UNUSUAL STRUCTURES IN DEVONIAN ATRYPIDAE FROM ENGLAND

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ABSTRACT. A distinctive group of Middle Devonian atrypoid brachiopods (Subfamily Palaferellinae Spriestersbach 1942), with cemented muscle platforms and remarkable apical structures and crura, is described. This group, forming part of the newly established genus *Mimatrypa* Struve 1964, is common in the thick stromatoporoid–crinoid reefs of Givetian age in north-western Europe. Type material of J. de C. Sowerby, Phillips, Davidson, and Whidborne is re-examined and revised. The affinity of *Mimatrypa desquamata* (Sowerby), from the Devonian of south-western England, to the genus *Desquamatia* Alekseeva 1960 is refuted. The Eifelian *Gruenewaldtia latilinguis* (Schnur) is sectioned in detail. '*Karpinskia*' *rhenana* Leidhold is removed from the Atrypida.

THE atrypoid brachiopod collections from Devon, on which J. de C. Sowerby (1840), Phillips (1841), Davidson (1864–84), and Whidborne (1893) based their early descriptions, were re-examined and found to be in need of thorough revision. This paper forms a small portion of the work completed in this revision, and was based on the material housed in the British Museum (Natural History), London, the Sedgwick Museum, Cambridge, and the Geological Survey Museum, London, as well as on the writer's own collections from Devon. Through the courtesy of Dr. Hermann Jaeger, comparative German material was examined in the Museum für Paläontologie, Humboldt Universität, Berlin.

Three common 'related' Middle Devonian brachiopods are treated. One of these, ?*Lycophoria rhenana* (Leidhold), frequently described as an atrypid, is removed from the order Atrypida and placed in the Pentamerida. Its true affinities still remain obscure. Most of the emphasis in this study is placed on '*Atrypa*' *desquamata* Sowerby (now in the genus *Mimatrypa* Struve 1964), which was investigated in detail in view of the paper by Alekseeva (1960). In her paper, Alekseeva established the subgenus *Desquamatia* (type species *Atrypa* (*Desquamatia*) *khavae* Alekseeva 1960) for a group of atrypids said to be similar to '*Atrypa*' *desquamata* Sowerby. A careful examination of Sowerby's species revealed, however, that it had internal structures quite distinct from those present in the Russian form, and which linked it to the atrypoid subfamily Palaferellinae Spriestersbach 1942 (emend. Struve 1955, p. 211). Struve (1964) recently established the genus *Mimatrypa*, in which the most important internal structures are cemented muscle platforms, very similar to those present in '*Atrypa*' *desquamata* Sowerby. The third form to be discussed is a species of *Gruenewaldtia* Chernyshev 1885, for which detailed serial sections (based on acetate peels) are given for the first time.

Three major structures, hitherto not well known in the atrypoid group of brachiopods, are described and illustrated. These include cemented muscle platforms, medially fused (not contiguous) deltidial plates continuing into pedicle collars, and minutely fibrous crura, which are almost vestigial and differ structurally from those present in normal examples of *Atrypa* Dalman 1828. A curious type of inner protrusion of deltidial plates and an anomalous type of jugal process are figured.

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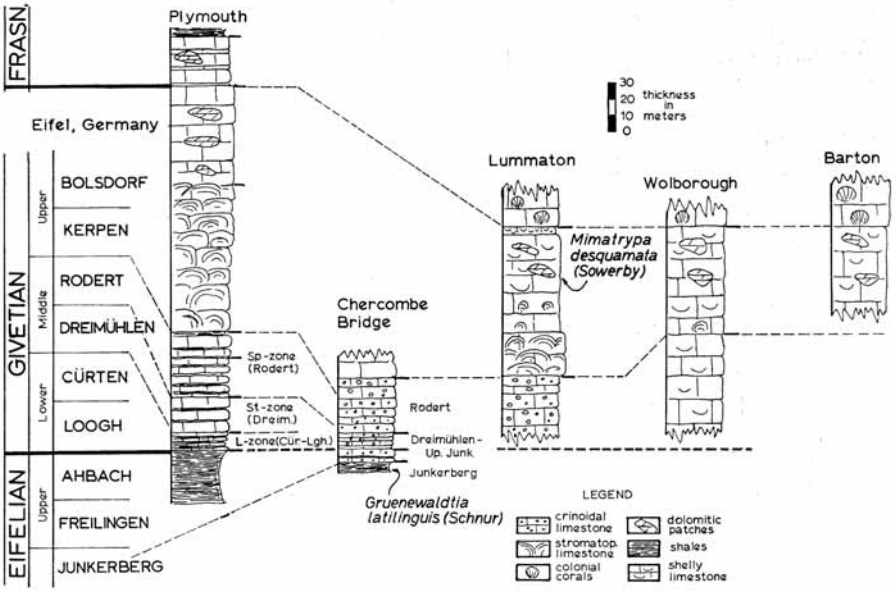
The abbreviations used in the text and explanations to plates and figures are as follows: BM, British Museum (Natural History); GSM, Geological Survey Museum; Geol. Soc. Coll., Geological Society collections (housed in the GSM); SM, Sedgwick Museum. The morphological terms common to the atrypoid brachiopods are described and figured in Siehl (1962) and Struve (1955).



TEXT-FIG. 1. Idealized stratigraphic table for Middle Devonian sections of south-west England. Plymouth section from Taylor 1951; Chercombe Bridge section from Middleton1954; Lummaton section from Jukes-Brown 1906; Wolborough and Barton sections were estimated and have not been measured; Eifel succession from Hotz *et al.* 1955 and Struve 1961.

Stratigraphy. A generalized Devonian succession for Devon, based chiefly on published research, is given in text-fig. 1. The correlations agree substantially with those of Elliott (1961) and House (1963). It is thought that some of the sub-stages defined for the Givetian of the Eifel region in Germany (but not yet internationally accepted) can be recognized in the sections at Plymouth and Chercombe Bridge. The Givetian is arbitrarily divided into lower, middle, and upper divisions based on the succession in the Eifel (Hotz *et al.* 1955; Struve 1961). In the Eifel, the upper Givetian–middle Givetian boundary is doubtfully placed below the Kerpen beds: the base of the Bolsdorf beds, which are characterized by thick stromatoporoid reefs and detrital limestones in the Eifel, would probably form a more natural lithological boundary. Further work is necessary to make such divisions satisfactory, and to revise them.

The material examined comes mainly from three fossiliferous localities in south Devon. These are Lummaton Hill and Barton (in Torquay) and Wolborough (south–

west of Newton Abbot). Sowerby's material was stated to have come from Plymouth, and was probably collected in part at Mount Wise, where fossiliferous upper Givetian rocks are known to occur (Taylor 1951, p. 154). Whidborne's atrypids were mainly from the Lummaton quarries, while Davidson appears to have based his descriptions largely on Wolborough material collected by W. Vicary.

The Lummaton quarries were described in detail by Jukes-Browne (1906), who was able to establish a fairly complete succession. This was reviewed by Elliott (1961, pp. 256–8), who confirmed the age of the Lummaton shell bed as Givetian, a view with which the writer concurs. In the shell bed Elliott found several specimens of *Spinatrypa trigonella* (Davidson), a very similar form of which also occurs at Büchel (near Herrenstrunden, Bergisches Land, Germany) in beds known to be of Givetian age. Stratigraphically directly below the shell bed large specimens of *Mimatrypa desquamata* (Sowerby), now known to be an upper Givetian fossil, are commonly found.

