# DEVONIAN ATRYPIDS OF NORTH-WESTERN EUROPE

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## Abstract

The Middle and Upper Devonian rocks of north-western Europe, especially those of Germany, have yielded a copious atrypid brachiopod fauna. A compendium of the families Atrypidae and Palaferellidae contains descriptions and figures of 53 species belonging to the genera *Atrypa*, *Atryparia*, *Anatrypa*, *Spinatrypa*, *Spinatrypina*, *Kerpina*, *Desquamatia*, *Gruenewaldtia*, *Mimatrypa* and *Carinatina*. Present atrypid classifications are refined. New taxonomic units include three new subgenera and 16 new species. Many old and well-established species are re-examined and revised. Several new internal structures previously unknown in the atrypid group are revealed; other basic internal structures are re-interpreted. In the Eifel region of Germany, individual atrypid genera are shown to have been adapted narrowly to special and limited environments and their distribution is plotted in sinuate, 3 to 10 km wide areal patterns which probably were parallel to ancient shore-lines. The chronologic distribution of atrypid genera displays marked changes in the Eifelian, Givetian and Frasnian stages which may be useful in large-scale correlations of Devonian sediments.

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# I INTRODUCTION

## Object of study

The atrypid brachiopods, a group of extinct, marine, bottom-dwelling shelled animals, are one of the most abundant fossil elements in Devonian rocks throughout the world. This is an account of their morphology, their distribution, and their evolutionary development in the classical geological exposures of northwestern Europe.

Three main problems exist in atrypid brachiopod studies. The first of these was to find suitable morphological criteria that could be used to sort out the multiplicity of variations. The second problem was to determine the stratigraphic value of the atrypid group of brachiopods, i.e. to determine the extent of vertical and horizontal distribution of species. The third problem was to determine the role of atrypids in their environments, to what extent they were influenced by associated faunas and to what extent they were restricted to particular environments.

Most atrypids described in the literature have been given one of three catch-all names : Atrypa reticularis (LINNE 1758), Atrypa aspera (SCHLOTHEIM 1813) and Atrypa desquamata SOWERBY 1840. The controversy over 'splitting' or 'lumping' these atrypid taxa, was succinctly outlined by KELUS in 1939 when he referred to A. reticularis, 'This well known species......has been examined, described and figured by so many authors that one would expect to encounter no difficulties in systematic studies. This is, however, not the case. The deeper the literature is penetrated, the more uncertainty, differences of opinion and contradictions are found. .....the majority of researchers, who are primarily interested in stratigraphic, rather than anatomical and zoo-systematical problems have avoided the difficulties by either uniting all Devonian and Silurian representatives of Atrypa under the name A. reticularis, or have retained Atrypa reticularis and distinguished in it countless varieties' (freely translated, KELUS, 1939, pp. 12-13).

In fact, little appears to have changed since KELUS wrote these lines. The Atrypa group has proliferated into large numbers of new species, but many of these new species are unrelated to the taxa to which they are assigned. Very little attention, except in isolated works, has been paid to the important and diagnostic biocharacters of the form and shape or ribs and growth lamellae, and, most significantly, internal morphology. Before the problem of species was approached, a sound systematic basis had to be established. Without such a basis, little could have been done to determine the chronological and ecological value of the species studied.

A second, equally pressing problem in Middle and Upper Devonian stratigraphy is the search for a precise and reliable macroscopic method of correlating sediments which are rich in corals and brachiopods. The present Devonian stratigraphic scale is founded on the ammonoid fossil group, but these fossils are rarely satisfactory implements in detailed correlations or coral-brachiopod rich rocks because of their extreme scarcity. There is a need, therefore, to find substitute media for dating such rocks. Zonations based on corals have been in existence since WEDEKIND established several 'Stufe' based on the rugose coral group in 1924-1925. But brachiopod zonations are of only recent origin, except for the widespread use of <u>Stringocephalus</u> <u>burtini</u> DEFRANCE and <u>Hypothyridina</u> <u>cuboides</u> (SOWERBY) to mark the Givetian and Frasnian stages and the use of rhynchonellids in zoning Famennian rocks. Brachiopods, particularly the atrypids, have been employed most extensively by Russian palaeontologists, such as NALIVKIN, LJASHENKO, RZHONSNITSKAYA and ALEKSEEVA, and used successfully in the correlation of the Devonian of the Russian Platform, the Urals and Siberia. Since the type sections of the Devonians are located in Germany and Belgium, a knowledge of the atrypid fauna in these areas may serve as a guide to correlations in other parts of the world.

A third critical problem, one frequently omitted in pure systematic-taxonomic studies, was to determine the tolerance of the atrypid brachiopods to different types of sediments and associated faunas. It has generally been assumed that the atrypid brachiopods, which are sessile benthos, showed marked infraspecific changes of morphology from one facies to the next, in other words, that individual atrypid species spread themselves over a wide range of environments. This view has resulted in the neglect of the atrypid brachiopods as potential index fossils. It was therefore necessary to find out how environment influenced the basic external features of shell convexity, beak incurvature and rib and lamellar structure, and to eliminate environmental changes from phylogenetic changes in morphology.

This three-pronged approach to the problem of the atrypid brachiopods, of morphology, of distribution and of ecology, yielded results which differed in many respects from previous work in this field. Many of the internal structures are described for the first time, or their structure redefined and modified. Several structures figured were previously completely unknown in the atrypid brachiopods; these include disjunct jugal processes tipped by jugal plates, spinose or nodose jugal processes, disconnected, feathery and vestigial crura, pedicle collars and hollow deltidial plates, cardinal processes (in several atrypid species-groups where they were not known), and the correct structure of lateral cavities, dental plates, muscle plates and the shell wall. It was found that some structures, particularly the crura and jugal processes were rather different from what was previously supposed, and that these could be used satisfactorily in the arrangement of new species-groups. The most striking aspect of the atrypid distribution in the area studied was the virtual disappearance at the end of Eifelian time of several important atrypid genera, including Atrypa, Desquamatia, Gruenewaldtia, and their replacement by the dominant group Spinatrypa and Spinatrypina in the Givetian. Atrypa and Desquamatia returned in Frasnian time. It is not known if these marked changes in distribution were reflected in similar rock sequences of other parts of the world. Another remarkable feature, of particular value in the reconstruction of biotope maps, was the narrow distribution of the major atrypid genera in parallel bands which probably roughly followed the shorelines in large continental areas or islands. These distributions were almost inevitably associated with particular sediment types and with different types of corals.

## Acknowledgements

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To my supervisor, Dr. D.V. AGER, I am deeply indebted for a great deal of sound and valuable advice, in particular on all aspects of palaeoecology. Dr. W. STRUVE is singled out for his generous gift of Senckenberg reprints and the loan of numerous specimens, and Dr. H. JAEGER for his assistance in making available hundreds of specimens from now inaccessible localities in Germany. Mr. J. FERGUSON (British Museum of Natural History), Mr. A.G. BRIGHTON (Sedgwick Museum, Cambridge), Mr. M. MITCHELL (Geological Survey Museum), and Dr. R. HUCKRIEDE (Geologisch-paläontologisches Museum, Marburg, Germany) provided type specimens which were of considerable assistance in revision of species. There are many others who gave of their own time and ideas, all of which have a share in this study.

## Methods of study

A collection of more than 24,000 atrypid brachiopods from some 800 different fossil localities of Eifelian to Frasnian age was assembled for study. In addition, type or comparative material was consulted. Two thirds of the specimens were collected personally and the remaining one third was received on loan from the Natur-Museum und Forschungs Institut Senckenberg, Frankfurt am Main and the Institut für Paläontologie und Museum, Berlin, Germany. Type material of SCHLOTHEIM, KAYSER, LEIDHOLD, and SPRIESTERSBACH was made available by the Berlin Museum and SCHNUR's type material was loaned by the Senckenberg Museum. PAECKELMANN's syntypes of Spinatrypina tubaecostata were borrowed from the

Text-fig. 1. Idealized palaeogeography of the Devonian marine environment about late Eifelian - early Givetian (Middle Devonian) time. The map is compiled from GIGNOUX 1955, ERBEN 1962, BRINKMANN 1960, CHLUPAC 1956, 1958, WILLS 1952, RIETSCHEL 1962, HERMANN SCHMIDT 1926, KEGEL 1950, STRUVE 1963, DELEPINE 1951, Wo. SCHMIDT 1952, TERMIER & TERMIER 1960. Areas from which fossil material was collected are numbered :

1. Torquay, England.
2. Aachen, Germany.
3. Eifel, Germany.
4. Westfalen (Bergisches Land, Sauerland), Germany.
5. Boulonnais Palaeozoic inlier, France.

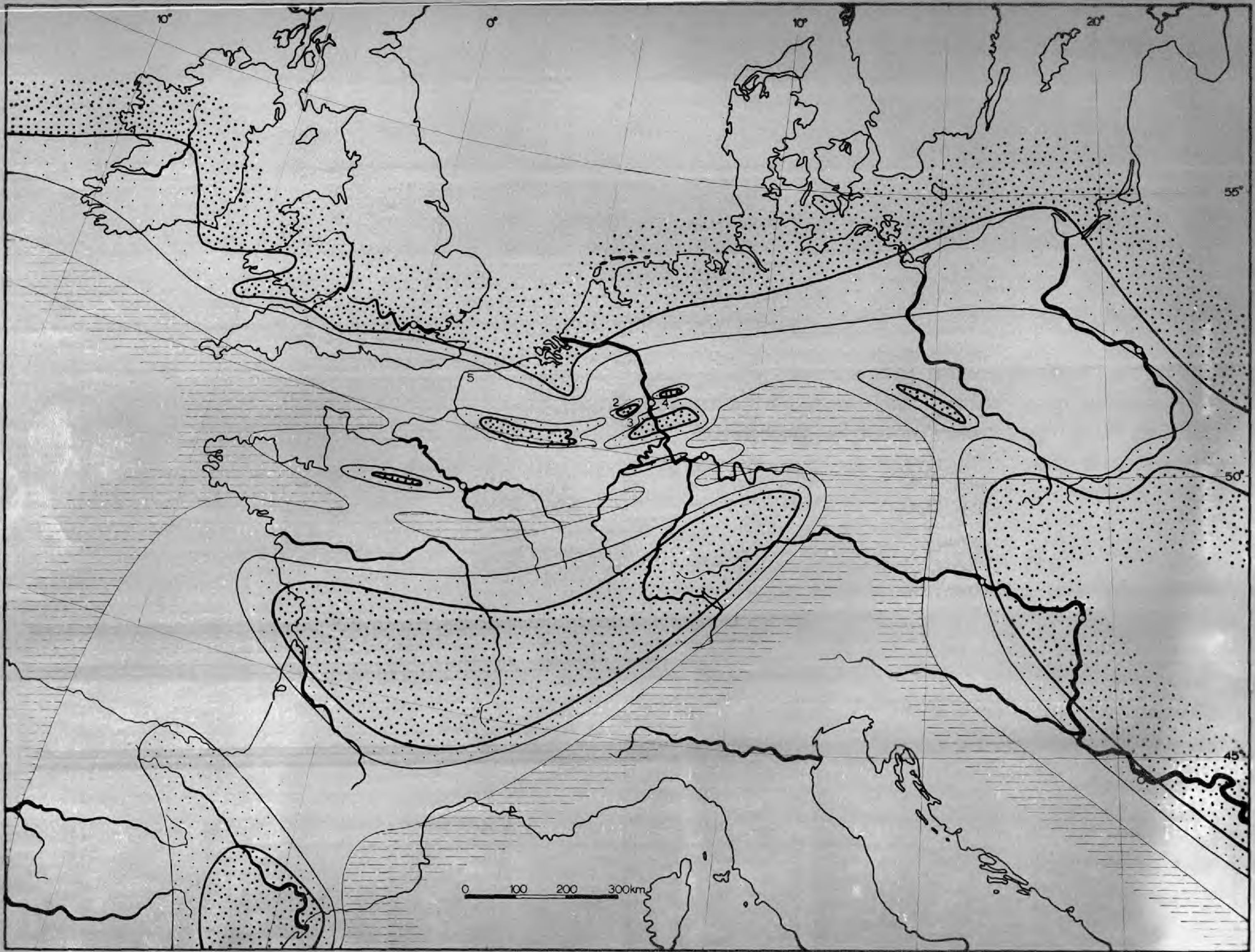
Four major facies bands are outlined :

A. (heavy stipples), continental, 'Old Red' facies with sandstones, conglomerates, volcanics, fresh or brackish water sediments, plant and fish remains.

B. (light stipples) brackish water, shallow marine, 'rhenish' facies with sandstones, siltstones, shales, lamellibranchs, inarticulate brachiopods and long-ranging, hardy articulate brachiopod stocks.

C. (blank), shallow marine, closed shelf sea, 'Eifel', 'Misch' or 'Normal' facies with calcareous shales and limestones, rich in brachiopods, corals, ammonoids scarce.

D. (dashed lines), fully marine, open sea, 'hercynian' facies with non-argillaceous limestones, bank reefs (massive), some black shales. Abundant ammonoid fauna. Refer to p. 50.


10°
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Geologisch-paläontologisches Institut der Universität Marburg (Lahn), Germany. The custodians of the brachiopod collections at the British Museum (Natural History), the Geological Survey Museum, London and the Sedgwick Museum, Cambridge provided original material of SOWERBY, PHILLIPS, DAVIDSON and WHIDBORNE. The collections of the Paläontologisches Institut, Universität Köln, which contained type material of WEHRLI, were destroyed during the war. Comparative Canadian atrypid brachiopods were sent by Dr. C.H. CRICKMAY of the Imperial Oil Company Ltd., Calgary, Canada and Dr. W.G.E. CALDWELL of the University of Saskatchewan. Dr. R.E. ALEKSEEVA of the Institute for Geology and Geophysics, Novosibirsk, Russia sent invaluable atrypids from the Kutznetsk and Minussinsk basins of Russia. The lectotype specimen of the Silurian atrypid Atrypa reticularis, type species of Atrypa, was examined and photographed through the courtesy of the Linnaean Society of London.

During six months of field work in 1963, all the German type localities previously mentioned in the literature were visited. Some localities were found to be inaccessible, being filled in by debris or covered by vegetation. During laboratory studies later in 1963 and 1964, the field collections were labelled, washed and sorted. Initial work began on the two species groups Desquamatia and Spinatrypa. Specimens of these two genera which were from the same stratigraphic level were plotted roughly on a base map of the Eifel synclines, and found to conform to sinuate patterns. On the basis of these patterns, suitable areas for further collecting were marked out and a short return field trip to the Eifel in 1964 turned up valuable additional material roughly at the predicted sites.

After sorting the collections into species groups, the more abundant and important species were measured and plotted on scatter diagrams and frequency curves. The statistical information obtained was used to supplement the species descriptions. Care was taken to orient specimens for measurement in the position shown in text-fig. 19. Therefore the length plotted on diagrams became maximum length relative to the commissural plane rather than absolute length. A lack of time prevented measurement of all the available specimens.

One or more specimens of each species was selected for transverse serial sectioning and detailed examination of internal strucutre. Plaster reproductions of potential section specimens were made with the use of Vinamold, a low temperature melting rubber compound. Some specimens also were photographed before sectioning. After this, each specimen was dipped quickly in a bath of molten sealing wax to give it an even, roughly 0.5 mm thin, coating to prevent later etching of the shell other than the grinding surface. Wax-coated specimens were mounted in plaster blocks so as to leave the upper 5 mm free and prevent the acetate sheets from wetting. The shells were ground away on a hand-operated Croft's parallel grinder. Every 0.1 mm (or less), the ground surfaces were examined for morphological internal changes and acetate peels taken if these were warranted.

Acetate peels were made by the 'dry' technique : each polished surface was etched for about ten seconds with dilute HCl (5% solution), washed and cleaned with water, dried, and then the dull side of a small strip of acetate film pressed to the etched surface. The acetate film, 0.03 to 0.04 mm thick, purplish, Acetobutyratfolie-Triafol BN, was supplied free of charge by the BAYER Chemical Company of Germany. The advantage of this material was its thinness (easy to press flat and mount) and its drying speed (about 30 seconds). The purple colour seemed to provide extra contrast.

Each acetate strip contained an impression of the etched brachiopod surface. Innumerable strips could be removed from the same surface. These strips were mounted temporarily in 35 mm transparency frames for viewing. The frames were projected and images traced and the acetate strips later stored in postage stamp files. For each sectioned brachiopod (108 specimens were serially sectioned), about 100 peels or more were made, two for each section (in case of defects). The growth lines and calcite crystals observed on the acetate peels were traced on white bond paper with rapidograph ink. Outlines of the shells were traced with a thick pen (0.9 mm nib), and growth lines with a thin pen (0.6 mm). Fibrous layers of the shell were marked in by closely spaced concentric lines and the columnar layer by coarse lines at right angles to the fibrous layer. The umbonal parts of the teeth, representing transverse sections of vertically oriented crystals, were marked in by dots.

In the systematic descriptions care was taken to describe the internal structure realistically in three dimensions to avoid pitfalls of 'time' and 'two-dimension' terms, e.g. saying the tooth comes in 'early' when it is apical, and the septum 'long' when it is deep. Acetate peels were photographed microscopically in order to clarify many previously unknown or poorly known internal structures.

Specimens were coated with magnesium oxide by holding over the white smoke of ignited magnesium ribbon, then photographed with a Leica M-3 camera (90 mm lens) using Adox KB 35 mm film. Photographs of specimens were mounted on a black background and re-photographed with 3¼ by 4¼ inch Ilford N5-31 'fine grain ordinary' film. The plates were reproduced on 8 by 10 inch Dalcopy '250 glossy normal paper', but with only middling results. It is recommended that other paper be used. Serial section drawings were reduced to plate size negatives by Hall-Harding Ltd. and copied on Dalcopy 'standard' photographic paper.

In the systematic studies, the importance of the associated fauna and the source sediment has been stressed and its main elements outlined. Also, in order to prevent subsequent confusion or doubt about specific descriptions, a precise type locality and type stratum were named. This was not, however, possible for some of the old collections consulted. Type and other localities were given the standard German, five digit grid references based on the kilometer scale. For example MTB Hillesheim r11111: h22222, reads Messtischblatt Hillesheim rechts 11111 and hoch 22222, i.e. topographic sheet Hillesheim, reading to the right 11111 and upwards 22222. These grid references are theoretically accurate to within 10 m. Under Material, for each species, the catalogue number is quoted first, and followed, in parentheses, by the number of collected specimens from that locality.

It will be noticed that some of the species are treated unevenly and that for many only the minimum information was cited, such as type localities, type strata, diagnosis and remarks. This study is basically a compendium of a larger scale work, The species originally described in greater detail were not abridged to suit the standard of the later descriptions. During the study, three small sections were prepared for publication, two synopses were published, and a revised classification of the atrypid group submitted for a symposium. These sections, some of them still in press, are not repeated in the systematic descriptions. Two of the papers are contained in a pocket at the back of the thesis.

## Historical background

The study of Devonian atrypid brachiopods of western Europe has a long and complex historical background dating from the eighteenth century. Many of the earlier publications are extremely rare and some of the pioneering work appears to have been completely forgotten. The faunas of the European Devonian rocks were undoubtedly the first to be described. A record of them is essential to later descriptions. It is also a matter of scientific interest to trace the development in the atrypid palaeontological literature because it gives an insight into many different concepts and ideas, and why some failed and others succeeded.

Only references which described or figured atrypids or monographic studies in which reference is made to the atrypids, are listed. The study of the atrypid brachiopods has passed through three broad phases. The first phase was a period of pioneering research from about 1770 to 1860, during which many of the classical faunal studies were made. This was the heyday of LINNE, SCHLOTHEIM, SCHNUR, BARRANDE, ORBIGNY, LAMARCK, SOWERBY and STEININGER. The second phase, lasting until the turn of the nineteenth century, was mainly a static one : new faunal discoveries were made in different parts of Europe, but the nomenclature was frozen by the use of already well established, catch-all names such as Terebratula, or Atrypa reticularis and A. aspera. These names soon lost their original meaning. The third phase of study was initiated by SCUPIN and GORTANI in 1906-1907 and saw a host of new specific, subspecific and varietal names injected into the European literature. Much attention was also paid to the less rewarding, more poorly preserved Lower Devonian faunas. However, during this phase no major advances were made either in taxonomy or palaeoecology of the Atrypida and ideas similar to those of the previous century remained entrenched. The 1950's have seen a marked revival in the study of the atrypids as a whole. For the first time, a new look was being taken at the details of internal structure, though in only a few studies. The present literature shows a rapid, almost yearly turn-over of taxonomic-evolutionary ideas and this fluidity and instability is an encouraging sign.

