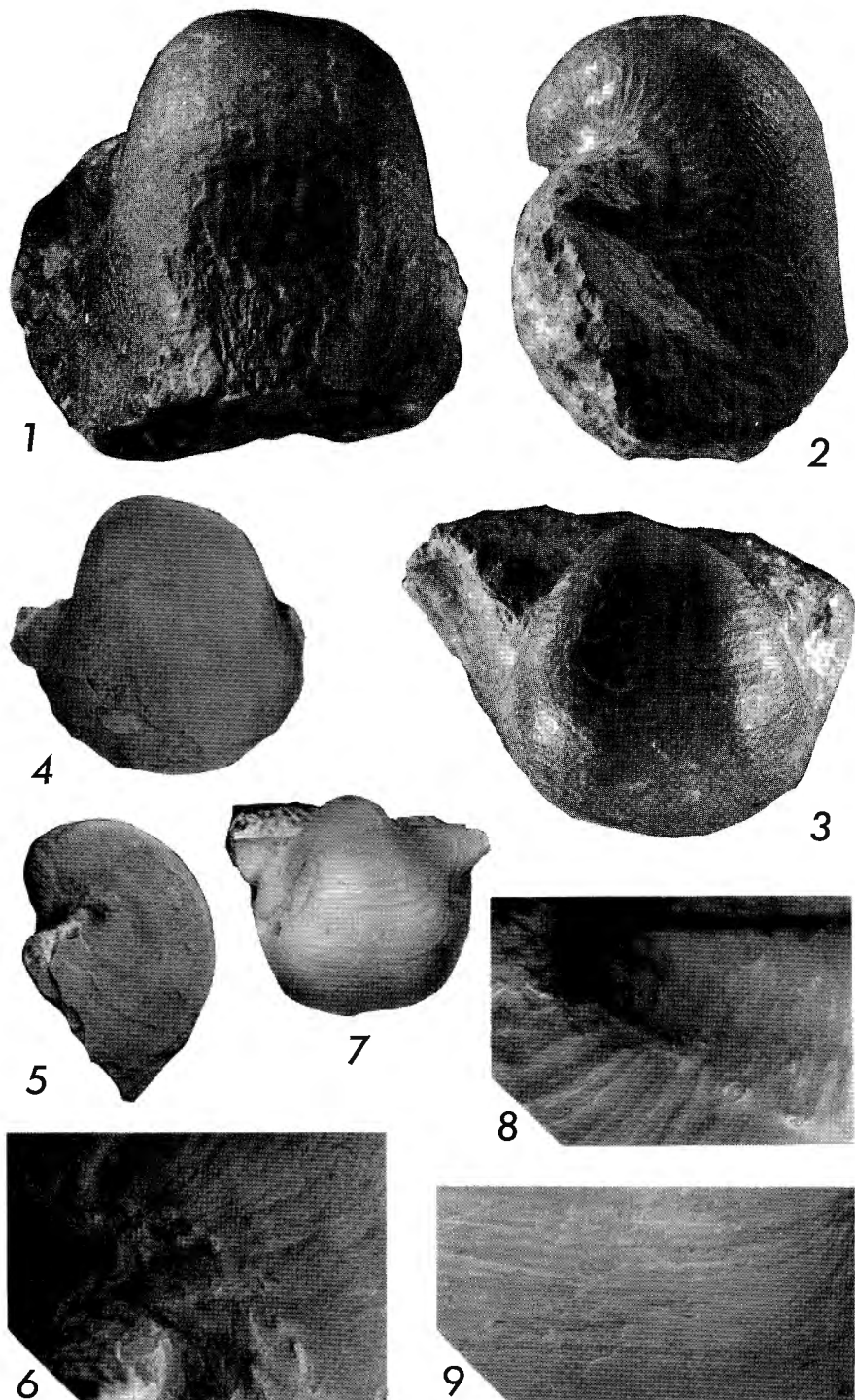


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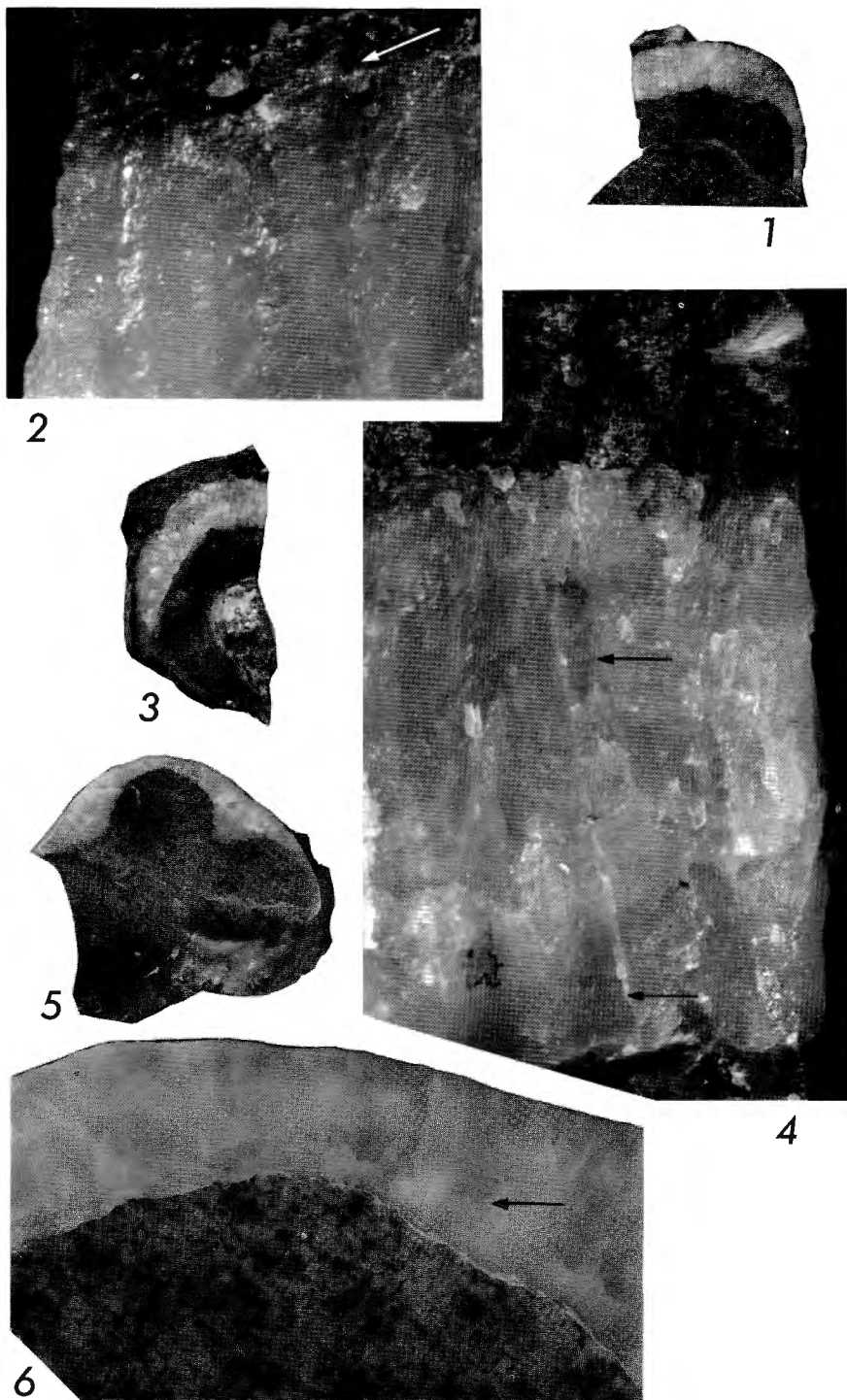
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 genus *Levitusia* MUIR-WOOD, H. M. and COOPER, G. A., 1960
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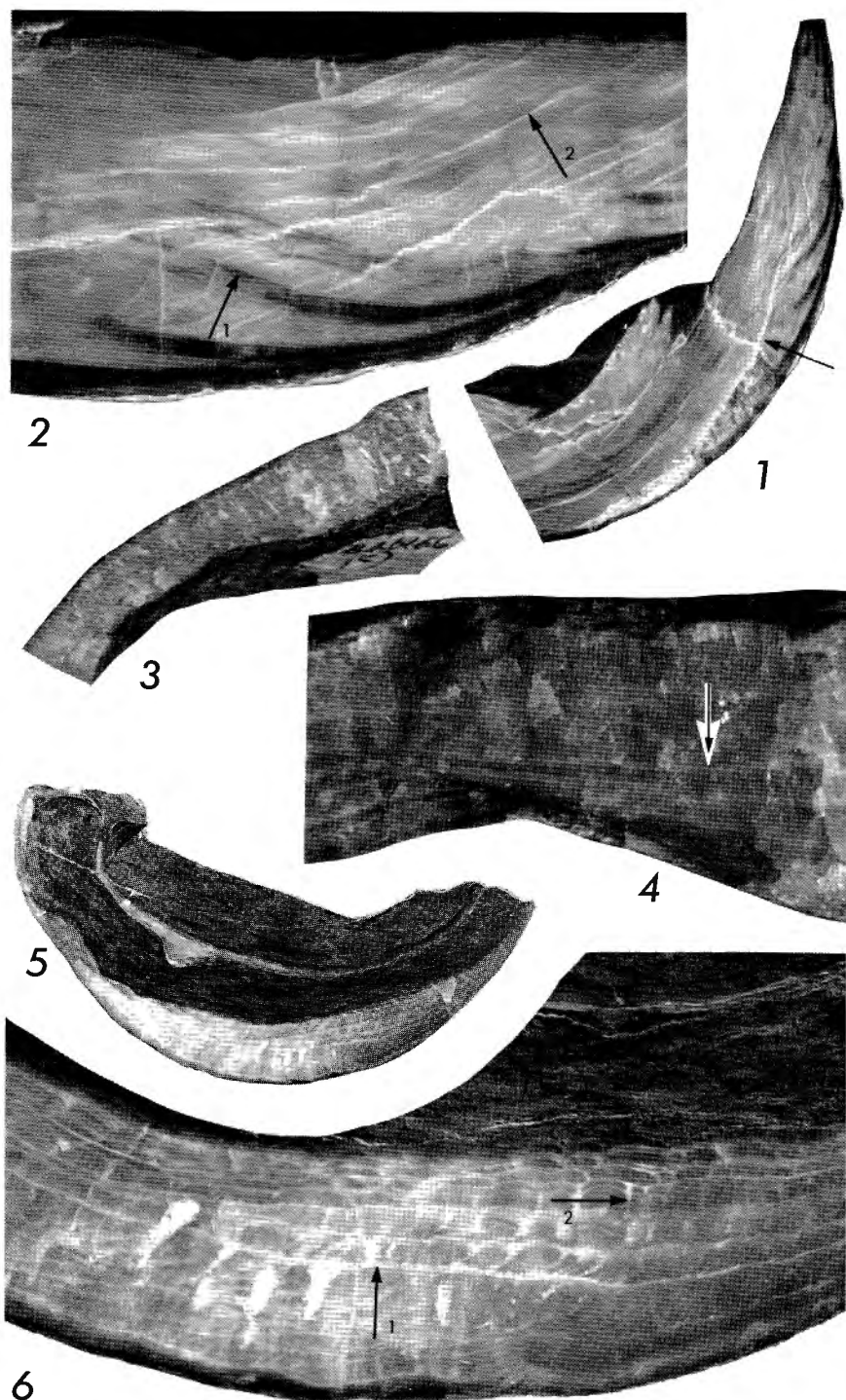
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EXPLANATION OF PLATES