The Barton quarry is not well known. It is thought that only a small portion of the Givetian, mainly upper, is present. Typical examples of *Mimatrypa desquamata* (Sowerby) are not uncommon, but the globose, flattish, and coarsely ribbed varieties are apparently absent.

Most of the well-preserved atrypids come from the Wolborough quarry, which is unfortunately no longer accessible. Collections from this quarry contain a large number of *Mimatrypa desquamata* (Sowerby), small specimens of which tend to resemble *M. insquamosa* (Schnur) of the Eifel. There are also a few coarsely ribbed specimens which are similar to, but far from identical, with *M. flabellata* (C. F. Roemer). *M. insquamosa* and *M. flabellata* are of lower Givetian age, and the presence of intermediate forms in the Wolborough quarry would suggest that more than merely the upper Givetian is present there.

SYSTEMATIC DESCRIPTIONS

Order Atrypida
Superfamily Atrypacea
Family Atrypidae
Subfamily Palaferellinae Spriestersbach 1942

The classification of the atrypoid brachiopods is a controversial matter, and several differing systems have recently been proposed. The elevation of the atrypids to the order level, as separately adopted by Alekseeva (1962), Ivanova (1962), and Tiasheva (1962), is supported. There is strong evidence that the atrypoids as a group are more closely related to rhynchonellid than spiriferid brachiopods. It is rather striking that in some forms of atrypids (e.g. *Mimatrypa flabellata* (C. F. Roemer) and *M. insquamosa* (Schnur)) detailed examination of hundreds of specimens has failed to reveal the presence internally of calcified spiral cones. A similar phenomenon is apparently present in more primitive atrypoid genera such as *Eocoelia*, *Anabaia*, *Leptocoelia*, and *Australocoelia* (Boucot *et al.* 1964, p. 807). The presence of a spiral brachidium, at present the only ground for classifying atrypoids in the order Spiriferida, does not necessarily indicate the same descent.

The palaferellinid brachiopods are given the more conservative subfamily status of Struve (1955, p. 211) chiefly, however, because their origins are unknown and our

knowledge of the group is scant. The direct relationship between synchronous *Atrypa* and *Mimatrypa* is probably purely superficial and, phylogenetically, the discovery of *Mimatrypa* in no way strengthens the relationship between the divergent stocks of the Atrypinae and Palaferellinae (as argued in Struve 1964, pp. 433–4). If *Mimatrypa* were to form an evolutionary intermediate between *Atrypa* and *Gruenewaldtia* it would have had to occur in Lower Devonian rocks rather than upper Middle Devonian rocks. At present it appears more likely that *Mimatrypa* was an end-member of the divergent palaferellinid stock.

Rzhonsnitskaya (1960*b*), in the Russian brachiopod 'Treatise' (ed. T. G. Sarycheva) divided the Atrypidae into seven subfamilies, four of which are the Atrypinae, Palaferellinae, Carinatininae, and Karpinskiinae. Boucot *et al.* (1964) proposed six subfamilies, including the above four, and regrouped some of the genera. At almost the same time Struve (1964), mainly on the basis of similarity in external sculpture, reduced the total number of subfamilies to four by including the genera *Carinatina* Nalivkin 1930 and *Karpinskia* Chernyshev 1885 (type genera of two subfamilies) in the Palaferellinae. This last classification appears to be the most satisfactory. Studies have hitherto been hampered mainly by the lack of knowledge of shell structure (particularly umbonal structures which are valuable in atrypoid taxonomy) and it is clear that the classification of the family Atrypidae is still in an unsettled state.

The palaferellinids, typified by muscle platforms in both valves, include *Gruenewaldtia* Chernyshev 1885 (= *Palaferella* Spriestersbach 1942) and *Mimatrypa* Struve 1964 (= *Desatrypa* Copper 1964). Other genera are at present only doubtfully included: *Vagrania* Alekseeva 1959 (? ancestral to *Carinatina* Nalivkin 1930), *Karpinskia* Chernyshev 1885 (? alternative ancestor to *Mimatrypa* Struve), *Carinatina* Nalivkin 1930, and *Anatrypa* Nalivkin 1941 (possibly derived from *Mimatrypa desquamata* (Sowerby)). Not enough is known about *Pseudogruenewaldtia* Rzhonsnitskaya 1960*a* and *Nalivkinia* Bublichenko 1928 either to include or exclude them from the Palaferellinae. Ivanova (1962) favours their inclusion.

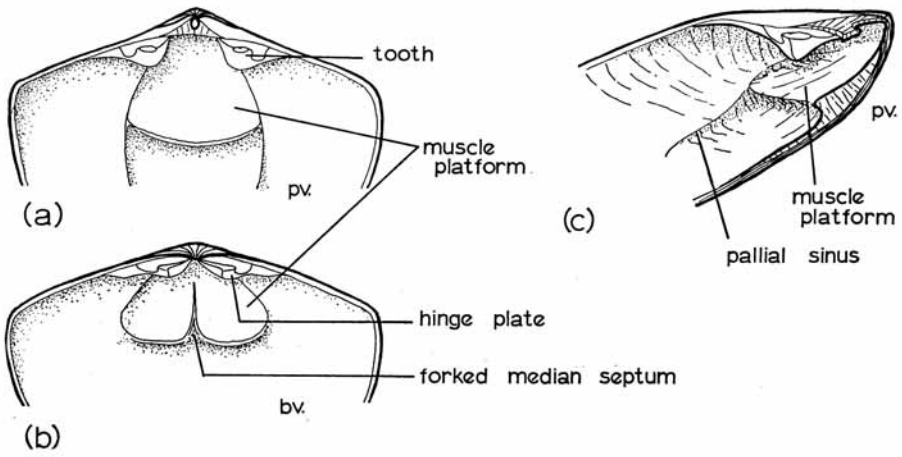
Genus *Mimatrypa* Struve 1964

Type species. Terebratula prisca var. *flabellata* C. F. Roemer 1844, p. 66, pl. 5, figs. 4*a*, *b*.

Diagnosis. Biconvex atrypids with even, continuous palmate ribs, few incipient marginal growth lamellae, a well-exposed inter-area and delthyrium, and 'cemented' muscle platforms in both valves.