In 1758 LINNE described *Anomia reticularis* as part of his monumental 'Systema Naturae', and this species subsequently became the type species of *Atrypa*. However, it may never be known whether LINNE did indeed describe an atrypid specimens for he referred to the Museum Tessinianum (LINNE 1753) in which there is a figure given (ibid. Pl. 5, fig. 5) which is not readily identifiable but has little in common with the morphology of an atrypid. This figure is probably a rhynchonellid. In the text of the Museum Tessinianum the figure mentioned is labelled *Anomia subrotunda*. What *reticularis* was is not clear from LINNE's (1758, p. 702) diagnosis and description. In the 12th edition of the 'Systema Naturae', LINNE repeated the previous description of *Anomia reticularis* (LINNE, 1767, p. 1152). The source of LINNE's material probably was the Silurian beds of the island of Gotland. Devonian material appears to have been unknown to him. A specimen from the Linnaen collectoon, selected as lectotype of *A. reticularis* by ALEXANDER (1949) is illustrated on Pl. 1.

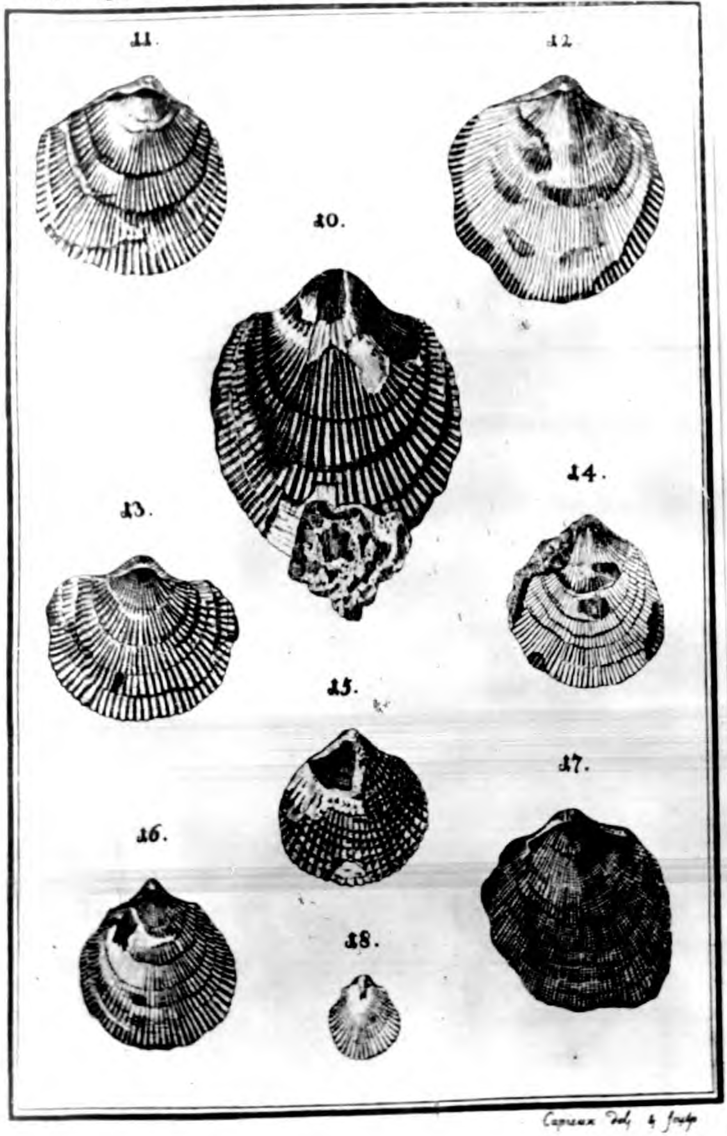
The first reference to Devonian atrypids is that of SCHRÖTER in 1777, who collected extensively in the Eifel region and east of the Rhine, who figured many specimens and who even proposed a simple classification of brachiopods. The name SCHRÖTER has almost vanished from the modern literature. It was mentioned by ALEXANDER (1949, p. 207) in her revision of *Atrypa*, but in the German literature is is unknown. Not even SCHLOTHEIM and SCHNUR, who followed in SCHRÖTER's footsteps some 50 and 80 years later, were aware of his work. Two of SCHRÖTER's plates are reproduced in Pl. A. In addition to his pioneering Devonian work SCHRÖTER was responsible for numerous other monographs on natural history during the period 1768 to 1805.

A number of species are clearly recognizable in SCHRÖTER's figures. SCHRÖTER described them as *Terebratula pectinata*, *T. striata* and *T. cancellata*. The most distinctive is the abundant *Desquamatia* of Pl. 3, fig. 10 (SCHRÖTER 1777). SCHRÖTER mentioned collections from Dollendorf, Gerolstein, Heisdorf and Nohn in the Eifel region. Some of the Middle Devonian atrypids he collected from there may be tentatively identified as *Atrypa (Isonatrypa) inglanda* n.sp. (fig. 21), *Gruenewaldtia prooemia* n.sp. (fig. 22), *Spinatrypa* cf. *dorsata* BIERNAT (fig. 23) and possibly *Gruenewaldtia latilinguis* (SCHNUR) (fig. 27).

## PLATE A

A reproduction of two plates from JOHANN SAMUEL SCHRÖTER's "Abhandlungen über verschiedene Gegenstände der Naturgeschichte" (1777, Part 9, "Von dem versteinten Anomiten und Terebratuliten, besonders von den Terebratuliten im Bergischen und in der Eifel", pp. 335-404, pls. 2-5, Halle). This rare publication is the first known palaeontological work devoted to Devonian brachiopods, and, for its time, a classical study of these fossils. SCHRÖTER, who was a deacon at the church of St. Peter and St. Paul in Weimar, Germany, published numerous volumes on the ancient natural history of Europe between 1768 and 1805 and was one of the first authors to adopt the binomial zoological nomenclature of LINNE.

Schroeters Abh. 2 St. Tab III



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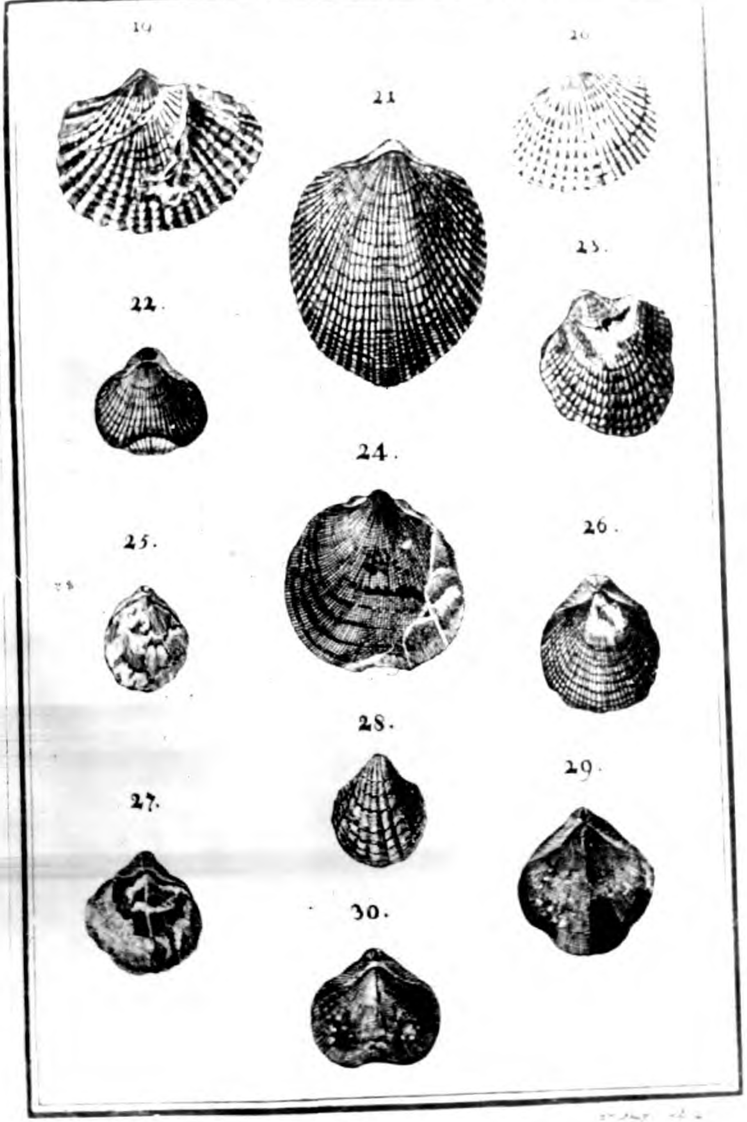
Schroeters Abh. 2 St. Tab IV



BEUTH (1776, pp. 132-147) listed and gave brief descriptions of nearly a hundred '*Terebratula*', most of which were stated to have come from Devonian localities especially around Bensberg and Paffrath (near Köln). BEUTH's work does not have the importance for atrypids that SCHRÖTER's study had, because he did not figure any specimens and his diagnoses, not fitted with Linnaean binominial nomenclature, are not recognizable. He listed the localities Elberfeldt, Glabeck (Gladbach?), Wipperfürth, Ruppigrath (Rupperoth?) and in the Eifel region, Iversheim, Zinsheim (Zingsheim), Tondorff (Tondorf), many of which are known to be atrypid localities.

In 1813, LEONHARD published a pocket book with a few figures of '*Terebratulites*', which were identified by SCHLOTHEIM and which included the first figures of the ubiquitous *Spinatrypa aspera*, which was later described by SCHLOTHEIM (1820, p. 263) as *Terebratulites asper* (Latin, *asper*, meaning rough, coarse, probably referring to the ribs on the shell), SCHLOTHEIM described two other species in 1820, *Terebratulites priscus*, and *T. explanatus*. The name *priscus* has been used in later literature to apply to Devonian atrypids resembling the Silurian *Atrypa reticularis* (LINNE), and since it was used as an 'ersatz' name it was rejected by other authors and now has fallen into disuse. In describing *Terebratulites priscus* SCHLOTHEIM made a reference to an illustration in the Encylopédie Méthodique (DESHAYES, 1827, Pl. 242, figs. 4a-c), which, as seen from the date, was not published until much later. SCHLOTHEIM referred to this figure (1820, p. 262) as the 'einzige mir bekannt gewordene ziemlich richtige Abbildung dieses Terebratuliten'. The figure in question is that of a coarsely ribbed atrypid resembling *Atrypa waterlooensis* WEBSTER. About the third atrypid described by SCHLOTHEIM, *T. explanata*, little doubt exists, though again it was not figured until later in the Nachträge (SCHLOTHEIM, 1822, Pl. 18, figs. 2a-b). Curiously, SCHLOTHEIM only mentioned the 'Eiffel' (Eifel) in his localities, though some of his material unmistakably came from elsewhere, most likely the well known locality at Refrath in the Paffrath syncline.

In the first edition of his 'Animaux sans vertèbres'. LAMARCK (1819) did not describe any atrypids. But in the second edition (1836, pp.365-366), SCHLOTHEIM's *Terebratula prisca* was annotated, yet not figured, and no internal structure mentioned. LAMARCK (1836, p. 331) also described a *Terebratula dorsata*, which was said to 'habite la mer du sud, au détroit de Magellan' (therefore presumably a Recent brachiopod) and referred this brachiopod to Pl. 242, figs. 4a-c of the Encyclopédie Méthodique (see below). This figure of an atrypid brachiopod in the Encyclopédie was called *T. prisca* by SCHLOTHEIM (1920, p. 262).

The brachiopod description and figures of the Encyclopédie Méthodique were the work of DESHAYES and not the work of BRUGUIERE or LAMARCK to which many others have attributed it. The plates were published in 1827, and the text in 1832. The explanation to the plates were prepared by BORY DE ST. VINCENT, apparently from LAMARCK (1819), and the atrypid illustrated on Pl. 242 (figs. 4a-c) of the Encyclopédie, is labelled as Terebratula dorsata LAMARCK. There is no reference in the text by DESHAYES to this figure. DESHAYES stated in the text that T. dorsata came from the Indian Ocean and that T. dorsata was figured on Pl. 242, figs. 1a-d. It is also fairly certain that LAMARCK (1819) never intended his T. dorsata as an atrypid but as a Recent brachiopod. It seems that the only one to recognize Pl. 242, figs. 4a-c as an atrypid was SCHLOTHEIM in 1820.

An equally mystifying brachiopod is in the Mineral Conchology of JAMES SOWERBY (1823, p. 24, Pl. 324, fig. 2) and called Terebratula affinis. Many authors have referred this brachiopod to Atrypa and placed it in synonymy with Atrypa reticularis (LINNE). From SOWERBY's figure, however, this relationship is extremely doubtful, and it is possibly a rhynchonellid. SOWERBY himself (ibid.) mentioned distinctly the Carboniferous origin of the specimen ('from decomposing Mountain Limestone ......Horncastle'), even if he admitted that he had not collected it himself. At Horncastle, Carboniferous rocks are known to occur, but the nearest Devonian is several hundred miles away. Morever, if the specimen is of English origin, no similar one seems to have been collected since. It is, of course, also possible that the specimen was of Silurian age since SOWERBY mentioned also that similar ones were sent him from the Malvern Hills and Dudley. In a later work by J. de C. SOWERBY (1840, fig. 11) a 'Spirifera affinis' is described and figured but this form is strongly unlike the original affinis. It seems advisable to eliminate Terebratula affinis SOWERBY 1823 as an atrypid species. The original collection of JAMES SOWERBY was not traceable.

KOENIG (1825, Pl. 4, fig 44) repeated the figure of Terebratula aspera given by LEONHARD in 1813 and noted briefly its source, the Eifel region. He may have been the first author in Europe to recognize SCHLOTHEIM's species. Nevertheless, KOENIG (1825, fig. 219) also gave the name T. aspera to a species of Acanthothiris.

In 1825 the 'Manuel de Malacologie et Conchyologie' of BLAINVILLE was published. It contained a short, seven page section on brachiopods and on p. 512 an atrypid described as Terebratula spirifera. In the plates to the 'Manuel' (published in 1827) BLAINVILLE showed a view of an unrecognizable atrypid species and an opened shell with two exposed spiralia in the Atrypa-like dorsal direction (BLAINVILLE, Pl. 54, figs, 2, 2a). The author does not seem to have recognized the significance of the spires except in referring it to the Terebratula spirifera group.

It is probably DEFRANCE who can be credited with the discovery of spires in atrypids. In 1827, he published an article in the 'Dictionnaire des sciences naturelles' and described in it a new species, Spirifer sowerbyi, which is clearly an atrypid and in which the dorsally directed spires are mentioned. The Dictionnaire is accompanied by an atlas of plates prepared by BLAINVILLE which are an identical copy of plates which were published with the 'Manuel' of BLAINVILLE (1827). The dates given on the 'Dictionnaire' atlas are 1816-1830, and not even SHERBORN is more helpful than this. It is likely that they were post-1827, but whether BLAINVILLE published his own plates for the 'Manuel' first, or the plates for the 'Dictionnaire' first, is still not known. Nevertheless it seems certain that DEFRANCE, rather than BLAINVILLE first noticed the new orientation of the spires.

In 1828 DALMAN established the genus *Atrypa* (Greek, *a*, without, *trupa*, a hole). He included in this new genus 11 species of brachiopods and these were in turn divided into *Atrypa* 'striatae' and *A.* '*laevigatae*'. Some of these are now known to be meristellids, but DALMAN's unfigured species *crassicosta* , *lenticularis* and *micula* cannot be identified. DALMAN also included species which to-day are not recognized as belonging to *Atrypa*, but are still in the families Atrypidae or Lissatrypidae.

The first to acknowledge DALMAN's new genus was HISINGER (1829, p. 17) who took over the identifications without question. Later HISINGER (1837) figured and described some of the Silurian atrypids of Sweden and copied most of DALMAN's illustrations of 1828. HISINGER (1837, Pl. 21, figs. 11d-e) appears to have been the first author to illustrate the alate extensions or frills on *Atrypa*.

The 'Zoologia Specialis' of EICHWALD contains a figure of a possible atrypid (1829, Pl. 4, fig.11) with the name *Terebratula cancellata*, a name commonly used for atrypids by SCHRÖTER (1777). The figure is not clear and the locality referred to, 'regionem Vilnensem alluvionis' (alluvium from Vilna ) is of little value. The locality may refer to Villmar, east of the Rhine, from which a few specimens have been described.

STEININGER (1831, p. 36) described, but did not figure, *Terebratula prisca* and *T. aspera*. He specified that he wished to distinguish from *T. aspera* 'eine eigene Species.....welche ich *T. globosa* nennen möchte'. He must have had a rather different concept of *Spinatrypa aspera* (SCHLOTHEIM) to consider *T. explanatus* SCHLOTHEIM a variety and the original figure of *T. asper* in LEONHARD (1813) a new species. It is curious that the name *globosa* appears to have been so popular for it was used by four subsequent European authors as a specific or varietal name of *Atrypa*.

After SCHRÖTER, the first good illustrations of Eifel atrypids were those in BRONN's atlas (1837, Pl. 2, figs. 10a-d). BRONN (1834, pp. 72-74) had previously described the atrypids as *Terebratula reticularis* (the figured specimens are recognizable as *Desquamatia* and *Spinatrypa*). BRONN placed exclamation marks after the locality names Blankenheim (in the Eifel) and Bensberg (Paffrath syncline), probably to stress their richness. In the third edition of BRONN's work, published jointly with

F.A. ROEMER (1856, Pl. 2, fig. 18) an internal view showing the spires of 'Atrypa' was added.

In 1834 BUCH introduced new brachiopod terminology and coined the word 'Deltidium', dividing the brachiopods on this basis into three groups with deltidia which were 'umfassend' (enclosing), "sectirend' (partially closed), and 'discret' (separated). BUCH apparently failed to find the spiralia in Palaeozoic brachiopods yet he mentioned the spiral arms of Recent brachiopods. Under Atrypa he also grouped many rhynchonellids, as well as SCHLOTHEIM's species T. aspera, T. explanata and T. prisca. In a later edition of BUCH's work, which was translated into French (by H. LE COQ), the Geological Society of France decided to add to BUCH's own figures and therefore provided original illustrations from the works of several other authors. In the French issue (BUCH, 1838, Pl. 16, fig. 19) a copy of SCHLOTHEIM's 1822 figures of Terebratula prisca is given. A Jurassic brachiopod which BUCH described as T. reticularis also is figured.

One of the first palaeontologists to describe brachiopods from Central Europe was PUSCH (1836). In a monograph PUSCH figured specimens labelled as Terebratula amphitoma which had spiralia which were dorsally directed. These specimens from the Devonian at Kielce in Poland, may have belonged to the poorly known atrypid genus Dzieduszyckia which strongly resembles the Triassic brachiopod genus Halorella. The genus Dzieduszyckia must be re-examined.

Also in 1836, DESHAYES accepted the SCHLOTHEIM species Terebratula prisca but made no remark about the internal structure.

In the notes accompanying the classic 'Physical structure of Devonshire' by SEDGWICK and MURCHISON (1840), J. de C. SOWERBY grouped many brachiopods under the name Atrypa. Some of these are now known to be pentamerids or rhynchonellids, He introduced two new atrypid species, plus one varietal name. The first of these was Atrypa desquamata (=Mimatrypa STRUVE 1964), and a variety called compressa. The species desquamata came to be recognized throughout the world, but in almost every instance has been incorrectly identified (COPPER 1965a). SOWERBY also described a new form, Atrypa squamosa, but specimens of this atrypid are so rare and usually so poorly preserved, that it is difficult to establish the validity of the species. There is no doubt that it can be referred to Spinatrypa and it seems to have some affinity with S. orthoclina n.sp. On Pl. 57, fig. 11 (SOWERBY 1840), an atrypid specimen labelled Spirifera affinis is figured. SOWERBY recognized its relation to Atrypa aspera but why he grouped it under Spirifera and others under Atrypa ss puzzling. The specimen in question was examined : though it seems to resemble the genus Kerpina STRUVE, it is, in fact, a species of Spinatrypina, possibly S. soetenica (STRUVE).

McCOY (1840, pp. 197-199) adopted the genus *Spirigerina* ORBIGNY (1847!!) and accommodated in *Spirigerina* three species, *S. cuneata* (DALMAN), *S. marginalis* (DALMAN), and *S. reticularis* (LINNE). The first two species are not now delegated to *Atrypa*; *S. cuneata* is a rhhnchonellid. McCoy discarded the species *prisca*, *explanata*, *affinis* and *aspera* in favour of the Linnaean name *reticularis*.

PHILLIPS followed shortly after SOWERBY in 1841 with atrypid descriptions. He assigned the atrypids to *Terebratula (Atrypa)*, in effect to a subgenus of *Terebratula* and accepted the species *aspera*, *prisca*, *desquamata* and created a new atrypid species *T. insperata*. SOWERBY's *squamosa* was fitted into *aspera* and his *affinis* to *prisca*. *Terebratula (Atrypa) insperata* PHILLIPS is regarded as a *nomen dubia* : the type specimen was examined, found to be poorly preserved and virtually unrecognizable.

