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Some New Namurian Bivalve Faunas and their Significance in the Origin of Carbonicola and in the Colonization of Carboniferous Deltaic Environments

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SOME NEW NAMURIAN BIVALVE FAUNAS AND THEIR SIGNIFICANCE IN THE ORIGIN OF *CARBONICOLA* AND IN THE COLONIZATION OF CARBONIFEROUS DELTAIC ENVIRONMENTS

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Shells which have been attributed to the genus *Carbonicola* are known from certain Viséan and early Namurian (E_1) beds of Scotland, and were recorded from a single local Viséan horizon in the north of England. Re-examination of well preserved material from both these stratigraphic groups indicates that Viséan–early Namurian shells differ in internal features, as well as in external shape, from late Namurian (R_2–G_{1b}) and Westphalian *Carbonicola*, to which they do not appear to have been directly related. The former have been assigned to the new genus *Paracarbonicola*, with *Pleurophorus elegans* Kirkby 1880 as type species. *Paracarbonicola* is present in the Flora Beds of Poland, considered to be of E_1 age, and in Czechoslovakia, where it ranges upward into beds of E_2 age.

In Britain and northern Europe no *Carbonicola*-like shells have been reported in measures lying unquestionably between the top of Stage E_2 and the bottom of R_2. In beds of late R_{1c} age two newly found correlated assemblages of shells, the first in County Limerick, southwest Ireland, and the second near Clitheroe, northern England, are herein referred to cf. *Sanguinolites* Hind *non* M'Coy. These faunas existed in shallow-water marginally marine conditions, as evidenced by the associated Mollusca. Their shells were highly variable in both lateral outline and surface features. In the English Pennines, upward gradation of these faunas with unquestionable *Carbonicola* of R_2 and higher horizons may be demonstrated in terms of internal and external features of the shell. It therefore appears that British late Namurian *Carbonicola* faunas were probably derived from marine ancestors in late R_1 time. Limited evidence suggests a similar sequence of events in Belgium and the Netherlands.

Both in lithological facies and in ranges of variation of shape of shell, the Irish and north Pennine faunas of cf. *Sanguinolites* Hind *non* M'Coy compare respectively with established and invading faunas of later *Carbonicola*. Moreover, the comparison is made more close by the fact that bivalve burrows, referred to *Pelecypodichnus* Seilacher, have not been seen on horizons lower than those of late R_{1c}, but recur above this horizon, tending to become more nearly vertical, more numerous and longer, as *Pelecypodichnus* escape shafts, on higher horizons. These trends culminate in the well known, extremely abundant burrows of the Haslingden Flags, mid-Pennines, of G_1 age. It is concluded that during the time when *Carbonicola* was probably evolving from cf. *Sanguinolites* Hind *non* M'Coy, which has been found without burrows in the Shale Grit (middle R_{1c}) of Derbyshire, steep burrowing of bivalves was common, the long axes of the shell being near the vertical; that from this position rising movements of the shells took place, enabling the bivalves to escape burial from rapidly advancing delta lobes; furthermore, that in the process of rising the more elongate shells, having shorter anterior ends and relatively low measures of obesity, such as *Carbonicola bellula* (Bolton), held selective advantage over other shapes of shell. In these particular circumstances therefore the delta invaded the bivalves, rather than vice versa.

During the deposition of bands of established faunas of *Carbonicola*, when rates of deposition were evidently lower than in the case of invading ones, shallow burrowing appears to have taken place obliquely, the long axis of the shell making characteristically a small angle with the plane of the substratum. From work on Recent analogous bivalve species, functional advantage in shallow downward burrowing may be assumed to have lain with the more oval and more obese varieties. Established faunas with the latter trends characterized lower-energy muddy environments of the delta, including those which immediately followed coal-forming conditions. These environments tended mainly to succeed the phases of rapid deltaic growth, of sands and silts in Namurian time, and are reflected in the prevalence of established faunas of *Carbonicola* in Westphalian time.

INTRODUCTION: EARLIER WORK AND THE PLAN OF THE PAPER

No origin has been postulated for *Carbonicola*, the earliest genus of the Family Anthracosiidae of Carboniferous time (Weir 1969, pp. N406–7). Shells which have been attributed to *Carbonicola* have been found locally in the Viséan of the north of England (Garwood 1922) and within both the Viséan (Bennison 1960, 1962) and the Pendleian Stage (E_1) of the Namurian of Scotland (Bennison 1954). They have been described also from the lower Namurian of Poland (Tabor 1970) and Czechoslovakia (Rehor 1965, 1972). In Britain *Carbonicola* has been recorded from the Marsdenian Stage (middle R_{2b} of figure 46) of the Namurian of the Pennines and on many successive horizons ranging into the overlying Westphalian (Trueman & Weir 1948).

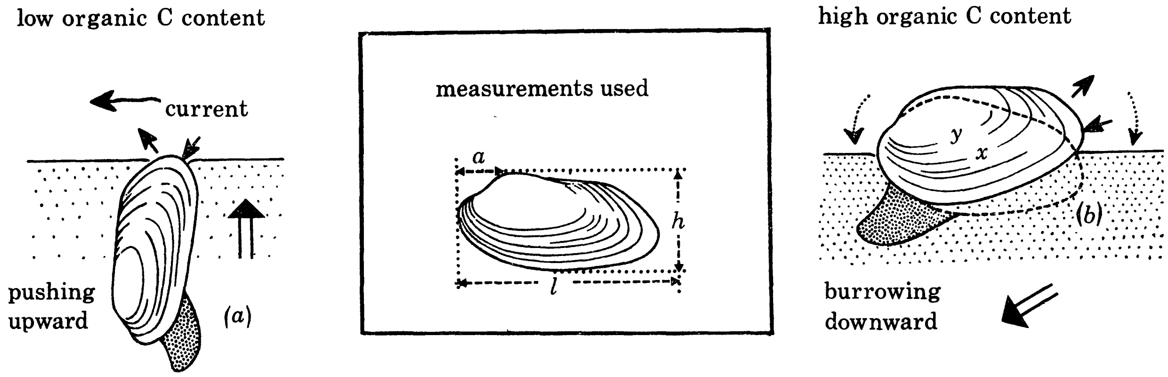

FIGURE 1. Shape of shell of *Carbonicola*, of the basal Westphalian of the Pennine Coal Measures, in relation to inferred characteristic living position of the bivalve (after fig. 12 of Eagar 1974). (*a*) *Carbonicola* aff. *bellula* (Bolton) and (*b*) *Carbonicola* aff. *protea* Wright, showing respectively the modal shapes of contemporaneous invading and established faunas. Small arrows denote inhalent and exhalent currents. The remaining arrows are concerned with bivalve movement and are explained in the text on p. 561. Standard directions of measuring the shell are shown inset. Obesity, the ratio t/l, is the maximum width of the bivalve measured perpendicular to the sagittal plane, divided by the length of the shell.

The concept of invading and established faunas of *Carbonicola* within the Pennine delta was deduced from palaeoecological work on lower Westphalian beds (Eagar 1971, 1973, 1974). Supplemented by broadly comparable results of work on shells attributed to *Anthraconaia* in late Pennsylvanian–Permian sediments of eastern U.S.A. (Eagar 1975, pp. 47–51), the essential data may be summarized: In invading faunas, shells tend to be elongate, having low height/length (h/l) ratios, short anterior ends (a/l ratios) and low obesities (t/l, figure 1*a*, and inset, centre). They characterize silty to sandy sediments commonly showing evidence of comparatively rapid deposition and of episodes of turbulence. The shells may be associated with burrows, referred to *Pelecypodichnus* Seilacher† and with escape shafts which include *Pelecypodichnus*. In contrast, established faunas are characterized by more oval shells with greater h/l ratios, longer anterior ends and greater obesities (figure 1*b*). Their shells tend to be found in prolific abundance in shales and mudstones which are typically rich in organic carbon (of the order of 5–12 %). In invading faunas there is commonly direct evidence of a steep-burrowing or steeply inclined living position, whereas in established faunas, a shallow-burrowing or ploughing position has been deduced (figure 1, positions of shells only), that is, when the bivalves were not resting, with one valve (left or right) lying more or less flat on the substratum.

In the present paper the group of British Viséan and early Namurian '*Carbonicola*' are first given brief systematic revision and separated from late Namurian–Westphalian *Carbonicola*. Newly discovered Irish and northern English late Namurian marine bivalves are then described and compared with the earliest known faunas of *Carbonicola* of late Namurian time. Emphasis is placed on the palaeoecological features of these new faunas, on new evidence of associated

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† The genus *Pelecypodichnus* Seilacher 1953 is used in place of *Lockeia* U. P. James (Häntzschell 1957, p. W79) on the evidence of recent work by Hakes (1977).

bivalve burrows and escape shafts in late Namurian measures, and on some new palaeoecological work on established faunas of Westphalian time. With the support of evidence from functional activity in some Recent analogous bivalves, a hypothesis is finally advanced to relate certain persistent trends in shape of shell to both periodic and long-term phases in the colonization of the developing late Namurian–Westphalian delta of the Pennines.

British and northern European Viséan and early Namurian non-marine Bivalvia

(*a*) *Introduction*

Within the Calciferous Sandstone Measures of Fife, Scotland, attributed to the Asbian and Brigantian Stages of the Viséan (George *et al.* 1976), shell bands considered to have been formed in non-marine, but probably including near-marine, conditions (Bennison 1960), have yielded *Naiadites obesus* (Etheridge junior), a small ?*Anthraconaia* (figure 18, plate 1) and shells attributed to the species *Carbonicola elegans* (Kirkby) and *C. antiqua* Hind *non* Brown (Bennison 1960; Weir 1968, pp. 416, 421). In north Ayrshire, shells from a single horizon in the Limestone Coal Group, deduced to be of early Namurian (E_1) age on indirect evidence from goniatite horizons (Currie 1954), have been placed in a third species, *Carbonicola pervetusta* (figures 4, 6, 7, plate 1) by Bennison (1954). These three biospecies (Bennison 1962) all had relatively small, tumid, evenly swollen shells, characteristically with more strongly marked adductor impressions than those of late Namurian and Westphalian Anthracosiidae. Their recent re-examination has indicated common internal features of the shell which are unknown in *Carbonicola* M'Coy 1885, as described by Trueman & Weir (1946, p. 2), necessitating their separation from this genus.

(*b*) *Systematic notes and discussion*

?Family Anthracosiidae Amalitsky 1892

Paracarbonicola gen.nov.

Type species *Pleurophorus elegans*, Kirkby, 1880

Pleurophorus Kirkby 1880, p. 586.
Carbonicola Hind 1895, p. 82.
Carbonicola Garwood 1922, p. 291.
Carbonicola Bennison 1954, 1960.
Carbonicola (pars) Weir 1968, pp. 421–2.
Carbonicola Rehor 1965, p. 299.
Carbonicola Tabor 1970, p. 120.

Type material. The type of *Paracarbonicola* is designated as *Pleurophorus elegans* Kirkby 1880 as interpreted by Weir (1968, pp. 421–2) in the lectotype illustrated by Bennison (1960, fig. 3, pl. 25).

Diagnosis. Shell with both lunule and escutcheon, the latter having sharply defined edges. Immediately behind the umbo the sides of the escutcheon are inclined at an angle of less than 30° to the sagittal plane, the angle increasing backward along the dorsal margin. The hinge plate consists of an anterior and posterior part set at an angle to one another, being either edentulous or bearing a single subumbonal tooth or swelling corresponding to a broad depression on the opposing valve. An elongate anterior accessory scar begins at the postero-dorsal extremity of the anterior scar and extends in the direction of the umbo, often forming a cleft in thick shells.

Further description and comparisons. Shells are characteristically oval to subelliptical, being typically of smaller size than those of *Carbonicola* and having adductor impressions of nearly equal size (cf. Trueman & Weir 1946, p. 4). *Paracarbonicola* is most readily distinguished from *Carbonicola* by its sharp-edged, steep-sided escutcheon, which has slightly concave sides and characteristically approaches closure near the termination of the dorsal margin (figure 3, plate 1), and by the elongate anterior accessory scar (Hancock Museum, G.66.03; cf. Trueman & Weir 1946). On internal moulds this feature may be seen as a ridge (figures 2*a*, *b*, plate 1), which may grade to a gentle fold of low relief (as in G.66.01 of the same collection). Where preservation is good, as in *Paracarbonicola elegans*, the curved path of the inclined grooves for the opisthodetic ligament may be clearly seen (figure 3, plate 1), the same feature being seen in the slightly eroded shell figured by Hind (1895, fig. 14, pl. XX) drawn in oblique (dorso-lateral) view. Both escutcheon and elongate anterior accessory scar are clear in *Paracarbonicola antiqua* Hind *non* Brown, the latter being well displayed in some internal moulds (e.g. in L.24514, Brit. Mus. (N.H.)), although sandstone moulds do not always show this scar. The type material of *P. pervetusta* (Bennison) consists of partly crushed shells in dark carbonaceous shale, but faint traces of the elongate accessory scar may be seen in all the types. The escutcheon is clearly visible with the lunule and characteristic anterior accessory scar – and in two cases with broad swellings indicating teeth – in *Paracarbonicola pervetusta* from the Flora Beds of Poland (for example in the collections of the Geological Institute at Sosnoviec, Coll. 85, Nos 48, 116, 126, the last cited being figured by Tabor (1970, fig. 16, pl. I)). It should be noted that teeth are almost invariably absent in Viséan species (Bennison 1960).

Paracarbonicola differs from *Anthracosia* in lacking a robust median dorsal ridge in the internal mould, and in being without trace of a pit for the anterior ligament (cf. text-fig. 18 of Trueman & Weir 1951). *Paracarbonicola* also tends to differ from both *Anthracosia* and *Carbonicola* in being more obese, primarily in the curvature of the shell profile in the vicinity of the ventral commissure, as may be seen in fig. 15*a*, pl. XX of Hind 1895. Since no morphic links are known with marine bivalve genera, the new genus is grouped only tentatively with the Anthracosiidae, on the basis of its general internal and external similarities to members of this Family.

Distribution. Paracarbonicola is present on several horizons through nearly the total thickness of the Calciferous Sandstone Measures (Viséan) of Fife, Scotland, *P. antiqua* Hind *non* Brown being restricted to the lower part of the group (Bennison 1960). The associated fauna suggests a brackish water environment (Bennison 1960, p. 151). In England, *Carbonicola*, associated with a gastropod referred to *Viviparus*, was recorded by Garwood (1922, fig. 3 of his pl. XII) from a restricted exposure of a thin limestone formerly seen in a quarry at Horton in Ribblesdale (a locality 40 km north of Burnley – figure 45). The horizon has been tentatively referred to the Holkerian, lower Viséan (W. H. C. Ramsbottom, personal communication). Nine poorly preserved shells from Garwood's locality show considerable resemblance, both in lateral outline and in the suggestion of a narrow escutcheon, to *Paracarbonicola elegans* (Inst. Geol. Sci. Coll. Leeds, Nos 64999, 65001–3), but are about half the size of this species as collected at Randerstone, Fife. Attribution of the gastropod to *Viviparus* has not been subsequently questioned (Yen 1949), but Viséan associates of *Paracarbonicola* elsewhere raise the possibility that the Horton Band may have been laid down in brackish water.

Description of plate 1

Figure 2a. *Paracarbonicola elegans* (Kirkby), an internal mould of a left valve in dorsal view, from Limestone No. 10 (of Kirkby 1880), Randerstone, Fifeshire, Scotland; shown in lateral view in fig. 5, pl. 25 of Bennison 1960, and in fig. 12, pl. XX of Hind 1895. Paralectotype of *Carbonicola elegans* of Weir 1968. The arrow marks the ridge formed by the cleft of the anterior accessory scar (see figure 2*b*). The matrix around the mould has been painted white and the photograph very slightly re-touched to remove 'glare' from an attached shell fragment. Brit. Mus. (N.H.) Coll. L.47162. (Magn. × 3.2).

Figure 2b. Part of the mould shown in figure 2*a*, taken from the same viewpoint, to show detail of the ridge extending backward from the anterior accessory scar. The umbonal tip of the mould is incomplete and is estimated to have lain about midway between the sides of the photograph and at about one quarter of its height. (Magn. × 15.)

Figure 3. *Paracarbonicola elegans* (Kirkby), a shell viewed dorsally to show the steep-sided escutcheon and the groove for the opisthodetic ligament which extends backward from the umbo to about the central point in the photograph, where it is seen to run off the hinge margin. The curvature of the groove is just discernible. Topotype, Kirkby Collection, Hancock Museum, No. G.66.00. (Magn. × 4.)

Figure 4. *Paracarbonicola* aff. *pervetusta* (Bennison) from the top of the Johnstone Shell Bed, Limestone Coal Group, in Powgree Burn, Kersland Glen, 1.6 km east of Glengarnock, north Ayrshire, Scotland. Hunterian Mus., Glasgow, S.13499. (Magn. × 2.4.)

Figure 5. *Paracarbonicola* aff. *pervetusta* (Bennison) from a depth of 620 m in Borehole No. L, near Grodziec, in the northeastern part of the Upper Silesian Basin of Poland; fig. 12, pl. I of Tabor (1970). The horizon lies near the top of the Flora Beds of E_1 age. Geological Institute, Sosnoviec, 85/104. (Magn. × 2.4.)

Figure 6. *Paracarbonicola pervetusta* (Bennison), as for figure 4. Text-fig. 6*b* of Bennison (1954). Paratype, Hunt. Mus. S.13384. (Magn. × 2.4.)

Figure 7. *Paracarbonicola pervestusta* (Bennison), holotype. As for figure 4. Text-fig. 6*a* of Bennison (1954). Hunt. Mus. S.13383. (Magn. × 2.4.)

Figure 8. *Paracarbonicola pervetusta* (Bennison), from 621.5 m in Borehole L. Fig. 6, pl. I of Tabor (1970). (Magn. × 2.4.)

Figure 9. Cf. *Sanguinolites* Hind *non* M'Coy a shell, with corrugations in the antero-ventral region. From a 0.13-m band lying 3 m below shales yielding *Reticuloceras gracile* Bisat and 'late *gracile*' in a stream exposure 1 km N 12° W of Mountcollins Post Office and 4.5 km SSE of Abbeyfeale. Killarney 1-inch Sheet 715D30, County Limerick, Ireland. Manch. Mus. LL.4986). (Magn. × *ca.* 1.5).

Figure 10. Cf. *Sanguinolites* Hind *non* M'Coy, an *Anthraconaia*-like variety, crushed, in dark shale 0.05 m from the base of the Mountcollins band (see figure 9). Somewhat irregular corrugations appear over the greater part of the lateral area of the shell, but much of the anterior lobe of the left valve is missing. Manch. Mus. LL.4987. (Magn. × 2.4.)

Figure 11. Cf. *Sanguinolites* Hind *non* M'Coy, as for figure 9 and showing the loss of all but the most anterior corrugations, which are irregular. Manch. Mus. LL.4988. (Magn. × 1.5.)

Figure 12. Cf. *Sanguinolites* Hind *non* M'Coy, from 0.63 to 0.69 m below the top of the shell band lying 1.4 m below *Reticuloceras gracile* and 'late *gracile*' on the east and west banks of Sabden Brook, 2.6 km southeast of Whalley, near Clitheroe, Lancashire. Geol. Surv. Six-inch Sheet 73 SW, SD 746343. Manch. Mus. LL.4989. (Magn. × 1.5.)

Figure 13. Cf. *Sanguinolites* Hind *non* M'Coy, as for figure 12. Although the *Anthraconaia*-like lateral outline is similar to that of figure 12, the surface of the shell shows more corrugation. Manch. Mus. LL.4990. (Magn. × 1.5.)

Figure 14. Cf. *Sanguinolites* Hind *non* M'Coy, as for figure 10. Part shell and part internal mould, showing *Carbonicola*-like characteristics in both. Manch. Mus. LL.4991. (Magn. × 1.5.)

Figure 15. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould closely similar to *Anthraconaia angulosa* Pastiels and lacking shallow corrugations (compare figure 16). Shown also in figure 47*a*, series C, number 18. As for figure 9. Manch. Mus. LL.4992. (Magn. × 1.5.)

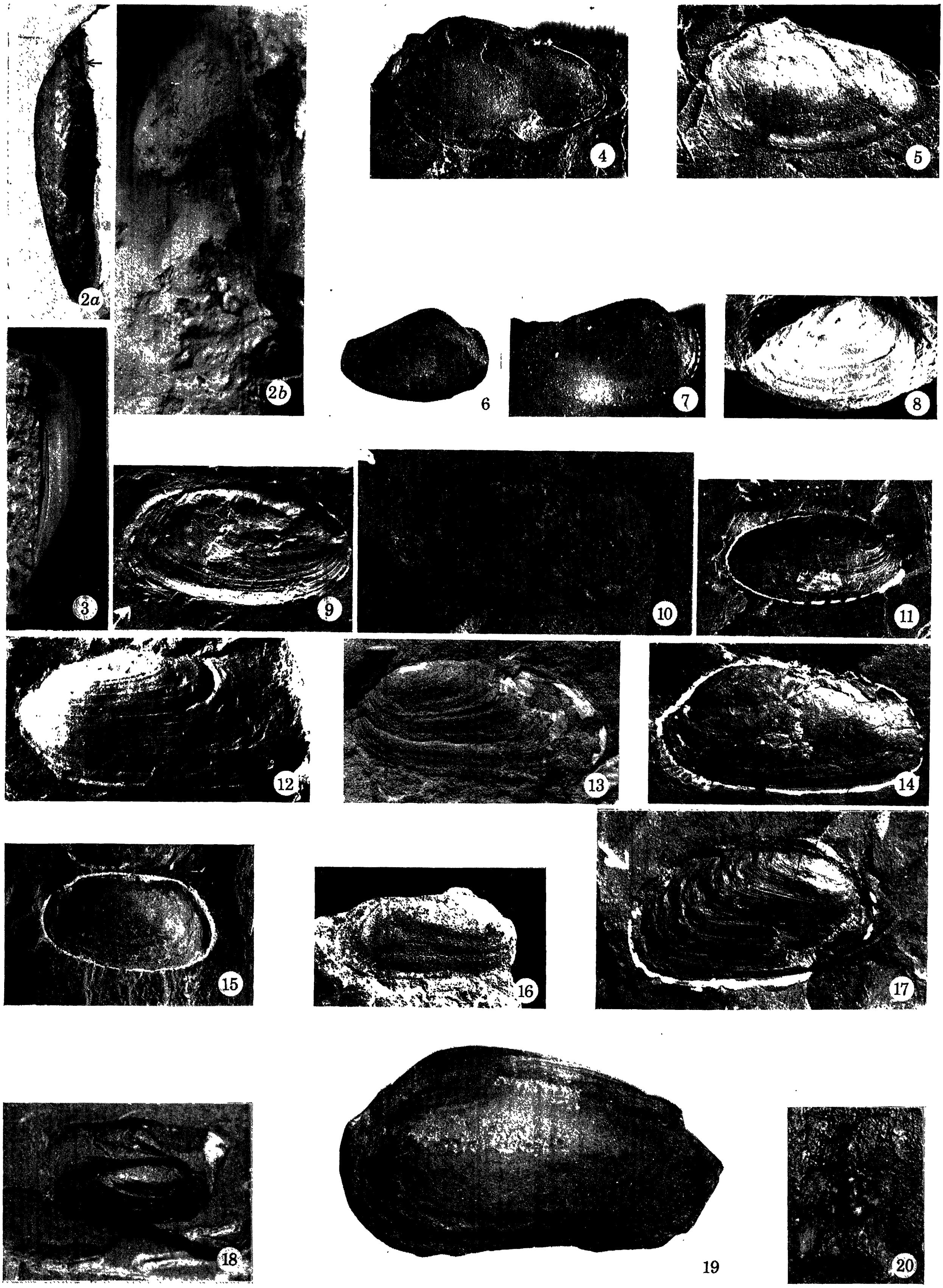
Figure 16. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould showing broad shallow corrugations, from 0.25 to 0.39 m below the top of the shell band at Sabden Brook, Whalley, as for figure 12. Shown in mirror image in figure 48, series E, number 15. Manch. Mus. LL.4993. (Magn. × 1.5.)

Figure 17. Cf. *Sanguinolites* Hind *non* M'Coy, showing a trend towards the outline of *Anthracosia phrygiana* (Wright). As for figure 9. Shown in mirror image in figure 47*a*, group D, number 66. Manch. Mus. LL.4994. (Magn. × 1.5.)

Figure 18. Cf. *Sanguinolites* Hind *non* M'Coy. Holotype of ?*Anthraconaia kirki* Bennison, from mudstone in the Calciferous Sandstone Series, Kilrenny Mill, Anstruther, Fife. Figured by Bennison (1960) as fig. 13, pl. 25. Hunt. Mus. S.13440. (Magn. × 3.2.)

Figure 19. *Carbonicola* sp., cf. fig. 21, pl. XXI, in Trueman & Weir (1951). From 33.5 m below the Belper Grit and 9 m below *Reticuloceras superbilingue* (figure 46) in Bullbridge Borehole, 0.4 km southeast of Bullbridge, Ambergate, Derbyshire. Geol. Surv. Mus. zl.262. (Magn. × 1.6.)

Figure 20. Gastropod, associated with cf. *Sanguinolites* Hind *non* M'Coy. As for figure 9. Manch. Mus. LL.4995. (Magn. × 6.7.)



FIGURES 2–20. For description see opposite.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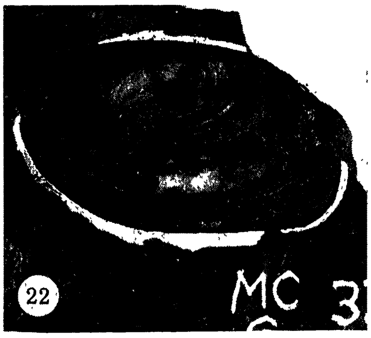
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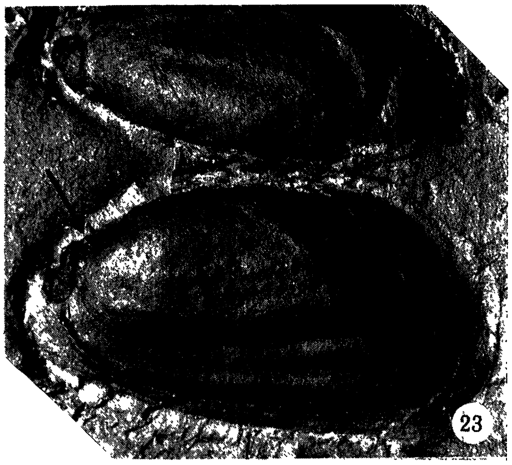
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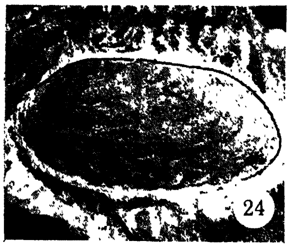
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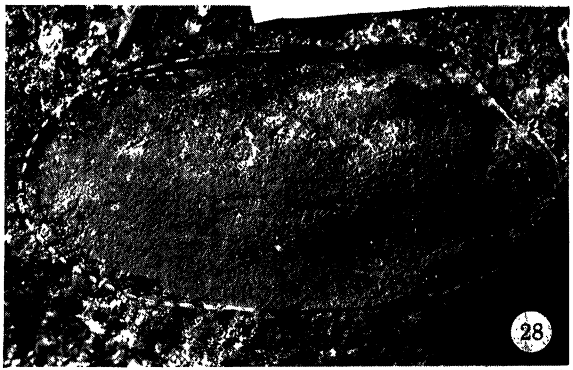
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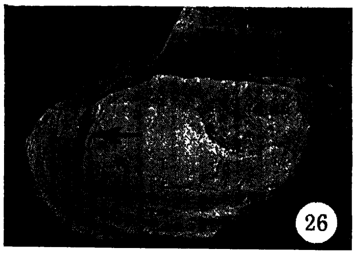
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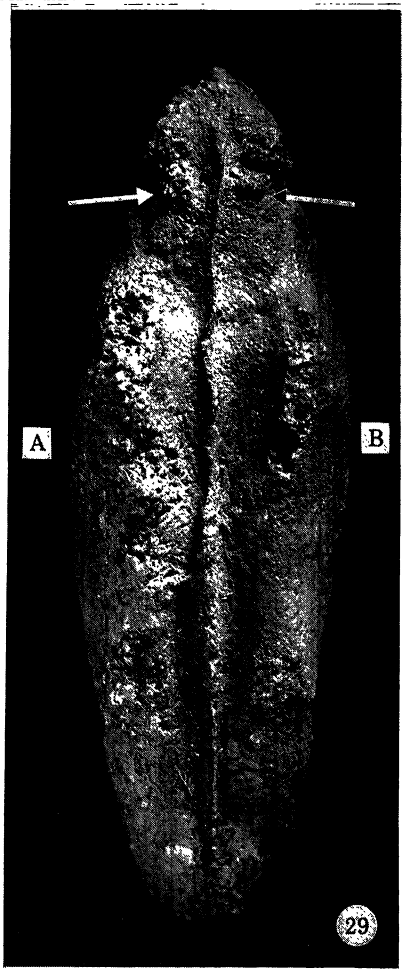
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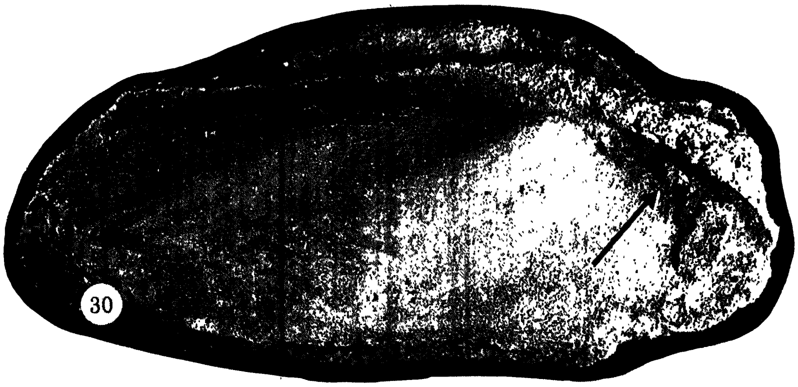
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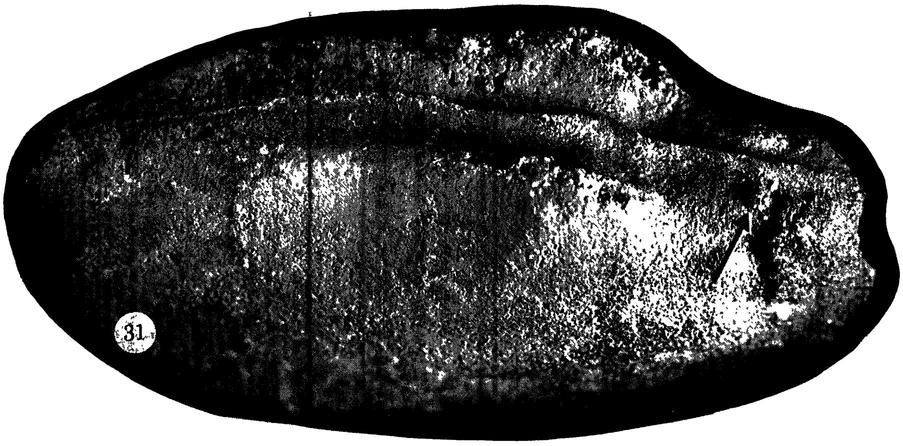
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Figures 21–31. For description see opposite.