Comparison. The genus is distinguished from *Gruenewaldtia* Chernyshev by its cemented rather than septally elevated muscle platforms, its vestigial crura, and in part also by its medially fused deltidial plates and lack of lateral cavities. *Vagrania* Alekseeva, which has a similar development of muscle platforms, is otherwise distinct in having a different rib structure. Adequate comparisons with *Anatrypa* Nalivkin cannot be made until inter-specific relationships in this genus are clarified. For example, the type of rib structure figured for *Anatrypa micans* (Buch) in Rzhonsnitskaya (1960*b*, pl. 55, figs. 7*a–d*) does not coincide with that figured for *A. kadzielniae* (Gürich) and *A. timanica* Markovsky in Alekseeva (1962, pl. 8, figs. 6, 7). *Mimatrypa* in part bears some resemblance to certain species of the genus *Desquamatia* Alekseeva; internally these two genera are quite different. *Mimatrypa* Struve 1964 (3. 8. 1964) is thought to be synonymous with

Desatrypa Copper 1964 (24. 9. 1964). Externally, specimens of the lower Givetian *Mimatrypa insquamosa* (Schnur) are almost indistinguishable from small specimens of the upper Givetian *M. desquamata* (Sowerby). Internally, both possess structures which are not present or are rare in other atrypid genera: medially fused, not contiguous, deltidial plates; massive dental plates without lateral cavities; thick cardinal blocks and hinge plates; and vestigial, minutely fibrous, short crura. The type species of *Mimatrypa* (*M. flabellata* (C. F. Roemer)) differs in having a slightly better developed muscle platform in the brachial valve.



TEXT-FIG. 2. Sketch diagrams showing the muscle platforms in *Mimatrypa desquamata* (Sowerby). Natural size.

Description. The typical features are a biconvex to dorsi-biconvex shell with large interarea, and prominent delthyrium containing two partially or wholly fused deltidial plates and apical foramen. Ribs are deep-troughed and round-crested (i.e. palmate), and are interrupted marginally by a few incipient growth lamellae. Spines are absent and frills are not likely to have been developed. A fine microscopic concentric ornament is preserved in rib troughs.

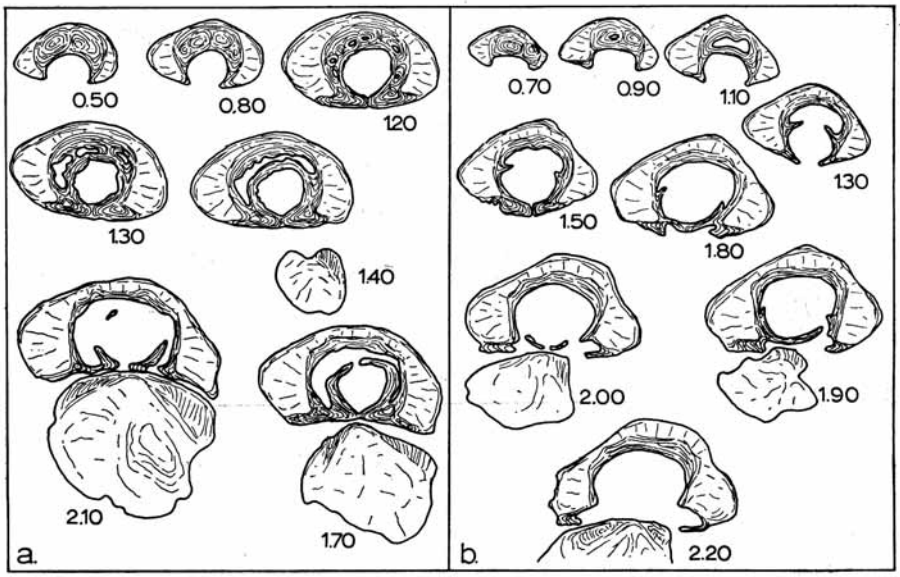
Internally, muscle platforms are weakly developed in the late Givetian species and somewhat more elevated in early Givetian species. A single unified muscle platform in the pedicle valve and, in the brachial valve, a platform divided by a bifurcating median septum, are illustrated in text-fig. 2.

A pedicle collar is well developed in at least one species (*M. insquamosa* (Schnur)), and, where present, forms a unified structure with the deltidial plates (compare text-figs. 3 and 8). This feature does not seem to have been previously described: pedicle collars are common to many atrypids, but in other genera they appear always to have been separated from deltidial plates. In *Mimatrypa* lacking pedicle collars, the deltidial plates are turned inwards to form what may be either an incipient or vestigial pedicle

collar, an anomaly also common to *Gruenewaldtia* (text-figs. 7, 8). Deltidial plates are wholly or partially fused medially, i.e. no suture-line is visible.

Teeth are massive, usually bilobed; dental plates are straight or zigzag in transverse section. No dental ridges or lateral cavities are known.

The cardinal process is weakly developed and overlaps the hinge plates. A thick cardinal block and massive hinge plates are typical.

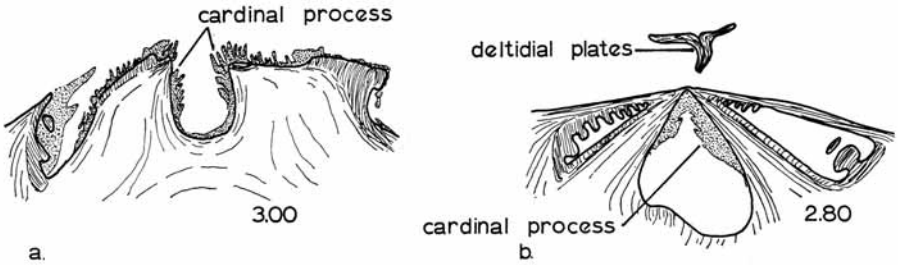


TEXT-FIG. 3. Transverse serial sections of *Mimatrypa insquamosa* (Schnur), lower Givetian, Baarley, Gerolstein syncline, Germany. Fused deltidial plates are typical of the genus. *a*, Pedicle collar freed from the shell wall; *b*, pedicle collar relatively short and not as well developed. ×3·6.

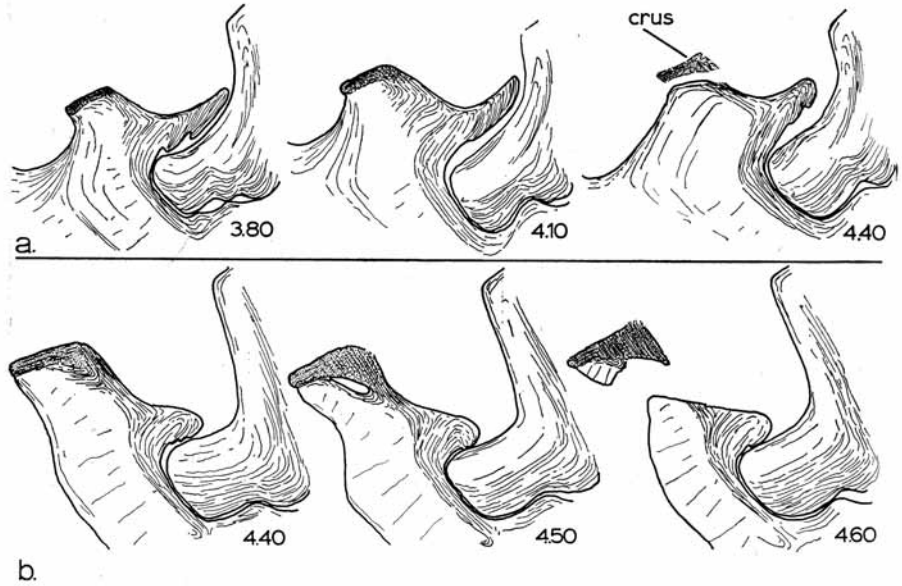
Crura are extremely weak, probably strongly degenerated structures; their curious development and mode of attachment to the hinge plates is not known in other atrypids at present (see text-fig. 5). In *Mimatrypa insquamosa* (Schnur) the normal connecting spiralia are absent. The crura of *Mimatrypa* are comparable with the rather short crura of some forms of *Gruenewaldtia*.

