

THE LAMELLIBRANCH GENUS *PROTHYRIS* IN THE UPPER DEVONIAN AND CARBONIFEROUS OF GREAT BRITAIN

by R. B. WILSON

ABSTRACT. The morphology and distribution of the species of the lamellibranch genus *Prothyris* Meek, occurring in the Upper Devonian and Carboniferous of Great Britain, are reviewed. Of the three Upper Devonian species described by Whidborne (1896), *P. scalprata* is regarded as conspecific with *P. contorta*, and it is concluded that *P. recta* should be removed from the genus. A new Upper Devonian species, *P. stubblefieldi*, is described. Four species are recognized in the Carboniferous: *P. breviformis* Wilson, *P. oblonga* Wilson, *P. scotica* sp. nov., and *P. carbonaria* sp. nov. Some general comments are made on the mode of life, environment, and evolution of the genus.

THE lamellibranch genus *Prothyris* Meek 1869, type species *Prothyris elegans* Meek, was first recorded from the Upper Carboniferous of Illinois and Nebraska (Meek and Worthen 1869, p. 172). American authors have since described several species, showing that the genus ranged from the Upper Devonian to the Upper Carboniferous in North America. Whidborne (1896, pp. 86–89) first recognized the genus in Europe when he described three species from the Upper Devonian of Devon. Hind (1906, p. 148) identified a shell as *Prothyris elegans* from the Scottish Namurian, the first record in the British Carboniferous. Since then, various occurrences of *Prothyris* have been cited from several horizons and the present paper attempts to examine the morphology and distribution of the known British species.

For permission to examine specimens in their care, the writer is grateful to the Director of the Geological Survey and Museum, Mr. A. E. Blackwell of the North Devon Athenaeum, Barnstaple, and Mr. A. G. Brighton of the Sedgwick Museum, Cambridge. This paper is published with the permission of the Director of the Geological Survey. Specimens with registration numbers prefixed by GSM are housed in the Geological Survey and Museum, London, and those by GSE are in the Collection of the Geological Survey, Edinburgh.

Genus *PROTHYRIS* Meek 1869

Meek (in Meek and Worthen 1869, p. 172) proposed the name *Prothyris* for a lamellibranch genus found in the Upper Carboniferous of Nebraska and Illinois, accompanying the announcement with a general description of the genus, but he did not assign any species to it. Later Meek (1871, pp. 8–9) gave a much fuller account, and selected *Prothyris elegans* Meek as the type species. His generic diagnosis is as follows: 'Equivalve, very inequilateral, longitudinally oblong, valves compressed or moderately convex, nearly closed or a little gaping behind and more or less widely gaping in front, where the hiatus is increased in size by a nearly rectangular notch in the margin mainly below the middle; beaks depressed and very near the anterior end with a small ridge usually extending from the anterior side of each to the corner of the anterior marginal notch; dorsal margin without escutcheon or lunule, being erect and sharp behind the beaks. Surface merely marked with striae of growth. Hinge and interior unknown.'

[Palaeontology, Vol. 6, Part 1, 1963, pp. 136–44, pl. 20.]

Only minor additions need be appended to this diagnosis. Immediately posterior and parallel to the ridge running from the umbo to the anterior marginal notch, here called the anterior notch, a shallow groove is present on well-preserved specimens of most species examined. Although the hinge has not been observed, several specimens of Carboniferous species show a structure in the umbonal region which may indicate some degree of dentition. It consists of two subparallel short lines, about 1 mm. long in a valve of 12 mm. length, running postero-ventrally from the umbo, and preserved as faint impressions or ridges. These may indicate poorly developed cardinal teeth; this would support the suggestion made by Meek (1871, p. 8) that the genus has affinities with the Solenidae.