PLATE I

Levitusia humerosa (SOWERBY, J., 1822)

- Fig. 1. — BM (NH) 97699. View of the anterior, trail region, of a large specimen from near Leek, N. Staffordshire, showing the median sulcation and, where the shell material is exfoliated, the V-shaped pattern of endospines projecting inwards. See also the internal mould of figure 2; $\times \frac{3}{4}$.
Fig. 2, 3. — Holotype BM (NH) B 60959. Internal cast viewed anteriorly showing the V-shaped pattern of pits made by endospines, and postero-laterally showing the casts of the brachial cones and muscle scar pits; $\times 1$.
Fig. 4. — BM (NH) B 55766. Internal cast, from the type locality, showing the way in which its morphology fits to the section of ventral valve of BM (NH) BB 13613 from Caldon Low, Staffordshire, the possible type locality of *Productus christiani*; $\times \frac{3}{4}$.
Fig. 5. — BM (NH) BB 13612 and BB 13613, the counterpart to BB 13612, showing the relationships of the dorsal and ventral diductor muscle scars; $\times \frac{3}{4}$.
Fig. 6. — MNHN 1942-1, 276 as *Productus christiani*. Lateral view. The specimen is almost entirely the external mould of a dorsal valve, to which small amounts of shell material adhere; $\times 1$.

PLATE II

Levitusia humerosa (SOWERBY, J., 1822)

Fig. 1-4. — Lectotype UPS D 812 of *Productus christiani*. Viewed laterally, posteriorly and ventrally. It should be noted that the hinge line on the right side, as viewed in figure 2, has been broken away to a position close to the line of ear spines; $\times 1$. Fig. 4: detail of the external ornamentation from a position in the middle of figure 3; $\times 2.5$.