In the succeeding Pendleian (E_1) Stage, *Paracarbonicola* is represented in Britain only at the horizon of the Johnstone Shell Bed of North Ayrshire, Scotland, near the middle of the Limestone Coal Group, where *P. pervetusta* commonly lies on the same bedding planes as *Lingula* and grades with occasional smaller shells referable to *P. ultima* (Rehor) (Hunterian Mus. S.13497–8). In Poland, *P. pervetusta* is present on several horizons within the Flora Beds of the Silesian Coal Basin, specimens showing striking similarity in both internal and external features to those of the Scottish Pendleian (figures 4–8, plate 1). The same beds have also yielded *P. ultima* (Rehor) (figs 13, 14, 16 of pl. I of Tabor 1970) and more elongate shells comparable with both *P. elegans* and *P. diversa* (Rehor) (figs 2, 5, pl. I; figs 1–6, pl. II, of Tabor 1970). The Flora Beds lie below the marine band Enna VII (Bojkowski 1967, p. 69) and have been correlated with the Hrušov Beds, of mid E_1 age, of Czechoslovakia (Rehor 1972, p. 129) by Kuchcińska, Musial & Tabor (1975) on the basis of a number of marine faunas extending through several boreholes. There is therefore independent evidence that the horizons of *Paracarbonicola pervetusta* and *P. ultima* are broadly the same in Scotland and in Poland. In the Flora Beds *Lingula* commonly lies near, but not on the same bedding plane as *Paracarbonicola* (Tabor, personal communication). Differences in the Scottish and Polish faunas consist mainly in the addition of more elongate

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DESCRIPTION OF PLATE 2

FIGURE 21. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould showing thickness of the shell and the impression of the flat dorsal edge of the shell margin, parallel to the sagittal plane of the bivalve. Provenance as for figure 9. Shown also in mirror image as figure 47*a*, number 34. Manch. Mus. LL.4962. (Magn. × 2.7.)

FIGURE 22. Cf. *Sanguinolites* Hind *non* M'Coy (cf. *Anthracosia regularis* (Trueman)). Some growth lines have been outlined in black on the print. As for figure 9. Manch. Mus. LL.4963. (Magn. × 2.0.)

FIGURE 23. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould from Mountcollins showing the anterior, anterior accessory (black arrow) and posterior adductor scars. As for figure 9. The shell is shown also as figure 47*a*, series C, number 13. Manch. Mus. LL.4964. (Magn. × 3.0.)

FIGURE 24. Cf. *Sanguinolites* Hind *non* M'Coy, a variety comparable with *Carbonicola fallax* Wright and shown also as figure 48*a*, series I, number 44. As for figure 12. Manch. Mus. LL.4965. (Magn. × 2.0.)

FIGURE 25. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould from below, or in the lower part of the Pule Hill Grit and above *Reticuloceras bilingue* Bisat at Holt Head, near Saddleworth, Oldham (figures 45, 46). The specimen lies on the same slab as the lectotype of *Sanguinolites ovalis* Hind. Figured by Hind (1900, fig. 14, pl. XLVI) and by Eagar in Jones (1969, pl. 24C), this shell has subsequently been cleared of matrix over the anterior end (compare the shells of figures 24 and 27, adjacent). Brit. Mus. (N.H.) L.47518A. (Magn. × 2.0.)

FIGURE 26. Cf. *Sanguinolites* Hind *non* M'Coy, an incomplete internal mould. Fig. 16, pl. XVLI of Hind (1900). Provenance and photography as for figure 25. Brit. Mus. (H.H.) LL.4750. (Magn. × 2.)

FIGURE 27. Cf. *Sanguinolites* Hind *non* M'Coy, an internal mould from 0.30 to 0.36 m below the top of the shell band at Whalley, as for figure 24, above. Manch. Mus. LL.4966. (Magn. × 2.0.)

FIGURE 28. *Carbonicola* cf. *lenicurvata* Trueman, from near the top of the Heyden Rock (R_{2b}) in a temporary excavation on the northern flank of Strines Dyke Gorge, 14 km WNW of Sheffield. Inst. Geol. Sci. Six-inch Sheet SK 29 SW, 2256 9071 (Stevenson & Gaunt 1971, p. 232). I.G.S. YPF9985. (Magn. × 2.0.)

FIGURE 29. *Carbonicola* sp., an internal mould in ferruginous sandstone, showing the impression of a single pit-like accessory scar from the right valve (B) and the suggestion of a more complex scar (A) in the left one. The same specimen is shown in oblique view in figure 31. I.G.S. PT9203. (Magn. × 3.3.)

FIGURE 30. *Carbonicola* sp., an internal mould in sandstone, viewed obliquely to show the impression of the deep anterior adductor scar and the small deep accessory scar (arrow), which is incompletely separated from it. The valves have been slightly displaced, so that they reveal the impression of a shallow curved hinge plate without signs of swellings or teeth on it. As for figure 28. I.G.S. YPF9982A. (Magn. × 2.0.)

FIGURE 31. *Carbonicola* sp., an oblique view of the shell shown in figure 29. Note the evidence for a deeper hinge plate than that of figure 30. (Magn. × *ca*. 3.3.)

varieties in Poland and in the absence there of some of the larger suborbicular trends which were found in the Johnstone Shell Bed (text-figs 3G, H, B, C of Bennison 1954). The Polish faunas are associated with less richly carbonaceous sediments than those of the latter Bed and include a number of very small shells of *P. ultima*, which all occur in grey, relatively silty mudstones. Together, therefore, the combined differences of morphological trend of shell and sediment in Scotland and Poland parallel those combinations described on other non-marine horizons, both in *Carbonicola* and supposed *Anthraconaia*, where high trophic levels of the palaeoenvironment were associated with increased size of shell, in *h/l* and *a/l* ratios, as summarized by Eagar (1975, pp. 47–51). The comparisons of these faunas therefore carry the suggestion that their morphic differences may have been primarily of palaeoenvironmental origin.

In Czechoslovakia, Rehor (1972) has illustrated shells of *Paracarbonicola*, including *P. ultima*, in a succession of measures from E_1 up to the middle of the Poruba Beds (middle E_2); above which there are no further records of the genus.

Horizons in the middle Namurian

In the British Isles, above Stage E_1 and throughout the greater part of the Namurian, that is from the Arnsbergian to the top of the Kinderscoutian Stage (R_1 of figure 46), no unquestionable non-marine bivalves have been found. In South Wales, where Eagar (in Jones 1969) recorded shells comparable with *Carbonicola ornata* Trueman, on a horizon which may lie within this interval, it is equally likely that the shells should be assigned to a low horizon in the Marsdenian (Jones, 1974). In Belgium and the Netherlands, where the absence of diagnostic marine faunas has resulted in lower and middle Namurian beds being assigned to the less precise divisions of Namurian A and B respectively, no shells remotely comparable with known variants of *Paracarbonicola* have been found (Pastiels 1960; Van der Heide 1943). There therefore appears to be no evidence that *Paracarbonicola* survived after middle E_2 time.

In Belgium however, Namurian A measures are characterized by several horizons yielding highly variable bivalves which Pastiels (1960) regarded as non-marine, describing from them the elongate *Anthraconaia angulosa* (figure 50, measurements), and in Namurian B, *A. perlongata* and *A. ventricosa* (figures 49, 50), and *Carbonicola willierae* Pastiels. Although none of these shells reveal evidence of internal features, and are thus generically uncertain, an appreciable number show evidence of original corrugations of the shell surface in their antero-ventral regions, notably those of fig. 1, pl. XIII, figs 9 and 21, pl. XXI, of Pastiels 1960, and the shell no. 2724 of the Heerlen Mining Bureau collection, from 288 m below the Sarnsbank in Diepe Boring 113, Winthagen, Netherlands. Similar corrugations are seen in ?*Anthraconaia kirki* Bennison (figure 18, plate 1) and in the newly found marine faunas of late R_1 age in Britain and Ireland (figure 11, plate 1, and p. 543).

Re-examination of Pastiels' Namurian bivalves indicates that many of his figured shells, referred both to *Anthraconaia* and *Carbonicola*, have been severely affected by post-depositional distortion, an effect well known in slates subject to regional pressures and seen in the fairly common situation where two shells lie flat on the bedding plane, adjacent to one another, but with their long axes at approximately 90°; one shell has an unusually low *h/l* ratio and the other an unusually high one (fig. 2, pl. XII of Pastiels 1960). Recognition of the distortion is important in interpreting the measurements of Pastiels' extreme variants recorded in the plots of figures 49 and 50. In general Pastiels' shells tend to be current-orientated, with their long axes parallel to subparallel. Moreover, this direction appears to have lain commonly at a wide angle to the minimum axis of the strain ellipsoid demonstrable on the bedding plane. It is therefore likely that the values of the h/l ratios for Pastiels' longer varieties are more often too small than too large, that the points for *Anthraconaia angulosa* and *A. perlongata*, when corrected, lie within, rather than marginal to, the scatter of figure 50, and that the middle Namurian shells of Belgium and of the Netherlands, where the same distortional effects may be seen, have wider dimensional overlap with new R_1 faunas to be described, than is apparent from their present state.

NEW NAMURIAN BIVALVE FAUNAS FROM IRELAND AND THE PENNINES

(*a*) *Mountcollins* (R_{1c-2a})

Shales yielding *Reticuloceras gracile* Bisat, including 'late *gracile*', crop out in a stream section near the village of Mountcollins, County Limerick, southwest Ireland (see p. 540). From about 3 m below the base of the marine band, through 0.28 m of dark grey richly carbonaceous shale overlying a 0.13-metre coal, shells superficially similar to *Carbonicola* (figure 47*a*) are very abundant. With them may be found much less common small *Modiolus* sp. comparable with the shell referred to cf. *Naiadites* in fig. 10, pl. VI, of Ramsbottom, Rhys & Smith (1962). Rare small turreted gastropods also occur, identical with the shell shown in figure 20 of plate 1.

The larger oval shells show a wide range of continuous variation (figures 9–11, plate 1; figures 21–23, plate 2; figures 41–44, 47*a*, 49, 50, plate 3). Whereas a few of these shells show traces of more or less regular corrugations, reminiscent of the 'ornament' of *Sanguinolites* Hind (figure 10, plate 1), this 'ornament' tends to be restricted to the antero-ventral region of the shell (figure 11) and grades into the finer pattern of growth lines characteristic of *Carbonicola* (figures 12, 14, 17) where postero-dorsal solution hollows of typically anthracosiid pattern are well seen. Wider corrugations may be impressed to a varied extent on internal moulds (figures 23, 27, plate 2, and compare the shell of figure 15, plate 1, where corrugations are absent). No correlation has been found between the lateral outline of the shell and the presence and degree to which both types of corrugations are expressed. However no corrugations on the surface of the shell are as clearly and regularly marked as those of *Sanguinolites* of figure 37, plate 3, nor is any 'ornament' as regular as that seen in the lectotype of *S. ovalis* Hind (pl. 24B of Eagar in Jones 1969).

Where preservation is good (figure 23, plate 2), the oval anterior adductor scar of the shell is deeply impressed, especially along its slightly irregular posterior margin, behind which there is occasionally a very slight bar-like swelling, comparable with that seen in the internal mould of cf. *Sanguinolites* of figure 25, plate 2. A single small round pit-like accessory scar is clearly separated from that of the anterior adductor, being dorsal and posterior to it, so that it leaves a small sharp protuberance lying towards the centre of the anterior umbonal slope of the internal mould (figure 23, plate 2, arrow). The pallial line is entire and the posterior adductor scar shallow, oval about one and a half times the area of the anterior scar, and situated near the dorsal margin of the shell (figure 23, plate 2). Over the umbonal region, which is often ill-defined in internal moulds, the shell is thickened very slightly, or inappreciably (figures 21, 23, plate 2). Posterior and dorsal to the umbo the latero-dorsal shoulders of the internal mould are usually well rounded (figure 21, plate 2; figures 39, 43, plate 3). The shell terminates dorsally in a flat hinge margin, parallel to the sagittal plane, without teeth and typically without thickening to form a hinge plate (figure 21). The dorsal surface of the margin is grooved for the reception of an external opisthodetic ligament, as in the Anthracosiidae. Anterior to the umbo, the shell is slightly thickened towards the cardinal margin, which remains smooth, parallel to the sagittal plane and edentulous. On internal evidence therefore the Mountcollins shells cannot be referred to *Carbonicola*. Of described and figured material they resemble most nearly shells associated with the types of *Sanguinolites ovalis* Hind (figures 25, 26, plate 2), which came probably from below the horizon of the Pule Hill Grit (figure 46) and above that of *Reticuloceras bilingue* (Eagar in Jones 1969). The latter are insufficiently well preserved to yield evidence of an accessory scar, but reveal a bar-like swelling posterior to the anterior adductor (arrows). The external oblique carina of *Sanguinolites* M'Coy (type species *S. discors*, Stoliczka 1871, Newell & La Rocque 1969) makes this generic name unavailable, and the internal features of *S. abdenensis* (Etheridge jun.) (see figure 48*a*, Series I) are unknown, although this species is included within the broader group of *Sanguinolites* Hind 1900. Accordingly identification can be made only comparatively with *Sanguinolites* Hind *non* M'Coy.

DESCRIPTION OF PLATE 3

FIGURE 32. Cf. *Sanguinolites* Hind *non* M'Coy (cf. *Carbonicola bellula* (Bolton)), from a parting in the Shale Grit (R_{1c}) in the upper part of Roych Clough, 4.6 km NNE of Chapel en le Frith, Derbyshire (figure 45). Inst. Geol. Sci. Six-inch Sheet SK 08 SE, 083844. Manch. Mus. LL.4967. (Magn. × 1.75.)

FIGURE 33. Cf. *Sanguinolites* Hind *non* M'Coy (cf. *Carbonicola bellula* (Bolton)). As for figure 32. Manch. Mus. LL.4968. (Magn. 2.7.)

FIGURE 34. Cf. *Sanguinolites* Hind *non* M'Coy, a shell comparable with *Anthraconaia perlongata* Pastiels (1960, figs 5, 13, pl. XXI). As for figure 32. Manch. Mus. LL.4969. (Magn. × 2.0.)

FIGURE 35. Cf. *Sanguinolites* Hind *non* M'Coy. The dorsal part of the truncated posterior margin may have been slightly straightened by post-burial distortion. As for figure 32. Manch. Mus. LL.4970. (Magn. × 2.0.)

FIGURE 36. Cf. *Sanguinolites* Hind *non* M'Coy, comparable with shorter varieties of the group of *Carbonicola bellula* (Bolton). As for figure 31. Manch. Mus. LL.4971. (Magn. × 2.0.)

FIGURE 37. *Sanguinolites* aff. *plicatus* (Portlock). From the middle of a 0.43-m siltstone parting in the Shale Grit of Whitebrow Quarry, 0.27 km WSW of the Filter House at Kinder Reservoir, near Hayfield, Derbyshire. Inst. Geol. Sci. Six-inch Sheet SK 08 NE, 0506 8802. Manch. Mus. LL.4972. (Magn. × 2.2.)

FIGURE 38. Cf. *Sanguinolites* Hind *non* M'Coy (compare *Carbonicola obliqua* Wright). From 1.45 to 1.50 m below shales with *Reticuloceras gracile* and 'late *gracile*' at Whalley; otherwise as for figure 12. The shell is shown also as figure 48*a*, series J_3, number 60. Manch. Mus. LL.4973. (Magn. × 2.0.)

FIGURE 39. Cf. *Sanguinolites* Hind *non* M'Coy (comparable with the 'anthraconaioids' of Eagar 1947, fig. 33). Mountcollins, as for figure 9. Shown also as figure 47*a*, between series E and F, number 34. Manch. Mus. LL.4974. (Magn. × 2.0.)

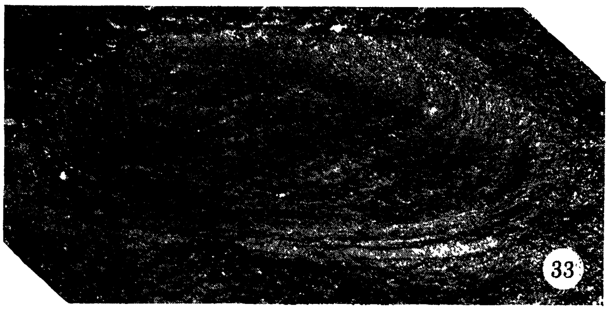
FIGURE 40. Cf. *Sanguinolites* Hind *non* M'Coy (compare with fig. 14 M in Eagar 1947). 2.10–2.48 m below *R. gracile* and 'late *gracile*' at Sabden Brook, Whalley. Shown also as figure 48*a*, series I_2, number 48. Manch. Mus. LL.4975. (Magn. × 2.0.)

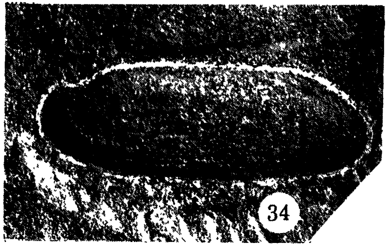
FIGURE 41. Cf. *Sanguinolites* Hind *non* M'Coy (compare with *Carbonicola declinata* Eagar). As for figure 12. Shown also as figure 48*a*, series F, number 25. Manch. Mus. L.4976. (Magn. × 2.0.)

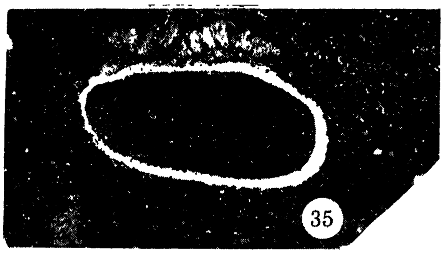
FIGURE 42. Cf. *Sanguinolites* Hind *non* M'Coy, an unusual variety, just comparable with occasional variants of the *Carbonicola bellula* group. As for figure 12. Manch. Mus. LL.4977. (Magn. × 2.0.)

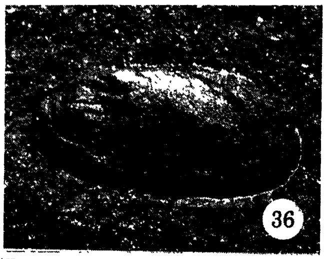
FIGURE 43. Cf. *Sanguinolites* Hind *non* M'Coy, an incomplete *Anthraconaia*-like internal mould showing the anterior adductor scar and the pallial line. As for figure 9. Manch. Mus. LL.4978. (Magn. × 2.0.)

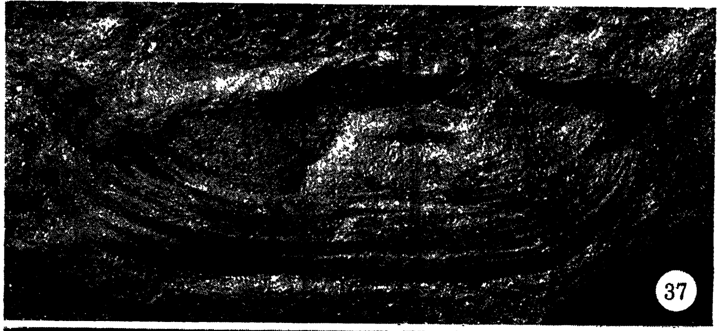
FIGURE 44. Cf. *Sanguinolites* Hind *non* M'Coy (compare figure 1 in plate XV of Trueman & Weir 1951, a shell which does not possess the gerontic snout of this individual). As for figure 12. Shown also as figure 48*a*, number 37, between series F and K. Manch. Mus. LL.4979. (Magn. × 2.0.)

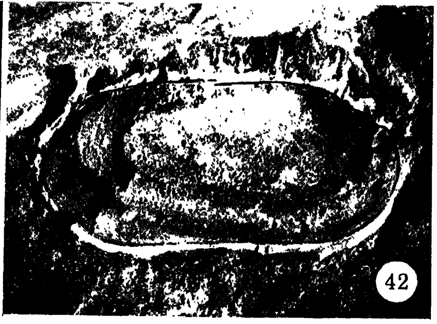






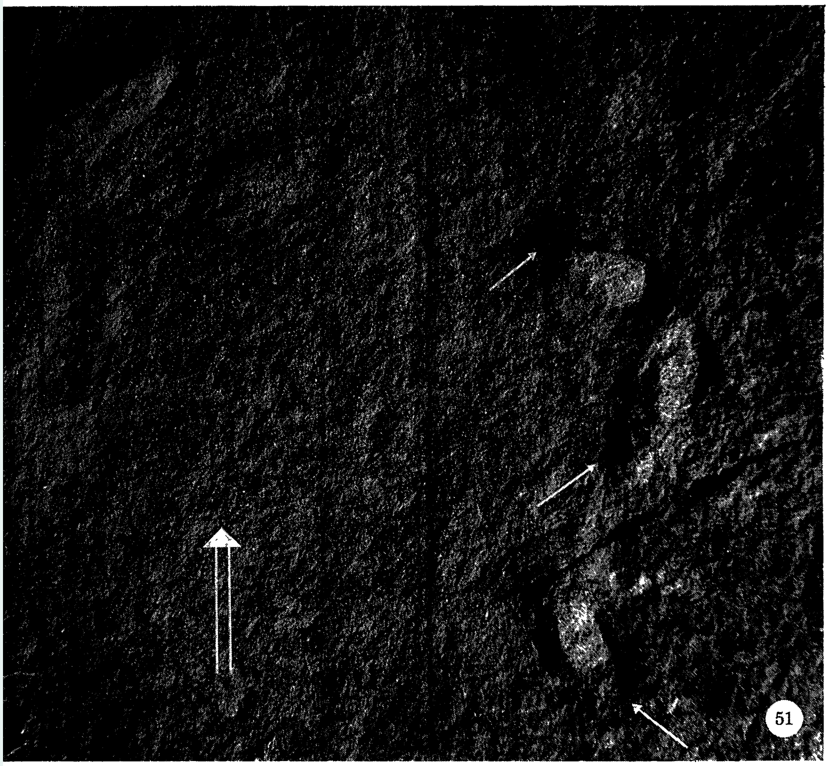


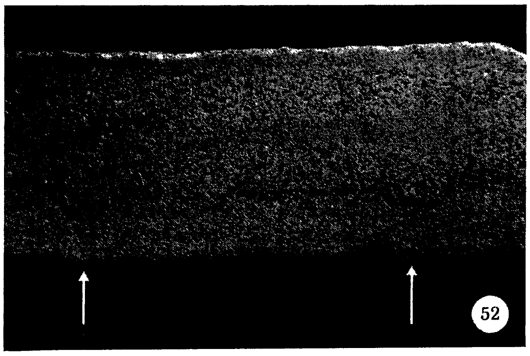




FIGURES 32–44. For description see opposite.

(*Facing p.* 544)



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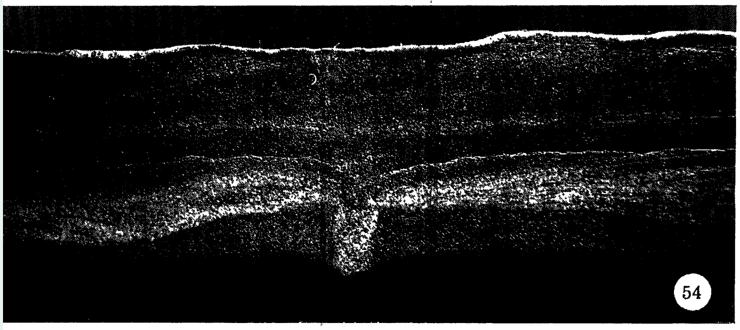

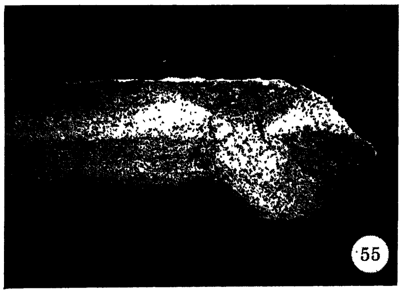

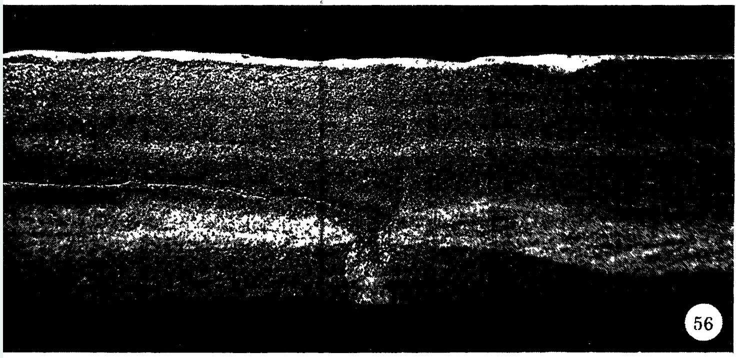

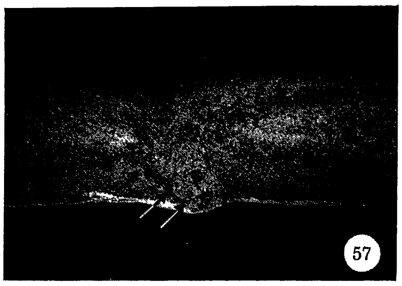

FIGURES 51–57. For description see opposite.

(*b*) *Sabden Brook, Whalley* (R_{1c-2a})

The succession exposed in Sabden Brook, Whalley (figure 45, northwest corner) has been described by Earp *et al.* (1961, p. 116, fig. 10), who recorded a band with *Reticuloceras gracile* and 'late *gracile*' above the Kinderscout Grit (figure 46). The following section, from the top of the marine band down to flaggy beds at the top of the Grit, has been collected in detail on both sides of the Brook at SD 746343, where just over 4.5 metres of measures are well exposed.

bed no.		metres
8.	Shaly mudstones with *Reticuloceras gracile* and 'late *gracile*', and with small bivalves, goniatites becoming very small in the lowest 0.25 m	*ca.* 1.00
7.	Grey somewhat pyritous mudstones with *Sanguinolites variabilis* M'Coy, *Palæoneilo* sp., *Polidevcia* cf. *acuta* (J. de C. Sowerby), *Aviculopecten* aff. *delepinei* Demanet, *Strobeus* sp., and with a basal leaf of *Lingula*, less common *Orbiculoidea* and small turreted gastropods	0.25
6.	Barren dark grey shaly mudstones with a 0.35-metre band of richly pyritous mudstone, including macroscopic blebs and nodules of pyrite and plant debris, 0.10 m from the base	1.02
5.	Dark grey shaly mudstone with occasional *Geisina* sp. and cf. *Sanguinolites* Hind *non* M'Coy	0.05
4.	Grey siltstones, rich in carbonate, with local lumachelles including crystalline pyrite 0.12 m from the top. Throughout the bed there are courses of abundant *Modiolus* sp., some with *Spirorbis* attached in commensal position (and closely	

Description of plate 4

Magnification is × 1.2 in all photographs.

Figure 51. Upper surface of a slab of siltstone with five burrows, *Pelecypodichnus* sp., all obliquely oriented to the bedding plane. The three right hand burrows (to the east) show infill by fine-grained lighter coloured sandstone, having subelliptical cross sections with one end sharpened (arrows), indicating the commissures of the shells. From a 0.43-metre siltstone-sandstone parting in the lower third of the Kinderscout Grit at Buckton Castle Quarry, Mossley, Lancashire, SE 991061 (figures 45, 46). Manch. Mus. M.3182.

Figure 52. Ground section, perpendicular to the bedding planes of fine-grained sandstone with darker carbonaceous siltstone laminae and showing parts of two small infilled bivalve burrows, *Pelecypodichnus* (arrows); from about the middle of a 9-metre sandstone lying immediately below the base of the Kinderscout Grit, in the upper part of Blackden Brook, 2.5 km N 10° E of Edale Church, Derbyshire, SK 1172 8832 (Stevenson & Gaunt 1971, p. 216). The left hand burrow shows, on the under surface of the slab, a clean-cut infilled section with sharpened end and long axis at 45° to the line of cut, whereas the right hand burrow is not visible on either upper or lower surface. Manch. Mus. M.3183A.

Figure 53. Ground section, as for figure 52, but with provenance as for figure 51. The burrow, *Pelecypodichnus*, has a structure suggestive of two phases (two arrows) of infilling by sandstone. Manch. Mus. M.3184.

Figure 54. Ground section showing siltstone laminae and infill of a single *Pelecypodichnus*. The section has been cut at 45° to the long axis of the burrow. Provenance as for figure 51. Manch. Mus. M.3185.

Figure 55. Ground section, as for figure 52, cut transverse to the long axis of *Pelecypodischnus*. The burrow shows marked inclination to the vertical and no evidence of more than a single fill of sandstone. As for figure 51. Manch. Mus. M.3186.

Figure 56. Ground section, as for figure 52, cut transverse to the long axis of *Pelecypodichnus* in banded sandstone-siltstone and with evidence suggestive of a single infilling of sandstone. As for figure 51. Manch. Mus. M.3187.

Figure 57. Ground section, as for figure 52, showing a strongly oblique burrow with constricted sides (arrows) suggestive of at least two periods of infill by sandstone. As for figure 51. Manch. Mus. M.3188.

bed no.		metres
	resembling the cf. *Naiadites* of fig. 10, pl. VI of Ramsbottom, Rhys & Smith 1960), and of fairly abundant cf. *Sanguinolites*, as above. Small turreted gastropods are rare. The siltstones have a basal 40-mm band of *Modiolus*	0.50
3.	Siltstones with carbonaceous fragments	0.13
2.	As for bed 4 (above), but without local lumachelles and with a 60-mm *Modiolus* band at the base	0.23
1.	Silty mudstones and siltstones grading down into fine-grained flaggy carbonaceous siltstones and thin sandstones with plant debris, with local bioturbation and occasional *Pelecypodichnus*. *Modiolus* is uncommon 0.15 m from the top	0.90

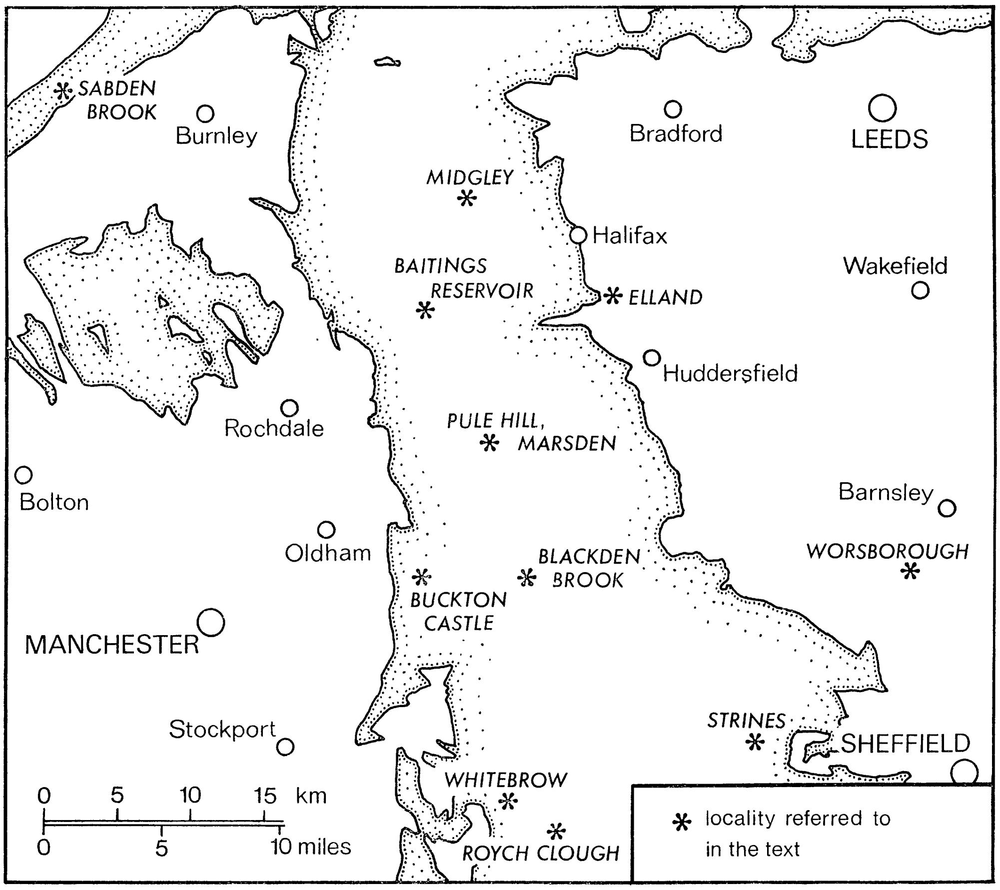

FIGURE 45. The stippled edge outlines the broad crop of Namurian rocks, the Millstone Grit Series of the Pennines, of which the upper part is shown in figure 46.