Hind (1908, p. 352) suggested that the ear-shaped process, anterior to the ridge running from the anterior notch to the umbo, here called the anterior lobe, contained the anterior adductor muscle. He also thought that the anterior notch marked a byssal opening. Wilson (1961, p. 102) questioned these suggestions as *P. oblonga* Wilson appears to have the anterior adductor scar posterior to the ridge bounding the anterior lobe, and it seems unlikely that a bivalve gaping at both ends, and probably of burrowing habit, would possess a byssus. Elias (1957, pp. 741–3) recorded radial markings on the valves of *P. soleniformis* and described, but did not figure, a simple hinge apparatus. He, also, regarded *Prothyris* as a subgenus of *Solen* Linnaeus, but the present writer considers that the internal and hinge characters are still not sufficiently well known and that the anterior notch and lobe are of generic significance.

DEVONIAN SPECIES

Whidborne (1896, pp. 86–89, pl. 9, figs. 12–18), in his study of the Devonian faunas of the south of England, described three species from the Upper Devonian of north Devon, which he assigned to *Prothyris*. All the surviving syntypes of these species have been re-examined.

'Prothyris' recta Whidborne

Plate 20, fig. 3

Discussion. The remaining type material of *Prothyris recta* (Whidborne 1896, pp. 86–87, pl. 9, figs. 12–14) consists of two of the three original figured specimens and several indeterminate cited specimens, all in the Geological Survey Collection, London. The specimen illustrated as fig. 13 cannot be found. Of the figured specimens, GSM 6085 (op. cit., fig. 12) is incomplete anteriorly and posteriorly, and is preserved in a dark-grey limestone. It is too poorly preserved to be used for determining the specific characters. GSM 87343 (op. cit., fig. 14), now refigured (Pl. 20, fig. 3), is an internal mould of a left valve, with the ventral margin missing; it is also preserved in a dark-grey limestone. It is subquadrate in outline, about 19 mm. long, and the height is estimated to be about 14 mm. An angular anterior umbonal ridge runs half-way towards the ventral margin, and a rounded posterior umbonal ridge extends to a point half-way down the posterior border. Between these ridges, the valve is moderately convex and there are several indistinct short ridges radiating from the umbo. The anterior margin has irregularities caused by the granular fracture of the matrix. The largest of these irregularities is about one-third of the way down; Whidborne interpreted it as the anterior notch of *Prothyris*.

There is no ridge extending from this feature to the umbo, and the present writer interprets it as fortuitous and of no morphological significance. Whidborne (1896, p. 87) stated that the species was of variable shape, but the specimen GSM 87343, just described, is the only one of the remaining syntypes which is reasonably well preserved; it is here selected as lectotype of the species '*P.*' *recta*. As it does not possess any of the diagnostic characters of *Prothyris*, the writer excludes it from that genus.

Prothyris contorta Whidborne

Plate 20, figs. 1, 2

Prothyris contorta Whidborne 1896, pp. 87-88, pl. 9, figs. 15-16a.

Prothyris scalprata Whidborne 1896, pp. 88-89, pl. 9, figs. 17-18a.

Discussion. An examination of the type specimens of *P. contorta* and *P. scalprata* has shown that only one species is involved. As the only factor relevant to determining which specific name is valid is that of page precedence, it is suggested that the name *scalprata* be regarded as a junior synonym of *contorta*.

Lectotype. The specimen figured by Whidborne (1896, pl. 9, fig. 15), marked as such, and housed in the North Devon Athenaeum, Barnstaple, is here selected as lectotype. It is an internal mould of a left valve, preserved in dark-grey limestone from Kingdon's Shirwell, north Devon.

EXPLANATION OF PLATE 20

All the lamellibranch photographs (figs. 1-9) are twice natural size. The accompanying outline drawings are natural size; they were prepared by drawing in waterproof ink the outlines of the shells on $\times 2$ photographs, bleaching the photographs, and then reducing the remaining outlines photographically. Figs. 1-9 were prepared by Mr. W. D. Fisher and the author.