Primary lamellae, spiralia, and jugal processes may be completely absent in *Mimatrypa insquamosa* (Schnur) and *M. flabellata* (C. F. Roemer), since an exhaustive search in hundreds of specimens has failed to reveal them. Quenstedt apparently also encountered similar difficulties for he states (1885, p. 702): 'Ich habe zwar die Spirallamellen an ihr nicht finden können, doch werden sie wohl nicht fehlen.' The apparent absence of spiralia may be related to the presence of vestigial crura.

Distribution. At present *Mimatrypa* seems to be largely restricted to western Europe. Breivel (1959, pp. 54, 55) appears to have found it in the Ural Mountains of the U.S.S.R.



TEXT-FIG. 4. Transverse serial sections of hinge-plates and cardinal processes in *a*, *Mimatrypa insquamosa* (Schnur), Baarley, Gerolstein, and *b*, *M. desquamata* (Sowerby), Lummaton, Devon. ×9.



TEXT-FIG. 5. Transverse serial sections of crural development in *a*, *Mimatrypa insquamosa* (Schnur), Baarley, Gerolstein, and *b*, *M. desquamata* (Sowerby), Lummaton, Devon. ×9.

Range. Middle Devonian: upper Eifelian to upper Givetian.

Member species. *Terebratula prisca* var. *flabellata* Roemer 1844, p. 66, pl. 5, figs. 4*a*, *b*; *Terebratula insquamosa* Schnur 1853, p. 182, pl. 24, figs. 5*a*, *b*; *Atrypa julii* Gortani 1911, pp. 159–60, pl. 17, figs. 9–11.

Mimatrypa desquamata (Sowerby)

Plate 46, figs. 1–11; Plate 47, figs. 7–10, 13–16; text-fig. 7

1840 *Atrypa desquamata* Sowerby, explan. to pl. 56, figs. 19–22.
1841 *Terebratula* (*Atrypa*) *desquamata* Sowerby; Phillips, p. 82, pl. 33, figs. 146*a–h*.

1864–65 *Atrypa desquamata* Sowerby; Davidson, pp. 58–59, pl. 10, figs. 9–12, pl. 11, figs. 1, 3–6.
1882–4 *Atrypa desquamata* Sowerby; Davidson, pp. 39–40, pl. 1, figs. 15, 15*b*.
1885 *Atrypa reticularis* var. *desquamata* Linné; Maurer, pp. 181–2, pl. 7, fig. 33.
1893 *Atrypa desquamata* Sowerby; Whidborne, p. 117, pl. 13, fig. 13.
1928 *Atrypa desquamata* Sowerby; Leidhold, pp. 96–97.
Atrypa circularis Leidhold, pp. 97–98, pl. 6, fig. 5; pl. 7, fig. 2.
Atrypa globosa Leidhold, pp. 94–95, pl. 6, fig. 4.
1934 *Atrypa desquamata* Sowerby; Torley, p. 123, pl. 9, fig. 73.
Atrypa circularis Leidhold; Torley, p. 124, pl. 9, fig. 74.
Atrypa globosa Leidhold; Torley, p. 124.

Type locality. This is designated as Plymouth by Sowerby. The stratigraphic horizon and precise locality are unknown. The species occurs most abundantly at the north-west end of the Lummaton Hill quarries, Torquay, Devon.

Material. Ninety-seven specimens from Wolborough, Plymouth, Barton, and Lummaton in Devon.

Range. Upper Givetian, Middle Devonian. The species is probably a good index fossil of the upper Givetian.

Source sediment. This is characteristically a massive to thickly bedded, light grey to whitish, stromatoporoid–crinoid detrital limestone with abundant large brachiopods, many of which occur in 'nests'. A turbulent, high-energy biohermal environment is indicated. The low argillaceous content of the limestones suggests clear, well-aerated waters.

Associated fauna. *Stringocephalus* cf. *burtini* DeFrance, *Uncites gryphus* (Schlotheim), *Hypothyridina cuboides* (J. de C. Sowerby). Most brachiopods occur in patches. Horn corals are rare; tabulate corals and colonial corals common. There is abundant stromatoporoid and crinoid debris. The fauna is probably largely indigenous. *Mimatrypa desquamata* (Sowerby) has not yet been found in argillaceous sediments of the same age.

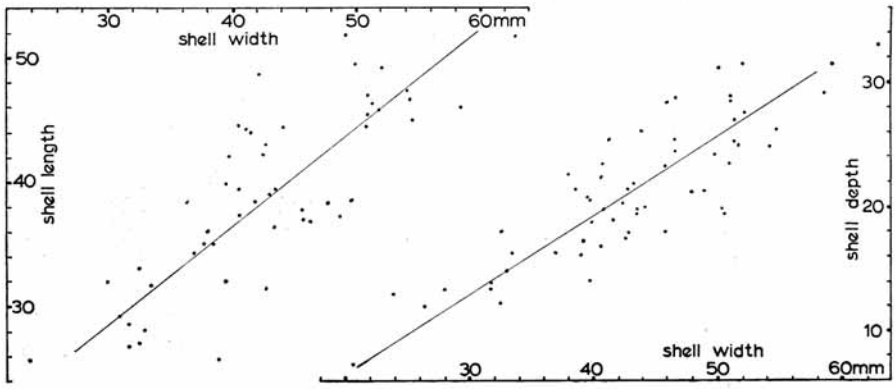
Diagnosis. Large, broad, biconvex, somewhat planar, subcircular palaferellinids with a prominent, blunt, protruding beak and moderately sized foramen. Internally, the main pallial sinuses are unforked. Spiralia are present. Pedicle collars not observed.

External morphology (terminology after Siehl (1962) and Struve (1955)). The species ranks among the largest known atrypids: the maximum size is about 65 mm., and the average mature size is between 40 and 50 mm. (text-fig. 6). The subcircular shell outline is truncated posteriorly by an obtusely angled hinge-line. Maximum width and maximum depth occur about mid-length. A broad weak fold is developed on the anterior commissure; globose specimens have a more prominent fold (as, for example, in Davidson 1864–5, pl. 11, fig. 1).

The pedicle valve is less convex than the brachial: it is somewhat planar, with a weakly and broadly convex mid-area (transl. German 'Mittelfeld') and flattened margins. The beak is blunt, orthocline (never incurved); it projects 3–4 mm. over the dorsal apex. The shoulder angle ('Schulterwinkel') is about 140 degrees but may be more acute. The shoulder line ('Schulterlinie') is only weakly indented. Hinge corners ('Schlossecke') are well rounded. The edge of the interarea ('Areakante') is sharp-edged apically but rounded and poorly defined laterally. The delthyrium is rather narrow and acutely angled (70 degrees at the apex). The apical hypothyrid foramen, rarely expanded into the ventral umbo, is 1 to 2 mm. across. Deltidial plates are crenulated.

The brachial valve is slightly more convex, and is well rounded. The dorsal apex is not covered by the deltidial plates of the opposing valve. A weak median furrow occurs apically in a few specimens.