Surface features of the shells referred to cf. *Sanguinolites* Hind *non* M'Coy vary in the same way as those of the Mountcollins fauna, but concentric corrugations in the antero-ventral regions of the shells are less in evidence. As at Mountcollins, however, broad shallow corrugations of the shell may be variably impressed on the internal moulds (figure 13, plate 1; figure 27, plate 2; figure 41, plate 3). Occasional fragments of internal moulds of the larger shells show the single accessory scar of the pattern shown in figure 23. The comparisons of figures 47 and 48, including the distribution diagrams, reveal a large field of overlap in lateral outline. On the basis of these internal and external characters, and with the additional evidence provided by the associated marine faunas and overlying goniatites, the cf. *Sanguinolites* band of Whalley is correlated with that of Mountcollins.

The wide range of continuous variation shown by both shell assemblages is unparalleled in previous descriptions of Namurian bivalves. Moreover, very striking similarities to basal Westphalian faunas of *Carbonicola* may be seen in varieties within the trends of Series A, E, F, G, and I–K of figures 47*a* and 48*a*.

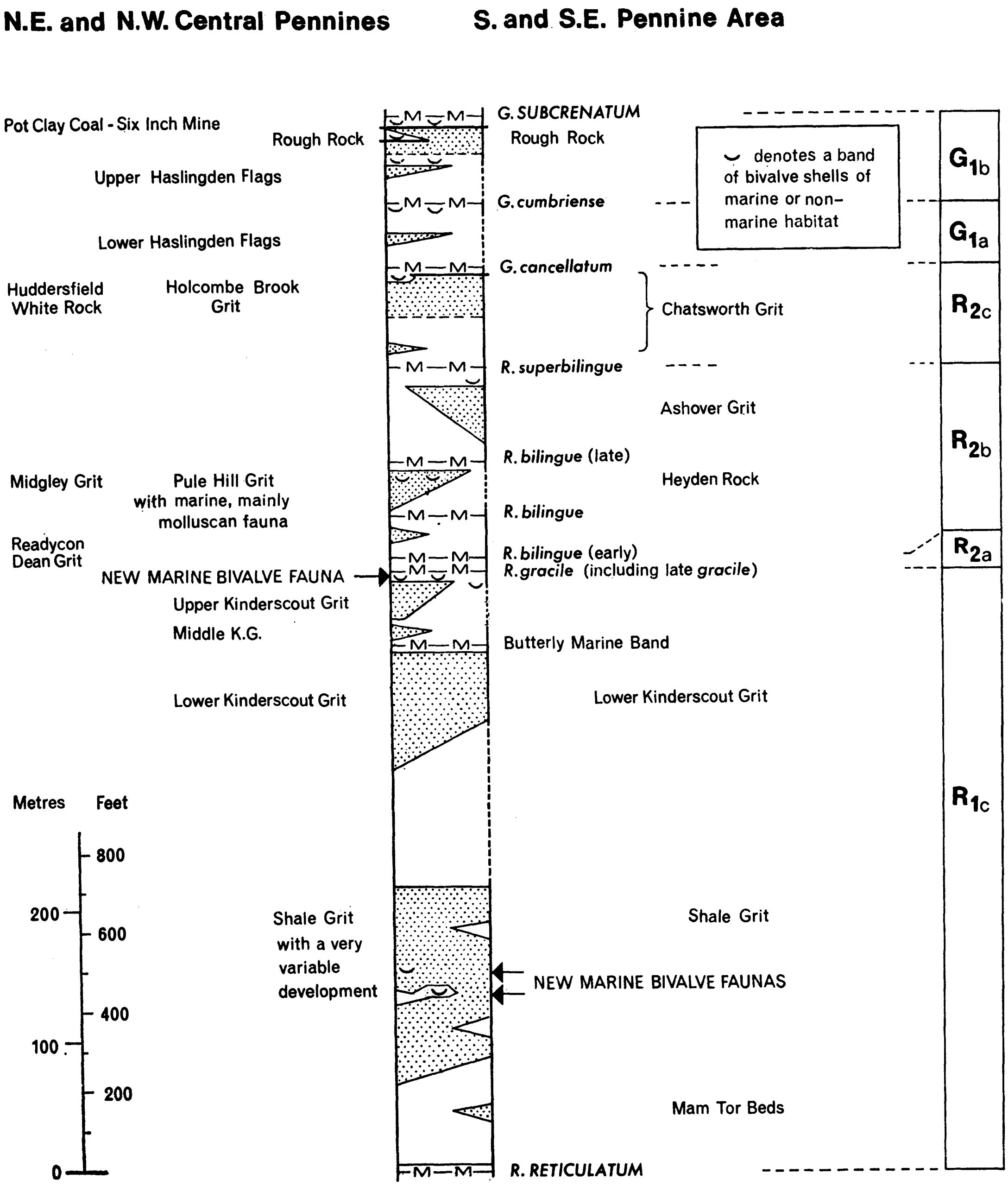

FIGURE 46. Schematic section of the succession in the upper Namurian Series of the English Pennine area. Major grits and sandstones are indicated by stippling. After Wright *et al.* (1927), Wray, Stevens, Edwards & Bromehead (1930), Bromehead, Edwards, Wray & Stevens (1933), Swinnerton (1946), Ramsbottom (1966) and Stevenson & Gaunt (1971).

(*c*) *The Heyden Rock* Carbonicola *of Strines area and of higher Namurian measures of the Pennines* (R_{2b})

Carbonicola was recorded from near the top of the Heyden Rock in the Strines area of Derbyshire (figures 45, 46) by Stevenson & Gaunt (1971). Internal moulds in sandstone of large, very variable shells occur as a death assemblage (Boucot 1953) and show a pattern of the anterior adductor and accessory scars (figure 28, plate 2, and the right valve of figures 29, 31) closely comparable with that of the faunas of Mountcollins and Whalley. Many of the shells from the Heyden Rock however have additional features which are unquestionably characteristic of *Carbonicola*, including evidence of a hinge plate posterior to the umbo (compare the internal moulds of figures 30, 31, and the thin median ridge of the mould of figure 29, which suggests swellings and depressions on the hinge plate). Less commonly the adductor scar appears to have been incompletely separated from the anterior adductor impression (figure 30, arrow) and its mould may bear a complex cusp (figure 29, left valve, arrow; cf. *Carbonicola*). Although there is considerable variation in both internal and external features of the Heyden Rock fauna, the more elongate *Anthraconaia*-like shells of figures 47*a* and 48*a*, series E, are lacking.

In a succeeding *Carbonicola* band, above the Ashover Grit and below *Reticuloceras superbilingue* (figure 46), external variation is again wide. The shells are commonly characterized by an early phase of oblique growth (figs 1–5 of pl. XV of Trueman & Weir 1951) and by the presence of high anterior lobes with very blunt antero-ventral rounding (cf. Series B, I, I_1, I_2, Series C, Group D, Series E of figures 47*a*, 48*a*). Blunting of the anterior end is particularly characteristic of the variable *Sanguinolites* of fig. 3 of Eagar in Jones 1969, although internal features, as far as they are visible, resemble those of the Heyden Rock fauna. Some varieties of the Ashover Grit assemblage show broad shallow corrugations in their antero-ventral regions (figure 19, plate 1), closely comparable with those of Mountcollins and Whalley and uncharacteristic of later *Carbonicola*.

In summary, the Strines fauna is referable to *Carbonicola* but shows a mosaic of mainly internal and some external features which grade with or are characteristic of those of Mountcollins and Whalley. The succeeding fauna, above the Ashover Grit, shows several features, mainly external, characteristic of both the Strines fauna and those of Mountcollins and Whalley. The approximate horizon of the Strines fauna is characterized by marine, mainly molluscan assemblages including gastropods at Pule Hill, Marsden (Barnes & Holroyd 1897, Ramsbottom 1966) and probably by *Sanguinolites ovalis* Hind *non* N'Coy (figures 25, 26) and by *Lingula* at Saddleworth near Oldham (Hind 1900, p. 411) (figures 45, 46). There are therefore both morphological links within a short stratigraphic interval and also palaeogeographic links, on more than one horizon, between late Namurian–early Westphalian *Carbonicola* on the one hand and the marine bivalve fauna of Mountcollins on the other.

(*d*) *The Shale Grit of Derbyshire* (R_{1c})

In a 0.43-metre parting, of siltstone with subordinate mudstone and thin sandstone layers, found in the middle part of the Shale Grit (figure 46) near the base of the exposure at Whitebrow Quarry, near Hayfield (figure 45), *Sanguinolites* aff. *plicatus* Portlock (figure 37, plate 3) is fairly common. A second, more oval, poorly preserved *Sanguinolites* occurs with it and includes shells which, on the basis of their surface features, cannot be distinguished from several varieties in the faunas of Mountcollins and Whalley. The shells are abundant, typically with both valves

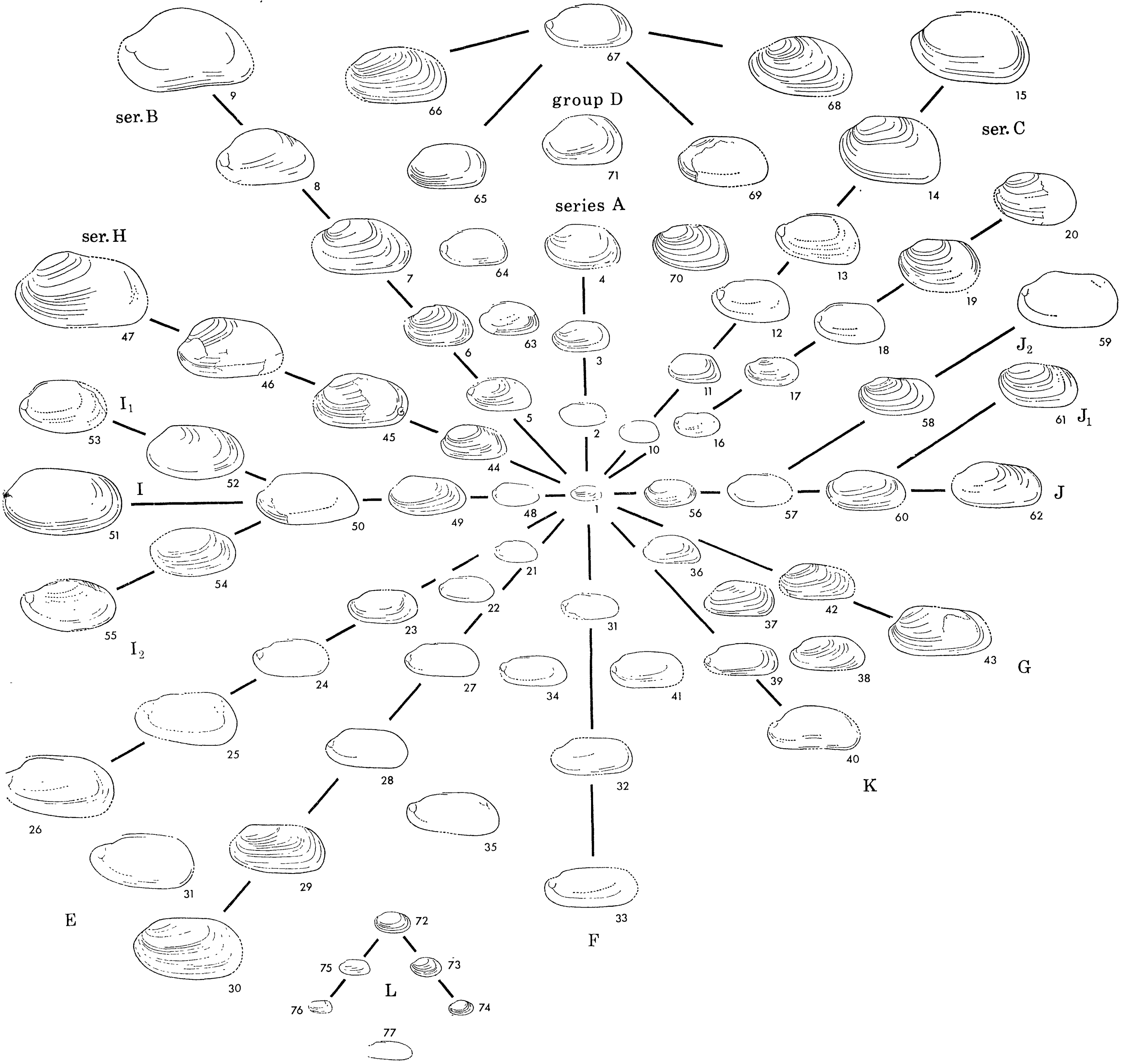

FIGURE 47*a*. For description see following page.

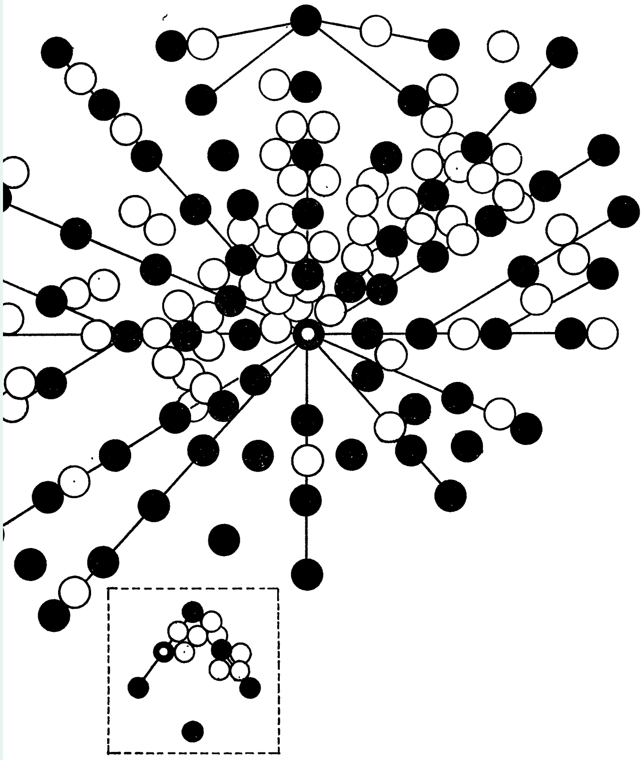

FIGURE 47*b*

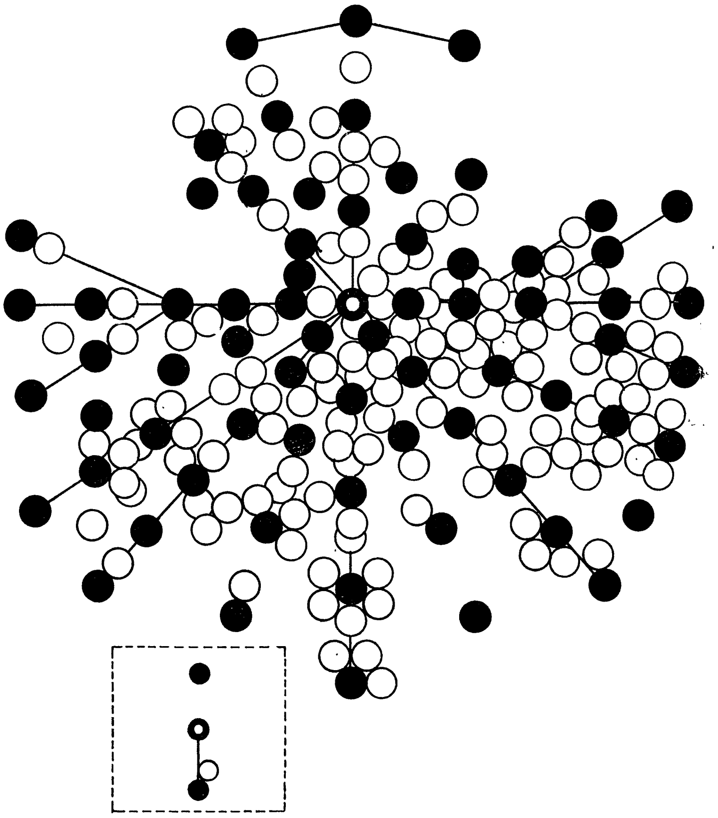

FIGURE 48*b*

FIGURE 47. (*a*) Cf. *Sanguinolites* Hind *non* M'Coy, from a 0.13-m band of dark shale lying below *Reticuloceras gracile*, including 'late *gracile*' at Mountcollins, County Limerick, Ireland (see the legend of figure 9). In the pictograph, in which account is taken of size as well as shape of shell, varieties with markedly increasing height/length ratios are shown in various 'northern' series outward from the norm, those with more elongate trends in the several 'southern' series. The series are lettered and the shells numbered for convenience of reference only. Shells in group D are in continuous variation with the remainder – compare series B, number 7, group D, numbers 66–68, series C, number 13; and note transitions between the varieties of series E, F, K (numbers 27, 34, 41, 39).

The norm (number 1) is repeated as number 75 in the separate diagram (L, bottom left) made to illustrate further variation in very small shells. In series E, numbers 24–26, 30, 31, 25, are closely comparable with *Anthraconaia ventricosa* Pastiels in both shape and size (compare figures 17, 18, 21, 24 in Pastiels 1960, pl. XXI). Similarities to *Anthracosia phrygiana* (Wright) and trends found in *A. aquilina* (J. de C. Sowerby) seen in series B and H were noted earlier (Eagar 1961, figs 3C, D) before the band was completely studied. All shells registered in the Manchester Museum, LL.5358–5403. (Magn. × 0.66.)

(*b*) Distribution diagram. Black circles denote figured varieties and white circles the remainder of the collected fauna, the position of each shell being controlled by its resemblance to one or more of the figured varieties.

FIGURE 48. (*a*) Cf. *Sanguinolites* Hind *non* M'Coy from 1.50 to 2.36 m below *Reticuloceras gracile*, including 'late *gracile*' in Sabden Brook, Whalley (figure 45 – see also the description of figure 12). The pictographic arrangement follows the same general plan as that of figure 47*a* but the letters of the series and groups denote usually comparable rather than precisely the same trends. Consistent differences within several of the series are greater elongation and more attenuation, or pointing of the shell towards the posterior end, in the Whalley assemblage.

Orientation of the shell is uncertain when the dorsum is strongly arched (cf. the different orientations of the shells numbered 6 and 12 in series B – the varieties are closely similar). In series K varieties compare with *Carbonicola limax* Wright, and in series J_1, J and J_3 with *C. obliqua* Wright. Other comparisons with *Carbonicola* of the *lenisulcata* Zone (basal Westphalian A) are referred to in the text. All shells registered in the Manchester Museum. LL.5404–5440. (Magn. × 0.66.)

(*b*) Distribution diagram, arranged as for figure 47*b*. The norm is repeated in the small diagram, bottom left. inset.

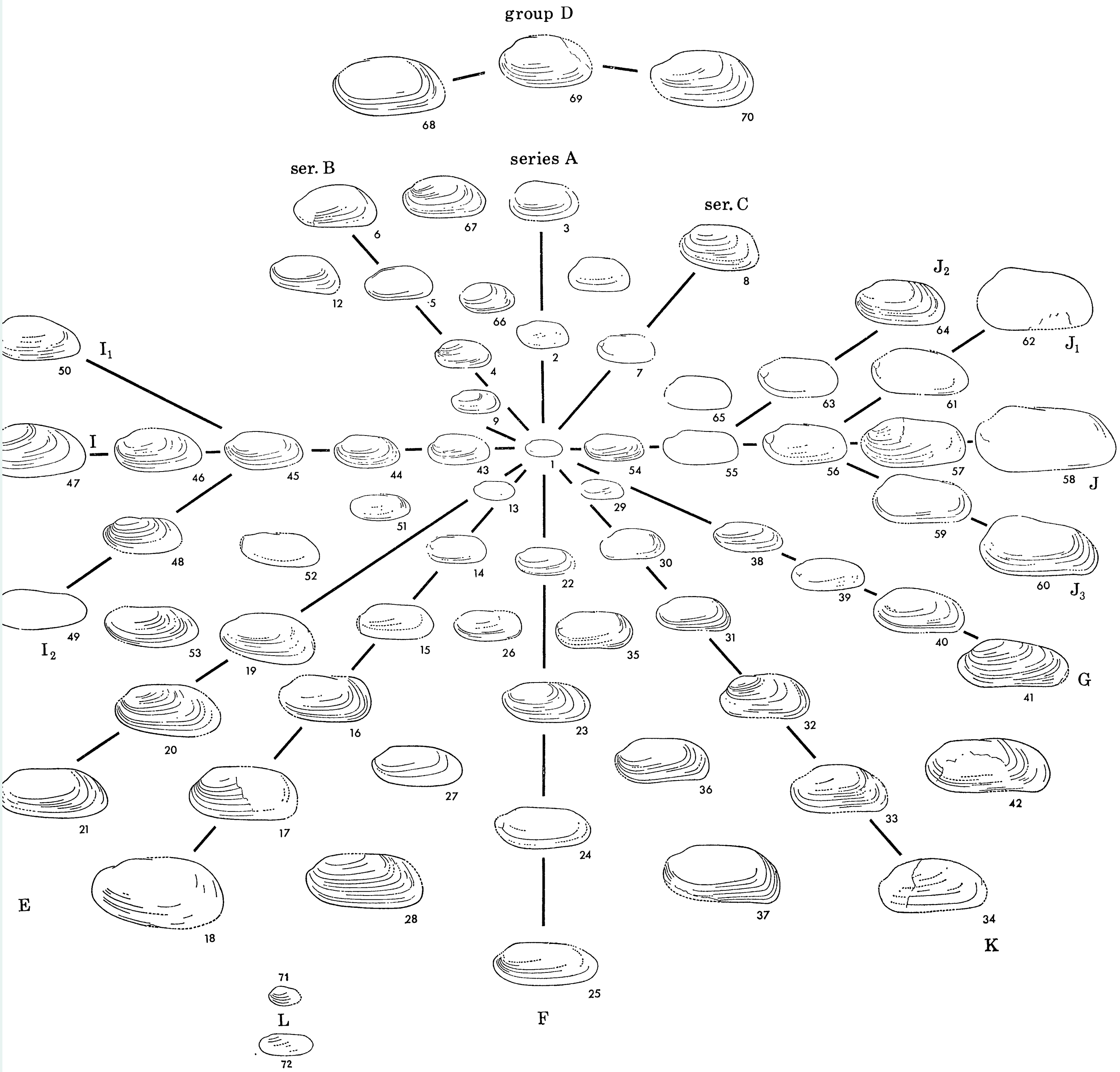

Figure 48*a*. For description see opposite.

present, lying immediately above two bands, each about 30 mm thick, of bioturbated carbonaceous siltstone and fine-grained white sandstone.

Slightly lower in the Shale Grit (figure 46), in a nearby exposure in Roych Clough (figure 45), smaller shells with comparatively fine lines of growth (figures 32–36, plate 3), but including occasional individuals to lengths of 40 mm, have been found sparsely within a 3-metre band of hard, richly micaceous siltstone with subordinate thin sandstones, underlying a sharp-based graded sandstone and grading down into darker, more fine-grained siltstones and mudstones. The shells, although comparable with members of the *Carbonicola bellula* (Bolton) group and, like these shells, being found commonly as pairs of open conjoined valves, include varieties with higher anterior lobes (figure 35) than any seen in later faunas of *C. bellula*. More than half of the Roych Clough shells show plications, or incipient corrugations, which tend to reach their maximum expression in their antero-ventral regions (figure 34). They are therefore referred, by inference, to the cf. *Sanguinolites* group of Whalley and Mountcollins, but are generally more elongate than these faunas (figures 49, 50, symbols), grading with and extending beyond the peripheries of the 'southwest' Series of figures 47*a* and 48*a*. Trace fossils, referred to cf. *Planolites*, occur at 2.63 m below the sandstone at Roych Clough and suggest a comparatively shallow-water origin for the band, as at Whitebrow Quarry, although both localities lie within a general succession of turbidites (Walker 1966).

THE SIGNIFICANCE OF THE NEW FAUNAS OF CF. *SANGUINOLITES* HIND

(*a*) *Generic features and comparisons: summary*

The newly found faunas of the Shale Grit cannot be separated from cf. *Sanguinolites* Hind on the basis of external features, no internal evidence being available. The same shells, and those of Mountcollins and Whalley faunas, are however closely comparable with and commonly indistinguishable from many of the forms attributed to *Anthraconaia*, and occasionally to *Carbonicola*, in Namurian A and B of Belgium and in Namurian B of the Netherlands. There is, furthermore, no evidence of the internal features of *Anthraconaia* lower than the middle of the *lenisulcata* Zone of Westphalian A, where much systematic work has been done (Weir 1966, p. 325). Since no member of unquestionable *Anthraconaia* has been seen to possess antero-ventral corrugation of the shell, it is very probable that the Belgian and Netherlands shells also belong to the marginally marine stock of cf. *Sanguinolites* Hind *non* M'Coy, of which ?*Anthraconaia kirki* Bennison, from the Scottish Viséan, may be the oldest known member. Thus on present available morphology, this stock of highly variable marine bivalves is very likely to have been ancestral to *Carbonicola*. However, until further taxonomic work can be done on the several groups recognized within *Sanguinolites* Hind (Wilson *in litt.* to me 4 February 1975), the newly found bivalve faunas appear more usefully left without a new generic name.

(*b*) *Palaeoecological aspects of the faunas of Mountcollins and Whalley*

The major features of the lithology and of the disposition or shells within the bands of Mountcollins and Whalley are summarized in table 1. Organic carbon and carbon dioxide from carbonates were determined by the methods of Groves (1951). All proportions are given as percentages. The figures for shells do not include any which were broken before burial.

The Mountcollins band is of almost uniform vertical extent, being slightly lighter coloured in the top few millimetres, where organic carbon content falls to 0.83 %. The sediment lies well within the clay grade, being closely comparable with that of grade 1 of Eagar (1947, p. 12), but has less disseminated pyrite and contains particles of quartz silt sporadically distributed within it. It shows cryptophyllitic texture (Dunham in Eagar 1952, p. 358). Shells lie in courses 5–15 mm apart, being usually distributed evenly and always without preferred orientation of their long axes. In different courses shells vary in concentration between 200 and about 1100 per square metre, all lying with their planes of commissure more or less parallel to the bedding. Disarticulated valves may be found occasionally, where they are associated with shell debris, much broken up and locally surrounded with secondary crystalline pyrite. *Modiolus*, which is comparatively uncommon, consists mainly of single values, some originally broken.

Table 1

	sediment			shells			
				paired			
	type	organic carbon	CO_2 from carbonates	closed	open	single valves	number used
Mountcollins	shale	9.97	0.04	61.3	27.5	11.2	80
Whalley	mudstone	0.92	7.84	21.0	4.0	75.0	124

Shells of cf. *Sanguinolites* are highly variable in outline (figure 47*a*, *b*), their dimensions being summarized in table 2, below. The h/l and a/l ratios are expressed as percentages, o.r., observed range. Obesities (t/l) are occasionally measurable. A mode of about 35 % for the Mountcollins assemblage is likely, whereas that of the Whalley Band is probably about 5 % lower.

Table 2

	length		height/length		anterior end/length	
	o.r.	mean	o.r.	mean	o.r.	mean
Mountcollins	8.6–36.0	21.07	43.6–64.8	53.24	17.6–29.4	22.99
no. measured	98		98		59	
Whalley	8.1–45.0	21.52	39.4–60.4	47.31	14.1–26.8	20.21
no. measured	131		131		81	

A comparison of the data in tables 1 and 2 with table 1 of Eagar 1974 (see also p. 537) indicates that the Mountcollins fauna is closely comparable, palaeoecologically and in terms of range of shell variation, with an established fauna of *Carbonicola* which lived under eutrophic conditions and beneath sedimentation which was sufficiently slow to allow slight displacements of open conjoined valves as the ligament decayed (cf. locality 4, fig. 14 of Eagar 1952; Band I, fig. 2 of Eagar 1961). Comparable data were noted and similarly interpreted by Broadhurst (1959) and by Pollard (1969, table 3, where conditions were less tranquil). The Mountcollins band therefore appears to represent a marine shallow-water epifaunal life assemblage (Boucot 1953), characterized by slow sedimentation and somewhat restricted circulation, which was disturbed only by occasional influxes of allochthonous shell debris. Palaeogeographical considerations (Calver 1969) suggest that these conditions could have existed in a somewhat sheltered shallow marine bay or lagoon which lay seaward of the late Namurian delta.

In the section at Sabden Brook, Whalley, shells of cf. *Sanguinolites* are mainly confined to thin leaves within finely banded quartz siltstones and shaly siltstones. These are interspersed with more numerous courses of *Modiolus* sp. and locally, towards the top of the band, with balled-up masses of shell fragments associated with thin lenticles of pyrite, which are absent elsewhere within the shell band. Single valves lying more or less parallel to bedding planes are more commonly convex- than concave-up. They show – rather uncommonly – a degree of preferred orientation in their long axes, about 5 % of them being found in positions inclined to the bedding (as in fig. 1 of Broadhurst 1959, right hand six attitudes). The few open valve pairs (table 1) all lie at inclinations to one another of less than 180° and all were found with ligament uppermost. Valves of the smaller *Modiolus* sp. proved more commonly articulated than those of cf. *Sanguinolites*. However within the band, single valves of the latter proved almost universal in its upper part, whereas towards the middle, nearly 50 % of the shells found were articulated valves. No differences in the range of variation of the shells were noted within subdivisions of the band.

Although successive leaves of the Whalley band obviously reflect variation in the operation of several environmental factors, the dominant influences in its formation were those of turbulent water and relatively rapid sedimentation. The Whalley band, in its low organic carbon content, with relatively high carbonate (table 1) and in its considerable proportion of disarticulated, commonly broken valves, is strictly comparable with a typical invading faunal assemblage of *Carbonicola* (Eagar 1974, p. 227). The parallel is reinforced by the differences in the variational patterns of the assemblages of Mountcollins and Whalley, which are in turn reflected in the dimensions of table 1, notably in the mean and ranges of the h/l and a/l ratios, and the probable decreases in obesity, both in the Whalley and in the invading faunas of *Carbonicola*. That the first two differences result from different patterns of growth in the shells is clear from figure 49, where there is a linear relation between height and length of shell above the length of 15 mm (broken line). By the method of Imbrie (1956) for the Mountcollins fauna

$$h = 0.654l - 2.51, \tag{i}$$

where $r_{hl} = 0.93$, and

$$a = 0.273l - 0.91, \tag{ii}$$

where $r_{al} = 0.90$.