Figs. 1, 2. *Prothyris contorta* Whidborne. 1, GSM 7044, both valves, Upper Devonian, Plaistow Mill Quarry (Sloly Beds), north Devon. Figd. by Whidborne as *P. scalprata* (1896, pl. 9, fig. 17). 2, Specimen in the North Devon Athenaeum, Barnstaple, lectotype, left valve, Upper Devonian, from Kingdon's Shirwell, north Devon. Figd. by Whidborne (1896, pl. 9, fig. 15) as *P. contorta*.

Fig. 3. '*Prothyris*' *recta* Whidborne. GSM 87343, lectotype, left valve, Upper Devonian, South Cave, Baggy, north Devon. Figd. by Whidborne (1896, pl. 9, fig. 14).

Fig. 4. *Prothyris stubblefieldi* sp. nov. GSM 87387, holotype, left valve, Upper Devonian, at 1,458½ feet in Willesden Borehole, north London.

Fig. 5. *Prothyris oblonga* Wilson. GSE 11755, holotype, left valve, Lower Carboniferous, at 3,775½ feet in Archerbeck Borehole, Canonbie, Dumfriesshire.

Fig. 6. *Prothyris breviformis* Wilson. GSE 11758, holotype, right valve, Lower Carboniferous, at 3,393 feet in Archerbeck Borehole.

Figs. 7, 8. *Prothyris scotica* sp. nov. 7, GSE 11719, holotype, right valve, from mudstone under Calmy Limestone, Scottish Upper Limestone Group, Namurian (E₂), shore 135 yards south-east of Hospital, Kirkcaldy. 8, GSE 11827, paratype, both valves, both valves, roof of Index Limestone, Namurian (E₂), at 284½ feet in Powis Mains No. 1 Bore, Stirlingshire.

Fig. 9. *Prothyris carbonaria* sp. nov. GSM 87388, holotype, left valve, Mansfield Marine Band, Coal Measures, at 1,724½ feet in Lindholme Borehole, Yorkshire.

Fig. 10. View of serial sectioning machine from side away from the operator showing general layout and position of the coolant drip-feed system. Height of machine to top of coolant tank 20 inches.

Fig. 11. Detail of compound slide rest viewed from operating side. Longitudinal feed handle on the right, cross-feed handle on the left. Magnetic positioner mounted on the tool post block in front of the cupped diamond wheel.

Fig. 12. Detail of magnetic positioner showing specimen attached to steel mounting block held by the positioner.

Description. Small, elongate, subrhomboidal, moderately convex, the maximum convexity occurs along the poorly defined umbonal ridge which fades out half-way to the posterior end of the valve. The umbo is situated at the anterior fifth of the length of the shell; it is prosogyrous and inconspicuous. The anterior end is symmetrically rounded but interrupted by a re-entrant notch from which a narrow, ill-defined ridge runs to the umbo. The dorsal margin is short and straight, passing into the long, gently convex, postero-dorsal border which ends in the acutely rounded postero-ventral extremity of the valve. The ventral margin is very gently convex. Two subparallel linear ridges run from the umbo half-way to the ventral margin. The postero-dorsal region is marked by two broad radiating ribs on the internal mould and by three radiating striae on the exterior of the shell. The musculature and hinge characters are not seen.

Dimensions.

	Length mm.	Height mm.
Lectotype	16	6
GSM 7044 (Whidborne, pl. 9, fig. 17)	17	6.5

Remarks. Whidborne (1896, p. 87), in his description of *P. contorta*, mentioned that the ventral margin is slightly concave, as shown in his illustration of the specimen now chosen as lectotype (op. cit., pl. 9, fig. 15). This outline was false, caused by some matrix, since removed, which covered part of the margin. The other specimen he figured as *P. contorta* (pl. 9, fig. 16) is very poorly preserved and indeterminate. Of the four specimens he illustrated as *P. scalprata*, GSM 7044 (pl. 9, fig. 17) is now refigured (Pl. 20, fig. 1) and referred to *P. contorta*; Sedgwick Museum specimen H 363 (pl. 9, fig. 18) is poorly preserved, but is probably *P. contorta* as now described, and the two specimens shown on pl. 10, figs. 16, 17, are indeterminate lamellibranch fragments.