Internal shell markings. The shape and size of the muscle platforms can be seen in text-fig. 2 and Plate 46, figs. 1, 2, 4. Muscle platforms are striated longitudinally. In the pedicle valve two long, but rather weak, pallial sinuses flank the muscle platform and extend roughly parallel towards the anterior margin, forming a shallow trough anterior to the



TEXT-FIG. 6. Scatter diagrams showing the size relationships in *Mimatrypa desquamata* (Sowerby). Data combined from localities at Lummaton, Barton, and Wolborough.

platform. Tributary pallial arteries are extremely weak (Pl. 46, fig. 3). The small nephritic adductor scars common to other atrypid genera are not present. Internal markings are well illustrated by Leidhold (1928, pl. 6, figs. 4–5; pl. 7, fig. 2). It is surprising that Davidson did not mention muscle platforms in his descriptions. It is suspected that Davidson's fig. 9 (1864–5, pl. 11) was a reconstruction drawn from other brachiopods, some possibly of Silurian age.

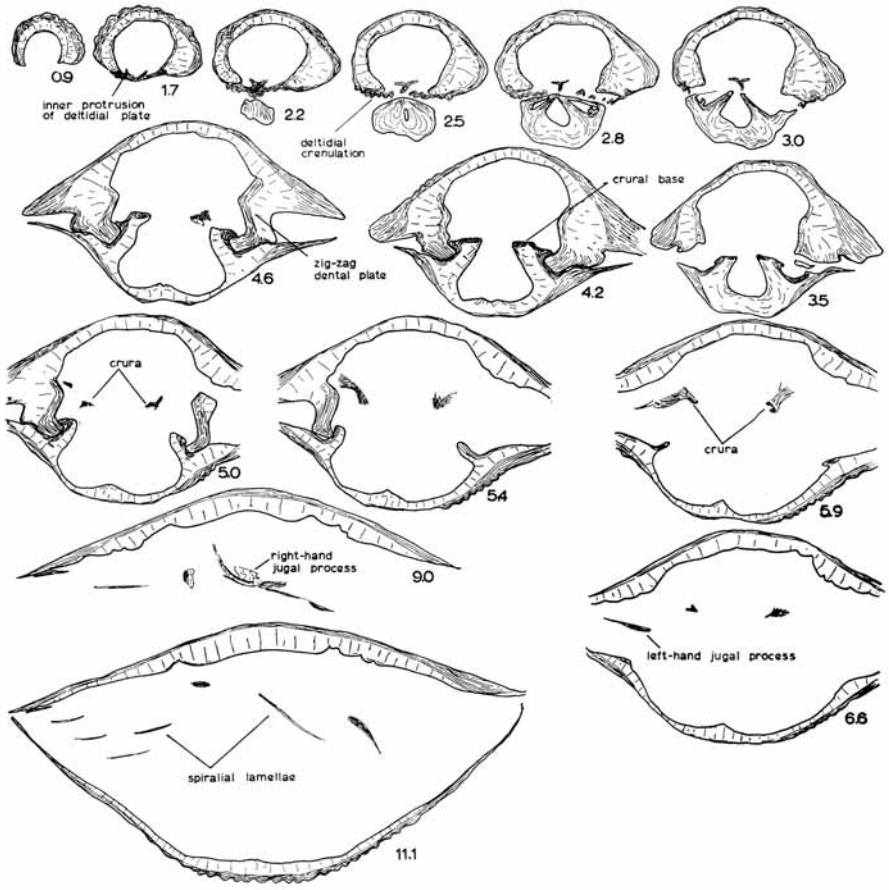
Interior structure. Enlarged transverse serial sections are shown in text-fig. 7. The internal description is based on more than 350 acetate peels taken from four serially sectioned specimens. Numerous specimens had a lining of dolomite crystals.

EXPLANATION OF PLATE 46

All figures natural size.

Figs. 1–11. *Mimatrypa desquamata* (Sowerby). 1, 2, Ventral and dorsal views of the pedicle valve figured in Sowerby 1840, pl. 56, fig. 19, paratype SM H3836, Plymouth (from preservation more likely Wolborough). 3, Ventral view of a decorticated shell showing pallial arteries, SM H3842, Plymouth. 4, Dorsal view of a broken portion of ventral valve (complete specimen probably figured in Davidson 1864–5, pl. 11, fig. 5), BM 22119, Wolborough. 5, 6, Poorly preserved flattish specimen figured in Sowerby 1840, pl. 56, fig. 21, paratype Geol. Soc. Coll. 6322, Plymouth. 7, 8. Ventral and posterior views of well-preserved specimen, rather globose and with angular beak, GSM 50855, Wolborough. 9–11, Dorsal, ventral and lateral views of *lectotype* figured in Sowerby 1840, pl. 56, fig. 20, Geol. Soc. Coll. 6342, Plymouth; note rib shape and pattern of bifurcation.

A pedicle collar was not observed, an effect possibly due to poor preservation. The inner margins of the deltidial plates show inward protrusions (text-fig. 7, 0·7–3·0 mm.). Deltidial plates are corrugated, thin, but not hollow, intricately interlocked medially,



TEXT-FIG. 7. Transverse serial sections of *Mimatrypa desquamata* (Sowerby), Lummaton, Devon. Intervals in millimetres from the ventral apex. ×2.

and fused near the dorsal umbo. Teeth are massive, squared, with a strong inner lobe and weak, stubby outer lobe. The inner margins of the dental plates are zigzag; no lateral cavities appear, nor are there any circular growth lines in the dental plates (as, for example, in *Atrypa* and *Desquamatia*).

In the brachial valve a weak, usually amorphous, cardinal process occupies the notothyrial cavity (text-fig. 4*b*); in one specimen three to five longitudinal striations were

observed. Hinge plates are thick. Crura (text-fig. 5*b*) are composed of minute, microscopic calcite fibres oriented normal to the hinge plate and commonly arched over the hinge plate to leave a small gap (text-fig. 5*b*, 4·5 mm.). The crural fibres radiate ventrolaterally, becoming increasingly more diffuse and tenuous towards the sides of the shell cavity. Jugal processes are not fully known: they appear to be disjunct. In text-fig. 7 (at 9·0 mm.) an anomalous structure, part of the right-hand jugal process, appears to be strikingly similar to one found in *Gruenewaldtia latilinguis* (Schnur) (text-fig. 8). Davidson's conclusions about the jugal processes are contradictory: in Davidson 1864–5, pl. 11, figs. 7–8, a disjunct set of processes is drawn, but in Davidson 1882–4, pl. 1, figs. 15, 15*b*, a fused jugum is shown. The spiralia have up to fifteen whorls.

Ribs. The wavelength of the ribs is roughly similar to that of the finely ribbed *Mimatrypa insquamosa* (Schnur) but not as coarse as in *M. flabellata* (Roemer). There is a predominance of the finer type of ribbing. In the mid-area, from eight to thirteen ribs occupy 10 mm. of arc; the average is about eleven.