For the Whalley assemblages the calculated lines are

$$h = 0.472l - 0.04, \tag{iii}$$

where $r_{hl} = 0.94$ and

$$a = 0.228l - 0.59, \tag{iv}$$

where $r_{al} = 0.87$.

The differences in the slopes of the fitted lines for h and l (figure 49) are significant at the 95 % level and also for a and l between Mountcollins and Whalley. Moreover, to complete the parallel between established and invading faunas of *Carbonicola*, the greater range of shell variation at Mountcollins is reflected in rises of the coefficient of variation of h and a from 20.96 and 25.60 at Whalley to 23.49 and 32.17 respectively at Mountcollins.

The smaller length classes are less well represented at Whalley than at Mountcollins (figure 49). Logarithmic plots of the two faunal assemblages (figure 50) indicates that in the Mountcollins fauna there is an inflexion around the length of 15 mm (compare fig. 13 of Eagar 1952 and fig. 10 of Eagar 1973). From the conclusions of Johannessen (1973), the inflexion may be interpreted as indicating loss of byssal attachment and therefore confirmation of an *in situ* fauna; whereas for the Whalley assemblage there is no inflexion and the full range of shell length may be represented by the line

$$\log h = 0.962 \log l - 0.635, \tag{v}$$

where $r_{\log h \log l} = 0.95$.

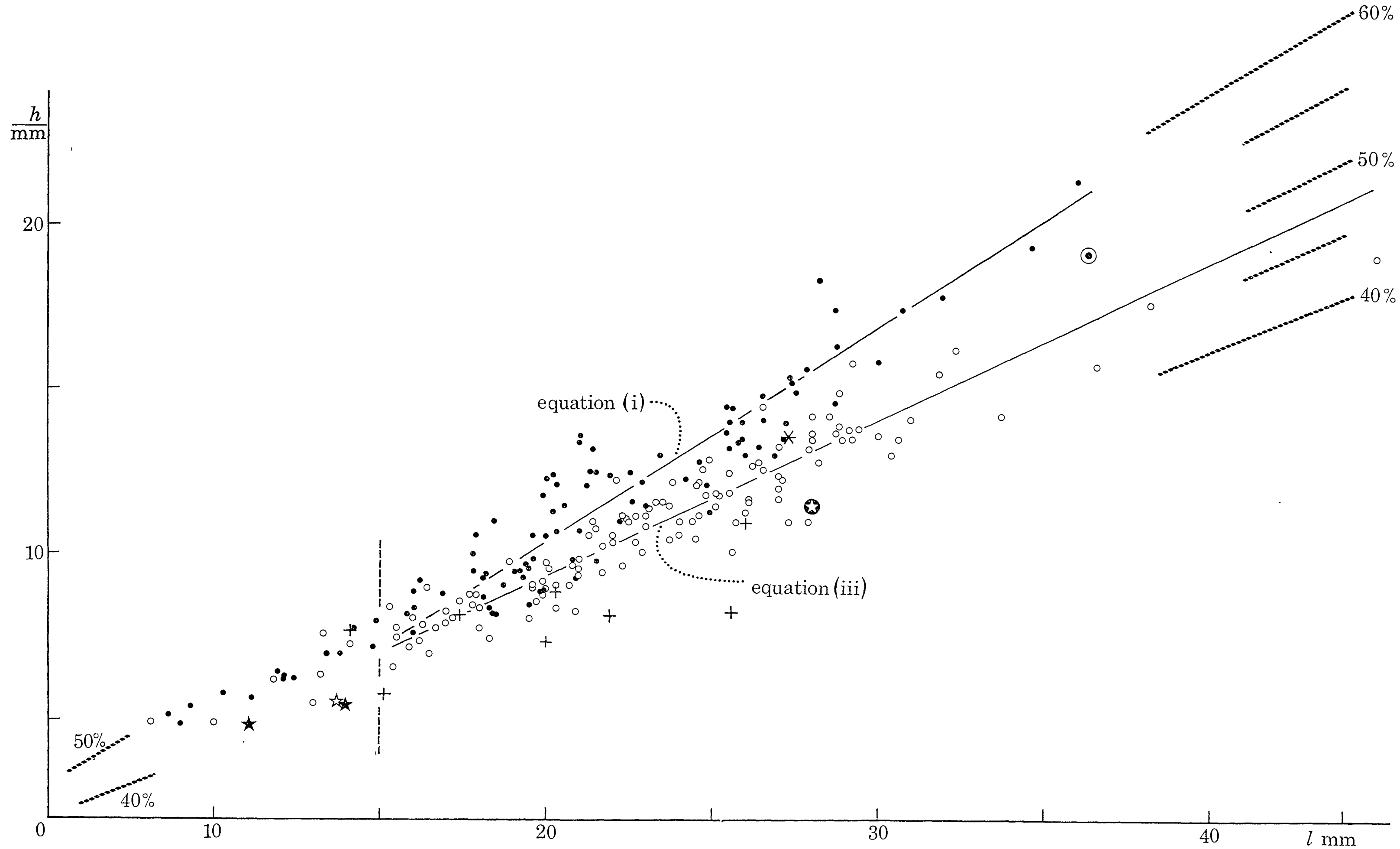

FIGURE 49. Height plotted against length of shells from the Mountcollins–Whalley faunas with positions of certain other shells indicated in the legend. The equations for the fitted lines for shells over the length of 15 mm (see the broken line) are given on p. 554. Faunas below *R. gracile*, late form. All cf. *Sanguinolites* Hind *non* M'Coy: •, from Mountcollins, Co. Limerick, Ireland, in dark richly carbonaceous shale; ○, from Sabden Brook, Whalley, northern England, in grey silty mudstone. Positions of other shells: ☆, *Carbonicola bellula* (Bolton), holotype, G_{1b}; ★, *C. bellula*, & *C.* aff. *bellula* topotypes, figured Eagar 1954; +, cf. *Sanguinolites* Hind *non* M'Coy, Shale Grit, R_{1c}; ✪, *C. limax* Wright, holotype, Westph. A, lower; ⊙, *C. lenicurvata* Trueman, holotype, R_{2c}, top; ⨯, *Anthraconaia ventricosa* Pastiels. Holotype, *ca.* G_{1a}.

The lack of the usual inflexion in the line of mean allometric growth may be interpreted as either a much earlier loss of byssal attachment in the more turbulent conditions of the palaeohabitat at Whalley, or the selective removal, by turbulence and current action, of the smaller, more nearly globose and consequently lighter bivalves (figures 47, 48, bottom left corners; compare the loss of small shells noted by Broadhurst (1964) in mudstone communities of *Anthracosia* and his discussion of the possible causes of this).

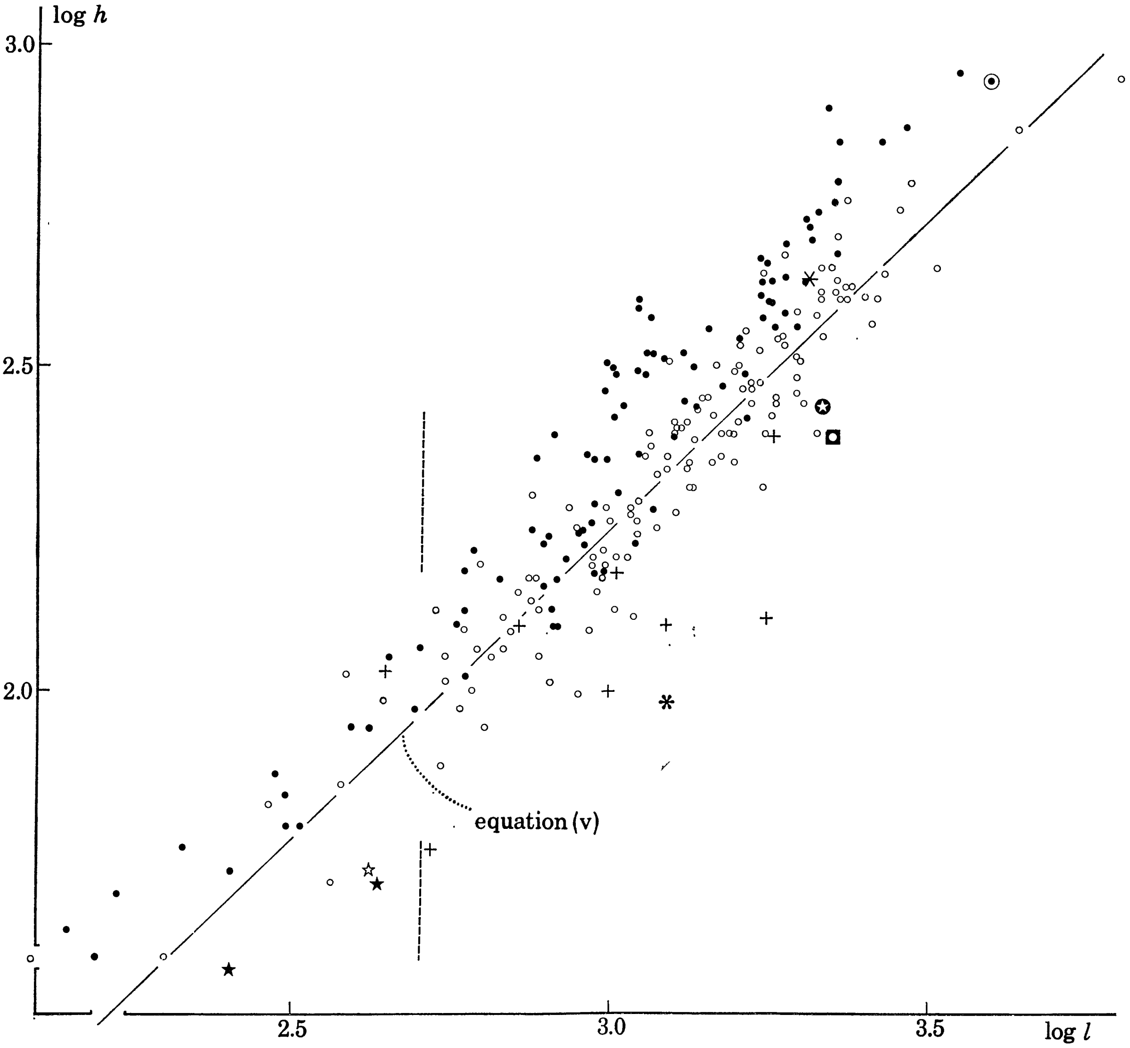

FIGURE 50. Logarithms of shell height and length for the faunas shown in figure 49. The same symbols are used and some further symbols for additional shells are utilized. The fitted line (equation (v)) has been applied to the full range in length of the shells from Whalley. The broken line shows the position of the natural logarithm for the length of l = 15 mm. Additional symbols ◘ *Anthraconaia angulosa* Pastiels. Holotype; ✱ *A. perlongata* Pastiels 160, fig. 4, pl. XXI topotype.

Although the Whalley band appears to be essentially a death assemblage (Boucot 1953), its numerous similarities to an invading fauna of *Carbonicola*, including the occasional presence of the burrow *Pelecypodichnus* beneath it (cf. Eagar 1974, p. 227), suggest that the original palaeohabitat was probably little if any different from that in which the shells were finally entombed. Moreover, on the basis of its summarized faunal and lithological detail, the band also compares closely with that of a subtidal delta-front, or delta top, as outlined by Donahue, Rollins &

Shaak (1975), who interpreted localized pyrite masses as resulting from the mass burial of opportunistic clam communities and the concomitant decomposition of their soft parts. In this situation the steep-burrowing position would have afforded stability during periods of turbulence, elevating the inhalent apertures of the shells to a maximum above the rapidly accumulating sands and silts, as the delta itself moved forward.

The invasion of the Namurian delta of the Pennines

(*a*) *The characteristics of bivalve burrows* (*late Namurian to Westphalian*)

Palaeoecological evidence of both downward burrowing and upward movement by bivalves is clear only in sediments subject to rapid alternations in grain size or in constituents (Eagar 1974). When these conditions have obtained, as for instance in the complex siltstone-sandstone facies of Elliott (1968), burrows referred to *Pelecypodichnus* and to *Pelecypodichnus* escape shafts, tend to reveal a series of asymmetrical subconical to elliptical depressions, with long axis of length about 15–18 mm and extending through some 0.02–0.25 m of strata. Both on the evidence of occasional conjoined closed bivalve shells found at the tops of burrows (Collinson & Banks 1975, quoting unpublished results of P. G. Hardy) and by inference from the measurements of burrows and those of associated bivalves (Eagar 1974), it is clear that *Carbonicola* of late Namurian and early Westphalian time burrowed with long axis of the shell vertical or near the vertical (Hardy 1970; Eagar 1971, 1974) as shown in figure 1*a*. The structures tend to be elliptical in sections parallel to the bedding (fig. 9 of Eagar 1974) where they commonly appear as infillings of fine-grained sandstone within darker siltstone. The ellipses are sharpened at one end (figure 51, plate 4, arrows) which marks the former position of the ventral commissure of the bivalve. *Pelecypodichnus*, seen as a depression on the upper surface of a slab of siltstone (figure 51, top left), or as an elongate subelliptical bulge on the lower surface, appears to have varied according to the thixotropic character of the sediment penetrated. The trace fossil is most clearly seen in vertical section when outlined by thin siltstone laminae including carbonaceous material, which are characteristically a millimetre or slightly less in thickness (figure 52, arrows). Shells have been found much more commonly above burrows than within them (Eagar 1971, 1974), a fact which suggests that upward movement of bivalves, resulted generally in their escaping burial by sedimentation. On the other hand, burrows have been found in prolific quantity, notably in late Namurian (Yeadonian, G_1) beds (figure 46), but without trace of overlying shells, and much the same situation may be found in the Elland Flags of Elland (figure 45), which lie near the base of the *communis* Zone of Westphalian A, some 300 m above the top of the Namurian in east Yorkshire (Eagar 1974, p. 231). Since new burrows may re-commence in positions different from those of terminated burrows (fig. 10*a* of Eagar 1974) in unfossiliferous sections several metres thick, it seems improbable that the total number of survivors of upward movement were periodically swept away and replaced immediately by new assemblages with the same population densities, and that these commenced upward movement once more to repeat the cycle. A more reasonable explanation of the absence of any fossils in these predominantly coarse-grained sediments postulates their original presence and subsequent removal in solution. In support of this view, it has been noted that large concretionary bodies of calcium carbonate, and certain richly calcareous sediments, both lying above heavily burrowed horizons, have been found locally to contain shells (for example in Eagar 1974, pp. 227, 233). It is much less easy to visualize conditions under which shells could be removed subsequently from more argillaceous measures, such as pale grey mudstones, which commonly succeed rich established faunas and reveal reduction in shell size immediately preceding disappearance of the faunas (Eagar 1952, Broadhurst 1959 – see also section (*e*) below).

To summarize, palaeoecological evidence is in conformity with the view that both downward burrowing and upward rising of *Carbonicola* took place in late Namurian and early Westphalian time during the deposition of silty to arenaceous beds, and that these movements were accomplished when the long axis of the shell was vertical or near the vertical, with posterior end upward; furthermore, that many of the sedimentary environments, including those of sandstone deposition, were at least locally more heavily colonized by bivalve life than the occasional relic of a shell in sandstone or siltstone now suggests.

(*b*) *The stratigraphical distribution of burrows* (R_{1c}–G_{1b})

No examples of *Pelecypodichnus* have been reported below Zone R_{1c} of the Namurian of the Pennines. In approximately the middle of the Shale Grit of Derbyshire the siltstone associated with cf. *Sanguinolites* Hind *non* M'Coy appears suitable for the retention of trace fossils, since it includes cf. *Planolites* at Roych Clough (p. 552), but it reveals no trace of bivalve burrows. At the slightly higher horizon seen at Whitebrow Quarry (p. 548) abundant shells, including *Sanguinolites* aff. *plicatus* and cf. *Sanguinolitus* Hind, immediately overlie bioturbated bands of siltstone and sandstone, but without recognizable bivalve burrows.

Unquestionable *Pelecypodichnus* (figure 52, arrows) indistinguishable from examples associated with *Carbonicola*, is present sparsely on a higher horizon, in the uppermost beds (Grindslow Shales, figure 46) below the base of the Kinderscout Grit in the upper reaches of Blackden Brook (figure 45). The burrows were found on a single horizon near the centre of the shale-siltstone-thin sandstone group, 9 m thick, recorded by Stevenson & Gaunt (1971, p. 216), but no shells were found with them. Burrows available for measurement have long axes of about 15 mm and show clearly the former commissural junction of the once present bivalve. Burrows were found to extend through 13 mm or slightly more than this thickness of sediment. There is therefore no evidence that these structures represent more than resting burrows, from which it appears shells were subsequently washed out (figure 52), but their general appearance is closely similar to those of the later escape shafts of *Carbonicola*.

Within the basal quarter of the lower leaf of the Kinderscout Grit at Buckton Castle Quarry, near Mossley (figures 45, 46, *Pelecypodichnus* is fairly abundant within a parting, dominantly of siltstone, through a maximum of 0.43 m, but again no bivalve shells have been found in their vicinity. A typical distribution is shown in figure 51, plate 4, where the burrows, which are not distinguishable from those of *Carbonicola*, have axes which make oblique angles with the bedding and may be seen more clearly in the ground sections of figures 53 and 55. The burrows do not commonly extend through a thickness of more than 10 mm, measured at 90° to the bedding plane the longest burrow seen reaching just over 20 mm. On bedding planes the long axes of the burrows show a preferred orientation through the greater part of their vertical extent, veering between NNE and NE, and in this respect comparing with the orientated burrows of *Carbonicola* (Eagar 1974; Collinson & Banks 1975). Whereas the vertical sections of figures 54–56 show no evidence of more than a downward burrow and the subsequent removal of the bivalve, two periods of infilling of the burrows appear probable in the case of the oblique structure of figure 53 (arrows) and in the constrictions of figure 57 (arrows), thus suggesting in each case two episodes of upward movement.

The burrow traces below the Sabden Brook shell band appear similar to those of Buckton Castle Quarry. On the succeeding horizon of the Scotland Flags, lateral equivalent of the Readycon Dean Grit (figure 46, lower R_{2b} Zone), bivalve burrows are generally more abundant and slightly larger, as in the region of Baitings Reservoir (figure 45), in stream sections at SE 002192 and 986182, the latter including oblique structures similar to those of figures 53 and 55. In Midgley district (figure 45) weathered quarried slabs of Scotland Flags are associated with burrows at SE 032267 and occasionally include what appear to be traces of internal moulds of shells with long axes strongly current orientated, others appearing to have accumulated, without obvious orientation, in the troughs of rippled surfaces. At Crow Hill Nook Quarry, Midgley (SE 021274) *Pelecypodichnus* is locally very common through just over 10 m of beds including sandstones up to 1.5 m thick. At the base of this section individual burrows in siltstone-sandstone laminae vary in minimum depth from 8.5 to 32 mm, with a mean, for 24 burrows, of 19.2 mm. They include unquestionable escape shafts, some with curved vertical axes, commencing obliquely to straighten upwards, with axes approximately vertical (Manch. Mus, LL.5447A, 5448). Oblique burrows tend to show displacement 'downstream', as evidenced by other sedimentary features (Collinson & Banks 1975).

Burrows are more generally vertical and commonly longer, forming *Pelecypodichnus* escape shafts, above horizons of undoubted *Carbonicola*, as in the Ashover Grit (figure 46, upper part of Zone R_{2b}), where they reach lengths of 0.22 m. In the Haslingden Flags (G_{1a-1c}) *Pelecypodichnus* reaches prolific abundance; the escape shafts reach their maximum length in the Namurian and may show striking current orientation (pl. 26 of Collinson & Banks), some horizons yielding sparse *Carbonicola bellula* (pl. 4 of Eagar 1971).

In summary, the stratigraphic distribution of bivalve burrows is in conformity with the continuity found between the stock of cf. *Sanguinolites* Hind and early *Carbonicola*. Available field evidence carries the suggestion that oblique burrowing commenced shortly after the arrival of the cf. *Sanguinolites* stock within the Pennine delta; that upward movement of individual bivalves, originally oblique, tended to become more nearly vertical with time and of longer vertical extent as bivalve populations increased within the deltaic area.

(*c*) *Sedimentation and the growth of the late Namurian delta of the southern Pennines*

The thick succession of clastic sediments occurring in Zone R_{1c} of north Derbyshire, north Cheshire and south Yorkshire, was deposited during the advance of periodic shallow water conditions into the southern part of the central Pennine basin (Reading 1964). The Shale Grit constitutes mainly a submarine fan of proximal and distal turbidites (Walker 1966) and these were probably generated by floods from the major distributaries of the delta rather than sediment movement on the upper part of the slope (H. G. Reading, personal communication 16 June 1976). The deep-water implications of the term turbidite are not necessarily applicable to the environments of the newly found Shale Grit faunas, since 'these same floods also produce sharp-based graded sandstones...which of course may look like turbidites, since the mechanism of deposition by waning flow is the same' (H. G. Reading, personal communication). The Shale Grit is succeeded by the Grindslow Shales (figure 46) which reveal trace fossils and indicate the commencement of the delta slope (fig. 2 of Collinson 1970). The horizon of the lowest recorded *Pelecypodichnus*, near the top of the Grindslow Shales, according to Collinson (1970) lies at or near the delta top, and those in Buckton Quarry probably within channel deposits of the Kinderscout Grit. The

Sabden Brook fauna may have entered the deltaic area following subsidence, or rise in sea-level, at the close of the deposition of the migrating fluviatile complex of the Kinderscout Grit – the latter had already been interrupted by the widespread incursion comprising the Butterley Marine Band, primarily yielding *Sanguinolites* (Bromehead, Edwards, Wray & Stephens 1933). Collinson, Jones & Wilson (1977), in recording turbidites in R_{2b} west of Blackburn, place the delta top in immediately pre-*Reticuloceras gracile* time over the area of Sabden Brook and Burnley with progradation of the slope, placed then north-north-west through Blackburn, proceeding west-south-west. There is therefore additional palaeogeographic reason for supposing that the Sabden Brook assemblage constituted that of a delta front or top under comparatively heavy sedimentation and subject to episodic turbulence as compared with the tranquil organic-rich muds of the Mountcollins band.

In the succeeding measures of R_2 Stage, notably beneath grits where the delta moved southward at this time (Ramsbottom 1966), and after the commencement of the Yeadonian Stage, the deltaic area shows evidence of considerably increased and persistent colonization by bivalves which lived under heavy sedimentation such as has been studied quantitatively in modern deltaic complexes. A delta front, for instance the Birdfoot delta of the Mississippi, moves seaward at speeds of the order of 75 m a year (Gould 1970, p. 75). A bivalve living in marginally marine conditions, such as a shallow marine bay, but in the path of an advancing delta front, would initially have to cope with an increasing rate of deposition of finer sediment, followed by coarser sediment. Its survival would therefore depend primarily on upward rather than lateral movement, as the delta front invaded the habitat of the bivalve. In a hitherto uncolonized environment, relatively rich in nutriment from the decay of swamp vegetation (Eagar 1974, p. 236), upward movement may be presumed to have kept pace with sedimentation (figure 1*a*). Moreover, it seems probable that a selective premium was placed at an early stage on bivalves best adapted to the function of remaining stable in these conditions and of rising, thereby avoiding burial.

(*d*) *Locomotor activity of bivalves in relation to type and shape of shell*

Ceteris paribus, bivalves with smooth shells burrow more swiftly, as measured by Burrowing Rate Index, than those with any kind of ornament (Stanley 1970, p. 57). Anthracosiids are all smooth-shelled and loss of shell 'ornament' within the postulated line of cf. *Sanguinolites*–*Carbonicola* has been emphasized in the transition from marine to non-marine environments, where there is evidence of increased locomotor activity of the bivalves. Krantz (1972) moreover drew attention to the reduced dentition characteristically associated with marine epifaunal suspension feeders, whereas the more active burrowers tend to have heterodont dentition, notably shallow burrowing genera (Stanley 1970). It may therefore be significant that in both *Paracarbonicola* and subsequently in *Carbonicola*, the earliest near-marine or marine forms were edentulous, and that primitive teeth appeared later, in non-marine deltaic conditions.

That burrowing downward to the position of figure 1*a*, followed by rising with the same orientation of the shell, is suggested by the experimental results of Krantz (1975) who observed the activities of bivalves of widely different taxa when subjected to anastrophic (localized catastrophic) burial. Members of the more primitive groups all moved upward in this way, pushing with the foot, but Krantz (1972) found that rate of upward movement tended to be slower, by an order of magnitude, than downward burrowing; furthermore, that the swiftest burrowers were also the most rapid risers, or escapers (compare the deductions in section (*b*) above).

Burrowing is a geotactically orientated response to exposure (Nair & Ansell 1968). A burrowing cycle (Trueman, Brand & Davis 1966*a*), which appears applicable to all living burrowing bivalves (Trueman 1975), includes a phase at which the shell is rotated to a varying degree, first to the anterior and then immediately to the posterior (figure 1*b*, left and right hand curved arrows respectively), through pull by the pedal retractors (Trueman *et al.* 1966*a*: Stanley 1970). Forward and backward rotation of the shell takes place about the centres *x* and *y* of figure 2*b*, so that the shell slices its way obliquely downward (figure 2*b*, large open arrow); but this angle can vary from 90° to the substratum (Stanley 1970) to nil, as when the bivalve moves on the surface (Thomas 1975), or ploughs parallel to it (cf. the postulated movements of shells in established faunas of the Carboniferous). The elongate *Margaritifera margaritifera* (Linnaeus), a unionid stream or river species, progresses horizontally this way over sand and gravel, but burrows steeply to reach a near-vertical living position (Trueman 1968), closely comparable with that of figure 1*a*. Entry of *M. margaritifera* into the sediment is facilitated by a small pedal gape between the valves in the antero-ventral region, so that the shell is pulled forward, with its long axis in the direction of movement (see restoration of the foot in figure 1*a*), presenting in this way minimum resistance to the sediment (Trueman *et al.* 1966*b*). Although it appears likely that shells of the *Carbonicola bellula* group entered the substratum in the same manner, evidence of a pedal gape is difficult to obtain because conjoined valves are uncommon and their preservation in relatively coarse grained siltstone is insufficient to indicate clearly whether or not a gape was once present. My examination of several hundred shells and internal moulds of *Carbonicola* of elongate type, that is with *h*/*l* ratio 50% or less, obtained from basal Westphalian measures and now in the Manchester Museum, has revealed the occasional presence of a very slight gape, invariably in the antero-ventral region of the commissure. An equal number of larger *Carbonicola* with greater *h*/*l* ratios, including excellently preserved shells of the *Carbonicola pseudorobusta* group (collections of the Institute of Geological Sciences) and some equally well preserved *Anthracosphaerium*, has failed to produce any evidence of a gape. There is therefore some indirect evidence that a gape may have been present in *Carbonicola* and its associates in late Namurian time. It appears also relevant that river unionids tend to live with their commissural planes at right angles to the plane of the substratum and with their posterior ends facing upstream, or approximately so (Dr M. B. Matteson, personal communication; Stein in Eagar 1974, p. 235). Elongate shells participate in these activities in river sands and silts and tend to have low obesities and to show 'streamlining' of the shell (Trueman *et al.* 1966*b*). It appears significant that shells of the *Carbonicola bellula* group have been found in current orientated position in the coarser sediments of the late Namurian and basal Westphalian of the Pennines (p. 558) and that they have low obesities, including low inconspicuous umbones, which would have contributed to 'streamlining' of the shell and would have facilitated their passage upward as well as downward (cf. Krantz 1975, above) when moving through the sediment.

Although ecological factors in the settling and early ontogeny of the spat cannot be entirely discountenanced as possible influences in the production of invading and established faunas (Eagar 1974, p. 236), growth studies do not encourage the belief that they were of major significance (Eagar 1947, 1952, 1961); nor does this appear likely in the contrasted morphic spreads of figures 47 and 48 (see figures 49, 50). The broad features of the shells of the *Carbonicola* *bellula* group are those which the action of steep-burrowing – and rising – might be expected to select from the wide variational range of the group of cf. *Sanguinolites* Hind *non* M'Coy.

(*e*) *Changes of sedimentational rate in relation to faunal change*

Increase in the length of the anterior end of the shell (a/l ratio), in h/l and t/l ratio, has been noted to accompany entry of a fauna of freshwater unionids, such as *Anodonta*, into eutrophic conditions (Agrell 1949). Comparable cases have been cited of supposed *Anthraconaia* showing the same general changes in late Carboniferous sediments (Eagar 1975, pp. 49–51). Increase in these shell ratios provides increased bulk of the soft tissues of the bivalve against its surface area, and therefore provides a higher energy or metabolic potential in conditions of comparative tranquility, although this trend can be of benefit to the bivalve only up to a limit (Wilbur & Owen 1964) and little or no work has been done to measure the effects of such a potential (E. R. Trueman, personal communication). Increased obesity however can be of selective value in providing support for shells on the softer more yielding bottoms of eutrophic environments, where the influence of ecological factors may be immediate, as witnessed within a year of transplant experiments of *Venerupis* (Eagar, in preparation). Furthermore, increased obesity, resulting in inflated umbones surrounding a well defined lunule, as in *Mercenaria* and *Anthracosphaerium*, can be of advantage in permitting faster oblique penetration of the substratum (figure 1*b*, broad arrow) with the same expenditure of energy (Stanley 1975). Muddy sediments in fact offer less resistance to burrowing than sandy ones (Trueman *et al.* 1966*b*), but lack of good pedal anchorage in mud tends to limit pedal activity on finer grained substrata (Nair & Ansell 1968). Thus the modal differences in the shapes of the shells outlined in figure 1*a*, *b*, where burrowing position is deduced from observation, are fully consonant with the functional advantages and limitations of the two contrasted palaeoenvironments.

It appears to be largely because of lack of good pedal anchorage that when established faunas of *Carbonicola* have been subject to increased turbulence, as is commonly found in Westphalian A measures, changes have taken place in the faunas in such a way that the survivors have shown a significant increase in specific gravity. The latter change has evidently occurred in assemblages of Recent *Margaritifera*, in certain venerids and in *Carbonicola* (Eagar 1968, papers 22, 23; 1973 p. 408 respectively). In view of the results of the present paper, which encourage the belief that selection broadly operated in maintaining the more elongate varieties as burrowers and risers under heavy deltaic sedimentation, it is relevant to search for any effects when later established faunas of *Carbonicola* were once more subjected to much increased sedimentation.

Generally within late Namurian and Westphalian faunas increased rate of sedimentation has tended to be associated with decrease in the size of bivalve shells and alteration in their relative growth rates, commonly leading to local extinctions (Eagar 1952; Broadhurst 1959, 1964). However, in a study of sedimentation and shell growth of *Carbonicola* near the top of the Pennine Namurian, it was noted that where sedimentation was deduced to have reached a local maximum within an established fauna, an invading fauna of *Carbonicola* cf. *bellula* appeared (fig. 1 of Eagar 1952). Moreover I have field notes which indicate that only at this locality were a few shells (5 out of 31) in the associated established fauna, found in steep-burrowing positions.