Prothyris stubblefieldi sp. nov.

Plate 20, fig. 4

Discussion. Stubblefield (1947, p. 20) reported an occurrence of *Prothyris* from a borehole sunk by the D'Arcy Exploration Company at Willesden, north London. It occurred at a depth of 1,458½ feet in a lilac-stained mudstone of Upper Devonian age. Although only one specimen is known, it is reasonably well preserved and merits description.

Holotype. GSM 87387, a left valve, in the Geological Survey Collection, London.

Description. Small, elongate, dorsal and ventral margins subparallel, diverging very slightly towards the posterior end. Umbo inconspicuous, placed at anterior end of dorsal margin. A rounded, posterior umbonal ridge extends almost to the postero-ventral angle, giving the valve a moderate convexity. The anterior end is incomplete ventrally but a distinct anterior lobe is present, separated from the remainder of the valve by a narrow, rounded ridge, posterior to which a shallow groove occurs. The dorsal and ventral margins are almost straight, the posterior border is obliquely truncate making an angle of about 45 degrees with the ventral margin. The postero-ventral angle is sharply rounded. Dimensions of the holotype are: length 18.5 mm., height 6 mm.

Remarks. *P. stubblefieldi* differs from the other British Devonian species, *P. contorta*,

by having a relatively longer dorsal margin, by the absence of radial striae on the postero-dorsal region, and by the subparallel alignment of its dorsal and ventral margins. It differs from *P. bergica* Drevermann, the German Devonian (Etröcung) species (Drevermann 1902, pp. 498-9, pl. 14, fig. 15), in that the latter species has convex dorsal and ventral margins. Several species were described in the last century from the Devonian of North America, but the descriptions are meagre. Some of them appear to lack an anterior notch and lobe, suggesting that they may belong to some other genus. Until these species are revised, any comparisons with them must be unsatisfactory but *P. stubblefieldi* shows no marked resemblance to any of the American species so far described.

CARBONIFEROUS SPECIES

The earliest occurring species recorded from the British Carboniferous are *P. oblonga* Wilson and *P. breviformis*, which were found in beds of Lower Visean age in the Archerbeck Borehole, Canonbie, Dumfriesshire (Lumsden and Wilson 1961, p. 11). They have been described already (Wilson 1961, pp. 101-3), but, for the sake of comparison, their salient features are given below.

Prothyris oblonga Wilson

Plate 20, fig. 5

Prothyris oblonga Wilson 1961, pp. 101-2, pl. 3, figs. 5-7.

Description. Relatively small, elongate, the average length/height ratio is 2.75. Dorsal margin slightly arched, the ventral one convex anteriorly and straight posteriorly, while the posterior end of the shell is bluntly rounded. The anterior notch is well developed, almost right-angled, situated about half-way up the anterior end. At this notch the valves gape appreciably. A poorly developed posterior umbonal ridge is present, antero-ventrally to which the shell is marked with fine, regular, concentric striae and obscure radiating striae. On the postero-dorsal area, only faint concentric striae are seen. Dimensions of holotype: length 9.8 mm., height 3.4 mm. The largest specimen seen is about 15 mm. long.

Prothyris breviformis Wilson

Plate 20, fig. 6

Prothyris breviformis Wilson 1961, pp. 102-3, pl. 3, figs. 8-10.

Description. Relatively small, elongate-quadrate, the length/height ratio is approximately 2, which feature distinguishes it from all other known species. The dorsal margin is gently convex, the ventral one convex at the extremities and straight in the middle, while the posterior end of the shell is bluntly rounded and subtruncate. The anterior notch is small and inconspicuous, and the anterior lobe is narrow in the antero-posterior direction. There is no umbonal ridge, the maximum convexity being in the sub-umbonal region. The only markings seen on the shell are fine, concentric striae and obscure radial striae, both confined to the antero-ventral part of the shell. Dimensions of holotype: length 8.9 mm., height 4.2 mm. The largest specimen seen is 10.5 mm. long.