Ribs typically are round and wide-crested and rather narrow-troughed (Pl. 46, fig. 10). Some specimens, particularly ones with angular beaks (Pl. 46, figs. 7, 8), appear to have narrower and more thinly crested ribs. The full variation cannot be determined because of the lack of well-preserved specimens. In specimens with decorticated shells it is common to see ribs reflected on the shell margins as short furrows (e.g. Whidborne 1893, pl. 13, fig. 13; and this paper Pl. 46, fig. 3; Pl. 47, fig. 13).

Growth lamellae. These are very weakly developed at the margins. No frills are present. Presumably Davidson incorporated this feature in the specific name '*desquamata*' (Latin *de*, without or loss of; *squamata*, covered with squamae or scales).

Growth and variation. A large variability in shape, ranging from extremely flat forms to rather globose forms, is common, and appears to be typical of reef-inhabiting organisms. A separation of forms does not appear to be feasible. Sowerby distinguished a variety which he called *compressa* (Pl. 46, figs. 5, 6; Pl. 47, fig. 10), a form which seems to be more common at Plymouth than elsewhere. At present this is treated as a minor variation. Rare globose specimens are found at Wolborough.

Three specimens of the variety *compressa* Sowerby were figured by Whidborne (1893, pl. 13, figs. 13–15), and they have been re-examined. Of these, only one (fig. 13) is in fact a small specimen of *Mimatrypa desquamata* (Sowerby); the other two belong to the genus *Carinatina* Nalivkin.

Davidson has clearly demonstrated the variety of forms present in *Mimatrypa desquamata* (Sowerby). His drawings are, unfortunately, almost wholly figurative and have obviously been restored (occasionally they have been drawn as mirror images, e.g. in his 1864–5, pl. 11, fig. 2). The narrow forms (Davidson 1864–5, pl. 10, figs. 12, 13) were not found in collections and appear to be a scarce variety. Extremely wide forms are not uncommon (op. cit., pl. 11, figs. 4, 5). The shape and outline most common to *M. desquamata* are those shown in pl. 10, figs. 9, 10.

Leidhold described two species, *Atrypa circularis* and *A. globosa* (1928, pl. 6, figs. 4, 5; pl. 7, fig. 2), from a quarry near Iserlohn, Germany. The type specimens of these two species, as well as other topotypes, were re-examined. Nearly identical specimens are present in the collections from Devon. Their rib structure is the same and very little difference, except in shape, could be found between Leidhold's own species. Further-

more, as support for their synonymy with *Mimatrypa desquamata* (Sowerby), is their synchronous upper Givetian occurrence.

Remarks. The species is distinguished from *M. insquamosa* (Schnur), to which it is most closely related, by its consistently greater size (almost 'gigantesque'), somewhat finer ribs, and internally by the presence of spiralia and lack of pedicle collar.

It differs more strongly from *M. flabellata* (C. F. Roemer) in its biconvexity and fine bifurcating ribs. Internally, the latter has a more strongly elevated dorsal muscle platform.

Mimatrypa desquamata (Sowerby) has been reported from all over the world, but it is likely that the resemblance to most other atrypids is only superficial. In England and Germany it is common in upper Givetian rocks and appears to have particularly favoured a biohermal environment. It is known in Germany at Iserlohn (Bilveringsen quarry), Waldgirmes and Balve. At present it is not known to occur in the Torringer beds and Plattenkalke of the Bergisch–Gladbach area near Köln, which also are of Givetian age.

Alekseeva (1960, pp. 421–4) described a new subgenus *Atrypa* (*Desquamatia*) based on the type species *Atrypa khavae* Alekseeva, and which, at that time, appeared to be related to the ubiquitous '*Atrypa*' *desquamata* described by Sowerby. A detailed examination of Sowerby's types revealed that this was not the case (Copper 1964). Biernat (1964, p. 282) has retained Alekseeva's interpretation that the large '*Atrypa*' *desquamata* Sowerby of the Rhineland, apparently also present in Poland, belongs to *Desquamatia* (and hence the subfamily Atrypinae).

Genus *Gruenewaldtia* Chernyshev 1885

Type species. Terebratula latilinguis Schnur 1851.

Diagnosis. An adequate diagnosis is given by Struve (1955, p. 211). As Struve (1955, 1964) has pointed out, the genus *Palaferella* Spriestersbach 1942 is a junior subjective synonym of *Gruenewaldtia* Chernyshev 1885.

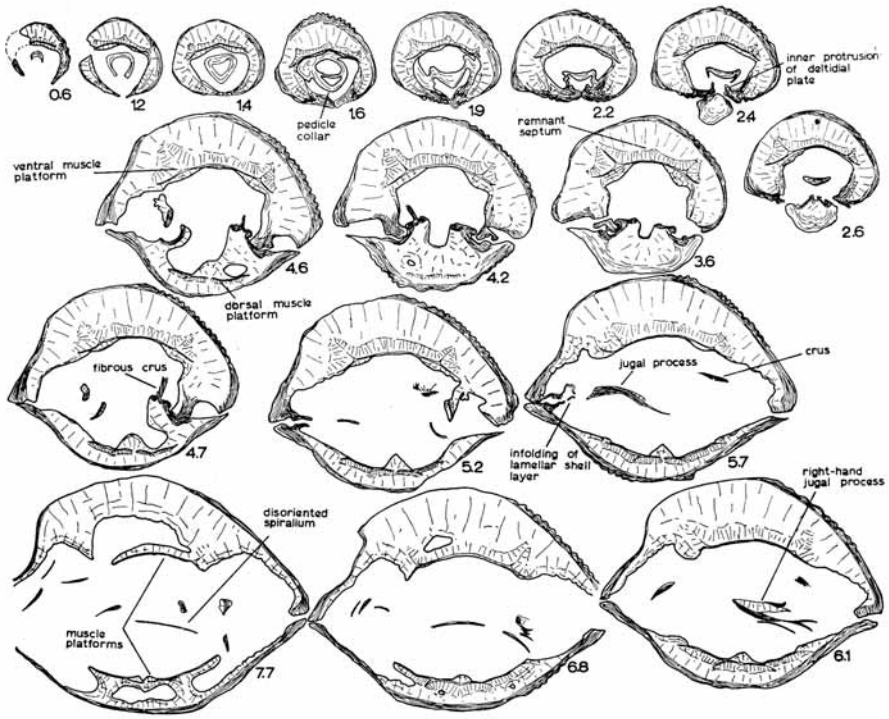
Gruenewaldtia latilinguis (Schnur)

Plate 47, figs. 1–3; text-fig. 8

Material. Eighteen specimens from Chercombe Bridge shales.

Remarks. This species, which is common to abundant in middle Eifelian sediments of the Eifel region in Germany, has not been described in detail. A short diagnosis is given by Struve (1955, p. 212) and a further revision is being undertaken by him. The specimens from Chercombe Bridge, Devon, are indistinguishable from the German forms. For this reason, a close correlation is drawn between these two areas.