Further evidence is now available from a section above the Flockton Thin Coal, of upper Westphalian A at Worsborough (figure 45). Alternations of established assemblages of *Carbonicola* (figure 58 'C') and of incipient *Anthracosia* ('A'), showing continuous variation between one another, occur through more than 11 m of measures, above which fossiliferous strata cease as the sequence grades up into siltstone and sandstone (figure 58, left hand side). Faunas of *Carbonicola* are confined to thin bands of dark, richly carbonaceous shale where palaeoecological evidence indicates that both turbulence and rates of sedimentation were at a minimum (fig. 2, Band I, of Eagar 1961; fig. 1 of Eagar 1962). In those with *Anthracosia* both the latter factors increased (Band II of Eagar 1961, fig. 2). The differences in the faunas of *Carbonicola* and *Anthracosia* are seen biometrically in the reduction of mean shell length (size) in the latter (figure 58, centre) and in changes in the pattern of growth of the shells as expressed by the equation $h = \boldsymbol{a}l + \boldsymbol{b}$, where $\boldsymbol{a}$ is the coefficient of relative growth and the slope of the fitted line,

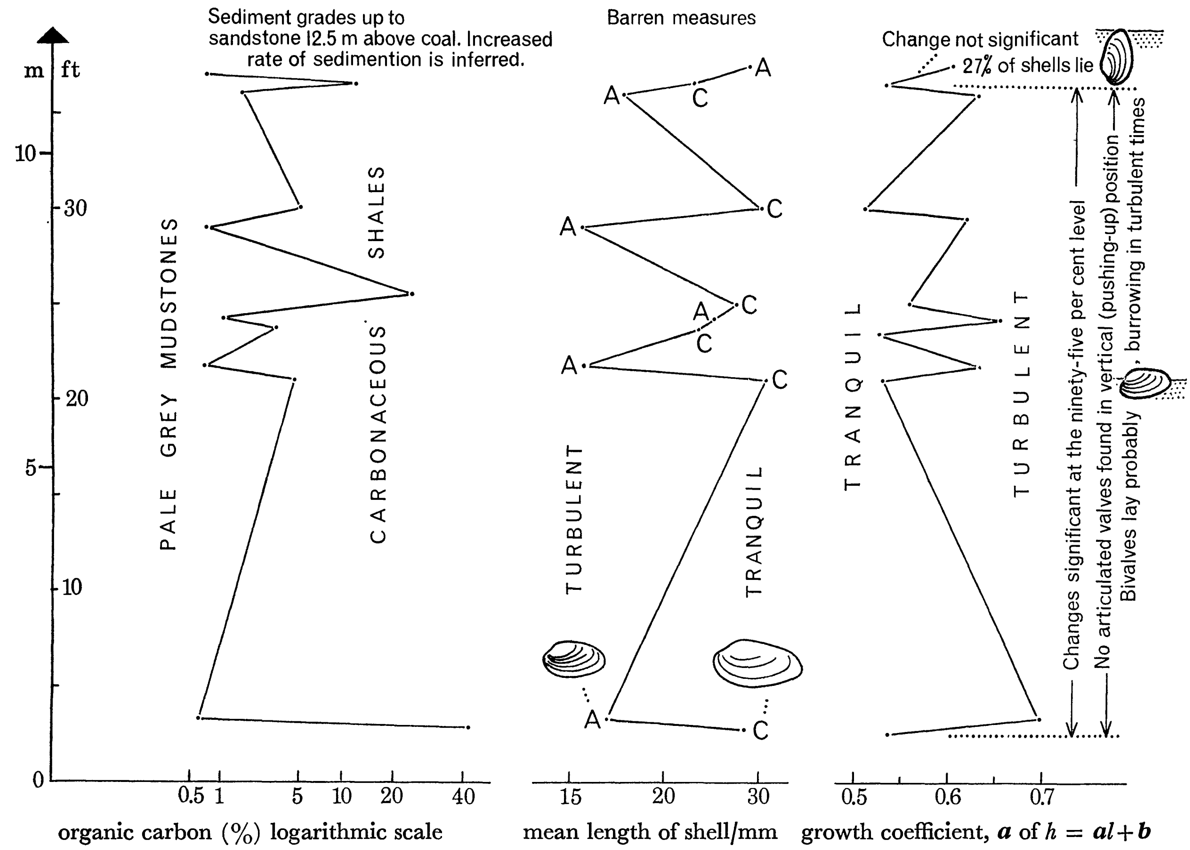

FIGURE 58. A summary of some chemical, lithological and biometrical data obtained from anthracosiid faunas in the lower part of the succession above the Flockton Thin Coal (Westphalian A) of Cold Bath Opencast, near Barnsley, Yorkshire.

and $\boldsymbol{b}$ is the initial growth index. The latter constant was found to vary insignificantly and is not recorded in figure 58. The value of $\boldsymbol{a}$, however, may be seen to vary antipathetically with the organic carbon content of the sediment throughout the section and to mean length of shell through most of it. With the exception of the uppermost fauna, each assemblage of incipient *Anthracosia*, by reason of its pattern of growth, may be inferred to have included living bivalves with higher specific gravities, and probably marginally better burrowing rate indices than those of the *Carbonicola* faunas, although no shell out of more than 3000 collected from these measures was found in a steep-burrowing position. In the highest fauna, of incipient *Anthracosia*, 13 specimens, 27 % of the conjoined closed valves collected, were found in vertical or near-vertical steep-burrowing position. In this fauna the value of the growth coefficient, $\boldsymbol{a}$, decreases insignificantly for the first time, whereas all the decreases in this constant on lower horizons in the succession have proved significant, by the *z* test, at the 95% level. There is therefore strong presumptive evidence that increased rates of sedimentation, which evidently led to a local termination of mussel life, prompted initially a re-orientation of the bivalves; that selection pressures changed their direction, from placing a premium on shell mass in a shallow-burrowing or ploughing fauna, to upward pushing, preceded by downward burrowing to near the vertical, as a means of survival. Yet perhaps the most striking result of this study is the immediate correlation found between sedimentological and faunal change, as seen in figure 58, and that such correlations appear predictable up to a palaeoecological threshold.

Conclusions

1. *Paracarbonicola* gen.nov. ranges from Viséan beds to the Pendleian of Britain, being found in the Pendleian of Poland and Czechoslovakia and up to the Czechoslovak Arnsbergian (mid-E_2).

2. Between late R_1 and R_{2b} *Carbonicola* evolved from marine stock herein referred to cf. *Sanguinolites* Hind *non* M'Coy. The same stock was probably represented in the middle Namurian of Belgium and the Netherlands.

3. In Britain marginally marine shallow-water colonies cf. *Sanguinolites* were invaded by seaward-moving delta lobes. Initially the living positions of the bivalve shell steepened, so that the long axes of the shells tended to approach the vertical. From these positions bivalves tended to push up vertically, with their resultant survival under increasing rates of sedimentation. Vertical movements tended to increase in magnitude with time, as the Pennine delta, pushing southward in the late Namurian, became progressively more heavily colonized. The characteristics of *Carbonicola*, notably as seen in the elongate thin 'streamlined' shells of the *Carbonicola bellula* group of the late Namurian to early Westphalian, may be viewed as resulting from the selective effects of high-energy sedimentation.

4. Bivalves which subsequently reached lower-energy uncolonized areas such as brackish and freshwater interdistributary lakes and lagoons, which became more common with the advent of the Westphalian, repeatedly proliferated in numbers and variety to become shallow-burrowing, or ploughing, established faunas. The latter developed in general more oval shapes of shell with greater obesities and often with lateral outlines closely comparable with those of their marine ancestors.

5. Deltaic 'invasion' and changes in the invading faunas themselves probably took place at the same time. Changes in internal features of the shell and in surface ornament were apparently irreversible. Those involving trends in shell outline and in obesity were commonly recurrent, as they are today.

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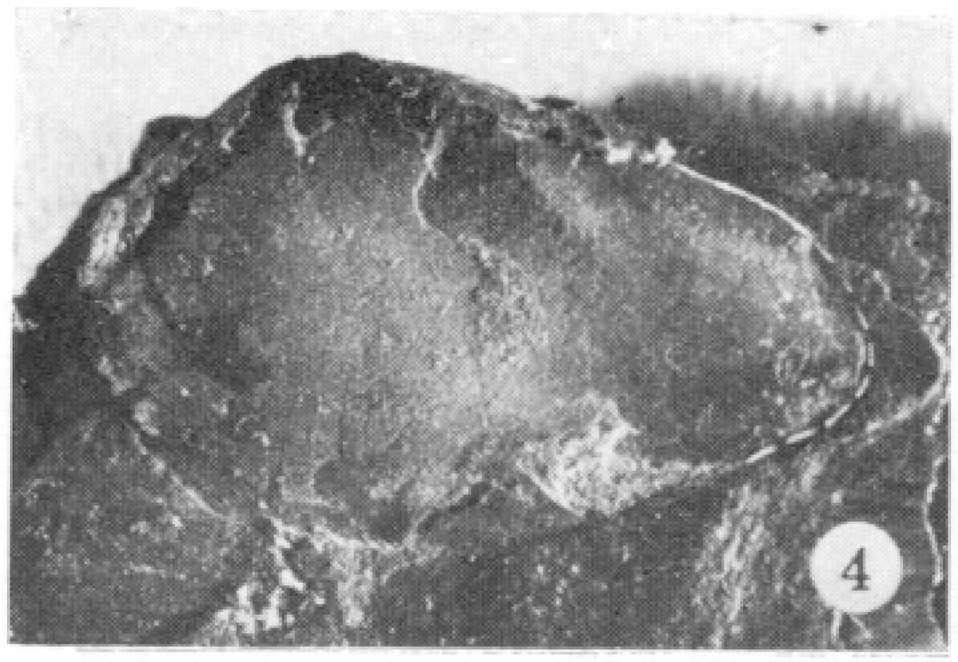