Fig. 5. — MM L3614. Ventral view. The lithology closely resembles that of the Lectotype of *Productus christiani*; $\times 3/4$.

Levitusia spinauris n. sp.

Fig. 6-8. — Holotype BM (NH) B 5799. Viewed laterally and anteriorly. Fig. 6, 7; $\times 3/4$. Fig. 8 shows the cluster of spine bases on the somewhat exfoliated shell of the right ear; $\times 3$.

PLATE III

Levitusia sublaevis (DE KONINCK, L., 1843)

Fig. 1-3. — Lectotype, MNHN 1942-1, 584b. Specimen viewed anteriorly, laterally and ventrally; $\times 1$.

Fig. 4-6. — BM (NH) 64690. Viewed anteriorly, and laterally. Fig. 4, 5; $\times 3/4$. Fig. 6: detail of figure 5 showing the double spine row along the flanks; $\times 3$.

Fig. 7-9. — BM (NH) B 5798. Fig. 7: viewed ventrally, showing shell damage on the left side; $\times 3/4$. Fig. 8: detail of figure 7 showing the single row of spine bases in a position antero-lateral of those seen in figure 6; $\times 3$. Fig. 9: detail of figure 7 showing the external ornamentation of growth lines but no ribs; $\times 2.5$.

PLATE IV

Shell structure in the genus *Levitusia* MUIR-WOOD, H. M. and COOPER, G. A. 1960.

Fig. 1-4. — *L. humerosa* (J. SOWERBY, 1822). BM (NH) BB 61648. Fig. 1: part of a transverse fracture surface through the visceral region of the specimen showing the thick ventral valve (uppermost) and thin dorsal valve below; $\times 1$. Fig. 2: detail of the top left corner of the ventral valve in figure 1; very thin laminar shell is preserved (arrowed) at the outer surface. The remainder of the shell is composed of calcite prisms more or less perpendicular to the shell surfaces; $\times 30$. Fig. 3: longitudinal fracture perpendicular to the surface seen in figures 1 and 2; $\times 1$. Fig. 4: detail from the right edge of figure 3 showing the prisms still perpendicular to the valve surfaces and faint growth lines within the shell fabric (arrowed); $\times 12$.

Fig. 5, 6. — *L. sublaevis* (DE KONINCK, L., 1843). BM (NH) BB 61647. Fig. 5: transverse polished section near the anterior margin of the visceral cavity of the ventral valve; $\times 1$. Fig. 6: detail from the middle of the valve in figure 5 showing the prisms perpendicular to the valve surface and faint growth lines within the shell (arrowed). Note the tendency to convexity towards the inner surface of the valve of these synchronous boundaries; $\times 10$.

PLATE V

Shell structures in the genera *Daviesiella* WAAGEN, W., 1884
and *Gigantoproductus* PRENTICE, J. E., 1950

Fig. 1, 2. — *Daviesiella llangollensis* (DAVIDSON, T., 1863). BM (NH) BB 61652a. From the S₂, Viséan of the Llangollen region, North Wales. Fig. 1: longitudinal polished

section showing the anterior muscle field area of the visceral cavity with the valve exterior to the right. Exfoliation of the shell follows isotopic boundaries and one such fracture plane dips into the shell from the external surface just above the figure (arrowed); $\times 1.5$. Fig. 2: detail of the upper half of figure 1 showing time-growth layering (synchronous boundaries - arrowed 1) and crystal-growth (isotopic) boundaries (arrowed 2). Exterior is to the bottom and anterior to the right; $\times 5$.

Fig. 3-6. — *Gigantoproductus giganteus* (SOWERBY, J., 1822). BM (NH) B 46166. From the upper Viséan of Ayreshire, Scotland. Fig. 3: oblique fracture surface at approximately 20° from the mid-line in the mid region of the ventral valve. Exterior uppermost and anterior to the right; $\times 2$. Fig. 4: detail of the mid region of figure 3 showing time-growth (synchronous) boundaries (arrowed) and fine crystal (isotopic) boundaries perpendicular to the external surface; $\times 7$. Fig. 5: longitudinal median polished section through the same specimen showing both valves, the dorsal valve uppermost within the sediment; $\times 1$. Fig. 6: detail of the mid region of the ventral valve showing the dark outer laminar shell, growth (synchronous) boundaries (arrowed 1), and crystal growth (isotopic) boundaries which are perpendicular to the valve surfaces (arrowed 2); $\times 4$.