Prothyris scotica sp. nov.

Plate 20, figs. 7, 8

Prothyris elegans, Hind *non* Meek 1908, p. 353, pl. 2, figs. 48-50.*Prothyris* sp. nov. Wilson 1962, p. 514, pl. 66, fig. 26.*Holotype*. GSE 11719, right valve, internal mould, in silty mudstone under the Calmy Limestone, Scottish Upper Limestone Group (E₂), on shore 185 yards south-east of Hospital, Kirkcaldy, Fife.*Paratype*. GSE 11827, both valves, open, attached, in mudstone above the Index Limestone, Scottish Upper Limestone Group, at 284½ feet, in Powis Mains No. 1 Bore 1959 (N.C.B.), Stirlingshire.

Description. Elongate, average length/height ratio (from twenty-three specimens) is 2.9, dorsal and ventral margins parallel. The umbo is situated near the anterior end of the dorsal margin, but not raised above it. The dorsal margin is straight, except for its posterior third which slopes ventrally in a very gentle convex curve to meet the almost vertically truncate posterior border. The ventral margin is almost straight for most of its length, but anteriorly it curves relatively sharply into the anterior notch which is almost rectangular. The anterior lobe is prominent, its height being about twice its length. It is separated from the main part of the valve by a narrow ridge running from the umbo and inclined anteriorly. Posterior to this ridge a shallow groove occurs. A distinct umbonal ridge runs to the postero-ventral angle, angular at its proximal end but becoming less well-defined distally. The anterior lobe and that part of the shell anterior and ventral to the umbonal ridge are marked by fine, regular, concentric striae, but over the umbonal ridge and on the postero-dorsal region the striae tend to coalesce into irregular plications. The valves gape at the anterior notch and at the posterior end. The shell is partly preserved on the paratype and is seen to be very thin. Hinge and interior not seen.

Dimensions.

	Length mm.	Height mm.
Holotype	20	7
Paratype	21.5	c. 8

The largest specimen seen is 30 mm. long.

Remarks. The species just described was first recognized as a *Prothyris* by Hind (1908), who identified it as the American species *P. elegans* Meek. This latter species differs from *P. scotica* in being relatively longer, length/height ratio 3.5 (Meek, in Hayden 1872, p. 223), its dorsal margin is arched, and there is no distinct umbonal ridge. *P. scotica* appears to be similar to *P. soleniformis* Elias, a late Mississippian form from Oklahoma, in its general dimensions and by possessing an umbonal ridge, but the illustration of the holotype of the latter species (Elias 1957, pl. 90, fig. 3) shows a shell markedly different in outline from that just described.

P. scotica is found in mudstones, silty mudstones, and, more rarely, in ironstones in the Scottish Midland Valley, ranging from the Hosie limestones up to the lower part of the Passage Group. In terms of the goniatite zonal scheme, this range is from the uppermost part of P₂ to the top of E₂ as it is represented in Scotland.

Wilson (1961, p. 93) named a specimen as *P. aff. soleniformis* Elias from the Archerbeck Borehole, Dumfriesshire. The horizon is in the roof of the Linns Limestone, probably near the top of the Viséan. A similar form has now been found at the same horizon

in Penton Linns, Canonbie. Neither specimen is well preserved but they show a close resemblance to *P. scotica*. This occurrence of *Prothyris* in the Canonbie area, Dumfriesshire, is about the horizon of the Tyne Bottom and Jew limestones of north-east England. From a band between these limestones in the Roddymoor Boring in Co. Durham (Woolacott 1923; Lee 1924), a specimen of *Prothyris* has now been recognized. It is numbered T 3897^f in the collections of the Geological Survey, Leeds. Both valves are present, but the shell appears to be a juvenile form, incomplete posteriorly, and it is specifically indeterminate.

Prothyris has recently been recorded from Northern Ireland (Fowler and Robbie 1961, p. 234). It occurred in the Millstone Grit (E) at approximately 150 feet in Palm Lodge No. 1 Borehole. The specimen, NIR 774, at present housed in the Geological Survey Collections, London, is part of a right valve, but both anterior and posterior ends are missing. Sufficient is preserved however, to suggest that it is a specimen of *P. scotica*.