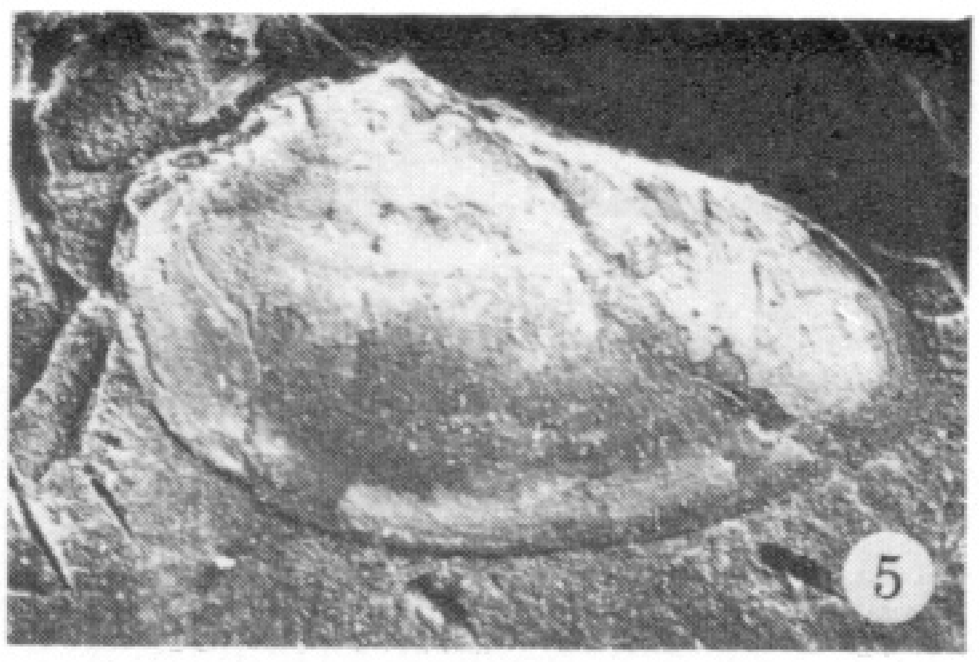

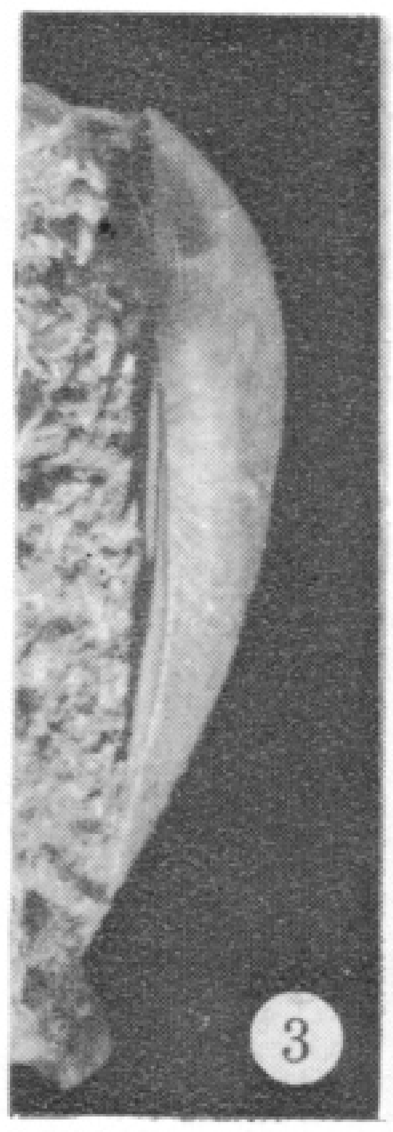

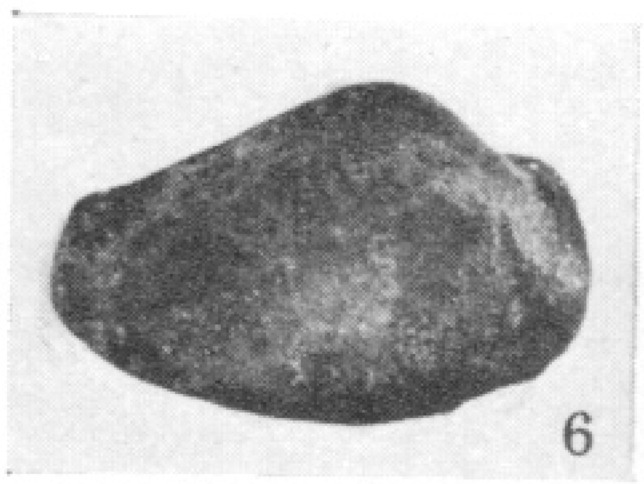

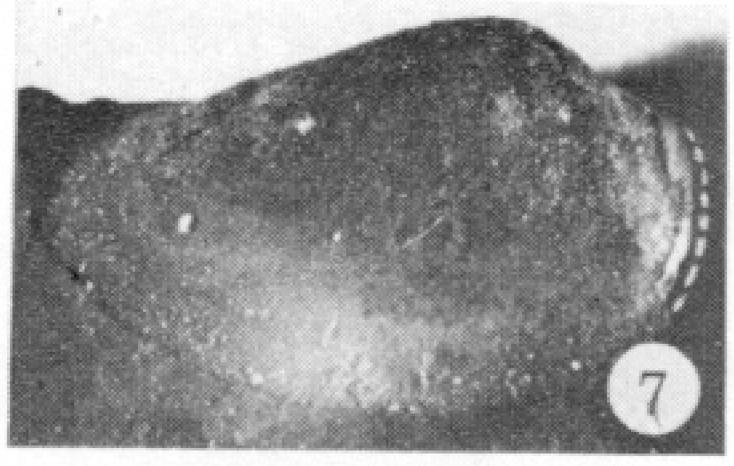

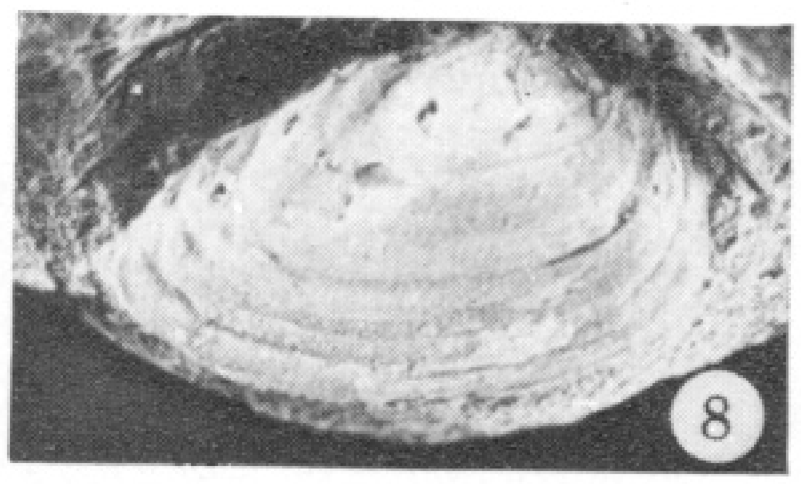

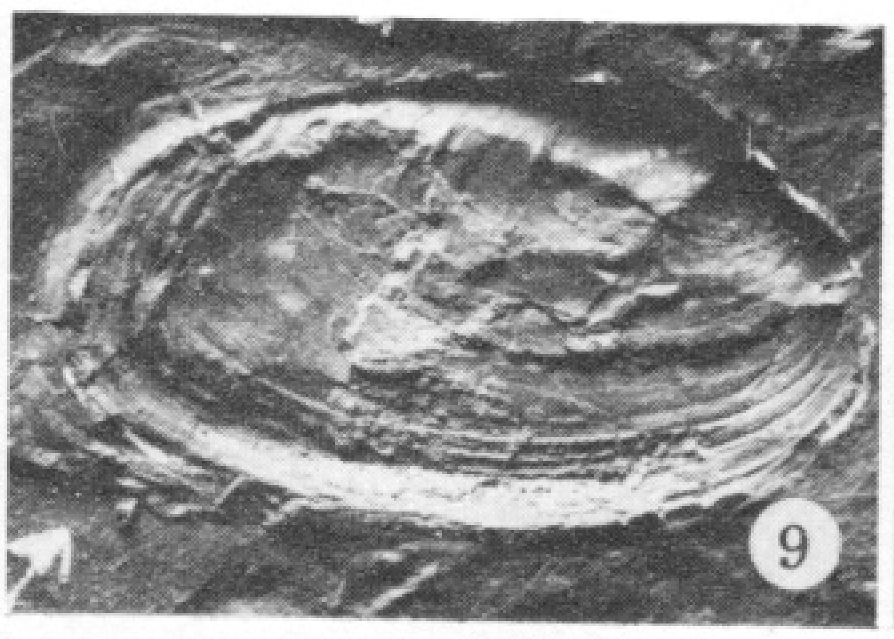

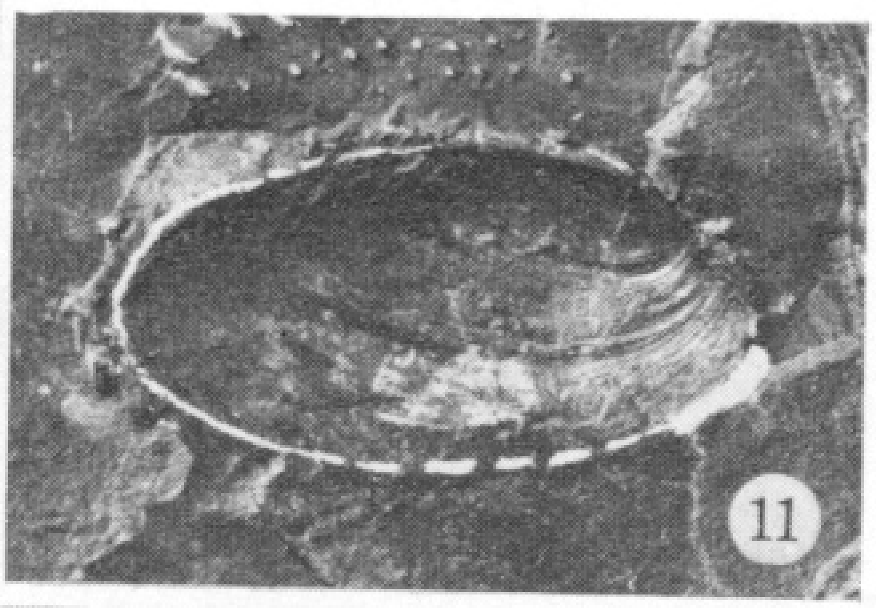

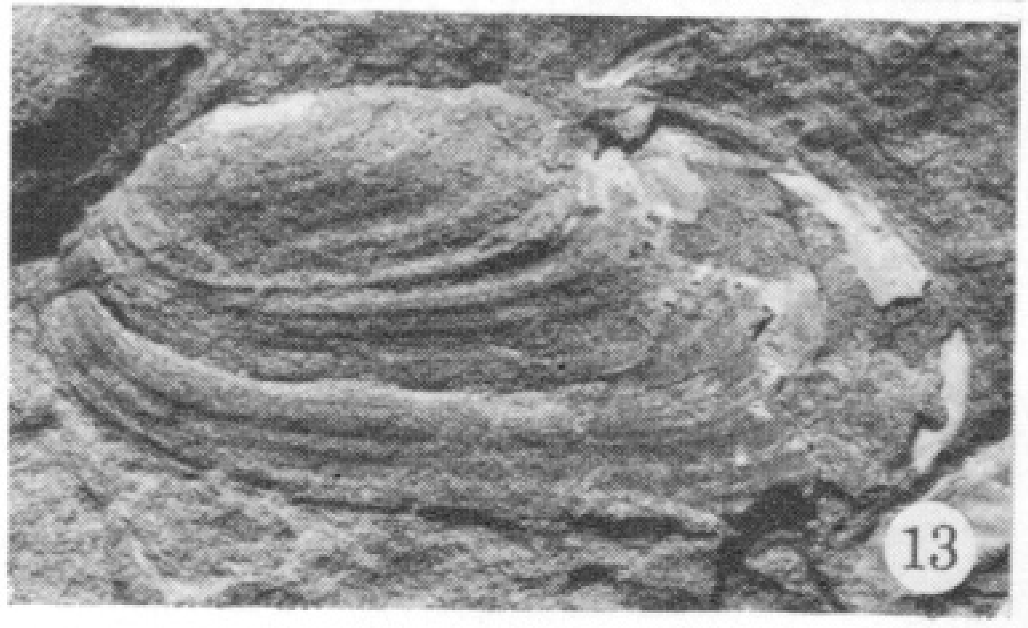

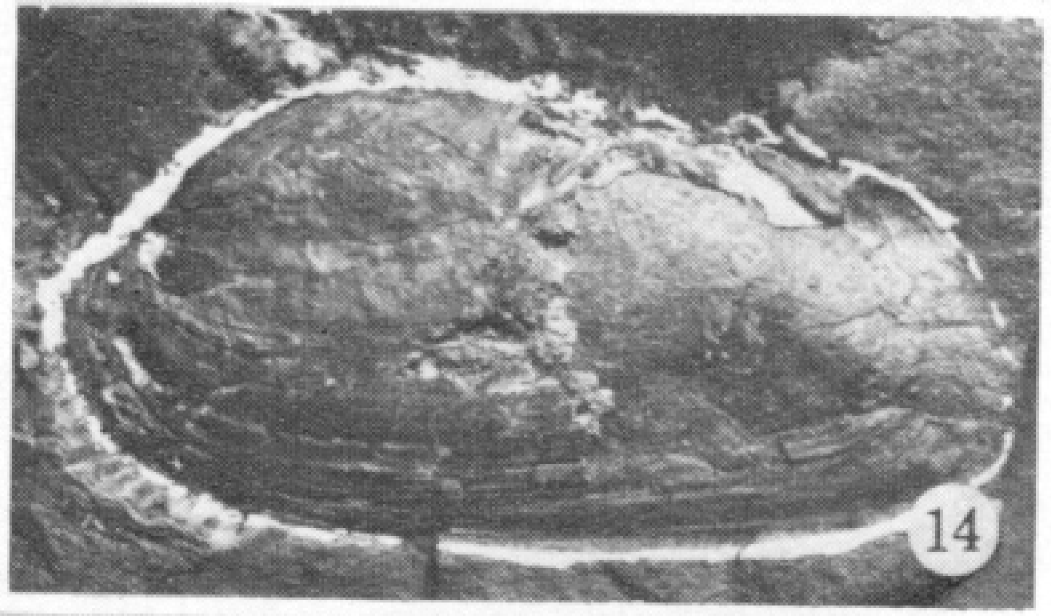

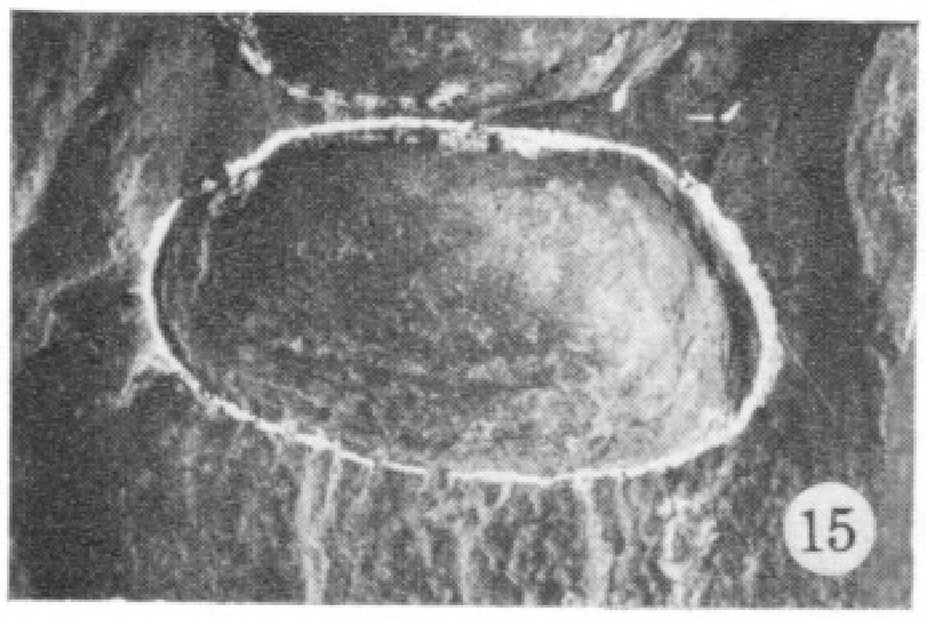

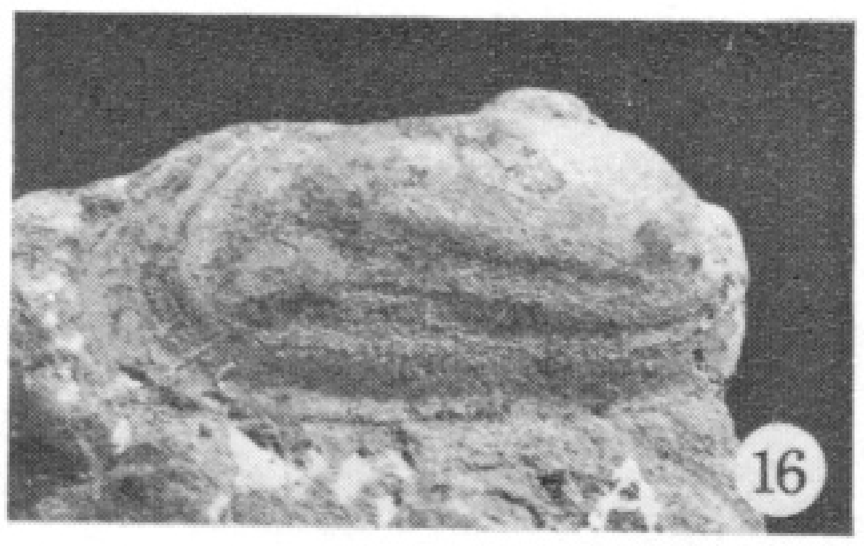

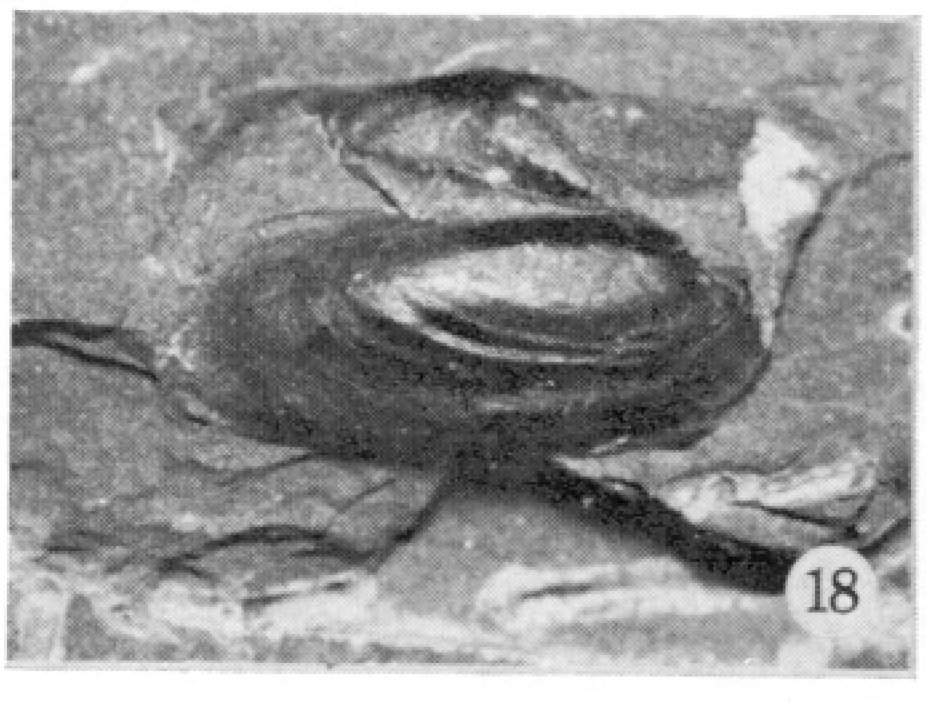

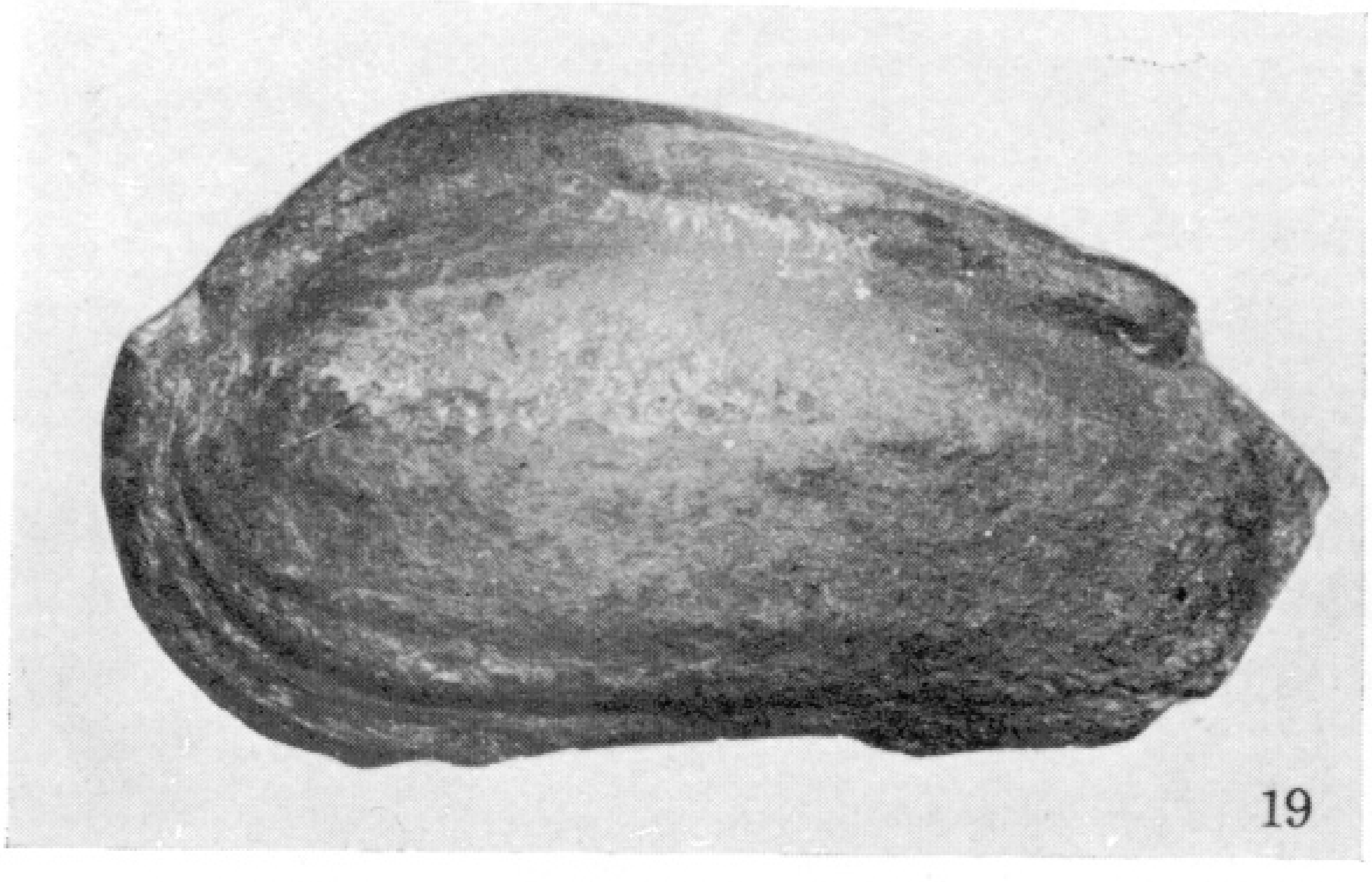

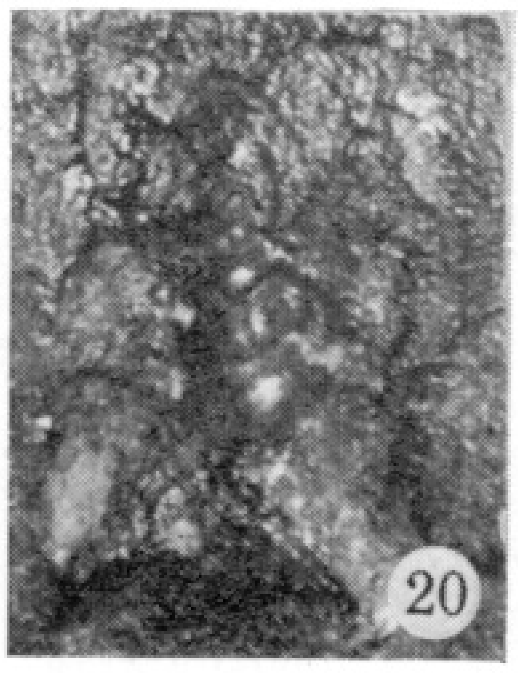

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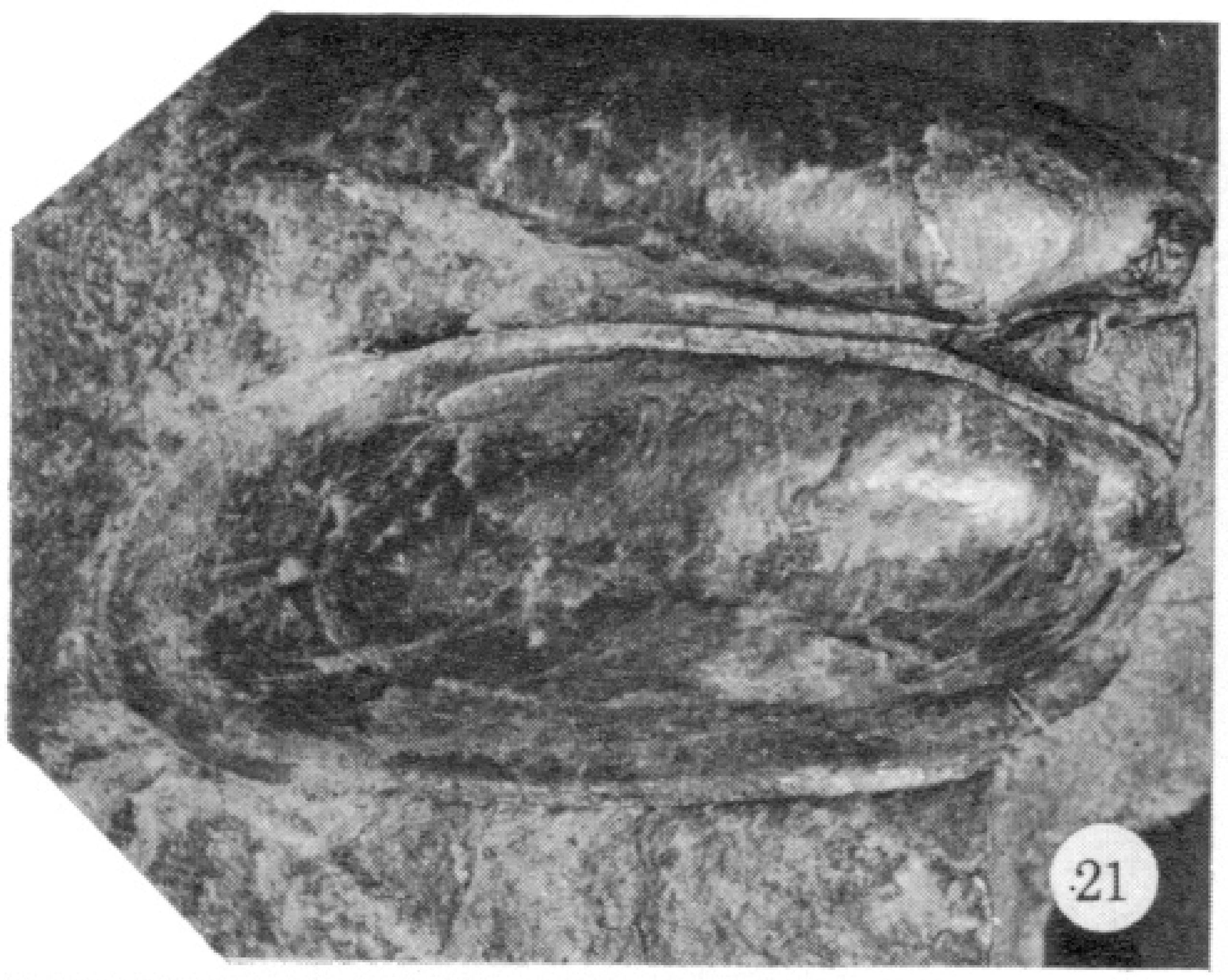
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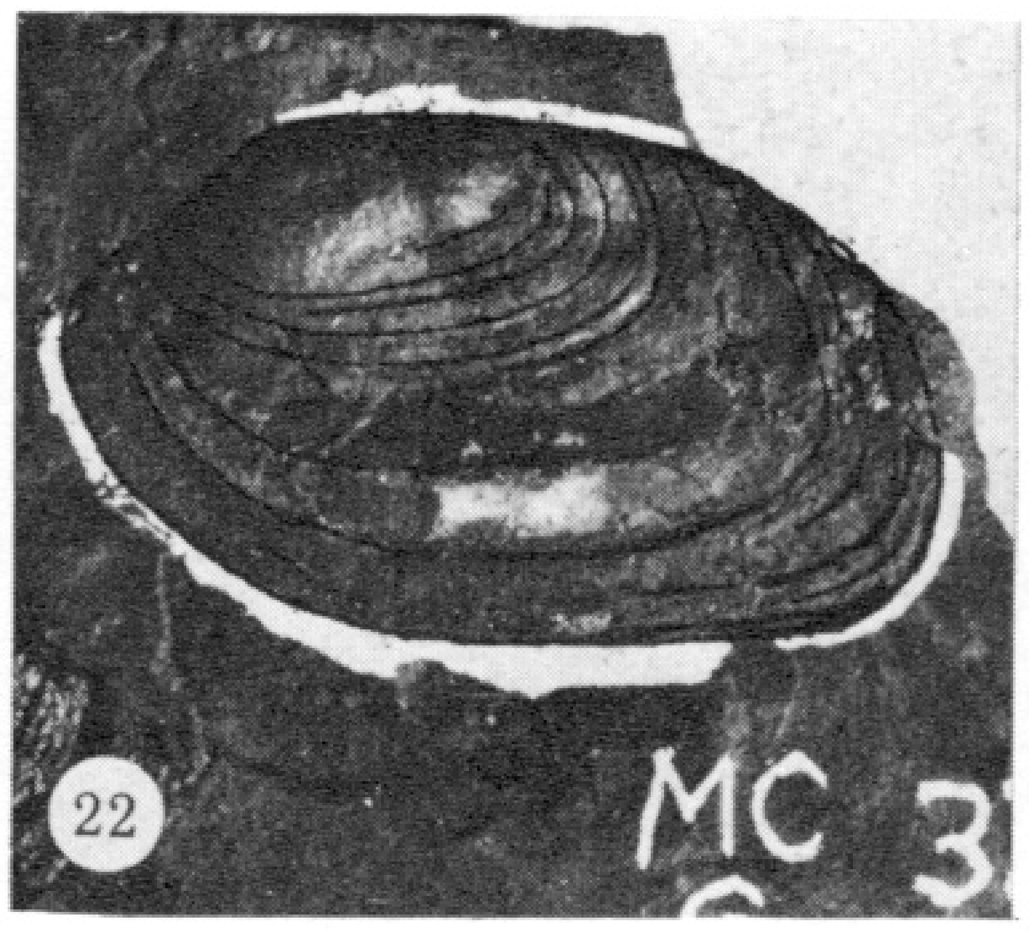
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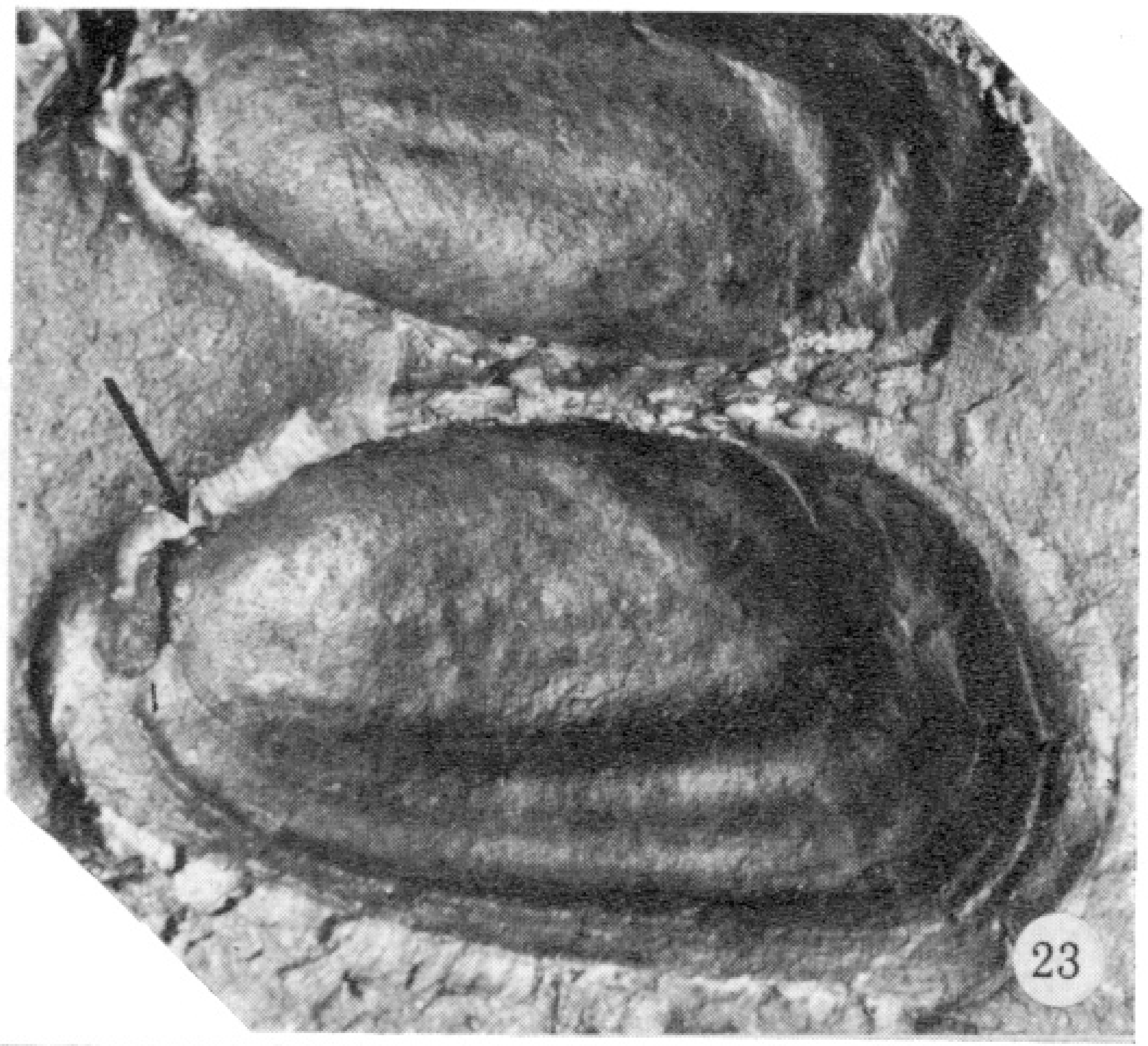
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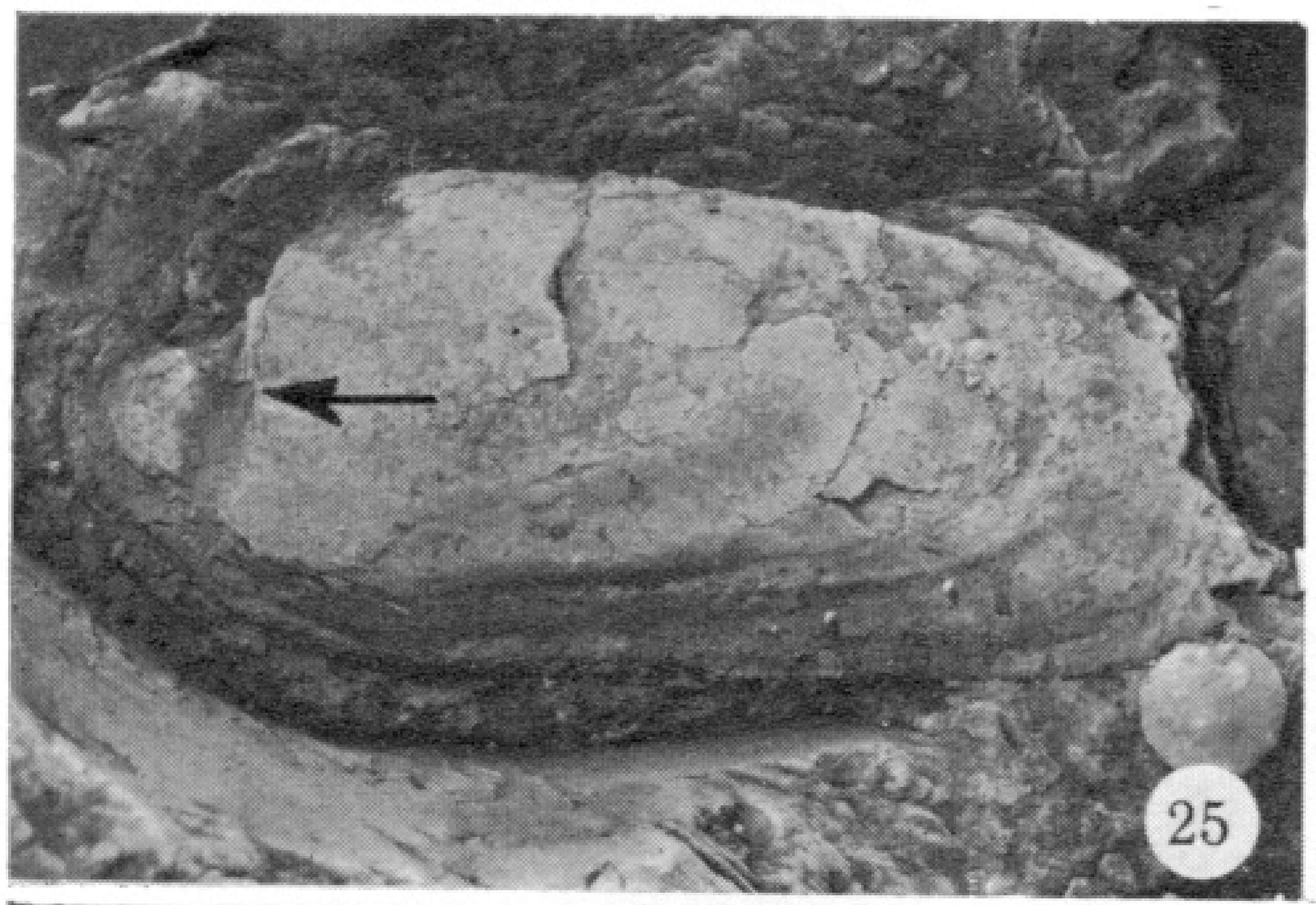
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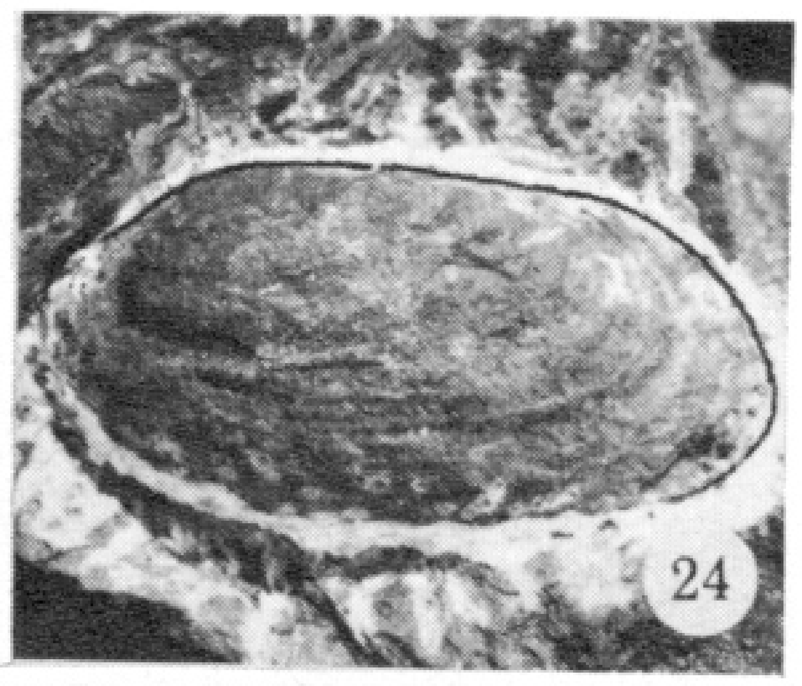
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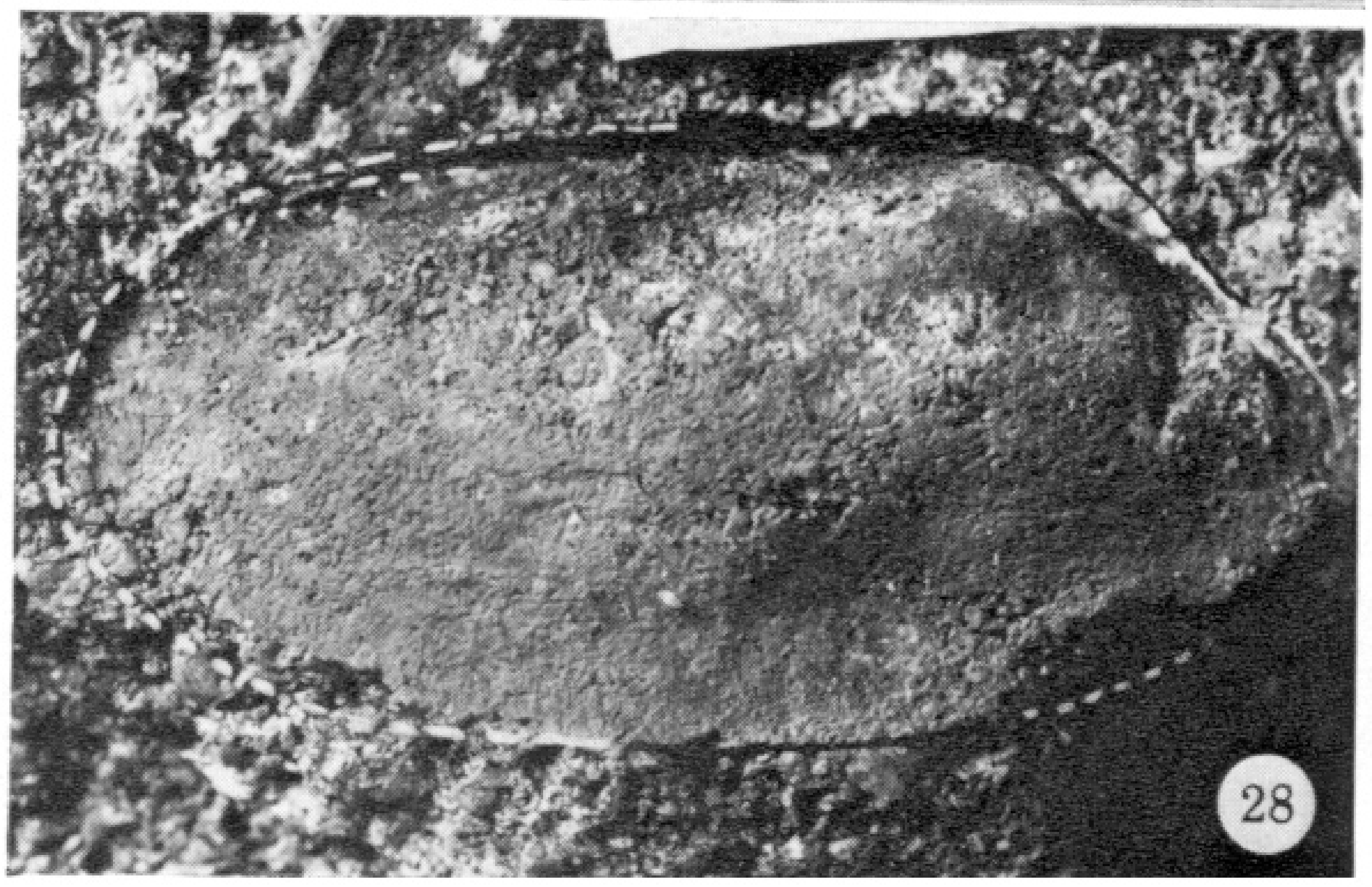