Davidson described an '*Atrypa*' *latilinguis* from Chercombe Bridge in 1882–4 (p. 41, pl. 2, figs. 9, 9*a*) and assumed correctly that it was closely related to the Eifel species of Schnur. In the Eifel, the genus is wholly confined to sediments of Eifelian age, although Biernat (1964, pp. 280, 333) dated the Skaly beds of the Holy Cross Mountains in Poland, containing *Gruenewaldtia latilinguis* (Schnur), as lower Givetian. Ivanova (1962) has shown that *Gruenewaldtia* also occurs in the Givetian of Russia. It is possible to come to the rather contradictory conclusion that the same fossils can have differing,



TEXT-FIG. 8. Transverse serial sections of *Gruenewaldtia latilinguis* (Schnur), Chercombe Bridge, Devon. The jugal process (at 6·1 mm.) should be compared with that in text-fig. 7 (at 9·0 mm.). ×2.

EXPLANATION OF PLATE 47

All figures natural size.

Figs. 1–3. *Gruenewaldtia latilinguis* (Schnur). Ventral, lateral, and posterior views of specimen serially sectioned in text-fig. 8, BM B22077, Chercombe Bridge.

Figs. 4–6. *Mimatrypa* cf. *insquamosa* (Schnur). Ventral, dorsal, and posterior views of well-preserved specimen, GSM 50859, East Ogwell.

Figs. 7–9, 14, 16. *Mimatrypa* cf. *desquamata* (Sowerby). 7–9, Ventral, dorsal, and posterior views of finely ribbed specimen, BM B22105, Wolborough. 14, Posterior view of finely ribbed form, BM B22098, Wolborough. 16, Ventral view of same variety, BM B49921, Wolborough.

Figs. 10, 13, 15. *Mimatrypa desquamata* (Sowerby). 10, Dorsal view of paratype figured in Sowerby 1840, pl. 56, fig. 22, Geol. Soc. Coll. 6323, Plymouth. 13, Dorsal view of small specimen figured in Whidborne 1893, pl. 13, fig. 13, SM H4290, Lummaton (?shell bed). 15, Dorsal view of large typical form, Geol. Soc. Coll. 6911, Wolborough.

Figs. 11–12. ?*Lycophoria rhenana* (Leidhold). Lateral and dorsal views of specimen figured in Davidson 1864–5, pl. 11, fig. 12, Geol. Soc. Coll. 6913, Wolborough.

Figs. 17–19. *Mimatrypa* aff. *insquamosa* (Schnur). Posterior, dorsal, and lateral views of well-preserved coarsely ribbed form, BM B44375, Lummaton (?).

restricted chronostratigraphic distribution in widely separated areas. Ivanova (1962) has advanced two highly plausible explanations for such contradictions: one of salinity controls of brachiopod distribution, and the second of 'facies' control.

Gruenewaldtia has so far been found in Britain only at Chercombe Bridge, in shales believed to be middle Eifelian in age (see text-fig. 1). This is the first time these forms have been examined for internal structure. Only a single transverse section of the pedicle valve of *Gruenewaldtia latilinguis* (Schnur) is available for comparison in the literature (Struve 1955, fig. 8*a*). Biernat (1964) did not describe topotype material from the Eifel. In sectioning topotype Eifel material I have not come across major internal differences between the Polish, Eifel, and Devon forms, although a few small, but important, structural details were previously omitted.

A distinctive internal structure, common to most examples of *Gruenewaldtia* Chernyshev and *Mimatrypa* Struve, and consisting of small internal projections of the deltidial plates, has also been found in specimens from Devon (text-fig. 8, 2·2–2·4 mm.). This structure is also present in *Gruenewaldtia matutina* Struve and *G.* cf. *rhenana* (Spriestersbach) from the Eifel. Similarly, it appears to be present in *G. sibirica* Ivanova (1962, fig. 36), where it seems partially to join a pedicle collar. In *G. latilinguis helenae* Rzhonsnitskaya (1960, pl. 2, figs. 1, 2) the protrusions extend from the pedicle collars rather than the deltidial plates. This feature may be useful in classification.

In the pedicle valve of specimens of *G. latilinguis* from Devon, two major septa support the muscle plate, which consists of a 0·5 to 1 mm. thick, monocrystalline sheet (septa and muscle plate together form a muscle platform); also, it is significant that one or two remnant septa are still found apically (text-fig. 8, 1·2–4·2 mm.). This is also true of the same species in the Eifel. The dorsal plate is supported by two lateral septa and a weak median septum.

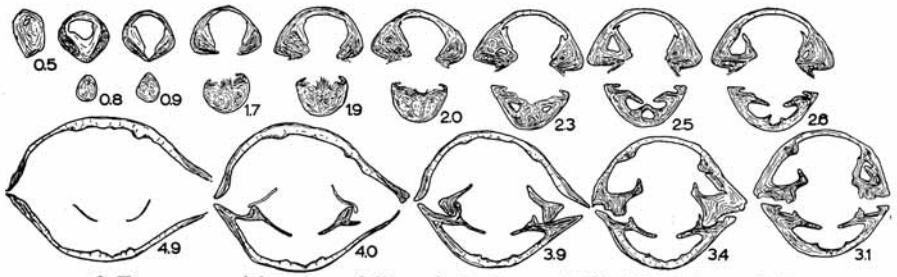
G. sibirica Ivanova and the Devon form possess a pedicle collar. Lateral cavities are absent.

Order Pentamerida
Superfamily Porambonitacea
Genus ?*Lycophoria* Lahusen 1885
?*Lycophoria rhenana* (Leidhold) 1928

Plate 47, figs. 11–12; text-fig. 9

1864–5 *Atrypa flabellata* (C. F. Roemer); Davidson (*partim*), pp. 59–60, pl. 11, figs. 10–12.
1928 *Karpinskia rhenana* Leidhold, pp. 98–99, pl. 7, figs. 4*a–d*, 5.

Remarks. An internal examination by means of serial peels of a representative specimen of a form previously grouped under '*Atrypa*' *flabellata* revealed a shell wall structure and internal morphology which are not found in atrypid brachiopods. However, the exact affinities of this form are still unknown and it is tentatively placed in the Pentamerida. Even Whidborne, who examined this form (1893, p. 120), was doubtful about its affinities and mentioned a resemblance to *?Mutationella guerangeri* (Verneuil). There is also a crude resemblance to *?Nanothyris primaeva* (Gosselet) (1920, p. 102, pl. 14, figs. 19–26). The form may also have affinities with the terebratulid genus *Notothyris* Waagen. A more detailed description must be left until better and more abundant material can be examined, and until its true affinities are confirmed.



TEXT-FIG. 9. Transverse serial sections of ?*Lycophoria rhenana* (Leidhold), Wolborough, Devon. The ?deltidial plates (2·5 to 2·8 mm.) and crude septalium (2·3 to 3·1 mm.) are of interest. ×2.

Conclusions

In the Givetian sediments of north-western Europe, the atrypids grouped under *Mimatrypa* Struve appear to have replaced the atrypid genera *Gruenewaldtia* and *Desquamatia*, which are abundant in sediments of Eifelian age. *Mimatrypa* lived in a biohermal environment almost exclusively, and appears to have been absent in synchronous argillaceous sediments.

Mimatrypa is believed to have been derived from *Gruenewaldtia*. A tentative lineage sketched by Copper (1964) is based on a number of internal morphological features which these genera have in common. *Mimatrypa* shows a strong tendency towards complete disintegration of structures connecting the spiralia to the hinge plates. *Mimatrypa* appears to have become extinct by the end of Middle Devonian time: it possibly gave rise to *Anatrypa* Nalivkin.