From the Millstone Grit of the north of England, two specimens of *Prothyris* are in the Geological Survey Collections, Leeds. They are HS 4591 and CS 844a and come from Chalk Beck, 2 miles north of Caldbeck, Cumberland, and the Cayton Gill Beds (Dunham and Stubblefield 1945, pp. 241–3) in Watergate Beck at Bay Croft Hill Farm, 3 miles west of Pateley Bridge, Yorkshire, respectively. They are both incomplete, but sufficient is preserved to suggest that they have affinity with *P. scotica*.

Prothyris carbonaria sp. nov.

Plate 20, fig. 9

Holotype. GSM 87388, left valve, internal mould, in mudstone from the Mansfield Marine Band, Coal Measures, at 1,724½ feet in Lindholme Borehole, about 10 miles east-north-east of Doncaster, Yorkshire. It is slightly incomplete on the ventral and posterior margins.

Description. Relatively small, elongate-oval, average length/height ratio (from seven specimens) is about three, dorsal and ventral margins almost parallel. The umbo is inconspicuous, situated almost at the anterior end of the cardinal border. The dorsal margin is very gently convex, with a shallow groove parallel and ventral to it. The anterior lobe is narrow, length about one-third of height, and its height is about one-third of the height of the valve. The lobe is separated from the main part of the valve by a faint linear ridge at right angles to the dorsal margin, with a shallow groove posterior to it. The anterior notch forms an oblique angle passing with a gentle curve into the ventral margin, which is straight for most of its length. The posterior end of the valve is almost vertically truncate, gently convex, its dorsal and ventral extremities symmetrically curved. There is no umbonal ridge, and the valves are only gently convex with slight gaps at the anterior notch and the posterior end. The anterior lobe and antero-ventral part of the valve are marked by fine, regular, concentric striae, whereas the postero-dorsal area has irregular plications apparently formed by the coalescence of groups of striae. Hinge and interior unknown. The approximate dimensions of the holotype are: length 15.5 mm., height 5.5 mm. The largest specimen seen is approximately 24 mm. long.

Remarks. Although *P. carbonaria* is similar in its dimensions to *P. scotica*, it differs from the latter in having an arched dorsal margin and no umbonal ridge; its anterior lobe is relatively smaller, and the ridge dividing the lobe from the valve is normal to the dorsal

margin, while in the latter species it is inclined anteriorly when traced from the umbo. *P. carbonaria* resembles *P. elegans* in having a groove parallel to the cardinal edge and in the general shape of the posterior end, but it is distinguished by being relatively shorter than the American species, by having a relatively smaller anterior lobe, and by the ridge posterior to the anterior lobe lying at right angles to the hinge line.

P. carbonaria appears to be a rare species in Britain. Few specimens were available for study, and they all came from the Mansfield Marine Band of the Yorkshire and Nottinghamshire Coalfields and the equivalent horizons in the South Wales and Bristol Coalfields.

GENERAL COMMENTS

Prothyris has been shown to range from the Upper Devonian to the Upper Carboniferous in Britain, as it does in North America. With the exception of *P. contorta*, found in limestone, it normally occurs in mudstones and silty mudstones. The shell matter is very thin, and the normal faunal associates are thin-shelled molluscs, suggesting that the environment was not rich in carbonates. The fact that the valves gape anteriorly and posteriorly, is evidence that the animal was a burrower. The valves are commonly found associated, either open wide or closed, but with one slipped slightly relative to the other. This suggests little disturbance of the bottom deposits, but it is also probably a reflection of the ability of the ligament to withstand decay until the valves were entombed.