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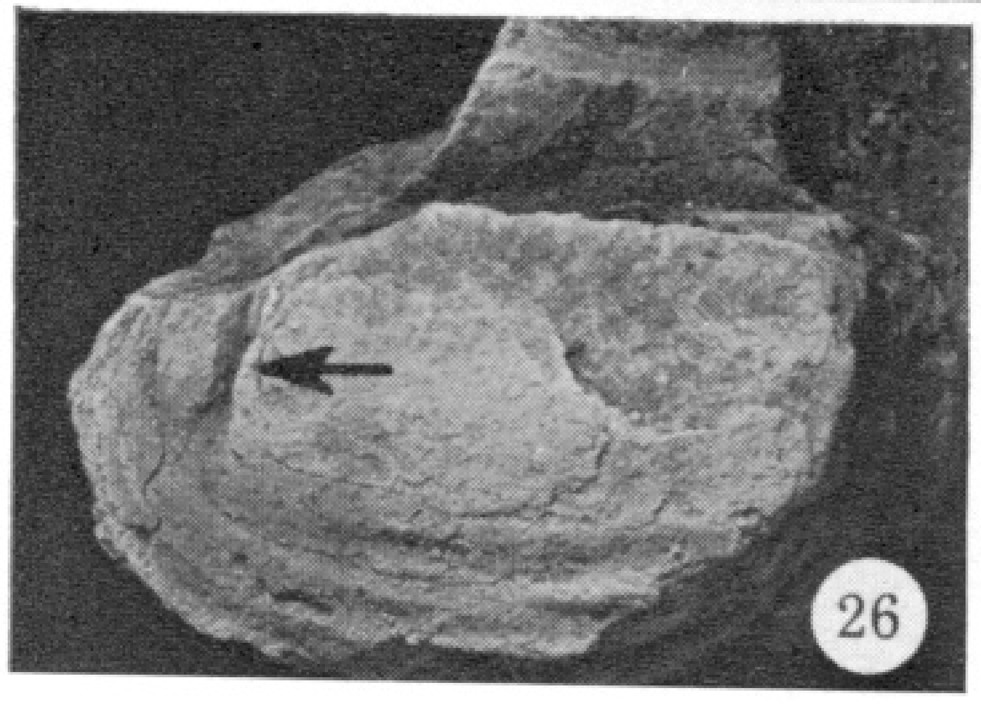
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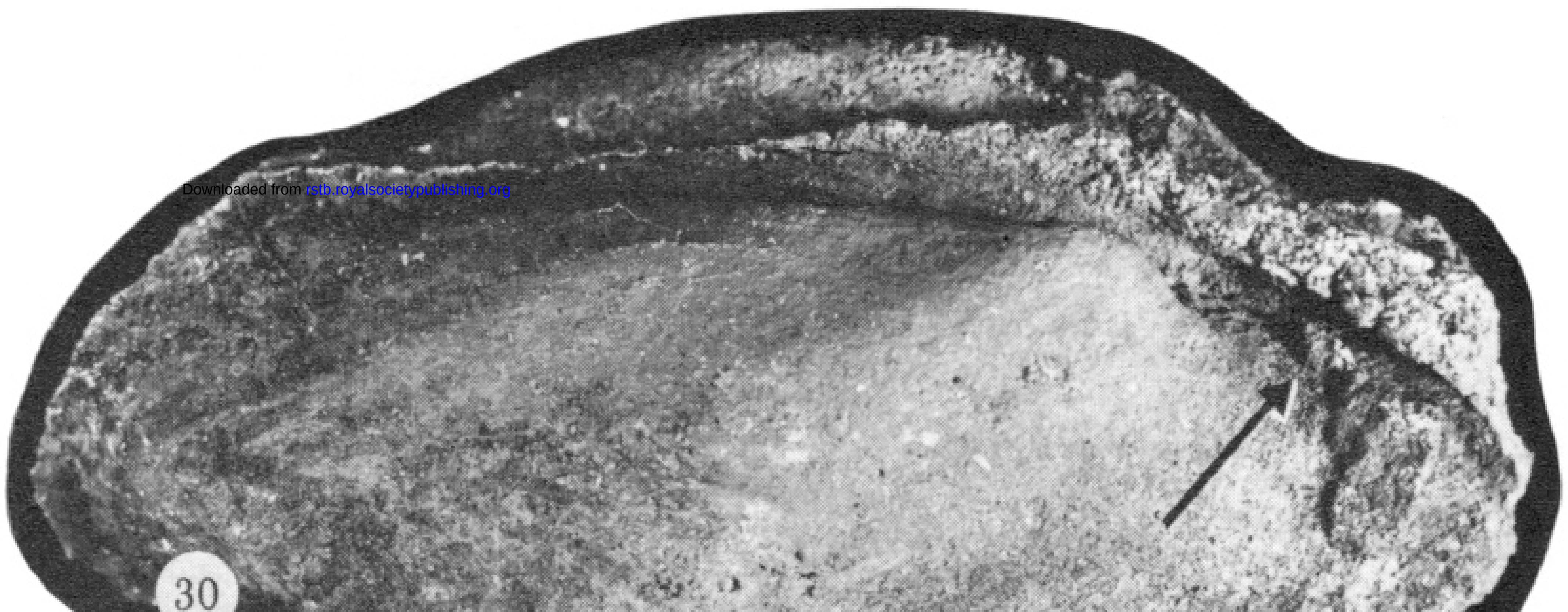
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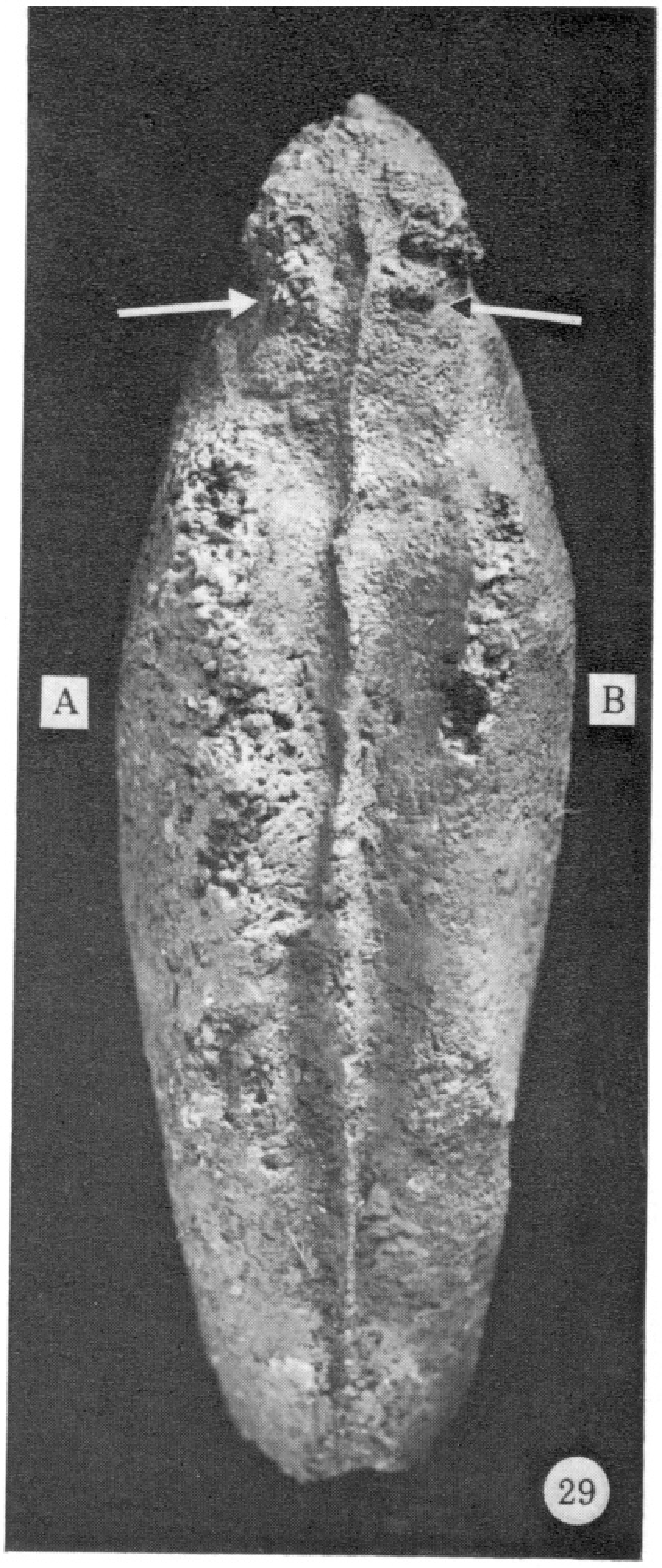
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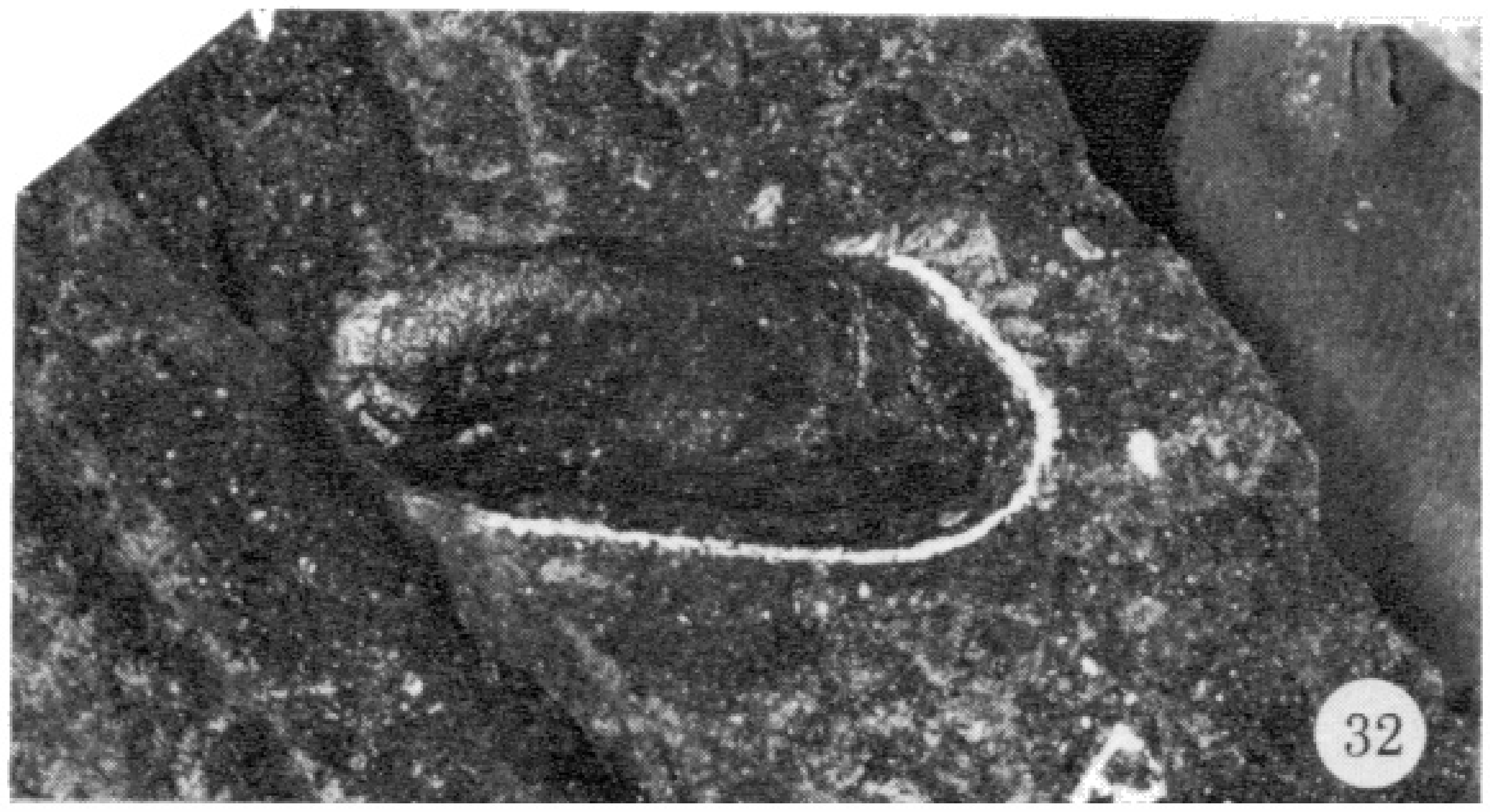
FIGURES 21–31. For description see opposite.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES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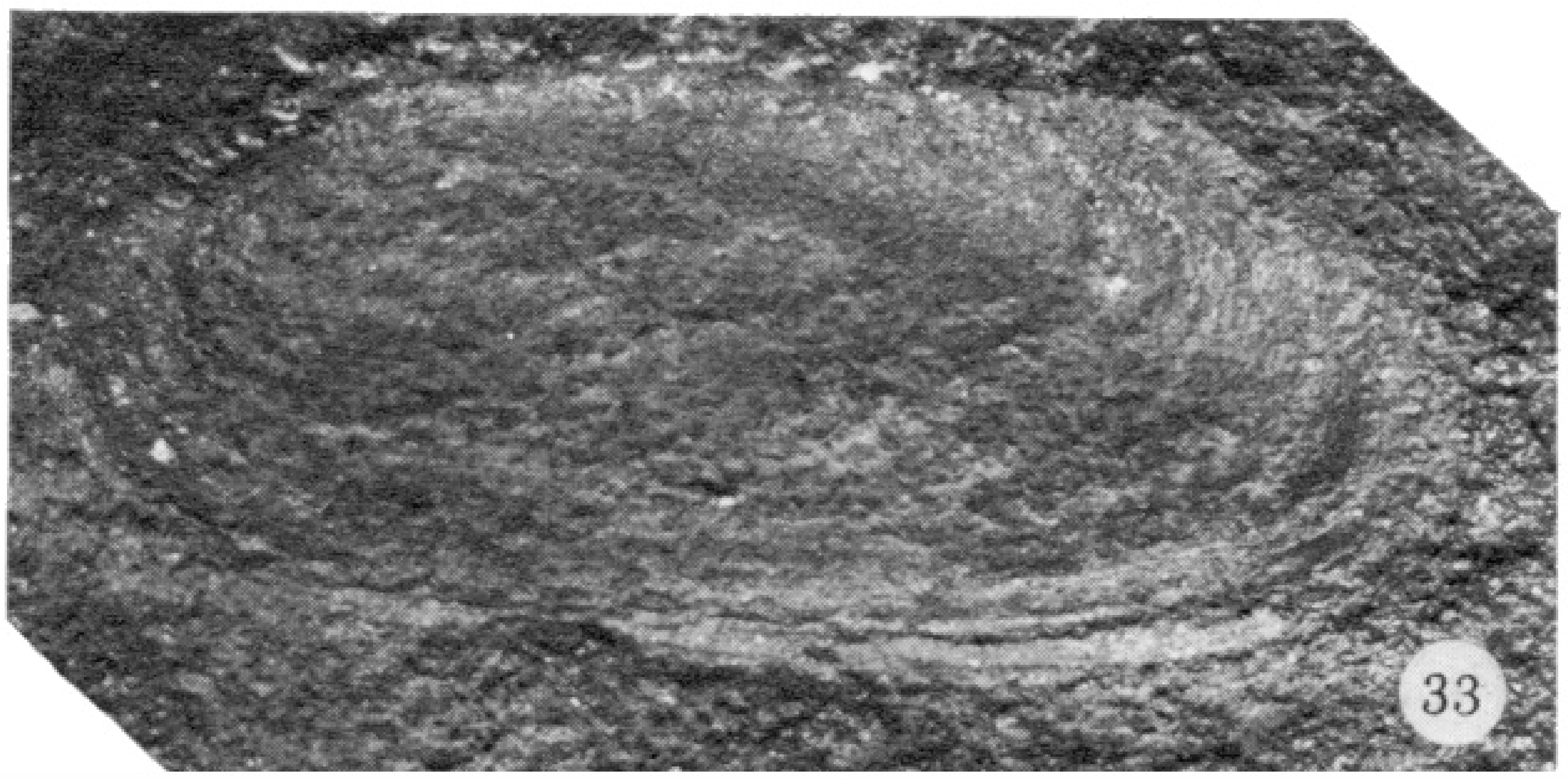
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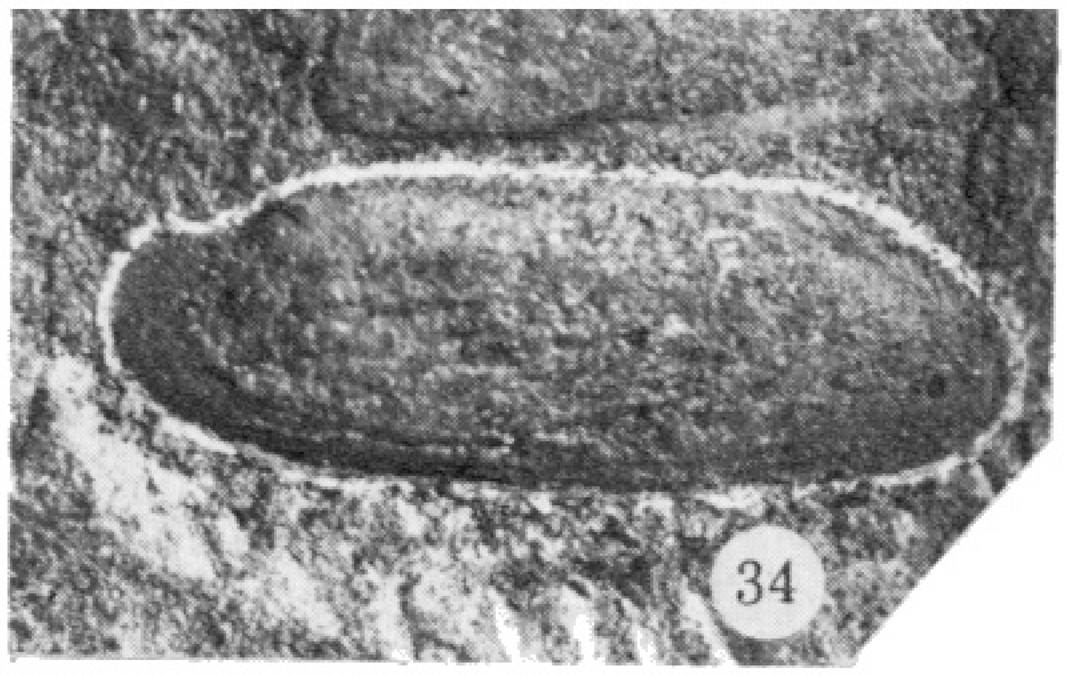
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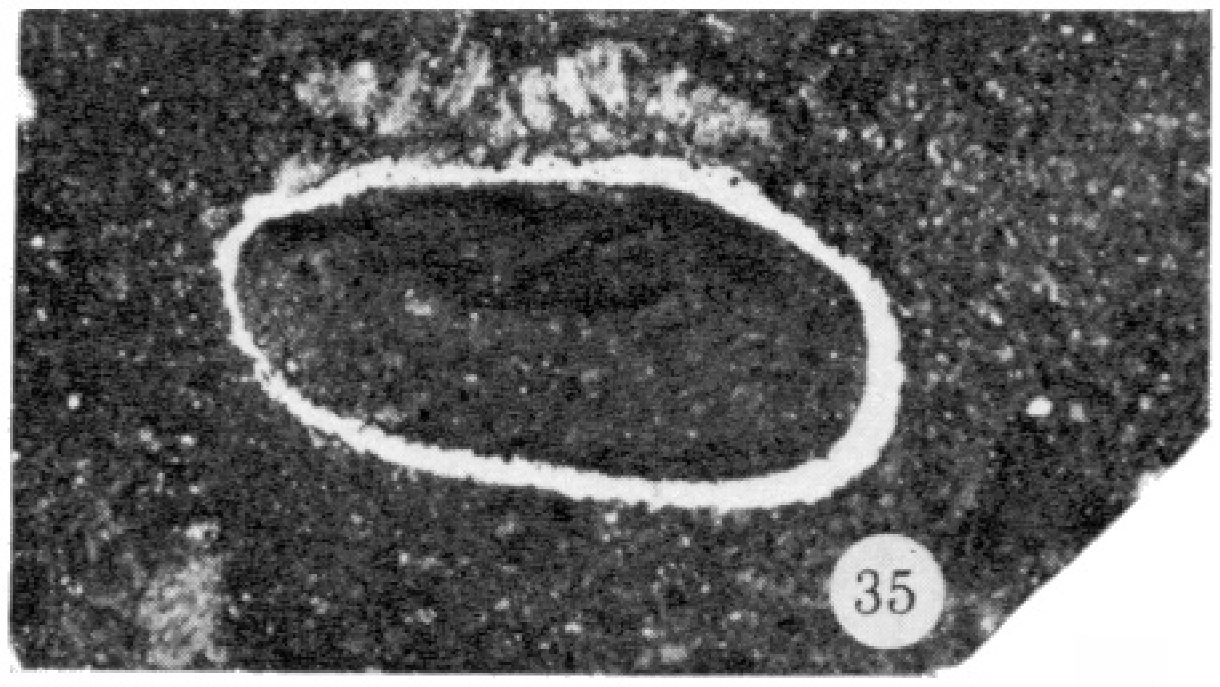
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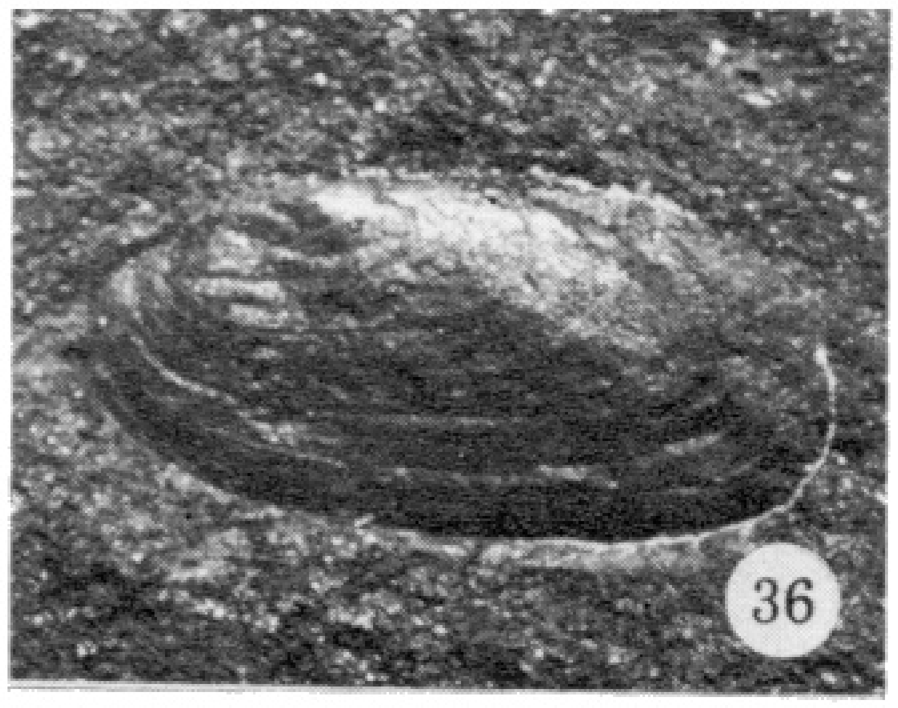
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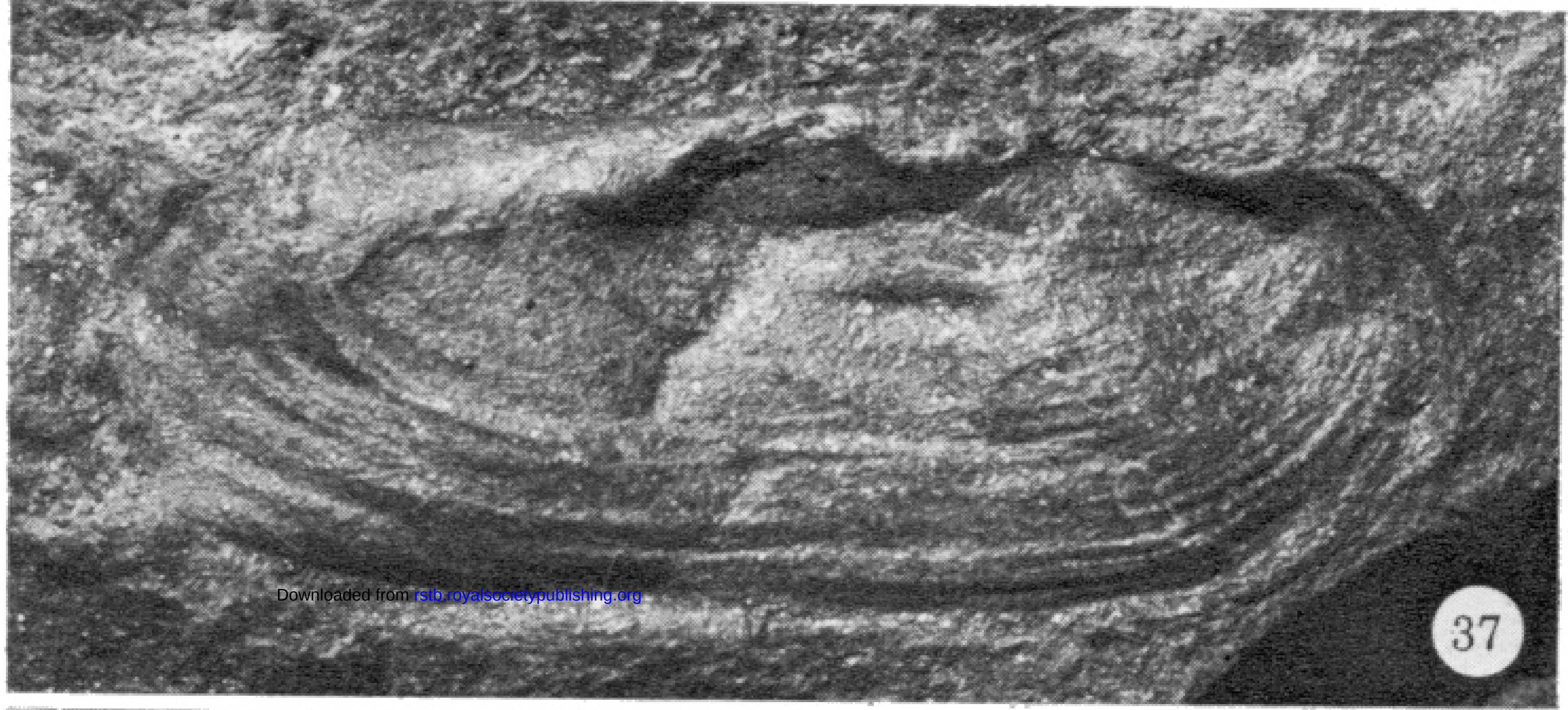
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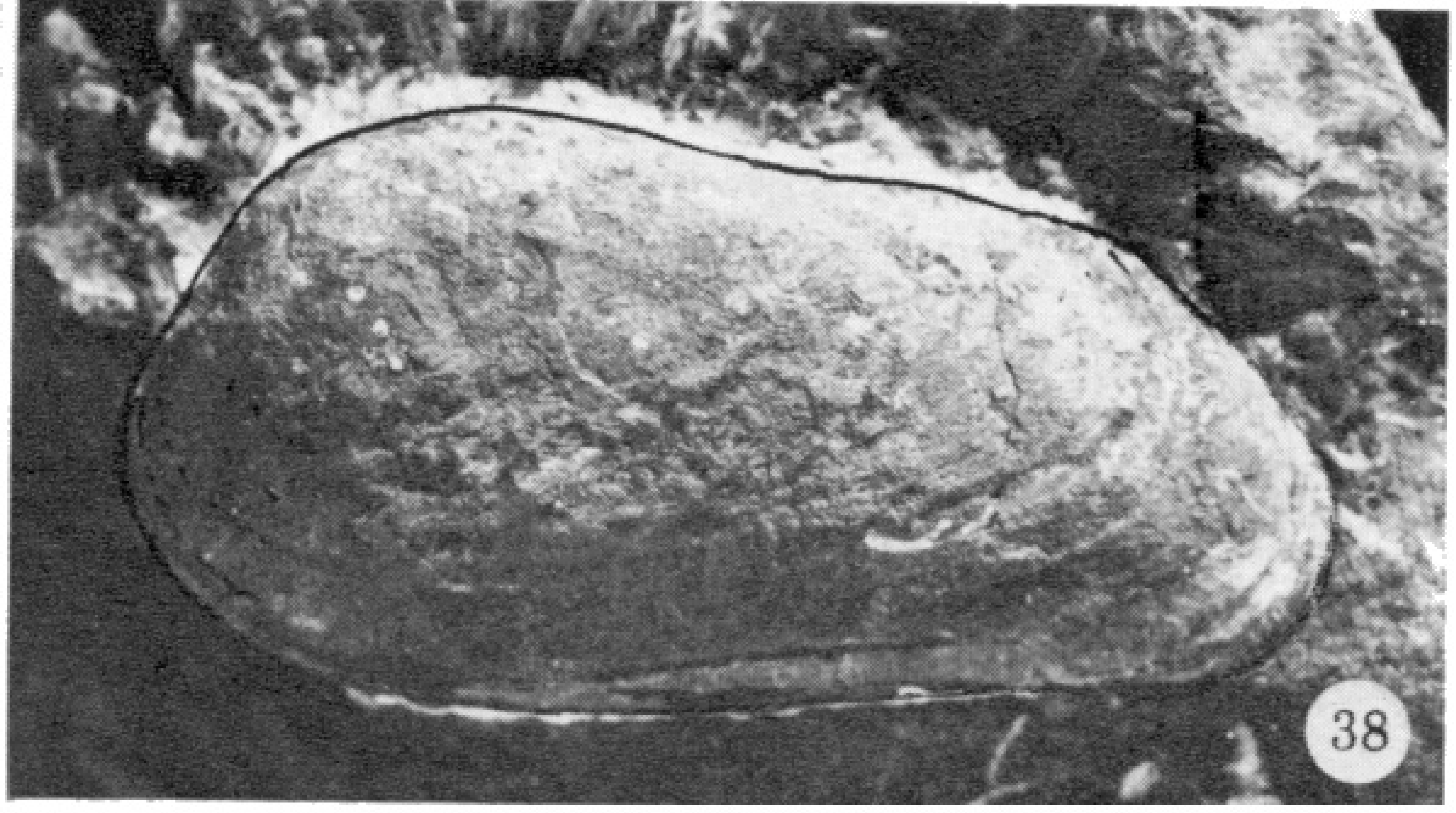
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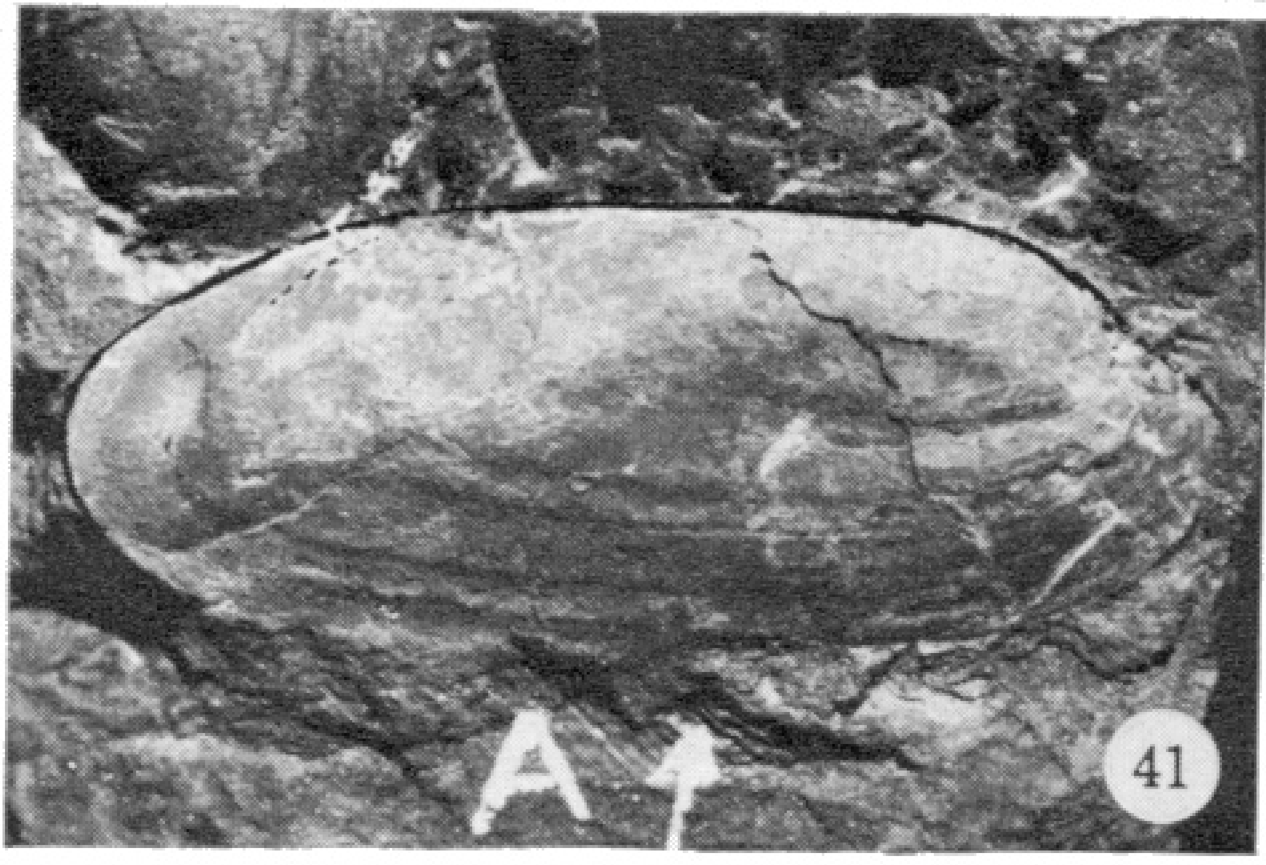