In an important paper SEDGWICK and MURCHISON (1842) which was read before the Geological Society of London in 1840, the first comprehensive survey of the German and Belgian Devonian rocks was made. They remarked on the occurrence of *Terebratula prisca* at the famous locality in Refrath. ARCHIAC and VERNEUIL (1842) described the fossils discussed by SEDGWICK and MURCHISON, but no figures of atrypids were included. ARCHIAC and VERNEUIL listed *T. aspera*. *T. explanata* and *T. prisca*, but also included hosts of species unrelated to the Atrypidae. Under *Atrypa*, the authors listed *A. desquamtia* SOWERBY. Their criteria for grouping some atrypids under *Terebratula* and others under *Atrypa* are not explained. Under the name '*Orthis arimaspus* EICHWALD', they remarked (ARCHIAC & VERNEUIL, 1842, p. 395), 'We believe that it is a *Terebratula*', though they do not quote a European locality for this atrypid species. They apparetnly also did not find *Orthis* (=*Anatrypa*) *micans* BUCH in Europe, inspite of mentioning it.

The Devonian fossils in the Harz region of Germany were described by F.A. ROEMER in 1843. The *Terebratula prisca* described and illustrated (ibid., p. 18, Pl. 5, figs. 11-13) seem to have Eifel region affinities. For example, fig, 11 possibly is *Desquamatia* (*Synatrypa*) sp.; fig. 12 *Atrypa* (*Isonatrypa*) or *Atryparia* and fig. 13 *Spinatrypa* or *Spinatrypina*. These figures are not more exactly identified. The original collection appears to be lost. The smooth shelled brachiopods shown by ROEMER may include atrypids such as *Cryptatrypa* or *Dubaria*.

More Eifel fossils are described by C.F. ROEMER (1844) in the 'Das Rheinisches Uebergangsgerbirge'. ROEMER defined a promising lower Givetian index fossil, '*Terebratula prisca* var. *flabellata*' (1844, p. 66, Pl. 5, figs. 4a-b), which recently became the type species of the genus *Mimatrypa* STRUVE 1964. ROEMER regarded all the atrypids as varieties of *prisca*, and in this sense regarded SCHLOTHEIM's *aspera* and *explanata* as varieties of SCHLOTHEIM's own *prisca*.

The 'Grundriss der Versteinerungkunde' of GEINITZ (1846, Pl. 21, fig. 11) contains a figure of an atrypid which cannot be defined. In the descriptions, (ibid., pp. 503-504), there is no mention of the internal structure of the atrypids, and specimens are included which are obviously unrelated to this group.

The problem of Atrypa interested KING (1846) and he allowed that DALMAN in his original definition of the genus had included a number of species which did not really belong there. He was stimulated to remark (ibid., p. 29) that, 'viz. Atrypa reticularis we are compelled to consider it as the typical one'. Thus KING appears to have been the first author to designate A. reticularis (LINNE) as type species of Atrypa DALMAN.

In 1847 ORBIGNY attempted a brachiopod classification and grouped a new genus Spirigerina (=Atrypa partim) into the spire-bearing brachiopod family Spiriferidae, which also included Spirifer, but also placed Atrypa (non Atrypa as emended by ALEXANDER 1949 and in the well known sense) in the Uncitidae. What ORBIGNY meant by his own definition of Atrypa is not clear. Recently, ALEKSEEVA (1960) resurrected the almost extinct name Spirigerina which had become a replacement of Atrypa, and used the name for a species-group resembling A. marginalis DALMAN 1828. This species group of A. marginalis had usually been placed in the genus Plectatrypa SCHUCHERT & COOPER 1930, to which it has strong affinities.

The classical work on the Devonian and late Silurian brachiopods of the Prague region, i.e. atrypids which can be grouped under 'hercynian' facies[1]., was done by BARRANDE. In 1847 BARRANDE began the first of a series of monographs on these faunas. He described numerous new species. For Terebratula reticularis LINNE he distinguished two new varieties, verneuiliana and murchisonia after the famous geologists by those names. In addition, BARRANDE separated T. semiorbis (=Spinatrypa), T. granulifera (=Punctatrypa), T. comata (=Carinatina or Vagrania), T. arachne (a genus related to Carinatina?) and several smooth shelled atrypids of the family Lissatrypidae. BARRANDE's faunas need revision to bring them up to date.

The 'Prodrome' of ORBIGNY (vol. 1, 1850, pp. 99-100) gives a list of the then known species of atrypids under the name Spirigerina. ORBIGNY continued to reject the name Atrypa for the atrypids and instead referred to Atrypa a mixed bag of orthoids and rhynchonelliods. However, ORBIGNY may have been the first to realize that Orthis arimaspus was a

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[1] In English usage (but not in German) the term 'hercynian' also has structural implications, e.g. as in 'hercynian orogeny'. Here the term 'hercynian' is used strictly as a facies concept for late Silurian-Devonian, limestone-rich rocks typified by exposures in the Harz region of Germany. The hercynian facies concept is defined by ERBEN (1962). The name 'Hercyn' is derived from the old Roman name for the Harz mountains.

member of the *reticularis* group of brachiopods. *Orthis arimaspus* EICHWALD is the type species of the atrypid genus *Carinatina* NALIVKIN.

One of DAVIDSON's first references to Atrypidae occurs in a revision of LAMARCK's collections. DAVIDSON (1850, p. 447, Pl. 14, fig. 55) correctly attributed a LAMARCK specimen labelled as *Terebratula granulosa* to the atrypids. To judge from DAVIDSON's figure, this specimen possibly is *Desquamatia pectinata* (SCHRÖTER 1777) from the richly fossiliferous locality at Refrath. LAMARCK's specimen was said to have come from exposures near Rome, but no Devonian is known there.

In his classification of brachiopods, KING (1850, pp. 72, 81, 137) made only brief mention of the genus *Atrypa* and again referred as type species LINNE's *Anomia reticularis*. ALEXANDER (1949, p. 208) stated that DAVIDSON was the type selector.

In 1853, DAVIDSON gave a generic discussion of *Atrypa* and assigned to it 6 species, only one of which is to-day strictly a member of *Atrypa*. He introduced no new forms and seems to have accepted that the atrypids belonged to the *Spirifer* group, in the tradition of ORBIGNY.

The first of QUENSTEDT's Petrefactenkunde came out in 1852. The atrypids were assigned to the "Terebratulae Calcispirae". Two species were listed, *Terebratula prisca* and *T. prunum* (*Atrypella*). Under the first, QUENSTEDT placed both *aspera* and *reticularis* (the latter attributed to WAHLENBERG). *Atrypa* is mentioned and rejected as a misnomer. On Pl. 37, fig. 1 (QUENSTEDT) an atrypid is illustrated which may be *Spinatrypina soetenica* (STRUVE). The significant spiral cones have been exposed in several figured specimens, but QUENSTEDT did not notice jugal processes.

SCHNUR (1853) rejected the name *Atrypa* (as did most other early German workers until the 1870's), and introduced three new species, also figuring for the first time a species described in 1851 (SCHNUR, 1851, p. 7). Unfortunately SCHNUR was prone to discard previous species as varieties of his own species. Thus SCHLOTHEIM's *aspera* became a variety of SCHNUR's *Terebratula squamifera*, ROEMER's *flabellata* became a variety of SCHNUR's own *T. insquamosa*. SCHNUR also arrived at some curious synonymies : under *T. squamifera* were listed the species *affinis*, *prisca*, aspera and the *reticularis* of some authors, under *T. insquamosa* came SOWERBY's *desquamata*, under *T. zonata* came some *reticularis* and *explanata*. What SCHNUR used as his criteria for the different species is not well understood. Nevertheless, SCHNUR's figures are excellent and his work has formed an important foundation of Eifel faunal studies.

In the same year brachiopods from the Eifel region also were treated by STEININGER (1853), who discussed the validity of *Atrypa* and *Spirigerina* but left his own described atrypids under *Terebratula*. STEININGER was the first author to accept the validity of a row of previously named atrypid species, i.e. *T. prisca*, *T. explanata*, *T. aspera* and *T. flabellata*. He described furthermore a new atrypid species *T. eifliensis* but stated it to be synonymous with *T. latilinguis* SCHNUR and did not figure this new species. Under the name *Orthis*, STEININGER described a new species *O. gerolsteinensis* (1853, p. 78, Pl. 8, figs. 5, 5a-b) which possibly can be assigned to the atrypid genus *Carinatina* and may be a senior synonym of *Carinatina plana* (KAYSER 1871). However, STEININGER's material is not known, his figures cannot be identified with certainty and since there is some doubt as to its identification it is probably better to consider it a *nomen nudum*.

The other paper, partly on atrypid brachiopods, written in 1853 was by GEINITZ. He described fossils from the Lower Devonian and possibly Silurian rocks of Saxony. A *Terebratula reticularis* is both described and figured (GEINITZ, 1853, Pl. 14, figs. 16-27).

In 1855 HANLEY revised many Linnaean species and firmly fixed the authorship of *Anomia reticularis* as the work of LINNE (1758). Many authors had also referred the species to GMELIN (who edited a later edition of the Systema Naturae), to WAHLENBERG and others.

G. and F. SANDBERGER (1856) grouped a large number of atrypid species under the name *Spirigerina reticularis*. Two figures of the SANDBERGERs are generalized and cannot be identified. They figured a frilled atrypid specimen (ibid., Pl. 33, fig. 1) though they were not the first authors to do this.

In 1860 GRUENEWALDT described a collection of atrypids from Russia which he thought were identical to *Terebratula latilinguis* SCHNUR 1851. Though he was mistaken in his identification, GRUENEWALDT's work is significant because he appears to have been the first author to use the technique of serial sectioning to describe an atrypid brachiopod.

DESLONGCHAMPS accepted the validity of *Atrypa* in 1862 (p. 4) and, in a continuation of the same work (1884), which was brought out in a series, gave a discussion of *Terebratula affinis* SOWERBY (1884, pp. 349-350), and referred it to *Atrypa reticularis* in 1886.

DAVIDSON's monograph of the Devonian Brachiopoda came out in 1864-1865. SCHLOTHEIM's species *aspera* was still described as a variety of *Atrypa reticularis* but *Atrypa desquamata* SOWERBY and *A. flabellata* (C.F. ROEMER) were accepted in full. DAVIDSON's specimens of *A. flabellata* are probably pentamerids (see COPPER 1965a) and the species wrongly attributed to GOLDFUSS.

The first Frasnian atrypids from Poland were described by DAMES (1868). DAMES described *Atrypa reticularis* and described and figured specimens he called *Atrypa zonata* (SCHNUR). The latter appears to resemble specimens of the genus *Gruenewaldtia* but type material from that area was sectioned and found instead to belong to *Desquamatia*. The affinities of RZHONSNITSKAYA's genus *Pseudogruenwaldtia* are still not clear, but the Polish specimens are not dissimilar. It is possible that the genus *Pseudogruenewaldtia* also can be assigned to *Desquamatia*.

QUENSTEDT (1871) gave excellent figures of many German atrypid species but he grouped all of them under the name *Terebratula prisca*. Many of the species only recently described can be identified from QUENSTEDT's figures. These include species of the genera *Spinatrypina*, *Atryparia*, *Desquamatia*, *Spinatrypa* and *Atrypa*. QUENSTEDT was one of the few authors who insisted that the atrypids were more closely related to the rhynchonellids than the spiriferids. This notion is supported. QUENSTEDT in fact accepted only one other atrypid species, *Terebratula flabellata*. QUENSTEDT (1871, p. 215) mentioned that BOUCHARD had named a brachiopod, *Atrypa longispina*, from the Devonian of Ferques in France, and gave a figure of part of the shell of this atrypid (Pl. 42, fig. 104). BOUCHARD had not published any description of *Atrypa longispina*, and in fact, never did. The first description of *A. longispina* is in RIGAUX (1873).

Another large-scale study of brachiopods from the Eifel region was that of KAYSER in 1871. Named as varieties of *Atrypa reticularis* are the species *desquamata*, *flabellata*, *latilinguis*, *aspera* and a new variety *plana*, a distinctive atrypid belonging to the genus *Carinatina*. KAYSER assigned the SCHNUR species *zonata* and *insquamosa* to *Atrypa reticularis* var. *desquamata*.

The first French atrypids to be described and figured were based on material from the Boulonnais Palaeozoic inlier. RIGAUX (1873) conserved the BOUCHARD authorship of the species *longispina*, which he referred to *Spirigerina*. RIGAUX (ibid., p. 47) mentioned that 'M. Bouchard .....se proposait un travail complet sur le Dévonien de Ferques', but BOUCHARD evidently never succeeded in publishing this work.

In his review of British fossils BAILY (1875) repeated one of DAVIDSON's atrypid figures and made some brief comments on *Atrypa desquamata*.

The atlas to the 'Lethaea Paleozoica' of F. ROEMER (1876, Pl. 28, fig. 5b) contains a figure of *Atrypa reticularis* from Gerolstein in the Eifel. This specimen shows the typical dorsally directed atrypid spiralia.

A second study of the Devonian fossils from the Harz region of Germany was oublished by KAYSER (1878). It followed ROEMER's pioneer work in 1843. The Harz region appears to have few elements in common with the Eifel faunas. KAYSER described *Atrypa reticularis*, a variety *aspera* (SCHLOTHEIM and *Atrypa* sp. indet. The figures are not clearly recognizable.

The monographic work 'Système Silurien' of BARRANDE (1879) which also contained Devonian brachiopods was one of the first detailed studies of atrypid shell morphology. Microscopic features of the shell surface such as growth lines and rib structure were given for the first time. BARRANDE also included excellent illustrations of spines and frills (e.g. ibid., Pl. 19, figs. 4a, 7b, 7c; Pl. 34, figs. 22-23) and the remarkable rib bifurcation of *Carinatina* *comata* (ibid., Pl. 30, fig. 7f).

The Greifenstein limestone fauna (a locality east of the Rhine), was made the basis of a study by MAURER in 1881. This fauna has strong east European (i.e. 'hercynian') affinities, though SIEHL (1962) showed recently that rare Eifel elements were also present. In addition to finding the BARRANDE species *Atrypa* *canaliculata*, *A*. *thetis*, *A. philomela* and *A*. *fugitiva*, common to the Devonian of the Prague area, MAURER described two varieties and a new species *A*. *verrucula*. These species were redefined by SIEHL (1962).

The Devonian faunas of Austria and Galicia in Spain received their first monographic treatment by BARROIS in 1882. BARROIS did not figure any brachiopods identifiable as atrypids but listed localities where *Atrypa* *reticularis* and *A*. *aspera* could be found. A specimen described and figured as '*Rhynchospira* *guerangeri* Vern.' possibly belongs to the atrypid family Palaferellidae. Very little still is known about Spanish faunas but they may bear a strong relation to faunas from the Eifel region.

DAVIDSON completed a supplement to his Devonian brachiopods in 1884. He correctly described (for the first time) the discovery of *Atrypa* (=*Gruenewaldtia*) *latilinguis* in the Devonian of England, and specimens of the English atrypid were recently sectioned (COPPER 1965a). DAVIDSON also described a new species *Atrypa* *trigonella* which can be identified as *Spinatrypa*, and is still to be described.

The formerly rich Middle Devonian faunas of the limestones at Waldgirmes (east of the Rhine) were studied by MAURER (1885). As the Greifenstein fauna mentioned before, the Waldgirmes fauna appears to contain a liberal sprinkling of hercynian atrypids and has little in common with faunas from the Eifel region. MAURER classed the following varieties of *Atrypa* *reticularis* : var. *insquamosa* SCHNUR, var. *explanata* SCHLOTHEIM, var. *desquamata* SOWERBY, var. *plana* KAYSER, var. *aspera* SCHLOTHEIM and a new variety *sagittata*. MAURER's *insquamosa* probably is *Atrypa* (*Isonatrypa*), his *plana*, probably *Carinatina* *signifera* (SCHNUR), his *aspera* not *aspera* sensu stricto, and his *sagittata* possibly a species of *Atryparia*. MAURER also described the hercynian atrypids *Atrypa* *eurydice* BARRANDE, *A*. *philomena* BARRANDE a new species *A*. *subcolumella*, *A*. *assula* BARRANDE, *A*. *canalicula* BARRANDE and *A*. *verrucula* MAURER 1881, as independent species. The hercynian elements probably belong in part to the genera *Glassia*, *Cryptatrypa* and others not treated in this thesis.

In 1885, CHERNYSHEV named as type of a new subgenus *Grünewaldtia*, the atrypid from the Eifel region, *Terebratula latilinguis* SCHNUR 1851. The significance of the remarkable internal structure of *T. latilinguis* was not realized until its discovery by STRUVE in 1955.

BARROIS described the first Devonian faunas of western France in 1886. These faunas, from the Maine-et-Loire regions, included "*Atrypa reticularis*" and '*A. aspera*', and descriptions and figures of *Atrypa* (=*Punctatrypa*) *granulifera* BARRANDE and a new species *Orthisina* (=*Carinatina*) *davyi*. BARROIS new species *davyi* may be synonymous with *Carinatina signifera* (SCHNUR).

BARROIS (1889) followed the above study with a faunal survey of the rocks of Erbray (lower Loire) in France. He grouped most of the atrypids under *Atrypa reticularis*, as var. A., var. B., var. *desquamata* SOWERBY, var. *aspera* SCHLOTHEIM and var. *sagittata* MAURER. He described a new variety *globosa* which is similar to *Atrypa* (*Isonatrypa*) *inglanda* but may also be related to *Atryparia*. From the figures this is difficult to judge.

In the same year OEHLERT (1889) described a Devonian fauna from Angers, in nearly the same area. He illustrated two specimens, one of '*Atrypa reticularis*' and one '*A. aspera*', but these cannot be related specifically to any known species. They are probably not of Eifelian age, but may be of Frasnian age.

In 1891 FRECH initiated Devonian atrypid studies in the eastern Alps (Austria). He designated a new atrypid *Atrypa desquamata* var. *alticola*. The affinities to *Mimatrypa desquamata* (SOWERBY) are obscured and the specimens must be re-examined. Under rhynchonellid or athyrid names, FRECH may have obscured a number of smooth-shelled atrypid species. The FRECH collection was not examined.

A re-assessment of Devonian faunas of England was completed by WHIDBORNE in 1893. WHIDBORNE was extremely conservative in his taxonomy, and he found it 'most difficult to decide their specific values or limits'. Therefore he returned DAVIDSON's and SOWERBY's species to varieties of *Atrypa reticularis* (WHIDBORNE 1893, pp. 115-116), but still described and figured them separately. WHIDBORNE figured two specimens of *Carinatina* (ibid., Pl. 13, figs. 14-15) but called them *Atrypa desquamata*.

HOLZAPFEL's perceptive study of the faunas of the Givetian Massenkalk at Frettertal in Germany correctly redefined some previous determinations. HOLZAPFEL (1895) dealt with *Atrypa flabellata* (ROEMER), *A. reticularis* (LINNE), *A. aspera* (SCHLOTHEIM), *A. desquamata* SOWERBY and figured and defined correctly for the first time *Atrypa signifera* (SCHNUR). He attributed *Mimatrypa fretterensis* n.sp. to *Atrypa* cf. *arimaspus* EICHWALD.

In one of his last monographic studies of North American brachiopods, HALL (1894) figured comparative material collected in the Eifel region and in the Paffrath syncline. He appears to have been the first author to figure a specimen of the Eifel atrypid Gruenewaldtia latilinguis (SCHNUR) under its correct name. In Europe the revision did not follow until 1955 in the work if STRUVE.

The rich Skaly faunas of Poland, which have a great deal in common with those of the Eifel region, were first studied by GÜRICH in 1896. He proposed several new names, but because he did not figure any specimens and because his descriptions were not clear, many names have not been accepted. Only one name has survived, Anatrypa kadzielniae (GÜRICH). As varieties of Atrypa reticularis, GÜRICH described Atrypa reticularis var. trigonalis, elongata, orbicularis and globosa. These may be regarded as nomina oblita. Type material of GÜRICH is lost. Under Atrypa desquamata two varieties are given, one the above mentioned variety kadzielniae and the other the var. applanata. GÜRICH recognized Atrypa plana and A. aspera as full species. His varieties probably would have been acknowledged as full species to-day if their description had been more complete, or figures included.

The fauna of the Langenaubach 'Tuffbrekzie' in Germany was discussed by DREVERMANN (1901). The Tuffbrekzie was recently dated by KREBS (1963) as lower Carboniferous in age, but the fragments it contains are derived from fossiliferous Frasnian rocks. DREVERMANN stated that he had found Atrypa aspera and A. duboisi, but unfortunately gave no figures. Collections were made at Langenaubach, and Frasnian atrypids of the Desquamatia group were found.