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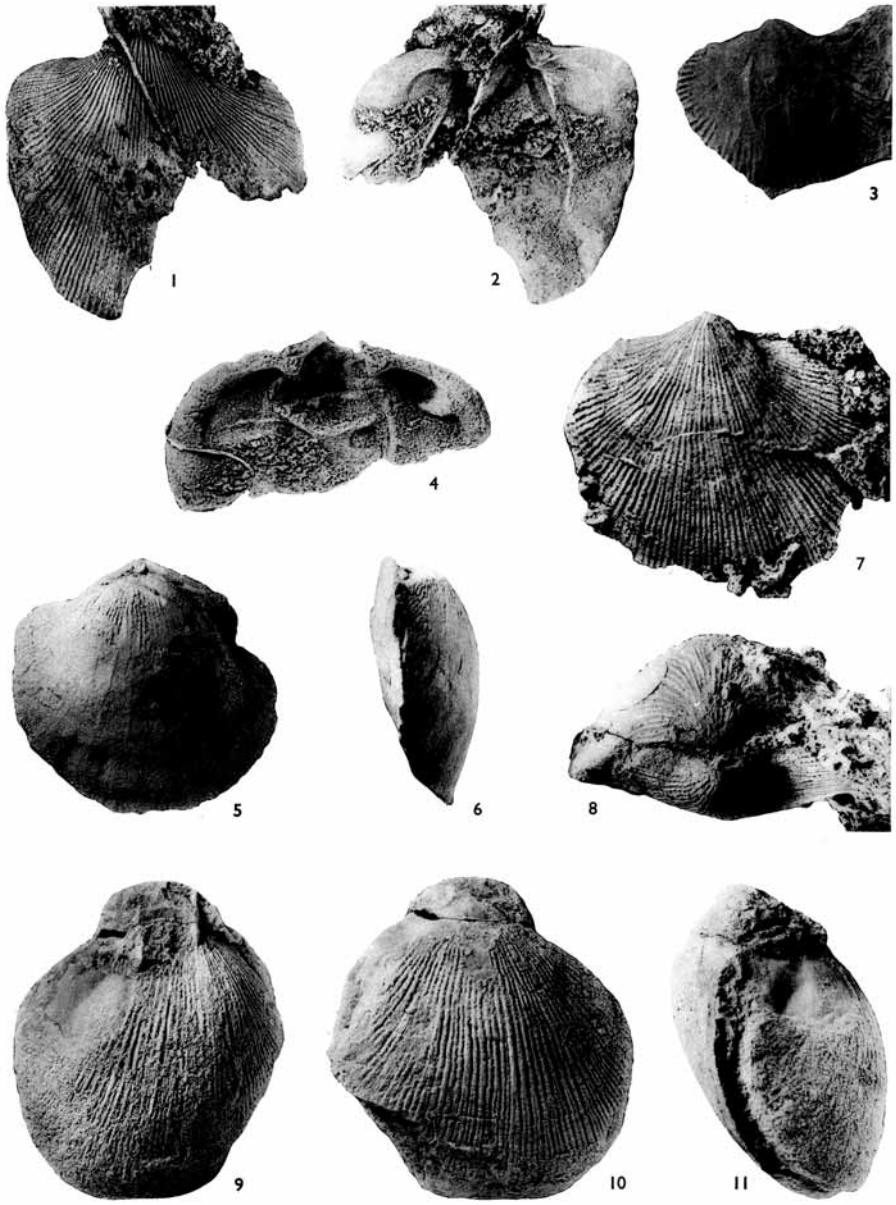
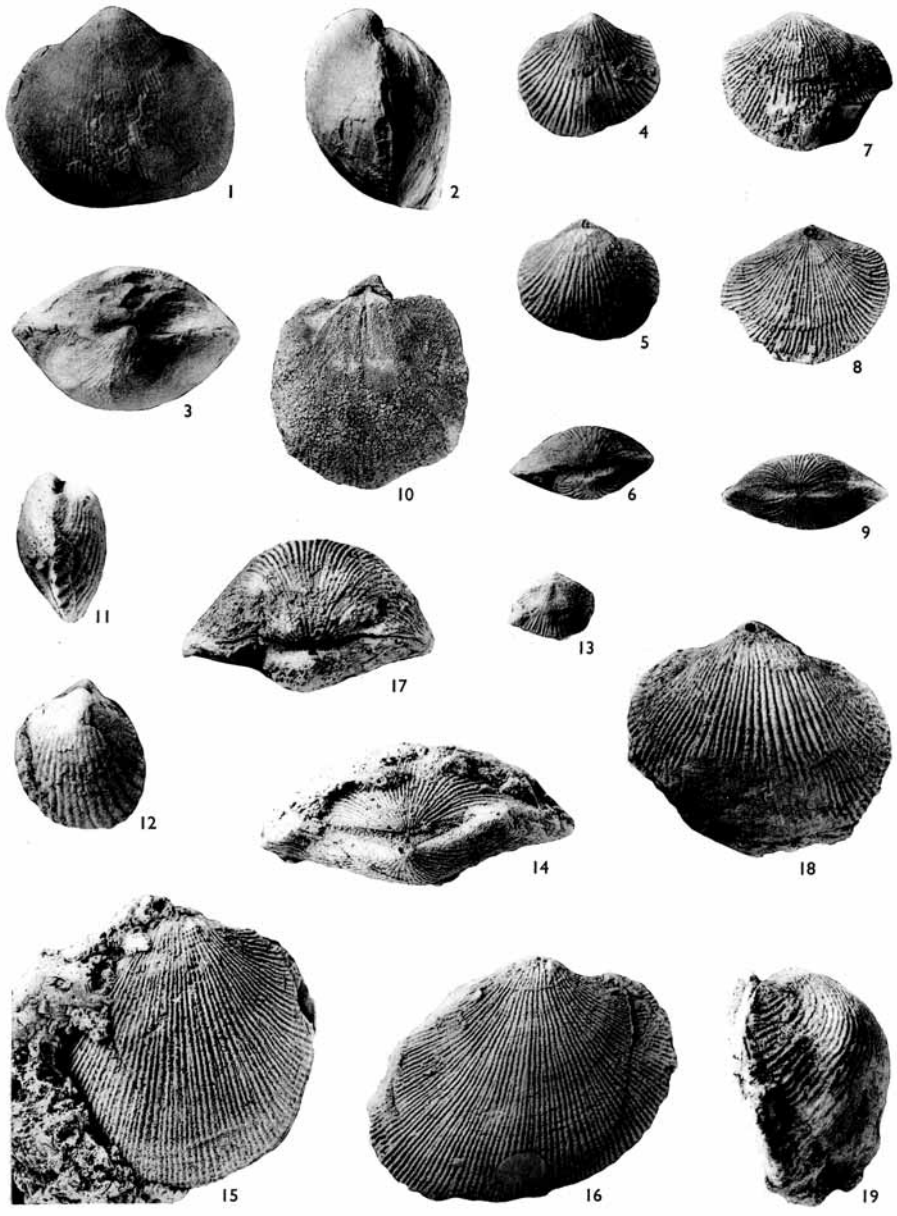


COPPER, Middle Devonian atrypoids



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