From the evidence of the five British species known at present, several changes took place in the valve shape during the evolution of the genus. The Devonian species have the dorsal and ventral margins diverging posteriorly, whereas the Carboniferous forms have these borders more or less parallel. The postero-ventral angle in the Devonian species is acute, but this angle increases to almost a right angle in the later species. The anterior lobe tends to be better defined in the Carboniferous, with the maximum development of this feature being displayed by *P. scotica*. These general trends in the evolution of the valve shape appear to have been paralleled in the North American species.

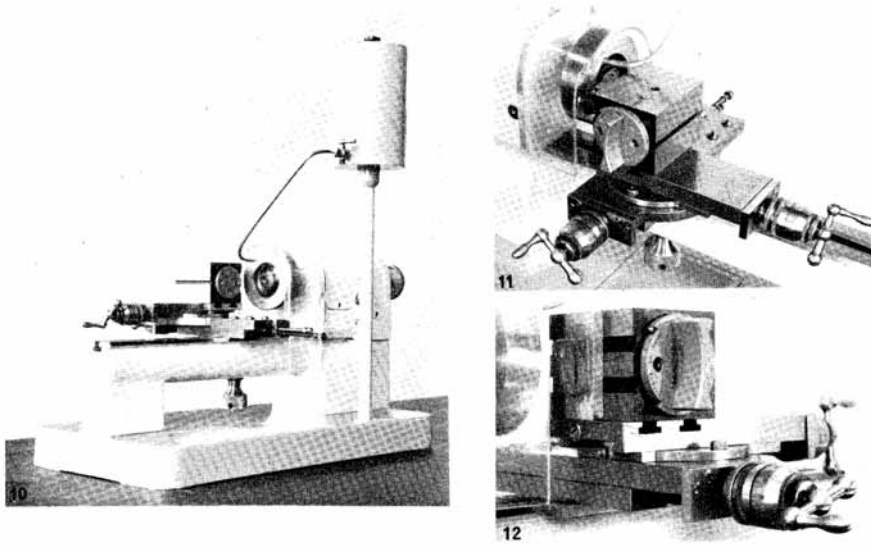
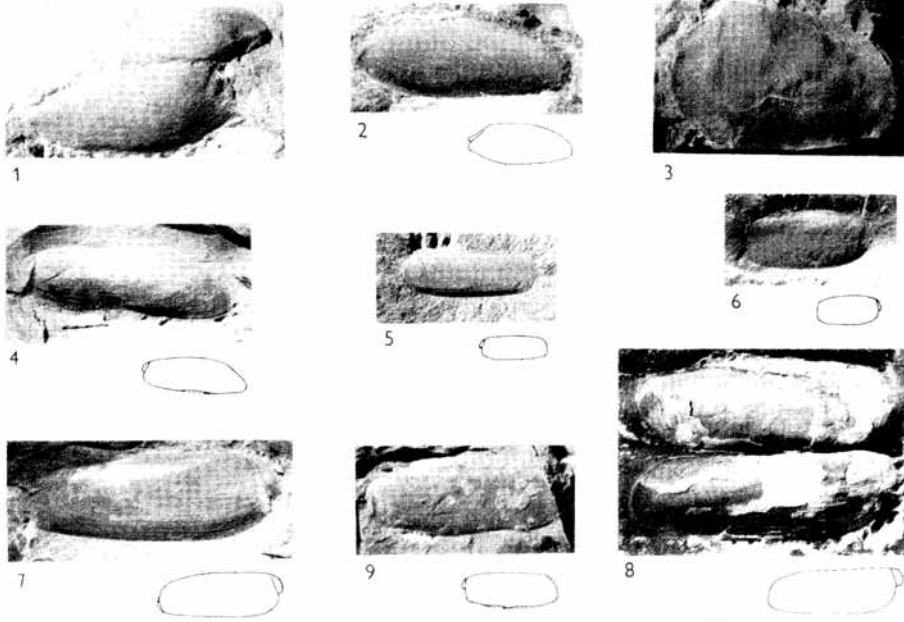
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R. B. WILSON
Geological Survey Office,
19 Grange Terrace,
Edinburgh, 9

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HENDRY, ROWELL, and STANLEY, parallel grinding machine