GÜRICH also studied the Devonian faunas of Debnik in Poland. These faunas contain atrypids which are very similar to Russian species from the Ural mountains. GÜRICH (1903) identified Atrypa bifidaeformis CHERNYSHEV (which he figured) and listed A. aspera and A. reticularis.

The first of a series of papers on the Devonian of Letmathe-Iserlohn in Germany, was that of W.E. SCHMIDT (1905). He quoted two popular species, Atrypa aspera and A. desquamata without discussion or illustration.

SCUPIN in 1906 gave the atrypids of the Austrian Alps comprehensive treatment. Faunas from this area have little in common with those of the Eifel region, and are of 'hercynian' character. SCUPIN discovered the Russian genus Karpinskia CHERNYSHEV for the first time in Europe, gave a generic diagnosis, and described two species K. conjugata CHERNYSHEV and a new species K. tschernyshewi. He also figured and described a host of Barrandian species, and another new species Atrypa (=Carinatina) paradoxa : SCUPIN suggested it might belong to a new subgenus.

With the renewed interest in the Austrian Alps, GORTANI began the first of a number of Devonian faunal studies of the Carnic Alps near the Italian border. This contribution included a new variety of atrypid *Atrypa desquamata* var. *rugosa*. GORTANI gave two text-figures of a new atrypid *Karpinskia carnica* but no descriptions, and described a new species of *K. consuelo* with two varieties, *taramelli* and *geyeri*. GORTANI apparently followed ZITTEL (1895) in changing the name *Karpinskia* to *Karpinskya* (the latter is an invalid homonym). The genus *Karpinskia*, a 'hercynian' faunal element, is not found in the Eifel region.

An unknown, probably Lower Devonian, atrypid brachiopod was illustrated by WALTHER (1907, Pl. 13, figs. 18a-c). This brachiopod came from the Thüringen part of eastern Germany, where 'hercynian' faunas are dominant.

TORLEY (1908 ) recognized a number of independent species in the Devonian of Iserlohn, Germany, He identified *flabellata* and *A. signifera*. Two of these, *A. desquamata* and *A. flabellata* belong to the genus *Mimatrypa* but not to the species indicated by TORLEY. TORLEY's figures are diagrammatic and difficult to identify correctly.

Shortly after, HOLZAPFEL (1908 ) made a further contribution to the Givetian faunal knowledge by describing more brachiopods from the well known locality at Frettertal in Germany. He noted the mass concentrations of *Atrypa flabellata* (=*Mimatrypa fretterensis*) at this locality. HOLZAPFEL's collections have been examined.

RIGAUX completed his promised work on the brachiopod faunas of the Boulonnais in 1908. He named *Atrypa reticularis*, and a new variety "*mutatio belliloci*", *A. desquamata*, a new species *A. legayi* and *A.* longispina BOUCHARD. A search through fine collections at the British Museum (N.H.) and a visit to the Boulonnais failed to reveal *Atrypa desquamata* SOWERBY. It is not likely to be present in the Boulonnais because the facies in which *Mimatrypa* is common is not present there. The other species described by RIGAUX are to be revised.

The brachiopod fauna on the eastern side of the Rhenish Schiefergebirge was reviewed by HERMANN in 1910, and in a second paper in 1912. The faunas described have strong hercynian affinities and arellinked to those of the Czechoslavakian Devonian. HERMANN added nothing that was new, and did not figure any atrypid brachiopods.

The second paper published by GORTANI (1911) on faunas of the Carnic Alps, appears to have marked the first attempt to subdivide the genus *Atrypa*. GORTANI established two form-groups, "Gruppo dell'*Atrypa reticularis*" and "Gruppo dell'*Atrypa desquamata*". The second group was separated as a subgenus by ALEKSEEVA in 1960. In the first group GORTANI also included *Atrypa flabellata*, a new "mutation" *prunulum* and a new species *A. julii*, which are to-day part of the genus *Mimatrypa* STRUVE. In the second group, GORTANI distinguished two new varieties *Atrypa desquamata* var. *forojuliensis* and var. *trigona*, and another new variety *A. signifera* var. *carnica*. For *Atrypa reticularis* he proposed the varieties *normalis*, *ephippium* and *semiovum*. It is not known and it seems doubtful that the *A. desquamata* of GORTANI corresponds to SOWERBY's original species. The GORTANI faunas must be revised.

The first study of the rich brachiopod faunas of the Aachen Devonian, very similar to synchronous faunas from Belgium, was made by KLÄHN in 1912. He described unnamed varieties of *Atrypa reticualris* and in the discussion of the French atrypid, *A. longispina*, named QUENSTEDT rather than BOUCHARD as the author.

For comparative purposes MEYER (1913, Pl. 5, fig. 2) gave a figure of an '*Atrypa reticularis*' from Gerolstein in the Eifel region, in a monograph of the Devonian faunas of Ellesmere island in the Canadian Arctic. This figured brachiopod is very likely *Desquamatia* (*Variatrypa*) *triangulata* COPPER 1965. Though not much is known at the present time about Arctic faunas (e.g. those of Arctic Canada and Novaya Zemlya) the comparison is of interest in a palaeogeographical context.

In the richly fossiliferous, but strongly localized Frasnian faunas from the Elberfeld region near DÜsseldorf in Germany, PAECKELMANN (1913) described one new species, *Atrypa tubaecostata*, and discussed the distribution in the Dorner Kalk of *A. reticularis*, *A. aspera*, *A. latilinguis*, and *A. flabellata*. Not one of these, except the new species, was found in the PAECKELMANN collections and not one is known to occur in rocks of Frasnian age. In examining PAECKELMANN collections most specimens were found to be incorrectly identified, even many forms previously fully described and correctly known in Germany. PAECKELMANN seems to have had the habit of finding every available species in his collections.

FUCHS (1915) who concentrated a great deal of his work on Lower Devonian faunas, added a new species, *Atrypa lorana*. Lower Devonian faunas have not been dealt with here, and *A. lorana* does not have a great deal in common even with the lowermost Eifelian atrypids from the Eifel.

GORTANI (1915) published the last of his triptych on Devonian faunas from the Carnic Alps, and introduced some new forms : *Atrypa aspera* var. *laevicosta*, *A. italica* (=*Carinatina*).

PAECKELMANN's second work on Devonian atrypids was published in 1922, The Givetian Massenkalk faunas he described were mainly labelled as *Atrypa reticularis*, *A. aspera*, *A. desquamata* and *A. tubaecostata*, mostly incorrectly. In the PAECKELMANN collections several of these could be redescribed as new species, e.g. *Spinatrypa orthoclina* n.sp.

and *Spinatrypina girzenensis*. In PAECKELMANN's handwriting were a few labels with *Atrypa scabra*, but the author never seems to have published this name.

LEIDHOLD's monograph on the Massenkalk faunas of Germany (1928) is well known and his palaeoecological conclusions about the diversity of atrypid species are sound. LEIDHOLD added three new species, two of which, *Atrypa globosa* and *A. circularis* were shown to be junior synonyms of *Mimatrypa desquamata* (SOWERBY) in COPPER 1965a. LEIDHOLD's holotypes for these species were examined and are figured on Pl. 56. The name *Atrypa globosa* (not the *globosa* of STEININGER 1831, or BARROIS 1889, or GÜRICH 1896) has been applied frequently to atrypids of the *Atryparia* group in the Eifel region. LEIDHOLD also described a new species *Karpinskia rhenana*, but the atrypid in question appears to be a pentamerid brachiopod (COPPER 1965a). LEIDHOLD was the first to show the shell interior of *Mimatrypa flabellata* (C.F. ROEMER), and, after GORTANI, one of the first to separate the *desquamata* group from the *reticularis* group.

SCHNUR's species Terebratula zonata lay dormant in the European literature until LEMAITRE made use of it in 1929, though not correctly. LEMAITRE also adopted *Atrypa lorana* FUCHS, and listed the species *Atrypa reticularis*, *A. aspera*. The name *Atrypa lorana* also became recognized by ASSELBERGHS in the Ardennes, Belgium and by LAVERDIERE working in the Pyrenees in 1929.

A new variety of *Atrypa aspera* (var. *paffrathi*) was proposed by WEHRLI (1931) when he described some rare specimens from the Paffrath syncline, Germany. WEHRLI's material is untraceable. It was deposited in the University Museum of Köln, whose collections were destroyed in the war. A visit to the type locality, which was accurately described by WEHRLI, failed to yield additional material. Dr. U. JUX (person. commun.) also searched the type locality without success. The figured specimens, said to be dolomitized, were poorly preserved and the critical beak structures not identifiable. WEHRLI's name becomes a *nomen dubia*.

In 1934, LEMAITRE drew a comparison between faunas from the Ancenis basin in western France with those from the Ural mountains and those of the Czech Devonian. She became one of the first to describe European atrypids under the name *Carinatina* NALIVKIN. LEMAITRE appears to have found 'hercynian' faunal elements in the French Devonian : this may be significant as the western-most occurrence of such faunas. In the same year, TORLEY (1934) repeated a previous study of the atrypid fauna of Iserlohn, Germany and accepted all of LEIDHOLD's new species without question. FUCHS (1934) restricted *Atrypa lorana* FUCHS 1915, which had gained a much wider interpretation than it deserved, into a form limited to the Emsian, and separated a variety *gedinniana* to include specimens described as *Atrypa lorana* by ASSELBERGHS in 1930. DAHMER (1942) redescribed and redefined *Atrypa gedinniana* FUCHS 1934, designating a type locality and type stratum.

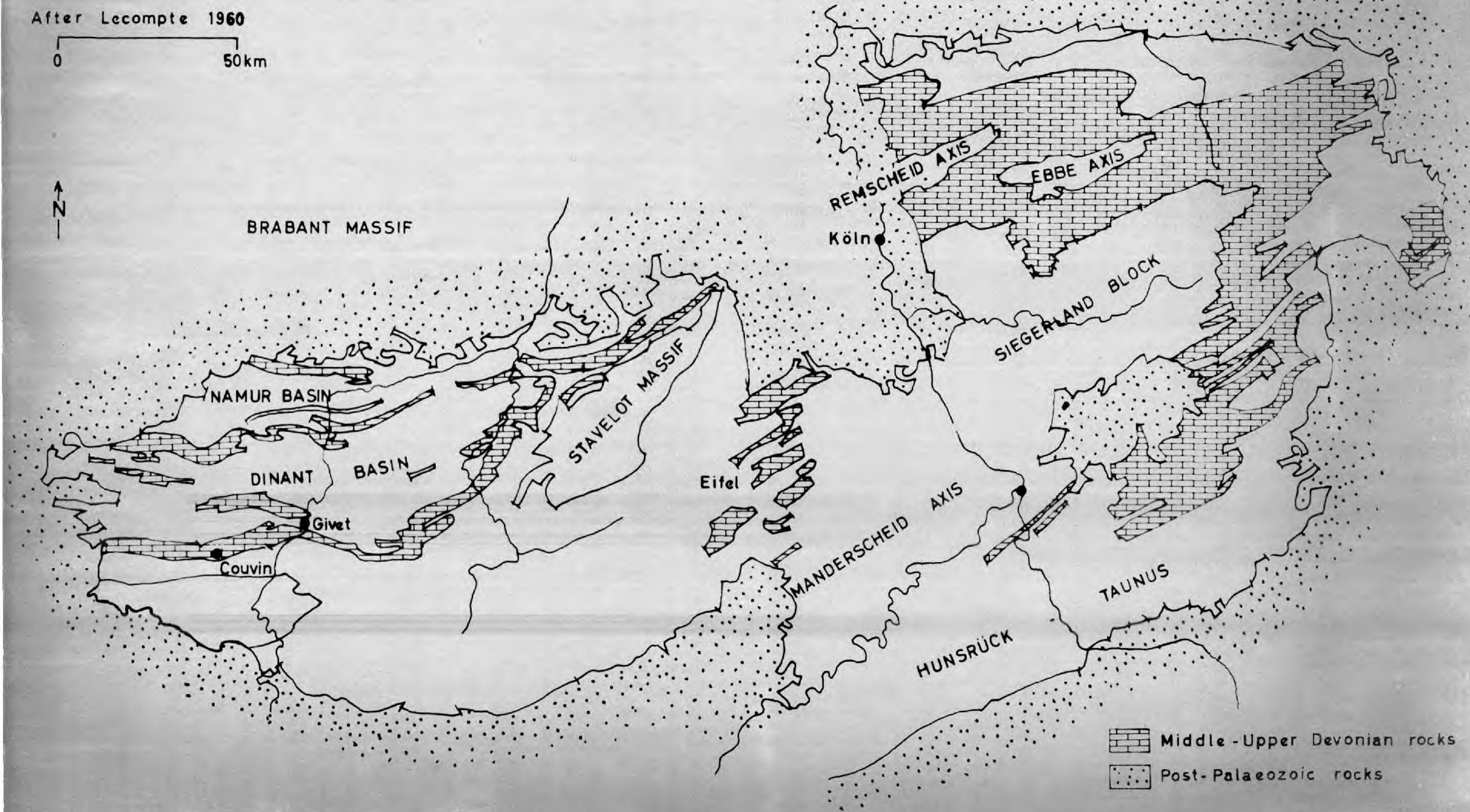
Though KELUS's work on faunas north of the Carpathian mountains in 1939 does not strictly fall into the province of west European faunas, his paper is important because it was one of the first to cast a critical eye on the generous use of *Atrypa reticularis* in the literature. He was also one of the earlier workers to employ serial sections in his descriptions of atrypids. Nevertheless, in spite of his critical view on the use of *A. reticularis*, KELUS described his atrypids as varieties of the Linnaean species and gave several new forms : var. *ventricosa*, var. *regularis*, var. *parazonata*, var. *orientalis* and var. *smordvica*. The first three varieties probably belong to the genus *Desquamatia*, and the last two to *Spinatrypina*.

A significant work in German atrypid brachiopods is one by SPRIESTERSBACH (1942). He described a new species. *Atrypa montana*, closely related to *Desquamatia triangulata* COPPER 1965, and established a new family, the Palaferellidae to include specimens of a new genus *Palaferella* of unknown affinities. This genus was later identified by STRUVE (1955) as a junior synonym of the atrypid genus *Gruenewaldtia* CHERNYSHEV.

The rich Polish faunas of Grzegorzowice, which contain many specimens very similar to those from the Eifel region, were described by BIERNAT (1954). For the family Atrypidae, only one species, new, was established. This species, *Atrypa varistriata* was subsequently re-identified by BIERNAT (1964) as belonging to *Desquamatia* ALEKSEEVA.

HAVLICEK continued studies of the Prague Devonian and a revision of BARRANDE species in 1955. He treated the following Atrypidae : *Atrypa verneuiliana* (BARRANDE), *Hystricina semiorbis* (BARRANDE), *Punctatrypa olgae* (NALIVKIN), *P. olgae nalivkini* HAVLICEK, *Falsatrypa admirande* n.gen., n.sp., and *Hystricina semiorbis latecostata* n.ssp. were introduced. The name *Hystricina* was changed by STAINBROOK to *Spinatrypa* in 1951. *Punctatrypa* and *Falsatrypa* seem to be atrypid genera foreign to the Eifel region.

Works published after 1955 in Europe are not discussed because all are revised and redescribed in some detail in this thesis. These include the atrypid papers by STRUVE (1955, 1956, 1961, 1964), JUX (1962, 1964), BIERNAT (1964) and SIEHL (1962).


After Lecompte 1960

TEXT-FIG 1A STRUCTURAL UNITS OF THE RHENO-ARDENNIAN MASSIF

# II STRATIGRAPHY

## Outline

A summary of the main stratigraphic units and the important facies developments of the Devonian in Germany is given. An exhaustive survey of the stratigraphy of northwestern Europe was not attempted. The important structural units are outlined in text-fig. 1A.

The main stages of the Devonian rocks in the classical outcrops located in Germany and Belgium are marked also by gross lithological differences. The Lower Devonian is characterised largely by siltstones and sandstones, the Eifelian by shales and limestones, the Givetian by biohermal limestones and the Frasnian again by shales. There is, therefore, no even continuous fossiliferous sequence and large facies differences are marked by gross faunal differences. These facies differences also had considerable effect on the distribution of the atrypid faunas.

Using the regression line of FRIEND & HOUSE (1964, fig. 1), which plotted cumulative thickness against time, each of the Eifelian, the Givetian and the Frasnian stages was estimated to last from 5 to 6 million years. The base of the Eifelian was drawn at about 369 million years ago and the top of the Frasnian at about 353 million years ago (ibid.). Therefore the atrypids under study cover a period of about 15 million years. The cumulative thickness of the calcareous shales and limestones with atrypid brachiopods in the Eifel, Aachen and Bergisches Land areas of Germany during this time, was about 1200 m. With this rough guide, each meter of sediment took about 13,000 years to be deposited and an estimate of the approximate length of each species relative to this scale can be made.

A comparison of the sedimentary thicknesses in the Ardennes, the Eifel region and Bergisches Land is interesting. Statistics are modified after BRINKMANN (1960). Only maximum thicknesses were calculated. The Eifel sequence is taken from STRUVE (1961).

| Stage | Ardennes | Eifel-Aachen | Bergisches Land | Sauerland |
|---|---|---|---|---|
| Famennian | 500 m | 500 m | 500 m | 250 m |
| Frasnian | 500 m | 400 m | 500 m | 500 m |
| Givetian | 500 m | 320 m | 1500 m | 650 m |
| Eifelian | 600 m | 450 m | 1350 m | 850 m |
| Emsian | 1000 m | 1700 m | 1000 m | 1900 m |
| Siegenian | 1500 m | 2000 m | 500 m | 3000 m |
| Gedinnian | 1000 m | 410 m | 1600 m | 1000 m |
| Totals: | 5600 m | 5770 m | 7150 m | 8150 m |

RICHTER (in GIGNOUX, 1955, p. 124) is quoted as having said that the Siegenian in the type area was more than 10,000 meters thick. W.E. SCHMIDT (1952) also reported thicknesses consistently greater than those given by BRINKMANN. For example, SCHMIDT gave the Frasnian-Famennian stages in Bergisches Land a thickness greater than 2400 m, the Eifelian more than 1500 m; similarly the maximum thickness of the Emsian in the rheno-hercynian zone becomes 2800 m, the Siegenian more than 2500 m. SCHMIDT's maximum total thickness reached 11,300 m.

There are marked facies differences in the Devonian outcrops of the Eifel synclines and the synclines east of the Rhine in Sauerland and Bergisches Land. The atrypid brachiopods were found chiefly and almost exclusively in the normal marine facies bearing corals and brachiopods, i.e. the 'Eifelfazies', the 'Normalfazies' of the 'Mischfazies' of different authors. And it is on these areas of coral-brachiopod sediments that attention is focussed.

During Eifelian time, only the Eifel synclines and the Attendorn syncline east of the Rhine, carried a normal brachiopod fauna. Elsewhere unfossiliferous sandstones and siltstones with plant remains characterise near-shore, continental areas.

During early Givetian time, previously emergent areas were flooded, and a normal marine environment ensued in the Paffrath syncline, and in the areas north of the Remscheid axis. Part of the southern Eifel was occupied by thick sequences of limestones but the northern Eifel carried faunas identical to those east of the Rhine. In Germany, and probably in Europe as a whole. the atrypid genera Atrypa, Atryparia, Desquamatia and Gruenewaldtia, so abundant during the Eifelian, vanished almost completely in the Givetian and were replaced by Spinatrypa and Spinatrypina. For the first time 'foreign' faunal elements are recognizable in the atrypid brachiopods of Germany. Such genera as Mimatrypa and Carinatina contained nearly indistinguishable synchronous species as far away as the Kutznetsk basin east of the Ural mountains. The middle and late Givetian marked the advent of large bioherms in the Germanic sedimentary sequence, in a facies well known as the 'Massenkalk', consisting of thick, massive units of light coloured limestones. In these limestones brachiopod remains are relatively scarce and many are contained in 'nests' or local concentrations, such as, for example, were formerly collected at Frettertal, at Bilveringsen near Iserlohn and in the Paffrath syncline.

Locally, as at Elberfeld north of the Remscheid axis, the 'Massenkalk' facies appears to have continued through the Frasnian. In other parts of Germany, the Frasnian again became a period of deposition of argillaceous sediments, much of which were sterile in brachiopods. Frasnian atrypid brachiopods are known in only a few areas, particularly at Refrath in the Paffrath syncline, around Elberfeld in the Dornap limestone and in the coral rich Gruiten beds, and also at Hofermühle 10 km NW of Elberfeld and in the brachiopod rich Frasnian of Aachen. The brachiopods in these isolated localities are difficult to correlate. In the Eifel region, the Frasnian is only preserved in one syncline, the Prüm syncline, and atrypids are here very scarce (refer to STRUVE 1964).