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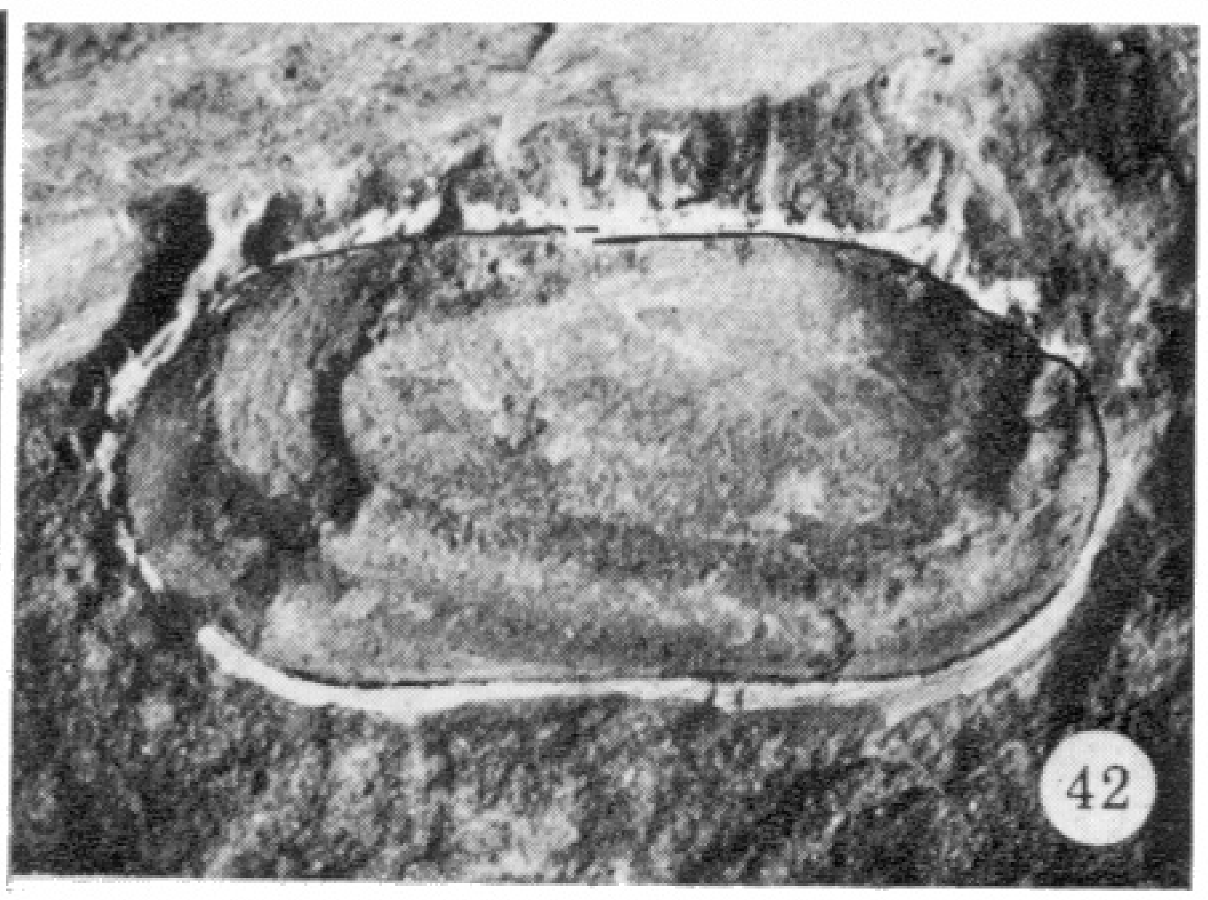
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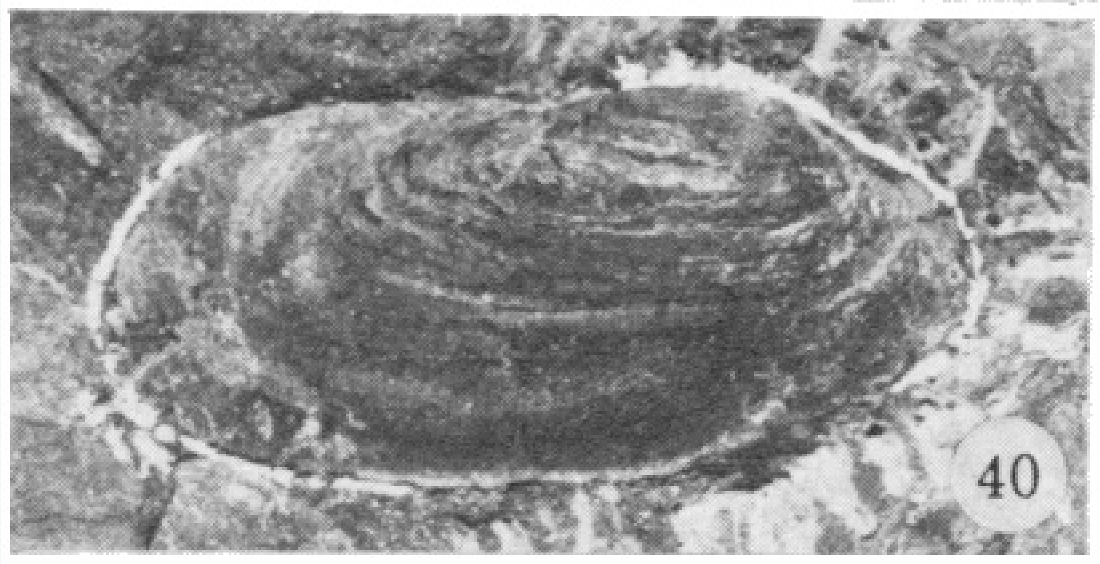
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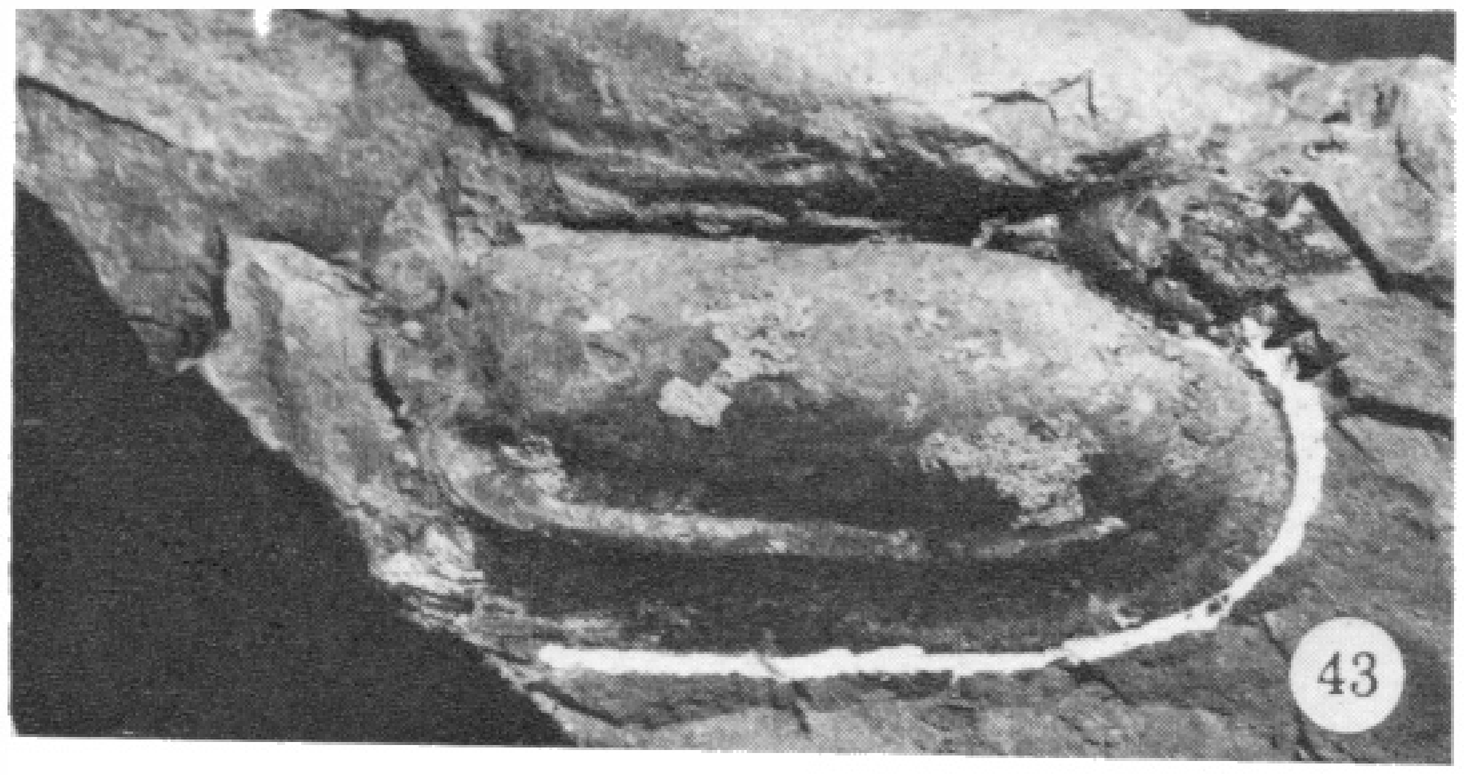
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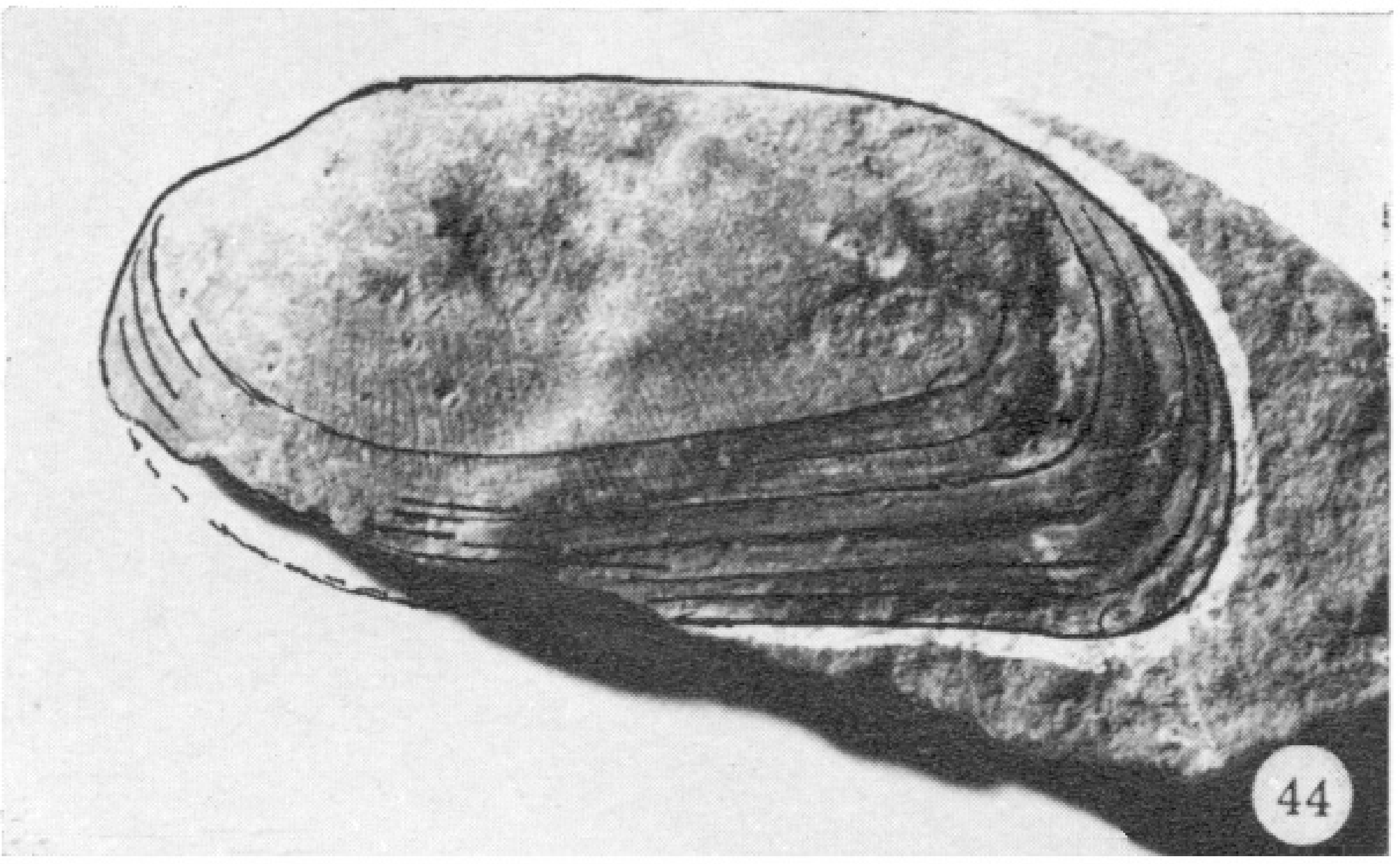
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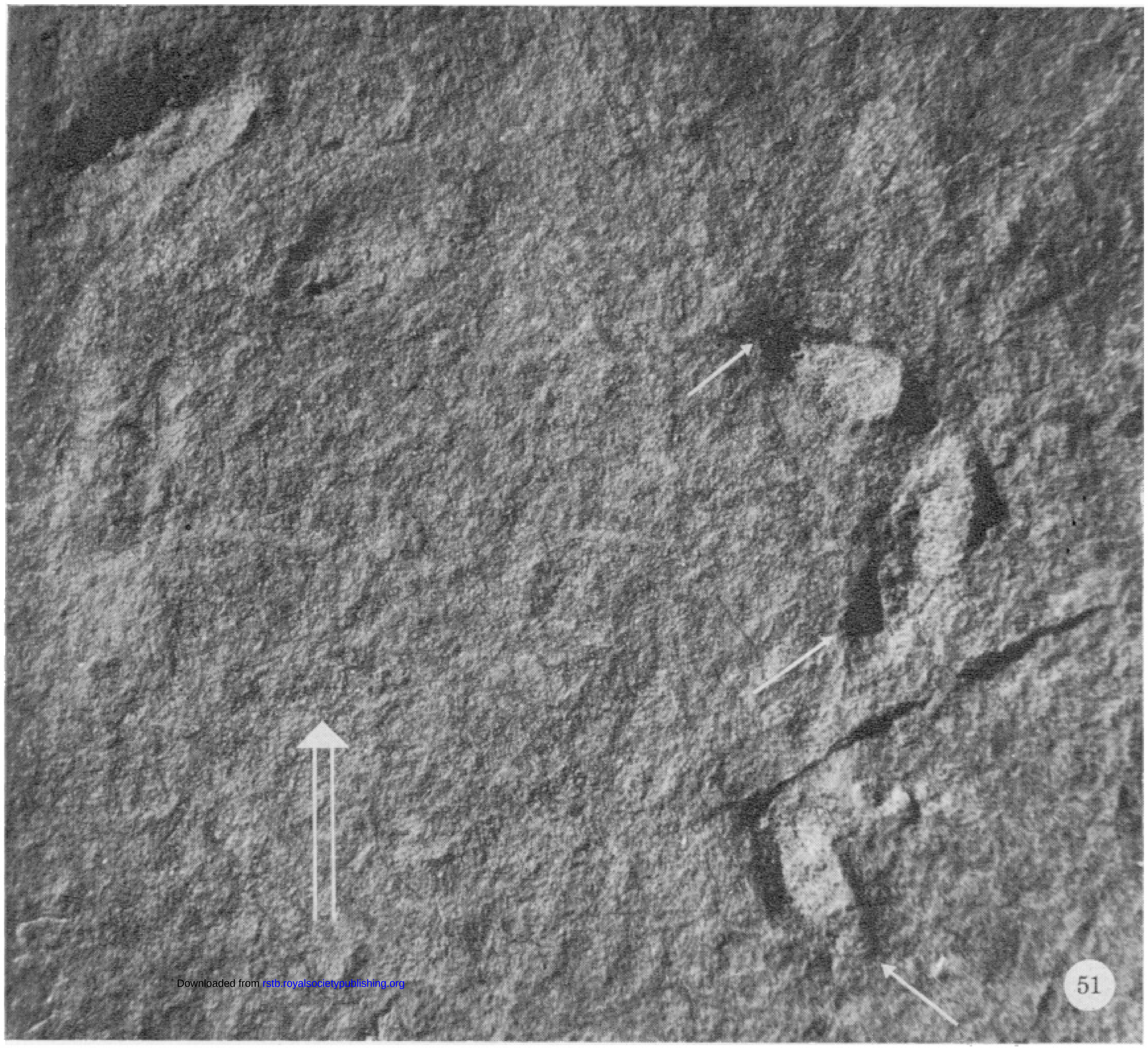
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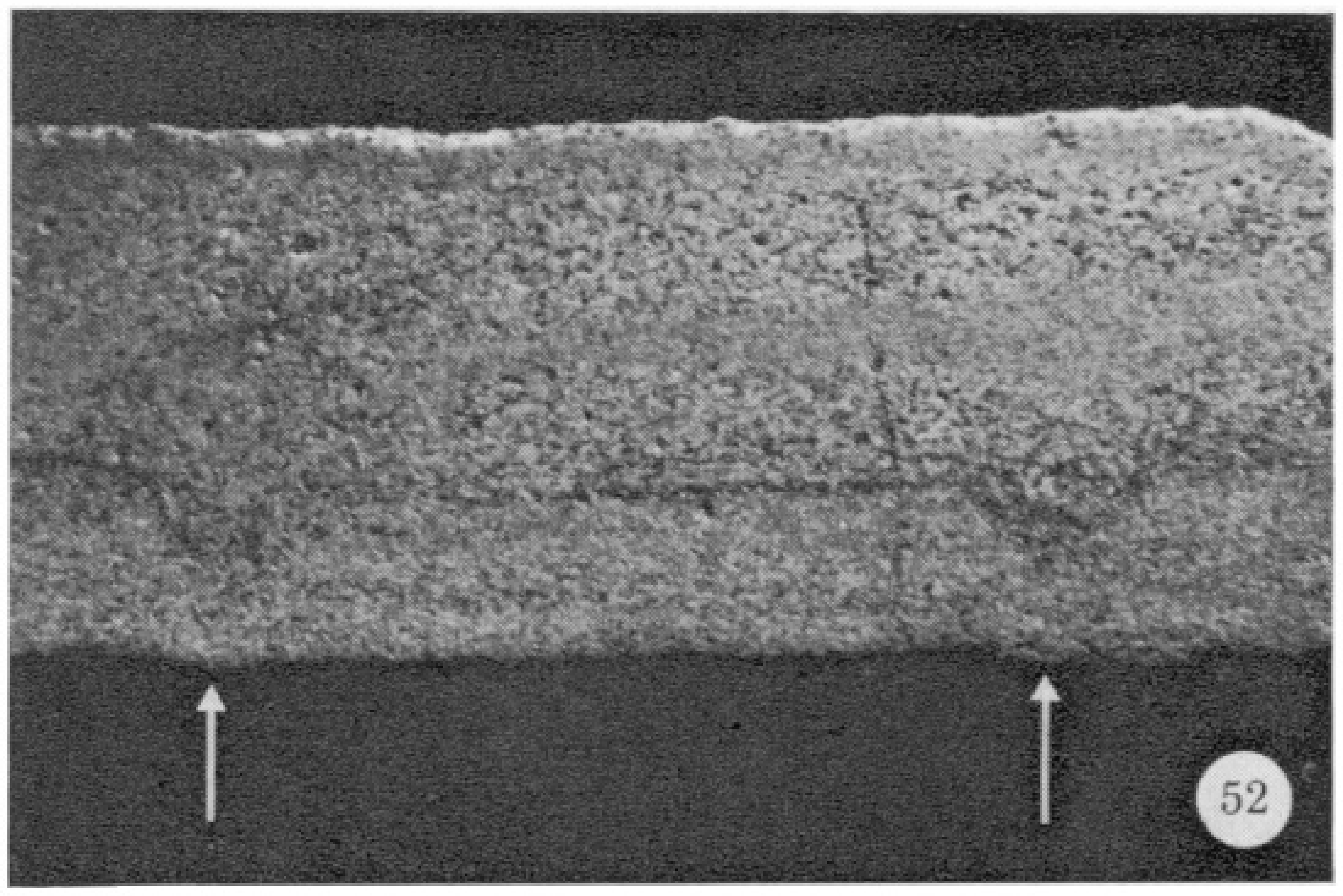
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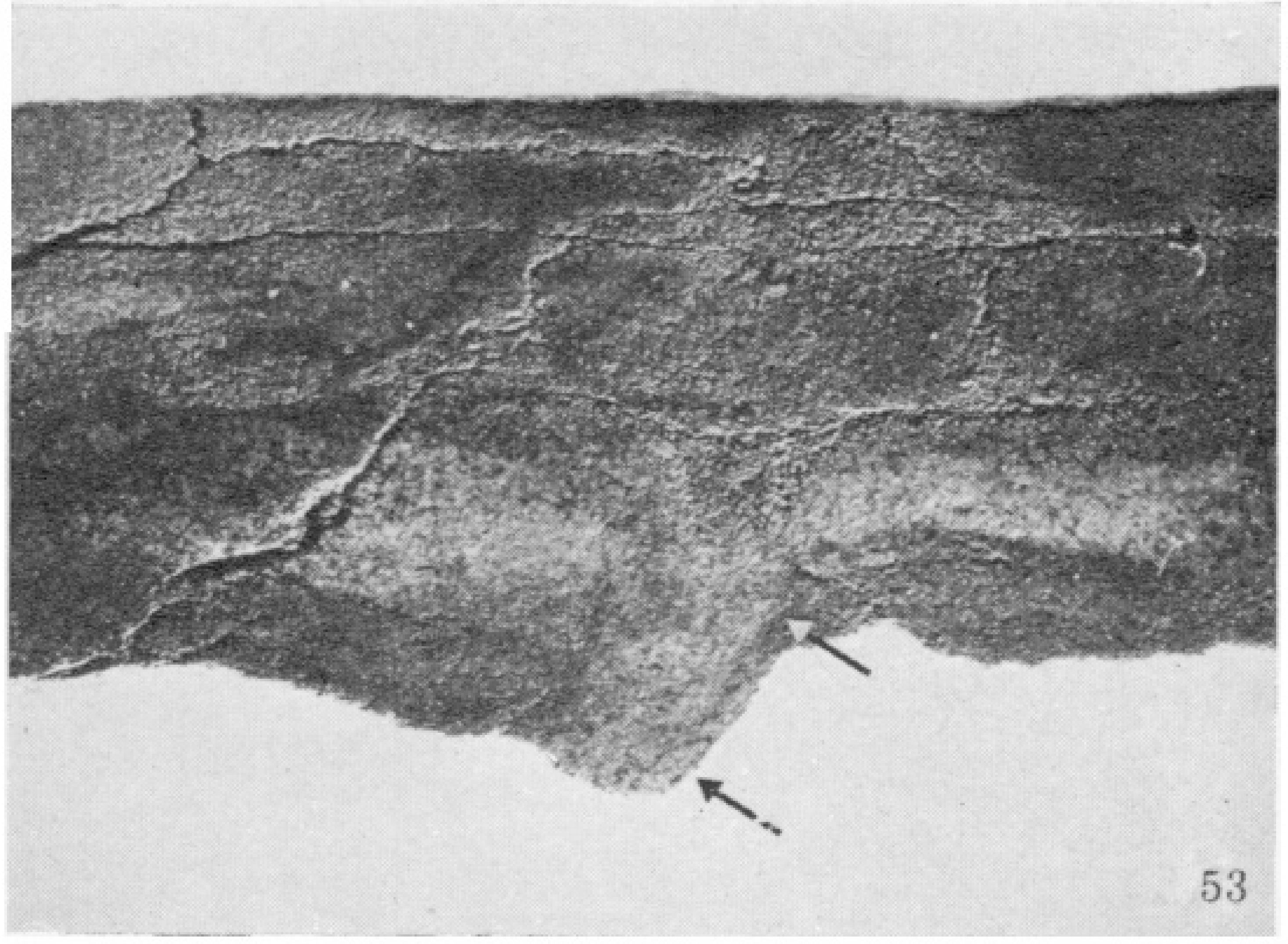
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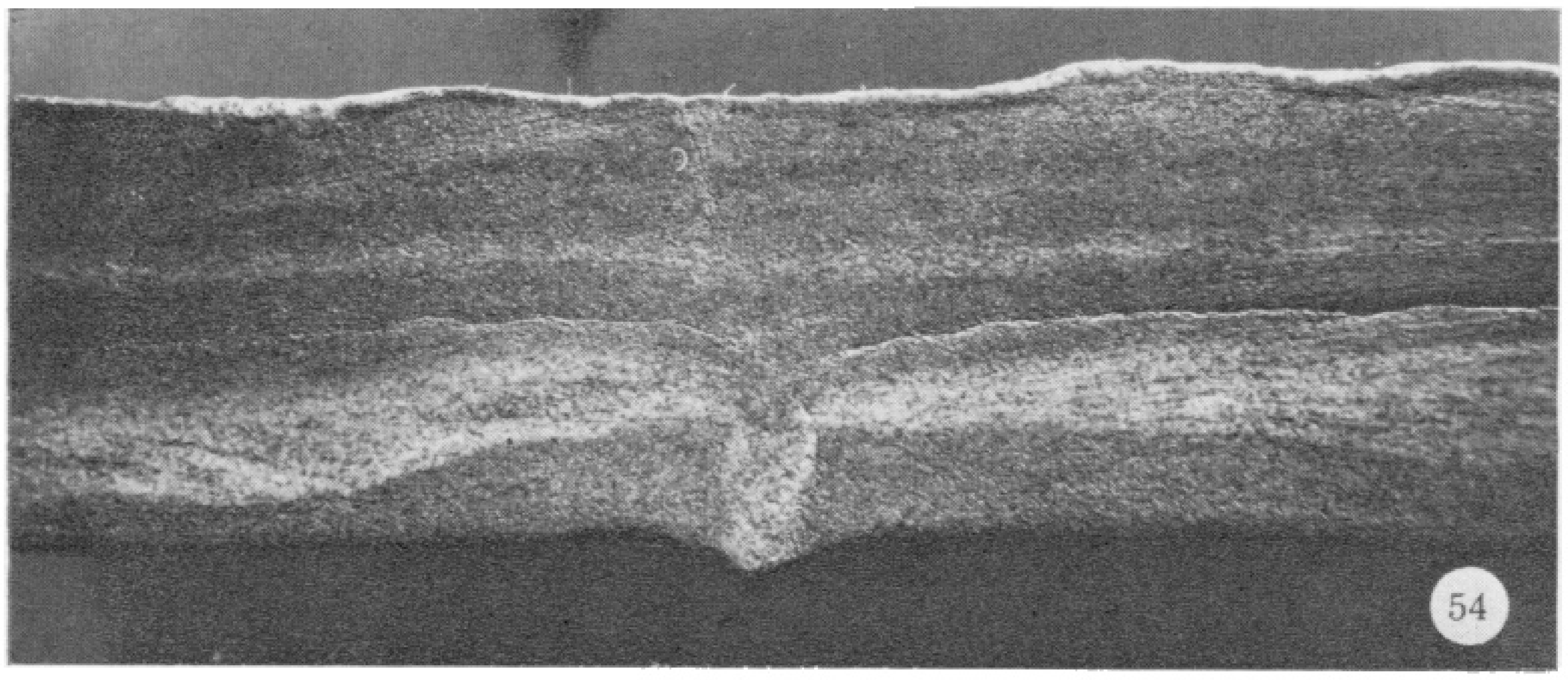
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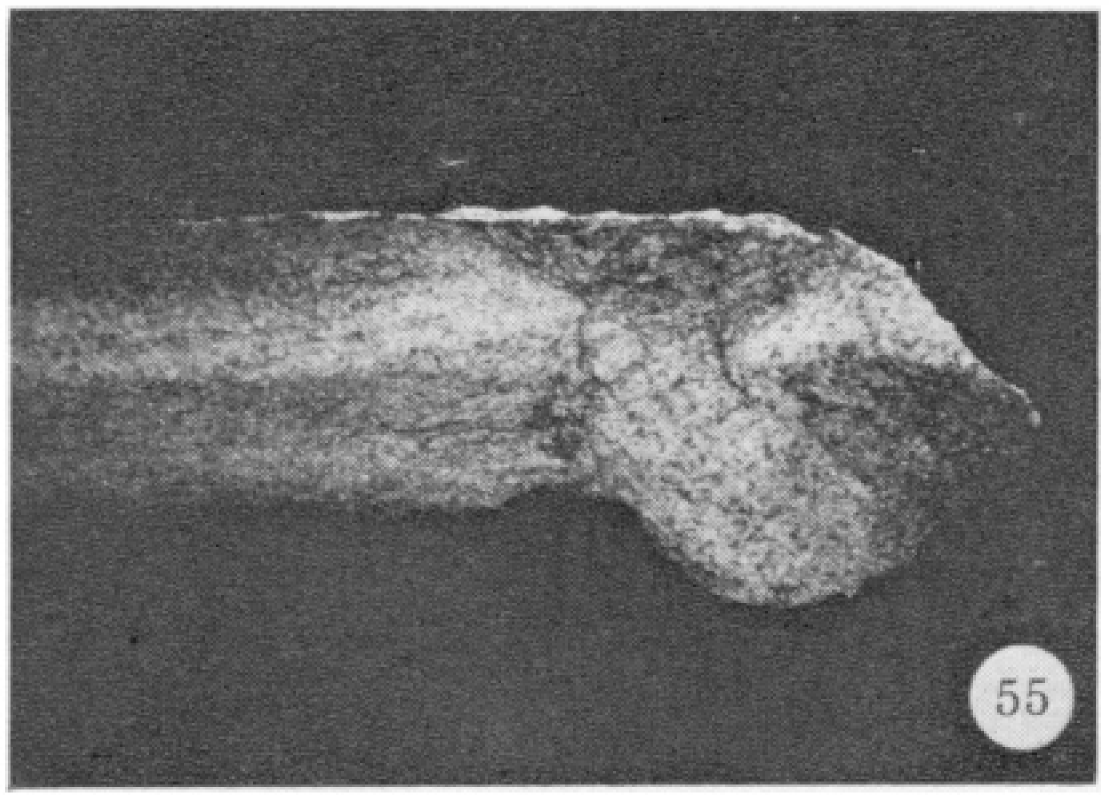
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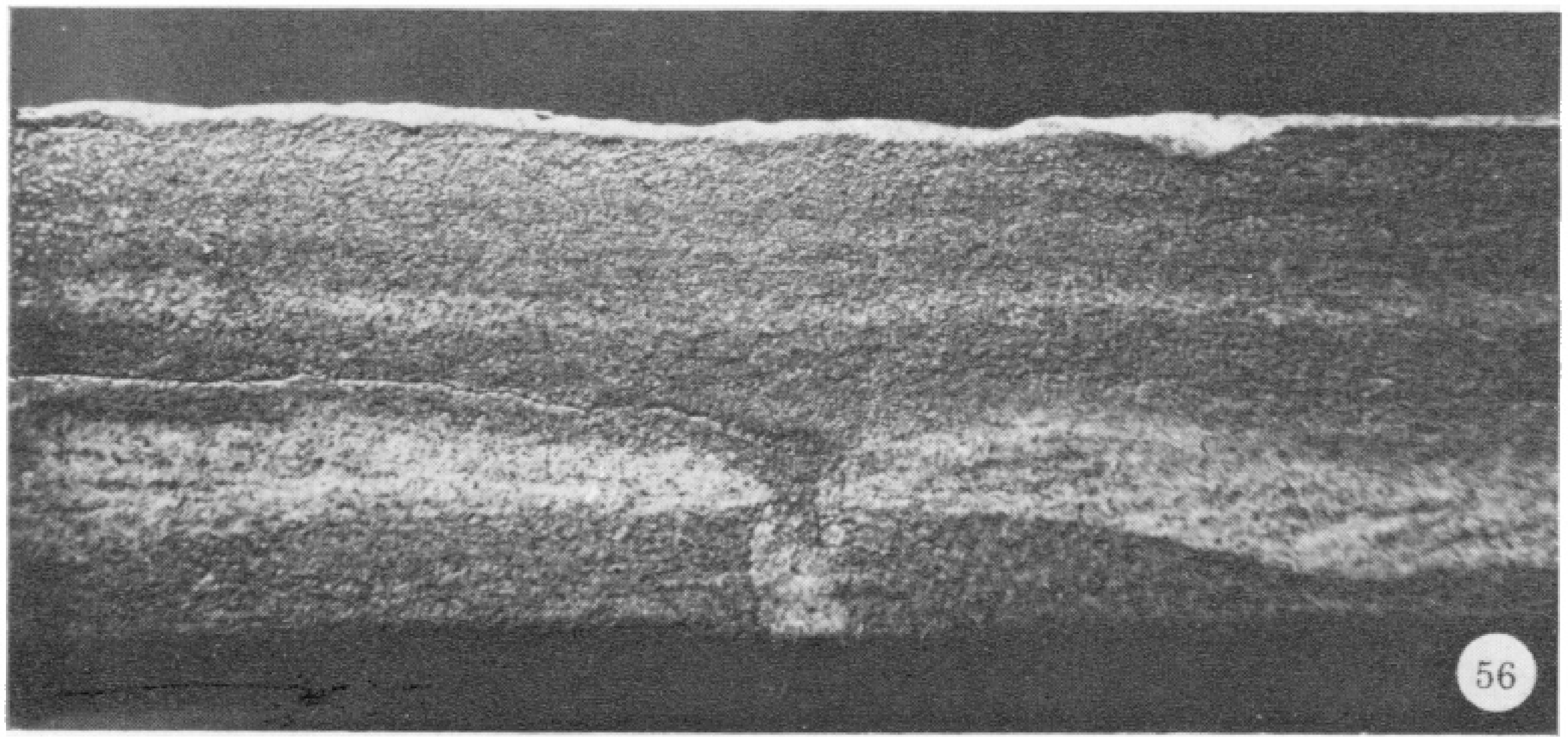
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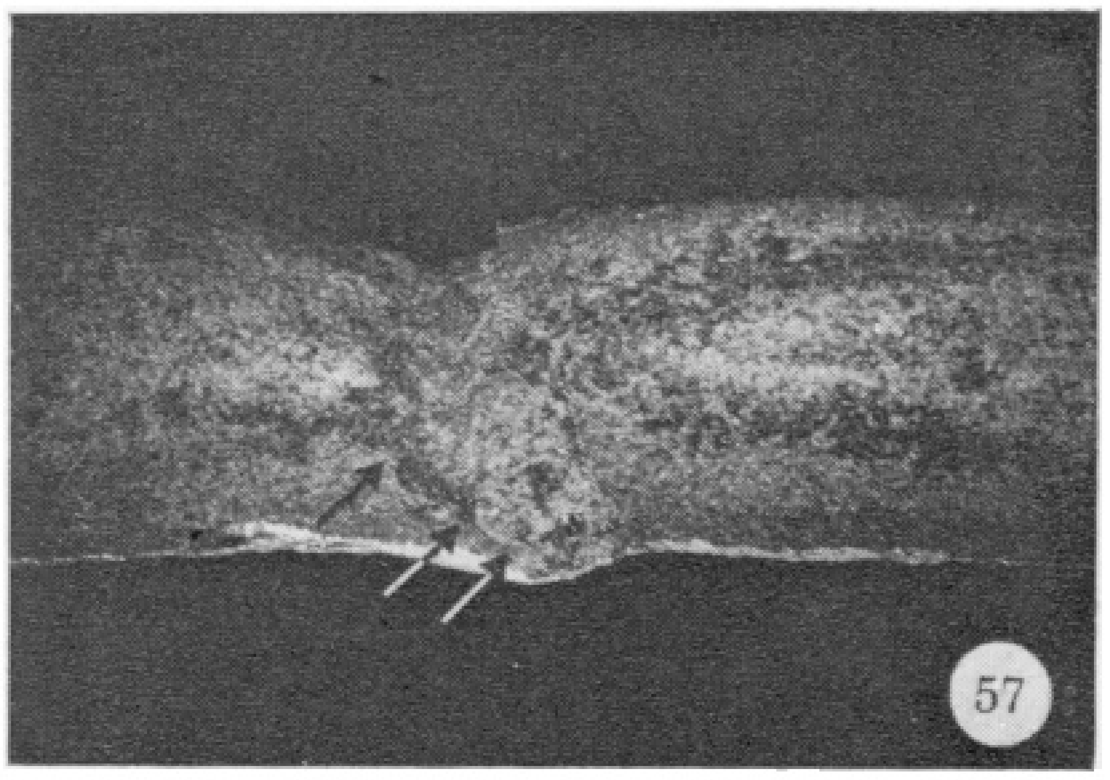
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FIGURES 51-57. For description see opposite.