## Eifel region

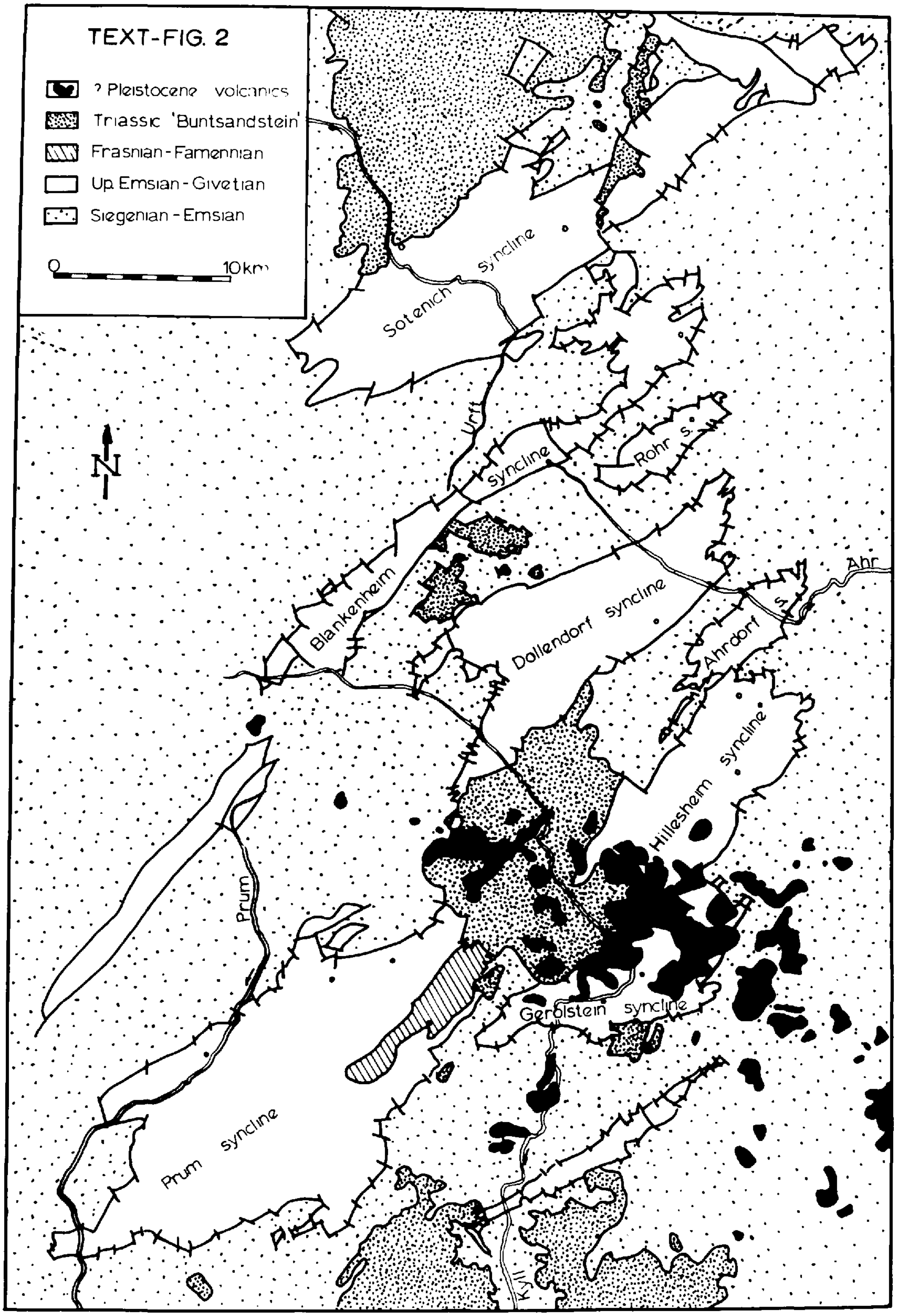
The Devonian synclines of the Eifel region occupy an area of about 1500 km$^2$ located between Aachen, Trier, Koblenz and Köln (text-fig. 2). The nine synclines, the largest of which is about 20 km long and 10 km wide, are situated in an area of rolling hills and winding streams at elevations of between 300 and 700 m above sea level. The synclines can readily be identified on topographic maps since they usually represent cultivated areas flanked by belts of forests which have taken root on the harder, more resistant weathering sandstones and siltstones of the Lower Devonian.

The Eifel was of interest to the natural historian nearly half a century or more before SEDGWICK and MURCHISON established the Devonian system in 1839. Nevertheless even to-day the richly fossiliferous synclines have been geologically mapped only in part. In the relatively small area of the Eifel synclines considerable facies differences exist between one syncline and the next and such facies differences have complicated accurate correlations. A broad faunal and facies distinction which varied from time to time during the Middle Devonian, existed between the northern synclines (the Sötenich, Blankenheim, Rohr and Dollendorf synclines) and the synclines to the south (Ahrdorf, Hillesheim, Gerolstein, Prüm and Salmerwald synclines).

No attempt is made to review the stratigraphical literature of the Eifel. A few of the more up-to-date references are cited and there is ample coverage of the early, pioneering work in these references. There also is no comprehensive geological map of the Eifel region available except for a few maps published before the turn of the century. A portion of the northern Eifel was included on a recent large scale (1:100,000) map prepared by SCHMIDT & SCHRODER (1962). The smaller synclines, e.g. the Blankenheim, Rohr, and Ahrdorf synclines have been mapped on a scale of 1:25,000. The remainder are under revision.

Pertinent stratigraphic references :

Sötenich syncline.- BERGER 1910; QUIRING 1913, 1914; RITZ 1931; Wo. SCHMIDT 1935; NOWAK 1956; PAULUS 1959, 1961; SCHMIDT & SCHRÖDER 1962.
Blankenheim, Rohr, Dollendorf synclines.- VORSTER 1918; KUCKELKORN 1924; KUCKELKORN & BORSTER 1926.
Blankenheim syncline.- OCHS & WOLFART 1961.
Rohr syncline.- GLINSKI 1961.

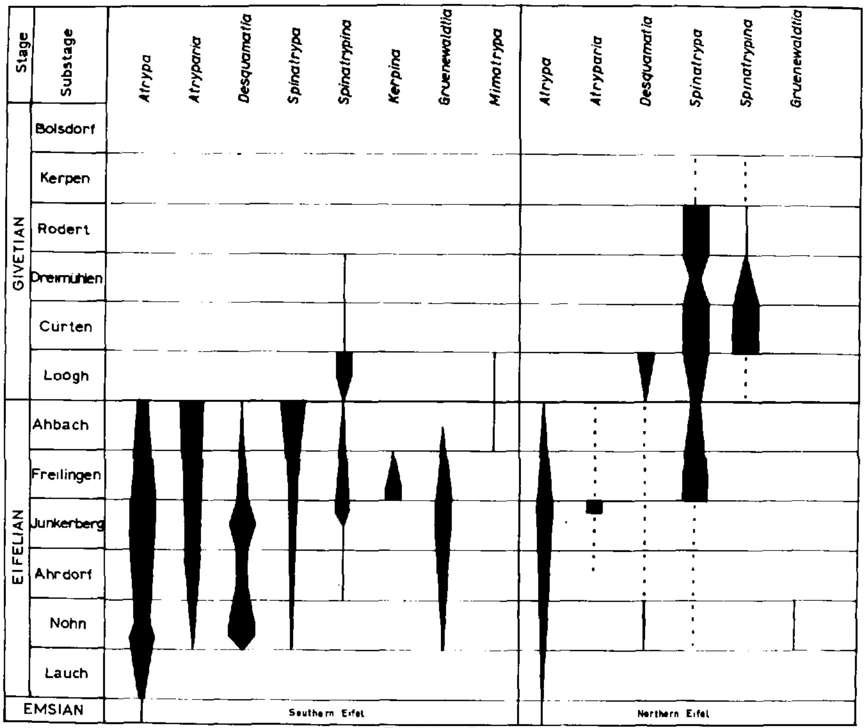


TEXT-FIG. 2

? Pleistocene volcanics
Triassic 'Buntsandstein'
Frasnian - Famennian
Up. Emsian - Givetian
Siegenian - Emsian
0
10km
N
Sotenich syncline
Urft
Blankenheim syncline
Rohr s.
Dollendorf syncline
Ahr
Ahrdorf s.
Hillesheim syncline
Prum
Gerolstein syncline
Prum syncline
Kyll

*Dollendorf syncline* (part).- METJE 1963.
*Ahrdorf syncline*.- QUIRING 1914b, HOTZ & KRÄUSEL (in HOTZ & KRÄUSEL & STRUVE 1955).
*Hillesheim syncline*.- HOTZ & STRUVE (in HOTZ & KRÄUSEL & STRUVE 1955), STRUVE 1961.
*Gerolstein syncline*.- RAUFF 1911; DOHM 1930; KRÖMMELBEIN 1957.
*Prüm syncline*.- HAPPEL & REULING 1937; STRUVE 1961, 1964.

The sequence in the Hillesheim syncline has become generally accepted by Eifel workers as the type succession in the Eifel region. The Middle Devonian sequence in this syncline is about 750 m thick and from the base to the top is marked by a gradual, much interrupted transition from a brackish water, littoral environment marked by lamellibranchs and plant remains to a fully marine environment with brachiopods, corals and reef-forming stromatoporoids. Accompanying this sedimentary change there is a gradual increase in faunal complexity from few, and rather primitive long-ranging atrypids to a rich and varied atrypid fauna. This complexity of atrypids culminated in the Freilingen beds (upper Eifelian) after which atrypids waned in their variety though not in their abundance. At the end of Eifelian time, the whole *Atrypa* group, (*Atrypa*, *Planatrypa*, *Isonatrypa*, *Atryparia*, *Desquamatia*) as well as *Gruenewaldtia*, disappeared en masse. *Desquamatia* lingered on for a short while until the end of Loogh (lower Givetian) time. *Atrypa* itself did not re-appear in Germany until late middle Frasnian time (approximately F2h-i), but *Desquamatia* came back in the late Givetian (text-fig. 3).



Text-fig. 3

To the north of the Eifel synclines, the vertical distribution of the atrypid brachiopods is different (text-fig. 3). The *Atrypa* was was never abundant in this area until late Junkerberg (middle Eifelian) time when it became briefly prolific. *Gruenewaldtia* already vanished much earlier in the lower Eifelian. It is to the north, however, that the *Spinatrypa*-*Spinatrypina* faunas reach their acme. An early forecast of the abundance of this group is the rich horizon with *Spinatrypa aspera aspera* (SCHLOTHEIM 1820) in upper Eifelian time. The lower and middle Givetian environment of the north seems to have been particularly favourable to *Spinatrypa* and *Spinatrypina*, while to the south this group is rare or absent. For the first time, correlations east of the Rhine with the Eifel are simplified because of similar facies and faunas.

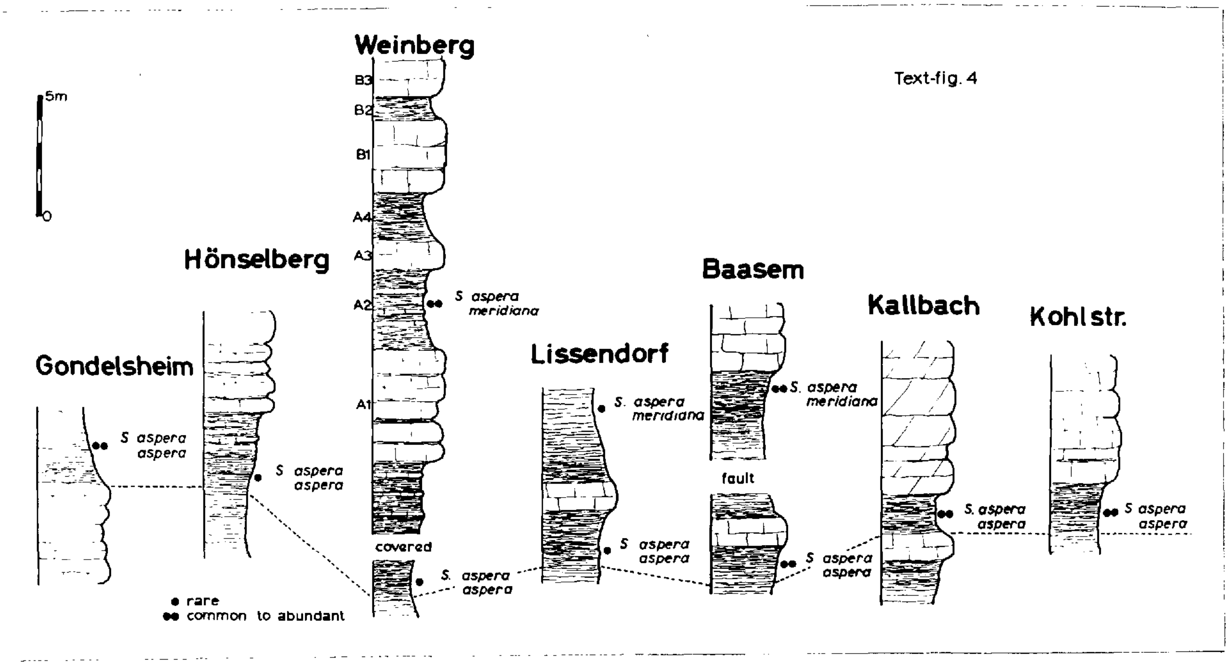
The chief stratigraphical units of the Eifel region have been grouped arbitrarily into lower, middle and upper divisions. The Givetian was divided previously (see COPPER 1965a) and the Eifelian divisions are as follows :

| | | |
|---|---|---|
| | Upper | Ahbach beds<br>Freilingen beds |
| Eifelian | Middle | Junkerberg beds<br>Ahrdorf beds |
| | Lower | Nohn beds<br>Lauch beds |

One of the important and critical points of correlations in the Eifel synclines is the boundary between the Junkerberg and Freilingen beds, i.e. the separation of the Giesdorf and Eilenberg horizons. This problem has plagued Eifel stratigraphers for many years and still is not wholly solved. There is no lack of fossils, but the fossil content varies from one locality to the next. In the Prüm syncline the Giesdorf horizon is easily marked by the conspicuous spiriferids *Spinocyrtia ostiolata* and this horizon has been taken arbitrarily, and very suitably as the top of the Junkerberg beds. However, *Spinocyrtia ostiolata* has a very local distribution and has recently been found in two other isolated localities outside the Prüm syncline, one northwest of Kerpen in the Hillesheim syncline, and the other near Lissendorf in the Dollendorf syncline. Directly above the *ostiolata* horizon on the north flank of the Prüm syncline are rich collectonss of *Spinatrypa aspera* (SCHLOTHEIM 1820).

In order to solve the problem it was necessary to find out what the real *Spinatrypa aspera* was. It was found that two subspecies of *Spinatrypa aspera* (SCHLOTHEIM) from the Freilingen beds, could be identified. In two stratigraphic sections (text-fig. 4), at Baasem (Blankenheim syncline) and at Lissendorf (Dollendorf syncline), the new subspecies *S. aspera meridiana*, a strongly ribbed, planar, orthocline beaked form occurs above the type species, *S. aspera aspera* (SCHLOTHEIM), a rounded, more golobose, shallow-ribbed form. It was also found that the *Spinatrypa aspera aspera* of STRUVE (1961, p. 313) was in fact different from the type *aspera aspera* and should have been referred to *S. aspera meridiana* n.ssp. The identification of these two subspecies as well as a note of their vertical distribution turned out to be critical in the separation of the Freilingen and Junkerberg beds.

STRUVE (1961, p. 310) supposed that the lower-most Freilingen did not contain *Spinatrypa aspera aspera* because he had not found this atrypid in the Eilenberg horizon. The Eilenberg horizon contained sediments apparently hostile to *Spinatrypa*. On the basis that the Eilenberg horizon did not contain *Spinatrypa aspera aspera* he had to assume that there were considerable stratigraphic hiatuses in the lower Freilingen beds of the Prüm syncline where this atrypid lies directly above the Junkerberg beds. As support STRUVE cited the presence of an ironstone bed at nearly the same position, and which, it was alleged, "ist eine typische Transgressions-Bildung" (STRUVE, 1964e, p. 239).



Text-fig. 4. Critical stratigraphic successions with *Spinatrypa aspera* (SCHLOTHEIM) in the Eifel region, Germany. Gondelsheim, MTB Gerolstein r36880:h65910; Hönselberg, MTB Dollendorf r53850:h74680; Weinberg, MTB Dollendorf r50980:h75720; Lissendorf, MTB Stadtkyll r42280:h75680; Baasem, MTB Hallschlag r35150:h81110; Kallbach, MTB Mechernich r38020:h96980; Kohlstrasse, MTB Mechernich r37910:h96450.

The writer found this theory difficult to accept and consequently collected many *Spinatrypa* at the critical horizons mentioned. At four localities on the north flank of the Prüm syncline (one is shown in text-fig. 4) the writer found typical Sötenich-type *Spinatrypa aspera aspera* directly above the Giesdorf horizon with *Spinocyrtia ostiolata* as was confirmed in STRUVE (1964e). There was no evidence at these localities of an ironstone formation, nor was there any sedimentological break observed (i.e. reworked sediment, mud-cracks, ripple marks, etc.). The sediments were calcareous shales and limestones of light gray to bluish gray colour.

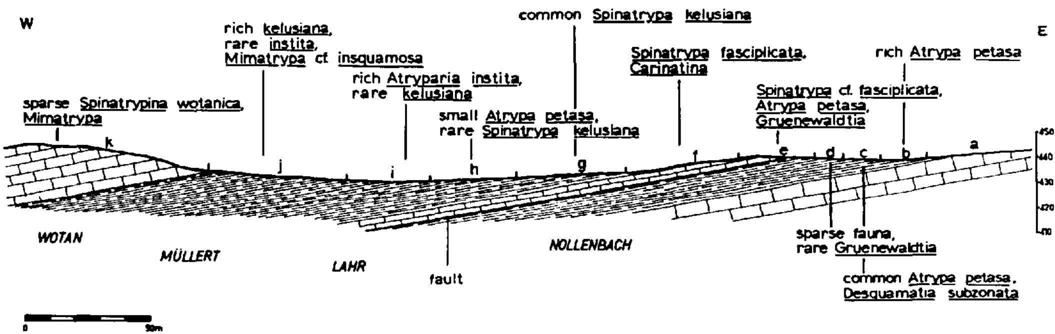
At the type locality and neighbouring localities of *Spinatrypa aspera aspera*, the fossiliferous beds are overlain by sterile limestones and dolomites, but at two other localities, Baasem and Lissendorf, the same species was followed by *Spinatrypa aspera meridiana* n.ssp. (the common form of the Hillesheim syncline). This led to the conclusion that *S. aspera aspera* should also be present *below* *S. aspera meridiana* in the Hillesheim syncline. They were indeed found in the predicted position at two localities, at Hönselberg and at the Weinberg quarry, and found not only at the base of the Eilenberg horizon but also below the Eilenberg horizon (beds with *Kerpina vineta goniorhynchia* STRUVE). This meant a sharp change in the definition of the Freilingen sequence, for no longer could these beds be divided into an upper unit with *S. aspera aspera* and a lower unit without it.

It also meant that the type locality of *Spinatrypa aspera aspera* should be dated as Eilenberg rather than Nollenbach age.

The change was not based on the redefinition of *Spinatrypa* alone, for strong corroboration was found in two other accompanying atrypid species. At the Sötenich type locality of *S. aspera aspera* and in the same horizon in the neighbourhood there are specimens of *Atrypa* (*Planatrypa*) *petasa* n.sp. which still have very strong links with the older *Atrypa squamifera* from which it was derived. In fact these specimens are almost intermediate. Another atrypid associated is the form typical of the Eilenberg horizon to the south, *Atrypa* (*Isonatrypa*) *inglanda* n.sp. There is then no doubt that *Spinatyypa aspera aspera* is of Freilingen age and also little doubt that it is in the Eilenberg horizon, probably at its base.

In the summer of 1963 a 1-2 m deep trench was excavated for a power line through the type locality of the Müllert horizon, Ahbach beds (text-fig. 5). It revealed part of the Freilingen beds, the Lahr and possibly the Hallert horizon (?fault), the Müllert horizon and the Wotan horizon. Hence it intersected the Eifelian-Givetian boundary. No specimens of *Stringocephalus*, index fossil of the Givetian, were found. in the Müllert horizon, and this supported its position in the Eifelian as suggested by STRUVE (1955, 1956). The first *Mimatrypa* (*M. insquamosa*) were found in the upper Müllert horizon and the last Gruenewaldtia in the Lahr (Hallert?) horizon. It is possible that the upper part of the Freilingen beds, the limestone of the Maiweiler sub-horizon, is missing here. Alternatively, the upper Freilingen is here in argillaceous facies or is overturned. Atryparia instita COPPER reached its peak of abundance about 10-15 m below Spinatrypa kelusiana rich beds. A fine collection of the rare Spinatrypa fasciplicata also was found for the first time.

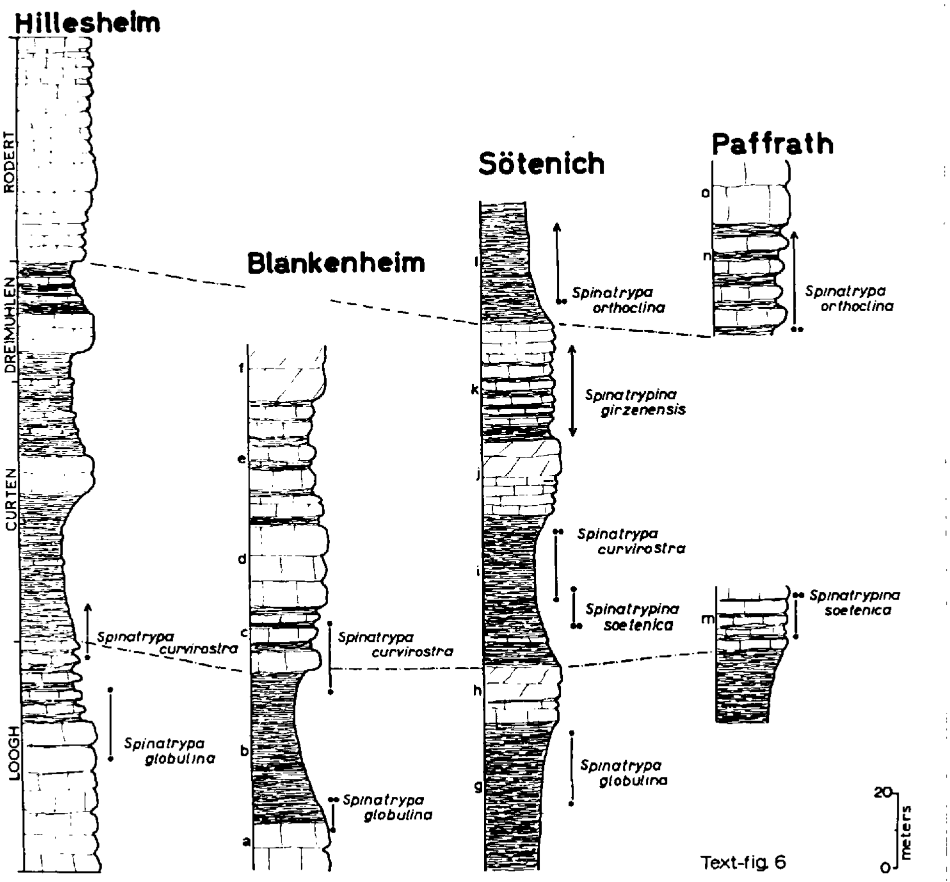
Text-fig 5



Exposures at the type locality, Müllert horizon

Text-fig. 5. Stratigraphic succession measured from trench through the type locality of the Müllert horizon (Ahbach beds). The trench intersects the Eifelian-Givetian boundary. MTB Dollendorf r55710-55430: h77390-77380.

Another critical correlation sequence (text-fig. 6) to which the Spinatrypa group makes a contribution is the lower and middle Givetian of the northern synclines, which, because of their distinct faunas, have been difficult to equate with the type Hillesheim syncline sections. In the Hillesheim synclines, these sequences unfortunately contain poor and dwarfed faunas and adequate comparison can be made only with the Loogh beds. The Wachtberg horizon of the Sötenich syncline and the Neuenbüsch horizon of the Blankenheim syncline are probably chrono-equivalents, and are best compared with the middle and upper Wotan and middle Rech horizons of the Hillesheom sequence. The age of the Spickberg dolomites is tentatively placed at upper Loogh. Spinatrypa curvirostra n.sp. of the Scheid horizon, can be dated as upper Rech to Felschbach (therefore high Loogh to Cürten). JUX (1962) dated the Scheid horizons as middle Eifelian and identified the above species Atrypa aspera. Spinatrypa soctenica (STRUVE) which occurs below Spinatrypa curvirostra at the north end of the Wachtberg quarry (locality C460), probably is of Felschbach age. Spinatrypina girzensis n.sp. is still uncertainly placed -- the thamnoporoid coral rich beds south of Keldenich in which it occurs are definitely younger than the Scheid horizon but probably not as old as the Rodert beds. They are therefore thought to be chiefly of Dreimühlen age.



Text-fig. 6. Critical stratigraphic successions in the Eifel region and Paffrath syncline. Hillesheim, about MTB Dollendorf r51500:h74300; Blankenheim, MTB Blankenheim r46410:h90050; Sötenich, MTB Mechernich r40160:h98850; Paffrath, upper section MTB Mülheim/Rhein r76800:h51120, lower section MTB Bürscheid r78430:h55350.

PAULUS (1959, p. 359) and SCHMIDT & SCHRÖDER (1962) date the age of the fossiliferous shales in the Urfey valley as Kerpen age on the basis of trilobites. This age is not supported! The Urfey beds carry a coral and brachiopod fauna with *Spinatrypa orthoclina* which is similar, if not identical, to the fauna of the Torringer beds with *Hexagonaria quadrigemina* at Hand in the Paffrath syncline. JUX (1962, p. 164) has dated these beds (as also HOTZ & KRAUSEL & STRUVE, 1955, p. 151) as Rodert age, and this agrees also with the interpretation of the atrypid faunas. It is possible that the upper parts of the Urfey beds (locality 17 in PAULUS 1959, p. 359) can be separated faunally from the lower part (locality 16, ibid.). The Spinatrypa orthoclina in the upper part are larger, and more coarsely and flatly ribbed than those in the lower part.

Near Odenthal in the Paffrath syncline a small quarry with atrypid-rich beds is found which can be correlated closely with the atrypid horizon of the Scheid beds in the Sötenich syncline. Therefore this makes the age of the Odenthal beds considerably older than is given by JUX (1964). JUX (1964 and person. commun.) places the Odenthal quarry level stratigraphically with the quadrigemina beds of Hand (Rodert age) when instead they are probably of Cürten age.

## Bergisches Land, Sauerland and Aachen area

The Devonian rocks of the Aachen area and east of the Rhine were thoroughly mapped geologically on a scale of 1:25,000 between 1890 and 1940. Large fossil collections from these areas accumulated by the cartographers and geologists were examined in the Paläontologisches Museum, Berlin, but many of the classical fossil quarries are to-day inaccessible. Since the 1930's little major revision of the chief stratigraphical formations have taken place. Much of the stratigraphy, particularly of the Upper Devonian, is based on conodont and ostracod microfossils, which are more suitable because macrofossils are rare.

A classical review of the rhenish facies was given by HERMANN SCHMIDT (1926) in his work on the Schwellen-Becken concept. Some of the facies concepts of SCHMIDT (see also SCHMIDT 1962, pp. 224-230 for a review) do not appear to agree with the distribution of the scarce atrypid faunas nor do they agree with the picture presented more recently by ERBEN (1962, pp. 42-61). As an example, the distribution of "Spirifer" ascendens in SCHMIDT (1962, fig. 1), which appears in the same facies as Spinatrypa of the S. orthoclina-curvirostra group, is quite probably much too widespread and does not take into account large gaps in the fossil record where these rocks are absent.

PAECKELMANN (1913, 1922) devoted a large part of his work to the Givetian-Frasnian reef limestones of the Massenkalk facies. A re-examination of PAECKELMANN's collection showed that the identifications left much to be desired. PAECKELMANN reported finding many genera which are absent in the Givetian and Frasnian and also not located in the collections. Nevertheless his reviews of the faunas broke much new ground.

THIENHAUS (1940) and SPRIESTERSBACH (1942) give a good account of the Middle Devonian stratigraphy of the Sauerland area. Valuable geological sections of the Bergisch and Sauerland areas are given in JUX (1960), and the stratigraphy of the classic fossil localities in the Paffrath synclines is reviewed by JUX (1964). The best reference to the brachiopod collections of the Aachen area is given by KLÄHN (1912). Recent Upper Devonian stratigraphy of Aachen is summarized by Wo. SCHMIDT & SCHRÖDER (1962).

The Upper Devonian sequence on the north flank of the Remscheid is shortened and generalized in the column below :

| | | | |
|---|---|---|---|
| | | Etroeungt beds | 60 m |
| Famennian | | Dashberg beds | 150 m |
| | | Hemberg beds | 50 m |
| | | Nehden beds | 50 m |
| Frasnian | F3? | Matagne beds | 150 m |
| | F2? | Iberg limestone | 100 m |
| | F1? | Dorper limestone | 250 m |

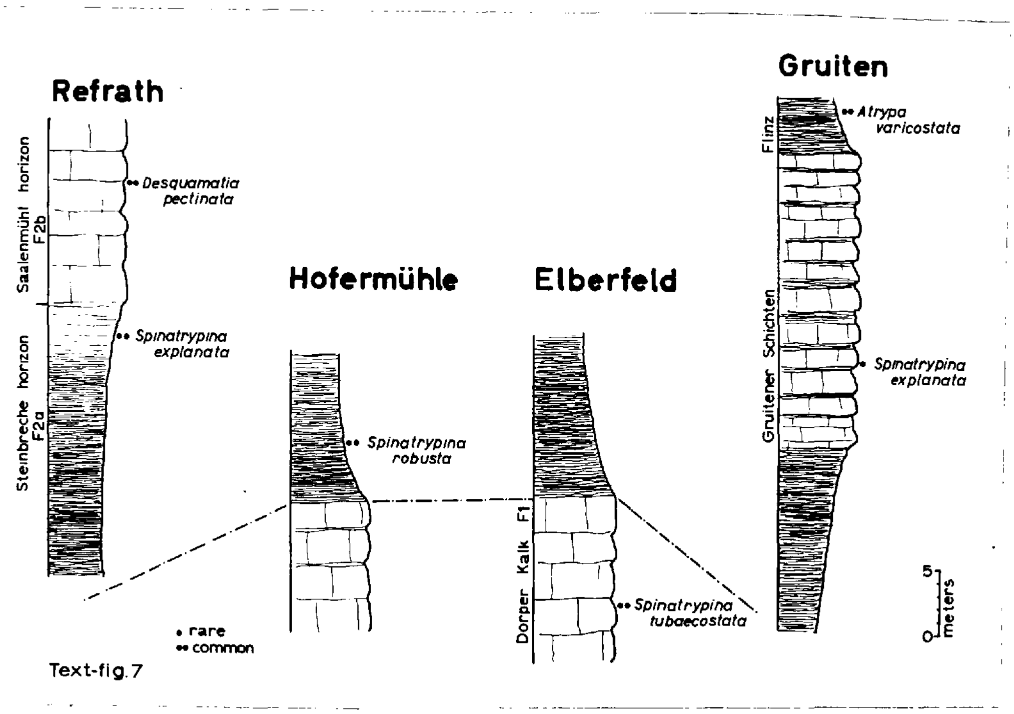
The Gruiten and the Refrath beds are to be expected somewhere above the Dorper Limestone, although not contained within the Iberg limestone which is only of very local distribution. Either of these limestones may be missing locally and replaced by black or dark gray nodular limestones of the 'Flinz' type.

The Frasnian atrypid faunas at Aachen and east of the Rhine can readily be separated into two units : a lower Frasnian part (F2a-F2e, some F1) with a *Spinatrypina* and *Desquamatia* fauna and an absence of *Atrypa*, and an upper Frasnian part (F2h-F3) marked by a return of *Atrypa* and many *Spinatrypa*, as well as the advent of *Anatrypa*. These two units are treated separately. No atrypids have ever been confirmed in Famennian or younger rocks, and reports of these e.g. VEEVERS (1959b), MANSUY (1912) need to be checked. THOMAS (1916) reported that in North America atrypids have been found in Mississippian rocks, and he cited WELLER (1914) who apparently found an *Atrypa frequens* in the Glen Park limestone (Kinderhookian?) of Illinois. This report needs to be examined.

The lower unit (F1-F2c) is exposed at several important localities, all of which were visited but only two of which are accessible to-day (text-fig. 7). These localities are difficult to correlate because they are wide apart and each fossiliferous horizon is only a few meters thick. The spinatrypid sequence is thought to be as follows.:

*Spinatrypina robusta* n.sp. F2b-c.
*S. explanata* (SCHLOTHEIM F2a.
*S. tubaecostata* (PAECKELMANN) F1.

Recently BRINCKMANN (1962) reviewed the limestone outcrops of the Elberfeld area and dated them on the basis of conodonts. From BRINCKMANN's work (ibid., p. 128) the Gruiten beds which locally contain a *Spinatrypina explanata*-like fauna are equated with 'Plattigen Kalke' and placed in the Adorf beds. BRINCKMANN advocated rejection of the name Gruiten beds which have been used as a name for coral and brachiopod rich horizons. From BRINCKMANN's work it is inferred that the Dorper Kalk of Elberfeld



Text-fig. 7. Critical stratigraphic successions in Bergisches Land, Germany carrying Spinatrypina faunas. Refrath, MTB Mülheim/Rhein r78140:h47540; Hofermühle MTB Kettwig about r66600:h86090; Elberfeld, MTB Elberfeld about r74410:h80600; Gruiten, MTB Mettman about r69680:h77110. Thicknesses estimated.

with a *Spinatrypina tubaecostata* is older than the Gruiten beds. The Gruiten beds can probably be correlated as the coral-brachiopod facies of the elsewhere unfossiliferous 'Flinz' (dark gray sterile limestone). PAECKELMANN (geol. map Elberfeld 1:25,000) placed the Gruiten beds below the Dorper Kalk, but this position is questionable.

There is little doubt that the Gruiten beds are more or less equivalent to the lower part of the Refrath beds. The position of the *Spinatrypina robusta* horizon in uncertain; it may be younger or older than the Refrath beds. Morphological evidence favours a younger age - *S. robusta* does not include intermediate specimens leading from *S. tubaecostata* whereas there are many coarsely ribbed *S. explanata* which show *tubaecostata* affinities.

The largest collections of *Spinatrypina* were found at Refrath, where topotypical SCHLOTHEIM material was found (these exposures are not accessible since construction of a sports field in 1963). The Refrath locality was already mentioned in the literature in the late 1700's and specimens have turned up from it in many major collections around the world. PAECKELMANN (1942) was the first to recognize the Upper Devonian age of the Refrath beds.

The Refrath beds can be separated into two horizons, a lower coral-rich shale horizon and an upper atrypid-rich limestone horizon. These are briefly described, as no previous mention of these is found in the literature.

## Refrath beds

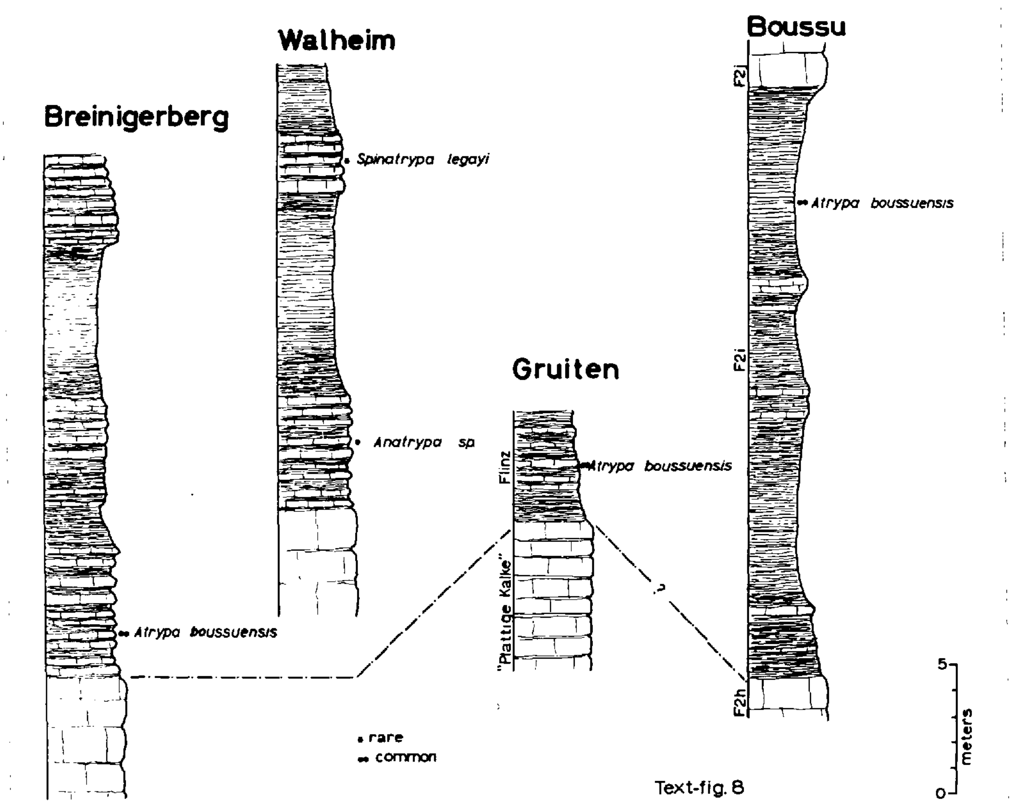
### Steinbreche horizon:

Name: After Steinbreche, the quarry formerly located on the site which provided the rich collections. Type locality: South side of the sport field in Refrath,Paffrath syncline, MTB Mulheim am Rhein r78140-200: h74550-80. Description: Pale brown to brownish or yellowish gray, richly fossiliferous calcareous shales with abundant tabulate corals, disphyllid corals and *Spinatrypina explanata*, *Atrypa* (*Devonatrypa*) *europaea* (STRUVE). Remaining fauna listed in JUX (1964, pp. 170-171). Thickness: Estimated 5-15 m.

### Saalermühl horizon:

Name: After Saalermühl Bach, a small creek which runs along strike of the fossil locality (in 1964 this creek was temporarily or permanently drained). Type locality: Quarry and exposure adjacent to Saalermühl creek, Paffrath syncline, MTB Mülheim am Rhein r78140:h47540. Description: Pale brown to yellowish brown, dull weathering thinly to moderately bedded argillaceous limestones rich in frilled specimens of *Desquamatia pectinata* (SCHRÖTER 1777) and isolated disphyllid corals as well as rare other brachiopods. Thickness: More than 10 m.

The upper unit of the Frasnian previously mentioned (F2h-F3) of Aachen and Bergisches Land contains an *Atrypa* and *Spinatrypa* fauna marked by an absence of *Spinatrypina* so abundant in the underlying Frasnian horizons. Atrypid collections were made at Breinigerberg, Walheim, and Gruiten and a comparative collection made at Boussu-en-Fagne in Belgium where rocks of the same age are fossiliferous (text-fig. 8). The entrance to the Walheim quarry yielded only small fauna. Notable was a dark shale and nodular limestone zone directly above the thick limestone unit used for quarrying. This zone contained what seemed to be a dwarf fauna in which a few *Anatrypa* were found. The Breinigerberg quarry was more prolific : many *Atrypa* were found but the horizon which must have provided the rich *Spinatrypa* collections in the Berlin Museum was not traced. It is suspected that it lies above the *Atrypa* beds, probably outside the quarry. These *Spinatrypa* from old collections have long been identified by QUENSTEDT (1871), KLÄHN (1912) and SCHMIDT & SCHRÖDER



Text-fig. 8. Critical stratigraphic successions in the Aachen area, Bergisches Land, and the Dinant Basin, Belgium. Breinigerberg, MTB Stolberg r17250:h22560; Walheim, MTB Stolberg r12960:h18800-760; Gruiten, MTB Mettmann r69680:h77110; Boussu, Carrière du cimetière, Dinant Basin.

(1962) as *S. longispina* (BOUCHARD) from the Boulonnais region in France. For this reason a topotypic collection was made at the Boulonnais Palaeozoic inlier. Two *Spinatrypa* species were collected there, *S. legayi* (RIGAUX) which occurred in the Ferques limestone and which was smaller, more finely ribbed, more dorsibiconvex atrypid, and *S. longispina* (BOUCHARD in RIGAUX) which occurred above the Ferques limestone, and which was larger, more coarsely and flatly ribbed and more equally convex. The former species, *S. legayi* was much more similar to the species from the Aachen area. *S. legayi* appears to be of late F2 age or possibly early F3, but not top F3. The Boulonnais atrypids still need to be revised.

# III ECOLOGY

## Outline

The sedimentological and palaeontological literature on Devonian shallow marine environments is extensive. Since all faunas, in the past as well as in the present, are critically related to their physical and biological surroundings, studies of the distribution of corals and brachiopods which formed a large part of the fossil record in the Devonian, are of great importance. Several such studies, notably those by WEDEKIND (1924) and LECOMPTE (1958, 1960, 1961) have been carried out. But, there is still no concrete information available on the distribution of many brachiopods in this framework. Most brachiopods are simply assigned to a rachiopod facies. It will be shown that the extinct group of atrypid brachiopods were highly adaptive organisms restricted in distribution to many different and specialized local environments and that because of their restrictions in distribution they are not only useful as index fossils but also as productive tools in the reconstruction of biofacies and palaeogeographical maps.

One of the first attempts to establish an order in the sequence and distribution of the main coral elements of the Devonian seas, was WEDEKIND (1924, p. 86) who gave a brief summary of the coral groupings. WEDEKIND distinguished two basic kinds of reefs, 'Monogene' or 'Sammelriffe'. WEDEKIND's original tabulation is repeated:

Monogene (monotypic) reefs.
-consisting of corals of one type.
a) Rasenriff - field reefs consisting of associations of a single type of tabulate, caespitose, rugose or amphiporid corals.
b) Blockriff - blocky reefs consisting of single elements of stromatoporoids, cerioid rugose corals, or tabulate corals.
c) Knollenriff - small, knoll-like corals in the form of groups of stromatoporoids or tabulates.

Polygene (polytypic) reefs.
-consisting of many mixed coral types.
a) Non-crusting tabulates and rugosans.
b) Encrusting tabulates and rugosans.
c) Impure associations of corals with much shale associated and not accumulated in bioherms.

In a later publication, WEDEKIND & TRIPP (1937, p. 299) compared the Eifel corals to those of the Silurian in Gotland and added one more element to the Rasenriffe, Blockriffe, and Knollenriffe and called associations of solitary corals by the special name 'Rübenriffe' (transl. beet reefs), a not inappropriate term.

In 1958 LECOMPTE suggested that the marine Devonian sediments could be scaled into six bathymetric zones, ranging from shallow to deep as:

1) Zone des Stromatopores, massifs, dominants.
2) Zone des stromatopores lamellaires.
3) Zone corallienne.
4) Zone des brachiopodes.
5) Zone des schistes steriles.
6) Zone des goniatites et Buchiola.

In 1961 LECOMPTE refined his faunal zones into five facies each with characteristic physical criteria and individual biota. These were (ibid., p. 33):

1) Le facies turbulent (massive stromatoporoids).
2) Le facies subturbulent (lamellar stromatoporoids).
3) Le facies sous-turbulent (ceroid and fasciculate colonian corals passing into a mixed phase with brachiopods).
4) Le facies quiescent (brachiopods, solitary corals).
5) Le facies profond (goniatites or sterile shales).

Also in 1961 STRUVE reconstructed the Eifel coral sea along lines previously attempted by WEDEKIND. STRUVE identified three main facies, in turn divided into smaller faunal associations. The first facies was a stromatoporoid-coral facies which was separated into stromatoporoid reefs, stromatoporoid-coral reefs, rugose, tabulate and crinoid thickets, and lastly horn coral reefs. The second facies was devoted to brachiopods and the third was a sandy-clayey facies with few fossils. In 1963 STRUVE broadened out these environments and identified seven zones which were compared to those of LECOMPTE (1961, fig. 3). It is in the framework prepared by STRUVE (1961, 1963) and BIRENHEIDE (1962) that the atrypid brachiopods will be fitted. This basic faunal division is as follows.

1) lagoonal area, 2) bank reefs, 3) knoll-block reefs, 4) thicket reefs, 5) beet reefs, 6) brachiopods, 7) zones with rapidly deposited and reworked sands and clays.

In his comprehensive study of the Devonian reefs of Germany, JUX (1960) described many localities where these were exposed, but did not make an attempt to build up a sequence of biotopes, or to zone the biotopes on a geographical basis.

The atrypid brachiopods are one of the main elements of Devonian sediments and appear to have reached a wider distribution in coral rich rocks than other brachiopod groups. The atrypids are not confined to the "zone quiescent" of LECOMPTE (1961) nor to the "brachiopod zone" of BIRENHEIDE (1962) and STRUVE (1961, 1963), but range through several biotopes from the bank reefs to the nearly sterile sands and clays. Though they range through many biotopes, the atrypids are in fact less facies tolerant than other brachiopods such as stropheodontids and orthoids because they disappear much more rapidly when conditions are unsuitable, such as on sand or silt substrates. It is in the coral-rich zones where atrypids are often abundant, that other brachiopods are scarce. The atrypids formed striking 'friendships' (symbiotic?) with many different types of corals and with each other. These will be described.

Some authors have treated brachiopods as accessory organisms in sediment construction in that they contributed very little to the bulk of sediment. This view is particularly prevalent in sub-surface correlations, and is not unfounded. For example, KLOVAN (1964, p. 41) assigned brachiopods to the organic reef portions and remarked that Atrypa thrived in turbulent waters. Neither of these views were corroborated by a study of the Eifel brachiopods. Brachiopods may take up only a small fraction of sediment volume and their distribution may be difficult, if not impossible, to plot through bore-hole information. Areally, however, brachiopod biotopes occupied large tracts of the sea floor on which often very little macroscopic life seems to have settled.

ZIEGLER (1964, p. 233) outlined a Silurian brachiopod community study in which evidence was presented that brachiopod distribution could be plotted so as to reconstruct a biofacies pattern. This appears to be the first study of its kind using Palaeozoic faunas. Similar biotopes were plotted independently for the Eifel region.

The Eifel area of Germany probably is unique in Europe in its rich and variable Devonian faunal structure, and the synclines of Couvin and Givet as well as those of Attendorn and Paffrath east of the Rhine, contain a sparsely fossilferous Middle Devonian sequence by comparison. The Eifel is therefore an almost ideal place for a detailed faunal study of this kind. The basic stratigraphic units have already been worked out (e.g. HOTZ & KRAUSEL & STRUVE 1955, STRUVE 1961) and some faunal patterns have already emerged in the studies of STRUVE (1961, 1963) and BIRENHEIDE (1962). By compariing the distribution of the previously plotted coral biotopes and the distribution of the atrypids, a somewhat different picture resulted. Several new interpretations are proposed.

The following study is biased in favour of the atrypid brachiopods, and the panoroma of the Devonian sea floor seen through 'atrypid coloured' spectacles.

The study of the Atrypids related to their environment is approached in two complementary ways : firstly, through the areal geographical distribution of atrypid biotopes and their contents, and secondly, through the special adaptations of atrypid shell morphology in relation to environment. Two important discoveries were made : individual atrypid genera were found to be confined to narrow bands whose width and extent could plotted on biofacies maps, and, within such bands the atrypid species developed unique morphologies. This sophisticated degree of adaptation may have been an important factor in the world-wide extinction of the atrypids at the end of Frasnian time, a period for which no 'catastrophic' geologic events such as major orogenies are known.

The direct applications of atrypid biotope maps are in the reconstruction of ancient coral masses. The method, of course, relies heavily on a precise taxonomic basis and a correct identification of atrypid genera. A reliable chronological scale must be established and material must be collected from numerous localities.

## European setting

A broad, two-fold division of marine Devonian sedimentary rocks in Germany and Europe into a 'rhenish' and a 'hercynian' facies has often been postulated in the literature. A good analysis of these two facies is given by ERBEN (1962). ERBEN has traced the historical development of these two concepts.

A third facies complex, a 'Grenzfazies', 'Mischfazies', 'Eifelfazies' or 'Normal fazies' also is found in the literature. In general, this third facies refers to the coral and brachiopod-rich areas of the Devonian in Europe. It is the facies which provided the bulk of the atrypid material under study. HERMANN SCHMIDT (1935) called the third zone, a Grenzfazies, and named the Koblenz quartzite of Lower Devonian age as typical of the 'rhenish' facies and the Tentaculites beds of the Harz region as the 'hercynian' facies. ERBEN (1962) called the third the 'Mischfazies' and split the hercynian into several intrafacies. ERBEN described several faunal types in each facies. The rhenish facies was said to have strongly ribbed brachiopods dominant, and very wide spiriferids as typical. The hercynian facies was said to be typified by smooth, round brachiopods (pentamerids, meristellids).

An outline of the main facies types is given in Text-fig. 1. The atrypids studied were from the Eifel region and fall into the range of the Mischfazies. It is probable that the atrypid genera Carinatina and Mimatrypa, rather rare elements in the Eifel area, belong at least in part to the hercynian type of facies, where they seem to be much more dominant. Text-fig. 1 is an idealized reconstructions of the late Eifelian-early Givetian (Middle Devonian) palaeogeography in western Europe. The continental, "Old Red" type of facies includes terrestrial fresh-water and brackish water environments. The second type of facies partly includes the rhenish facies and consists of brackish water to intertidal and partly marine environments. The third type figured is the Mischfazies, normal marine, probably closed or only partially open shallow marine shelf sea environment. The last type refers to the hercynian facies, with fully marine conditions and little influx of coarse detrital material

The individual fossil groups which inhabited the shallow marine 'Mischfazies' environment of the Eifel region are extinct. Parallels can be drawn, to a certain extent, with recent marine environments such as those of the well studied regions of the Bahama islandsd the Great Barrier Reef and on the Bikini Atoll in the Pacific, as well as many others, but comparisons remain purely morphological since it may probably never be known if similar extinct organisms occupied similar ecological niches. Some comparisons have been made, e.g. the recent colonial coral Manicina has been compared with the Devonian cerioid coral Hexagonaria (FABRICIUS 1964), and the recent 'organ pipe' coral Tubipora with the long ranging Palaeozoic coral genus Syringopora (HILL, 1960). But the fact remains that during Devonian times a highly complex marine environment existed, which, in most aspects, appears to differ markedly from organically similar environments of to-day. Horn corals, colonial rugose corals, thamnoporid corals, crinoids and brachiopods of the type and abundance of the Palaeozoic seas are now completely unknown. Modern brachiopods are scarce, geographically localized and many appear to live in colder and deeper waters than did their abundant, widespread, and probably shallow, tropical marine ancestors. The mode of life of ancient brachiopods and the bathymetry, temperature, salinity, oxygenation and current movement of their environment in the past will be known probably only in part. Deductions must depend on the field relationships of fossil brachiopods, the source sediment, the associated fauna, the position and alteration of specimens after death, their vertical and horizontal distribution, and not merely on the ecology of similar Recent Brachiopoda. Although recent marine lamellibranchs may have captured the ecological niche which brachiopods occupied in the past, they also cannot be used to reinterpret ancient brachiopod life assemblages.

In the re-interpretation of Devonian environments in the Eifel region, several acute problems arose, some of which required weighted evidence. In the biotope maps (text-figs. 10-14) the biotope lines were drawn around localities at which species were particularly abundant and not necessarily at all localities, some of which might contain only one or two specimens. It was inevitable that isolated members of some species would be scattered about biotopes in which they were not "at home". With rare species, or with monotypic faunas this problem was a light one, for mixed localities usually were scarcer.

The criteria for fossil communities are a minimum of pre-burial alteration and fossils found in life or near-life positions (FAGERSTROM, 1964, p. 1199). Such criteria are not easy to find. The most abundant atrypid brachiopod collections were gathered from soft-weathering, calcareous shales in which life positions are difficult to determine, Many atrypids appear to have had anchoring devices such as spines or frills, and therefore probably were moved very little, but other atrypids were attached by a pedicle muscle, a fleshy stalk not preserved as a hard part, and may have been buried after death in a position which did not reflect their mode of life. One of the atrypids with a functional pedicle was the genus Gruenewaldtia : the mode of life of this genus is not well known. Some of the evidence to determine transportation was, therefore, circumstantial, and rested on the appearance of the shell (damaged, eroded, disarticulated?), and the quantities of large and small shells or shells of only one type of morphology. Most of the rich atrypid collections seem to have been derived from in situ localities. At any rate, the biotopes which were plotted were several kilometers across, a distance beyond which it is unlikely that currents carried mature atrypid shells.. It seems likely also that the Eifel region was a shallow, at least partially closed shelf sea (see STRUVE 1963) well away from major currents comparable, for example, to the Gulf Stream of to-day.

It also was evident that a great deal of additional information was required about areas which were not as closely sampled. For example, parts of the Prüm syncline from which atrypid faunas had been described, were no longer accessible. The work of mapping the Eifel synclines also is only partially completed : the Prüm syncline, Hillesheim syncline (in part), Dollendorf syncline ($\frac{3}{4}$ unmapped), and Sötenich syncline are not known in detail and have not been correlated with the type sections of the Eifel region which are located in the Hillesheim syncline.

Probably less than 5% of the area once covered at any Devonian time interval in the Eifel area is exposed to-day. Some of this is dolomitized, or is unfossiliferous and cannot be dated precisely. The remaining 95% of the sediments which must have once covered the area is not exposed or is eroded. This naturally leaves large gaps in the record. Some of the facies patterns are even bound to coincide with outcrop pattern. For example, the broad facies plan which stretches across the Eifel region of synclines roughly in the shape of a loose S sinuating from NE to SW (STRUVE 1961, p. 85), is also nearly the area outlined by the outcrop pattern.

Another problem was that of correct correlation. Before parallels of environments can be drawn between one syncline and the next, there had to be some assurance that these sediments were of the same age. The detailed stratigraphy of small areas of the Eifel synclines is now known (largely in HOTZ & KRAUSEL & STRUVE 1955, STRUVE 1961), and with this as a base, more accurate comparisons could be drawn. But, no detailed petrographic-sedimentologic study of the type area of the lower Middle Devonian, the Eifel, has yet been carried out. It would be of great interest to know of the variation in sediment thickness, something of probable current directions, and so on. The lack of this knowledge hampered more accurate interpretations.

The Eifel sea lane was probably bounded to the south and southeast by a crustal high (called Istaevonia by STRUVE 1961), which coincides to-day with the Siegerland Block and Manderscheid axis (text-fig. 1a). Separating it from the Devonian area of Aachen to the north-north-west was another island core, Condrusia (STRUVE 1961), The Old Red continent occupying much of The Netherlands and northern Germany and further to the north/ There probably were direct connections with the Couvin-Givet sea lane and also to the east with the Lisa Gora area of Poland. The postulated islands Istaevonia and Arduennia (to the west) may have been separated by a channel which introduced, periodically, hercynian faunal elements. The main current possibly ran NE-SW (STRUVE 1963, p. 274). In late Eifelian time reddish coloured sediments were restricted to the northern Eifel synclines and sandy deposits to the west.

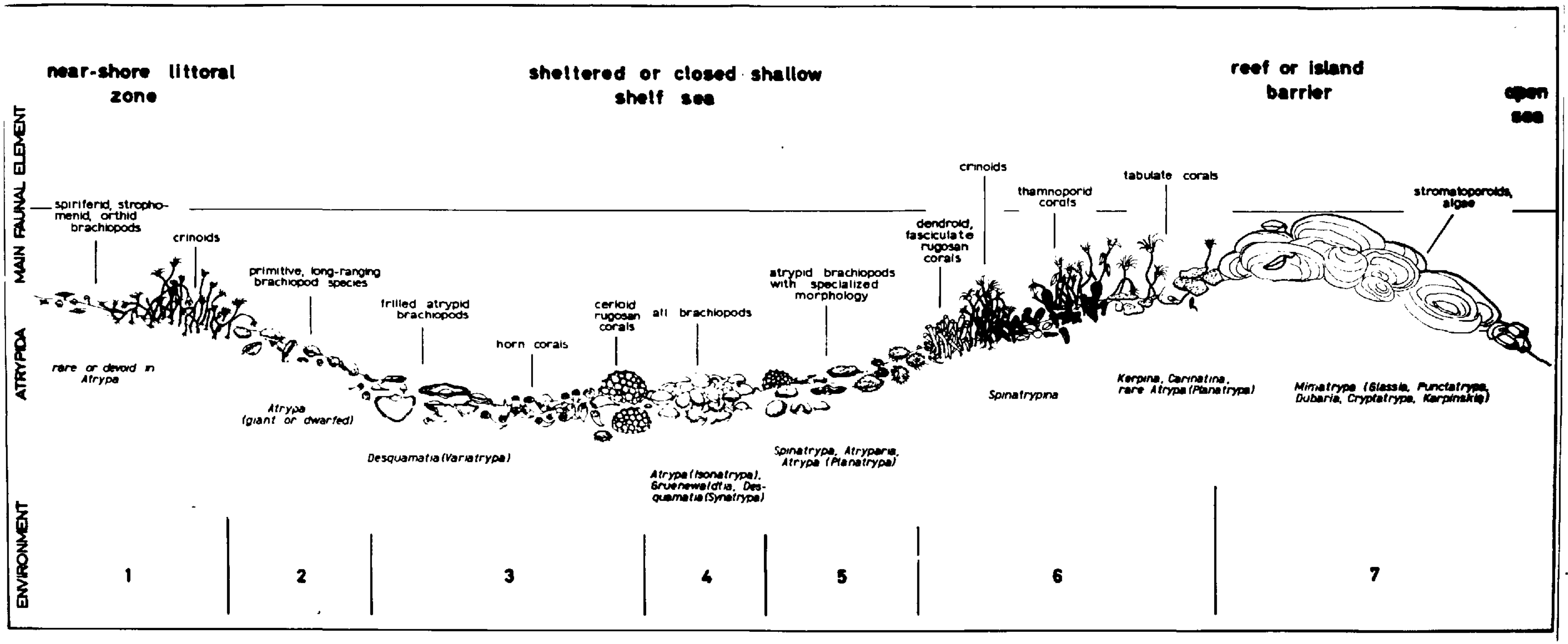
## Contents of the biotopes

Seven different atrypid brachiopod biotopes are recognized. These biotopes are best developed in the Eifel region of Germany, and particularly in the lower Middle Devonian sequence. It is doubtful if such biotopes can be distinguished in other groups of brachiopods in this area, because for many biotopes the atrypids are the only brachiopod faunal constituent. The next most abundant brachiopod in the Eifel region appears to be the athyrids, but their limited variability in external morphology do not make then well suited to differentiation. A summary of the main biotopes follows:

(1) Zone of facies-tolerant spiriferids, stropheodontids, orthids, rhynchonellids, athyrids and meristellids. Atrypids virtually absent, usually primitive.
(2) Zone of primitive atrypids, chiefly Atrypa.
(3) Zone of Atrypa, plus frilled atrypids like Desquamatia.
(4) Zone with multispecific, variegate atrypids, mostly biconvex, including Atrypa (Isonatrypa), Gruenewaldtia, Desquamatia.
(5) Zone of specialized atrypids Atrypa (Planatrypa), Spinatrypa, Desquamatia (last two spinose and frilled).
(6) Zone of atrypids associated with fasciculate, tabulate corals, e.g. Spinatrypina, Kerpina, Carinatina.
(7) Zone of bank-reef atrypids Mimatrypa, Carinatina (introduction of 'hercynian' atrypids, Glassia, Punctatrypa, Karpinskia, Vagrania, not present in the Eifel).

There is an increase in faunal complexity from the first to the last type of biotope. Bathymetric scales are hypothetical, but biotopes 3 and 5 probably are deepest water, although unlikely more than 60 meters. Biotope 1 may wholly or partially coincide with that usually called 'rhenish' facies, and biotope 7 may include large portions of the 'hercynian' facies.

Text-fig.9


near-shore littoral zone
sheltered or closed shallow shelf sea
reef or island barrier
open sea
MAIN FAUNAL ELEMENT
ATRYPIDA
ENVIRONMENT
spiriferid, strophomenid, orthid brachiopods
crinoids
primitive, long-ranging brachiopod species
frilled atrypid brachiopods
horn corals
cerioid rugosan corals
all brachiopods
atrypid brachiopods with specialized morphology
dendroid, fasciculate rugosan corals
crinoids
thamnoporid corals
tabulate corals
stromatoporoids, algae
rare or devoid in Atrypa
Atrypa (giant or dwarfed)
Desquamatia (Variatrypa)
Atrypa (Isonatrypa), Gruenewaldtia, Desquamatia (Synatrypa)
Spinatrypa, Atryparia, Atrypa (Planatrypa)
Spinatrypina
Kerpina, Carinatina, rare Atrypa (Planatrypa)
Mimatrypa (Glassia, Punctatrypa, Dubaria, Cryptatrypa, Karpinskia)
1
2
3
4
5
6
7

### (1) Zone of rare atrypids.

This biotope is similar to the one pictured by STRUVE (1961, p. 95) as 'kalk-arme, sandig-tonige Fazies' and may also partly contain the so-called '*Globithyris*' facies of BOUCOT (1963). The clay-silt-sand conditions which prevailed were unsuited to atrypid life. Small to medium-sized specimens do occur but abundant shell concentrations are very rare. Many specimens are preserved as casts or moulds in sandstones. Spiriferids, strophomenids, orthids, and rhynchonellids are, on the contrary, quite common and may locally be abundant. Worm tubes, trails, fucoidal markings, and other trace fossils are abundant. Plant remains reach sporadic distribution; many are preserved as carbonaceous impressions. Fossils often are bored or damaged after death (see JUX 1965). Pelecypods, and gastropods are dominant elements locally. This biotope probably was very near-shore, littoral or even intertidal, and may be compared to the littoral deposits of the North Sea to-day. Brachiopods and pelecypods possibly inhabited sheltered coves among sand-spits and sand bars or else may have lived in near-shore stream-channels. Brackish water pollution, strong tidal and wave disturbance were probably typical. Some sub-aerial erosion may have occurred when such environments were disturbed. Currents were probably sporadic, intermittent and irregular. On- and long-shore winds may have distributed some faunas. Faunas tend to be localized, monospecific and probably preferred muddy rather than sandy embayments. Lumachelles are not sedimentary features. Crinoid thickets appear to have thrived locally and may have protected or sheltered brachiopod patches in a similar manner to that in which seaweed tends to dampen or reduce onshore currents to-day. These brachiopods did not inhabit the crinoid patches themselves, but probably lived behind them, nearer shore. The Heisdorf beds of the Eifel region (Emsian, Lower Devonian) are characteristic of such environments.

### (2) Zone of 'primitive' atrypids.

In a type of biotope which frequently developed shortly after a period of sand-silt deposition, atrypids became locally abundant for the first time. Their morphology and affinity tended to be 'primitive', i.e. species belong to rather long-ranging, facies-tolerant atrypid genera. *Atrypa* prevails : some species may be very large in size, others small and consistently of the same size at many localities. The very large variety, such as *Atrypa* sp. in the Wolfenbach horizon, Lauch beds (lower Eifelian), are usually accompanied by a few immature specimens. Specimens less than 10 mm in width may even be absent. Similarly, other areas are marked by abundant dwarfed specimens (not merely stunted in growth). The latter are typical in the Bildstock horizon of the Ahrdorf beds (middle Eifelian). The first few corals also share this biotope. Small, ball-like *Alveolites* seem to be associated with some of the atrypids, a few growing around their shells. In the lower Eifelian a very common spiriferid associated with *Atrypa* is the giant (up to 50 or 60 mm wide) Paraspirifer cultrijugatus which serves as an index fossil. Large Schizophoria are not uncommon. Horn corals tend to be very rare.

Few criteria point to periodic sub-aerial erosion, and the biotope was probably wholly marine, with little brackish water influence. Sedimentary structures such as ripple marks, cross-bedding, mud-cracks, as well as fucoidal trace fossils are relatively rare, but corals are still never abundant. The shales still contain considerable silt content and are interbedded with sandstones (minor) with a more frequent interfingering of thin limestone lenses, some with crinoidal debris. The peculiar local faunal distributions indicate some current sorting, probably very active locally. The water appears to have been rather muddy and still unfavourable for permanent coral colonies. However, the substrate may have been more compacted and settled than in the first biotope, and not as liable to rapid erosion and deposition. The Wolfenbach and Weilersbach horizons, and probably the Bildstock horizon, can be included in this type of biotope.

(3) Zone of frilled atrypids.

A sign of increasing faunal complexity is marked by the introduction of Desquamatia, accompanied by many short-frilled Atrypa (only in some localities). Spinatrypa is very rare. This zone may follow directly after biotope 1 (as in the Klausbach-Mussel horizons). Association with horn corals is characteristic and these corals may crowd out the brachiopods or else be in turn replaced. Apart from atrypids, brachiopods belonging to the spiriferid-rhynchonellid-orthid groups are rare. Calcareous muds form the substrate, and may contain traces of pyrite. Shales tend to be dark brown or dark gray in colour. Faunas are localized and inclined to be limited in the variety of species. Athyrid brachiopods, some rather large, are fairly abundant. Gypidula is common in thin limestone bands.

The local abundance of pyrite, the dark colour of the shales and the lack of evidence for shell transport suggests deeper, quieter water, possibly somewhat stagnant water. The muddy bottom may have been interrupted by local mounds of colonial corals such as Hexagonaria, or else by mounds of algal or stromatoporoid origin. These hummocky ridges may have served as current guides or barriers. Possibly a comparison to the recent 'nigger head' mounds in sheltered areas or lagoons of reefs may be drawn (see STORR, 1964, p. ). It is possible that the faunas inhabited local depressions or channels on the sea floor. Some sort of faunal shelter is likely because many brachiopods are concentrated locally near more coral rich localities. The Klausbach and Mussel, Flesten and Schleit horizons may be drawn as examples. This zone may contain in part or in whole the "Rübenriff" zone of WEDEKIND & TRIPP (1930, p. 299).

(4) Variegated atrypid zone.

At several different horizons in the Eifel area sediments dominated by a rich and multispecific brachiopod fauna are found. The most typical development of this biotope occurs in the Junkerberg beds of the middle Eifelian, in the Eifel area. In the Eifel sea lane there appear to have been two separate environments, one dominated by atrypids, the other almost devoid of atrypids, yet both probably belonging to a similar type of biotope. To the north and west of the Eifel synclines, spiriferids, schellwienellids, orthids and productids were important elements and to the south, atrypids were richly developed and include the genera Atrypa (Isonatrypa), Gruenewaldtia, Desquamatia. These atrypids appear to have been gregarious or colonial, but their distribution is not merely localized. Rich beds are traceable over distances of several kilometers. Not only the biconvexity is typical, but the homoeomorphic atrypids Gruenewaldtia latilinguis (SCHNUR) and Desquamatia subditiva COPPER have orthocline beaks and prominent areas, probably indicating continuous, up to late ontogenetic attachment by the pedicle. Frilled atrypids virtually do not occur and the species with tendencies towards frill development appear to have only shortened frills. The biconvex atrypids would have been unstable unless partially buried in the mud. Complete ontogenetic series are present, and populations plotted show regular bell-shaped frequency curves indicative of little sorting.

Burial of brachiopod colonies in mud eddies or slumped muddy slopes may have been possible. The pedicles probably were not ideal for attachment to a muddy bottom and this may account for the gregarious nature of many specimens. Corals are relatively rare in this zone and firm surfaces for attachment may have been missing. Many brachiopods may simply have been attached to each other, settling on dead or even live compatriots. In the Eifel only the late Junkerberg, partly also Freilingen beds can be grouped in this zone. There are marked gradations with the brachiopod-rich faunas of the Schleit and Flesten horizons, and the latter may in part also be assigned here.

One of the interesting aspects of the atrypid brachiopods is the consistency of convexity. Planate, frilled and spinose atrypids are absent. MENARD & BOUCOT (1951), in a paper on shell movement in water, appear to have found that the more spherical recent terebratuloid brachiopods of the east American coast tended to grow in faster currents. The attached nature, and biconvexity of the atrypids of this biotope may have had a similar environment, suggestive of faster currents.

The northern Eifel synclines, mentioned above, had a rich brachiopod environment at nearly the same time as that of the Hönselberg horizon to the south. But these faunas have almost nothing in common and correlation has been very difficult. A partition of the Eifel sea lane at this time has been suggested by several authors, including WOLFART 1961 and COPPER 1965b. STRUVE (1961, fig. 7) has suggested that the faunal partition was due to an area of uplift called the "Krömmelbeinische Struktur". This crustal arch appears to have had some effect on younger sediments as well, although it was flooded and raised several times.

(5) *Zone of specialized atrypids*.

A peculiar atrypid biota typical of numerous late Eifelian and early Givetian horizons contains several mutually exclusive atrypid genera, which nevertheless probably occupied a very similar ecological niche. This niche is typified by *Spinatrypa*, *Atryparia*, *Atrypa* (*Planatrypa*) and sometimes also *Desquamatia*, genera which appear to have developed a striking specialized morphology which made them locally so successful as to crowd out all competitors. The chief morphological characteristics are strong beak incurvature or appression, lack of areas, growth of coarse ribs, and an external cover of spines, and frills or alternatively planate pedicle valves. It appears to be only in this environment that any of the above genera really become prolific. They are more sparsely distributed in the multispecific brachiopod zone and are rare with horn corals. The horn corals are, however, often scattered through this biotope. Exceptionally, this particular biotope may also be present in the midst of biotope 6 (see below), where local bare, muddy patches occurred. Large size is common, as in typical *Atrypa* (*Planatrypa*) *squamifera*, *Atryparia* spp.; but, small specimens also may become very abundant, examples of these including *Spinatrypa aspera*, *S. kelusiana*, *S. fasciplicata* and *S. globulina*. *Atrypa petasa* also tends to be small-sized. A large *Spinatrypa* is *S. curvirostra*. Locally some of these may complement each other, as is the case with the large *Atryparia instita* and small *Spinatrypa kelusiana*. *Spinatrypa* does not commonly appear to be associated with *Atrypa* (*Planatrypa*).

Rather soft, muddy bottom conditions appear to have prevailed - the specializations mentioned all appear to have functioned in their inimical ways to elevate themselves from a muddy substrate, and strikingly, not a single one appears to have been adapted towards pedicle attachment. The beaks are incurved and hide the pedicle openings. Frills, spines and planate pedicle valves may also have been more stable anchoring devices. The brachiopods (almost exclusively atrypoids) may have inhabited shelters protected by the adjacent crinoid, fasciculate coral thickets.

Locally there may have been very little movement of water, perhaps of stagnant, stale and nearly sterile bottom conditions. The spinous atrypids and also some (albeit few) of the strongly frilled forms are commonly associated with dark coloured argillaceous sediments, even dark gray or black shales. This correlation has been noticed previously. HERMANN SCHMIDT (1935, p. 143; 1938, p. 309) remarked on the relationship between the occurrence of spines and dark shales and believed that these were indicative of anaerobic, unoxygenated, rather sterile bottom conditions. This is elaborated on p. 80.

It has often been a problem to account for thick sequences of argillaceous sediments in near-reef areas. The detritus is unlikely to have been derived from the reefs. MAXWELL & MAIKLEM (1964), in a study of the source of muds in reefs along the Great Barrier Reef, obtained evidence that much of the muddy sediment was derived from streams and that the remainder may have had a loess origin. The muds of the Ahbach beds and other similar Givetian beds may have had a similar origin, though this is difficult to prove.

### (6) Coral thicket atrypids.

An environment, very rich almost solely in one generic group of atrypids is the striking thicket reef fauna so characteristic of the lower Givetian in Europe. This thicket reef biotope is composed of dendroid and fasciculate corals, small colonial tabulates of the thamnoporoid type and also some crinoids, and atrypid and a few athyrid brachiopods. Two somewhat different variations of this biotope are recognized : the Freilingen type and the Loogh type. These are grouped together because the faunal associations seem to have a number of features in common and probably are very similar physically as well as biologically. The brachiopods associated with these corals and crinoids show adaptions which point strongly to the idea that they were probably attached to the corals. These adaptations are mainly of a relatively large interarea, foramane and coarse, tubular ribs. The Loogh infra-biotope of fasciculate corals and thamnoporoid corals invariably contains a single atrypid genus, Spinatrypina. The dense network of corals probably provided an excellent harbour for small brachiopods of the Spinatrypina type. Many of these smallish Spinatrypina (width rarely greater than 30 mm ), are globose, equally biconvex and lack the rheotropic orientation of the Freilingen atrypids (see below). Faunas are few in species (since only one atrypid genus appears to thrive under these conditions), with atrypids dominant, and smooth, small, roundish to elongated athyrids next in abundance. Beaks are not twisted (or only rarely), interareas maintain a fairly constant size, although rib variation may sometimes be marked. There is no great deal of specimen crushing or deformation during growth. With changes in currents, these near-reefs thickets may have been effected by storm-created gaps in the reefs, may have been uprooted and scattered. Locally they may have been subject to wave action, perhaps from undertow. Lumachelles are common, and are marked by a phenomenon rare in the tightly shut shell of Atrypida, that is valves broken apart and current-sorted (Pl. B, figs. 1-2). These separated valves came to rest, concave side down. Many of the shells in this biotope are filled by a white, clear crystalline matrix instead of the muddy matrix which fills most of the atrypid shells that lived directly on the substrate of clay and mud. The lack of a

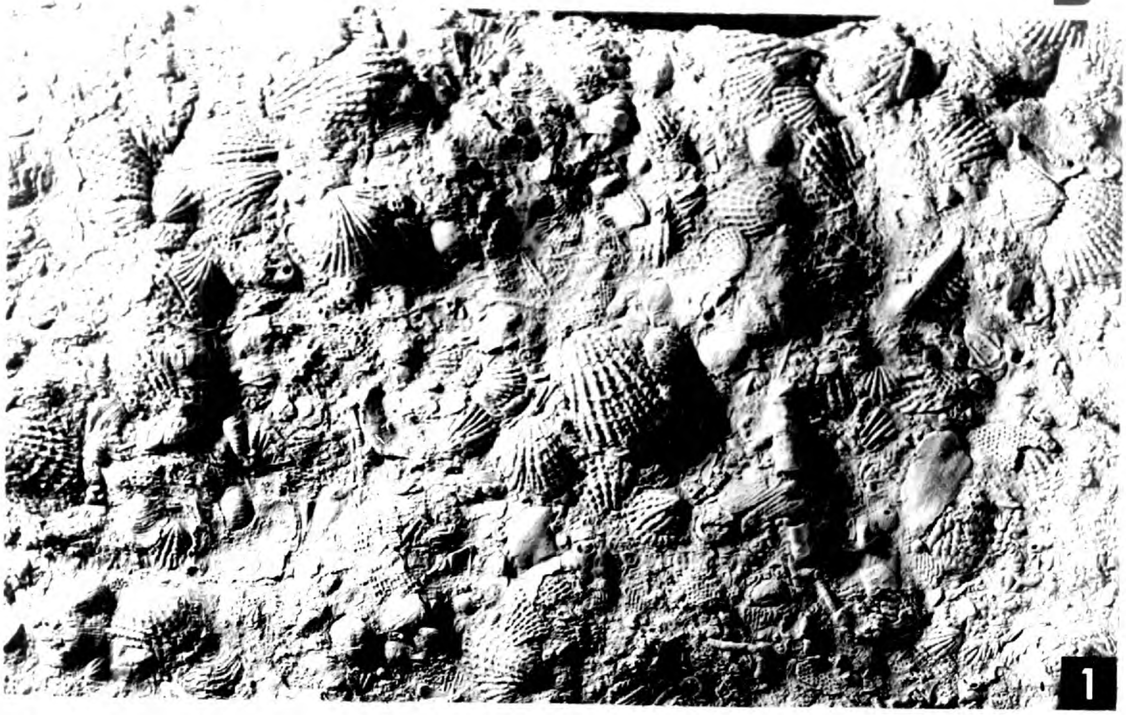
# PLATE B

Figs. 1-2. A single 3.5 cm thick limestone slab with current washed shells (nearly all single, separated valves) of *Spinatrypina wotanica* (STRUVE 1964). x1.

*1*. Upper side of the slab with single valves oriented concave side down. The nearly circular outline of the valves has precluded rheotropic orientation of the planes of symmetry. The matrix consists of *Fenestella*-like bryozoans, crinoid ossicles and small athyrid brachiopods fixed in a bioclastic argillaceous limestone.

*2*. Bottom side of the same slab.

B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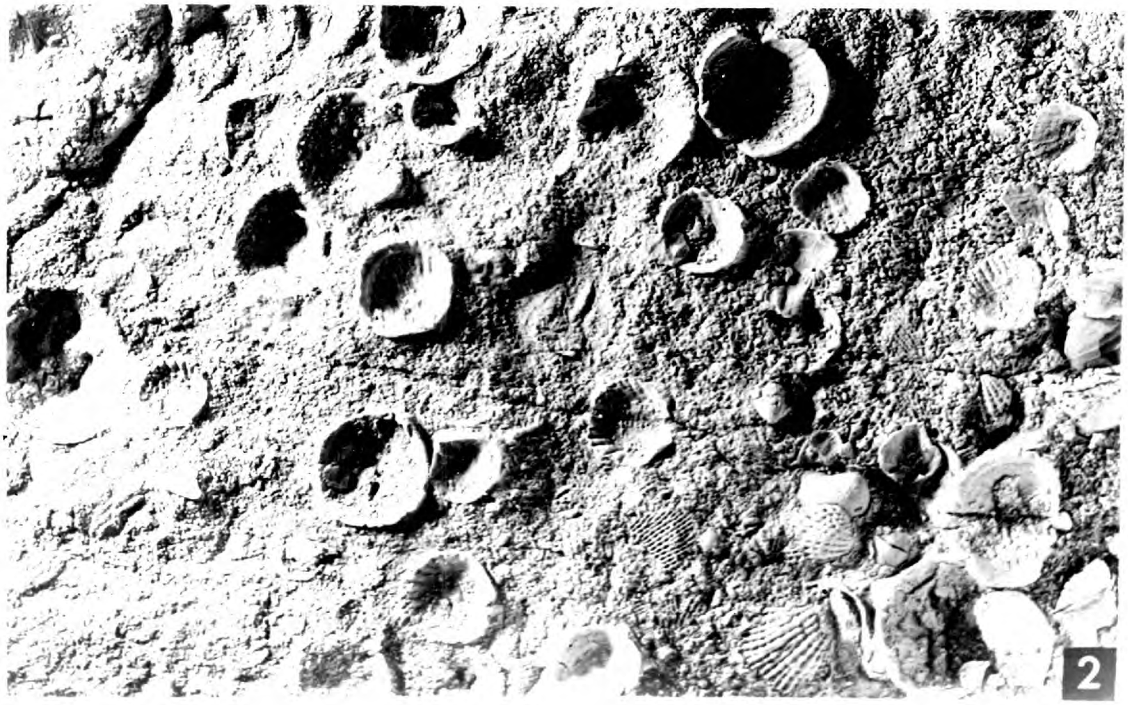

2

mud-infilling (not noticeable in other atrypids!) appears to be contributory evidence of the mode of life of these atrypids, a mode of attachment above the muddy bottom on a host, preferably a coral and usually the coral *Thamnopora*. These atrypids are not found with the tabulate coral, *Amphipora*, which resembles *Thamnopora* in size and shape. A few of the cynlindrical rugose corals in the Rech horizon (lower Givetian) had *Spinatrypina* imbedded in their calices. In a quarry near Rohr which yielded a lower Givetian fauna, mostly of intertwined and intergrown tabulates, horn corals and auloporids, *Spinatrypina* is ocassionally found, well-preserved, in the crevices of auloporid-alveolitid coral masses.

The wave-washed or current washed lumachelles mentioned above are not life assemblages. But, rich, probably 'washed' populations were found at some localities (e.g. Rechert horizon, Rohr syncline) and these localities yielded faunas which showed a complete size range from smallest to largest, and normal ratios. The thickest coral hosts may have prevented a great deal of distribution and the dead shells may also simply have been washed backwards and forwards, yet in situ. The process may be compared to the 'panning' method used in gold extraction.

The actual bathymetric location of the *Spinatrypina* beds is probably very shallow, less than 10 m deep water. A recent study of the Miocene-Pliocene coral thickets of Wairarapa in New Zealand (SQUIRES, 1964) has demonstrated an evolution of coral growths of *Lophelia* from colony thicket to bank which reflects the observed field relationships of the Givetian thicket reefs of the Eifel and Bergisches Land. Inside the New Zealand thickets molluscs are abundant and, "*Lima* sp. and the Brachiopod *Tegulorhynchia* *nigricans* are found in association with the coral and are not apparently found outside the thickets" (SQUIRES, 1964, p. 911). This rhynchonellid brachiopod is homoeomorphic with *Spinatrypina* (see below). SQUIRES cited a coral thicket temperature range of 6 to 10 degrees Cent. (relatively cold), strong currents, temperature stratification in the base of the thermocline and depths ranging from 1500-2500 meters (Hinakura thicket) and 400-600 meters (Lake Ferry thicket). SQUIRES stated that ecological conditions required for deep and shallow water structures are different. He specified that the criteria for ahermatypic corals are dendriform growth (relative absence of bank reefs), and general isolation of colonies, the absence of destructive agents, the slow rate of coral growth, and the relatively small portion of coral constituent and greater portion of fine sediment in the thicket reefs. The astonishing feature of SQUIRES' study is the depth at which these corals live. If the criteria are accepted and rigorously applied to Devonian thicket reefs, it would mean drastic changes in the environments postulated. Four of the criteria apply readily to the Devonian thickets, another (rate of coral growth) is difficult to establish. The chief drawback appears to lie in the absence of destructive agents which appear to have had some effect on Devonian thickets, otherwise comparison with the New Zealand thickets is nearly perfect.

CHAPMAN & CRESPIN (1923) made a study of the Tegulorhynchia nigricans species-group mentioned above in the coral thickets, and their figures show that the comparison to the Devonian Spinatrypina is remarkable. Rib structure, size, foramen and interarea are very similar. The species T. doederleini (DAVIDSON) also has spines. CHAPMAN & CRESPIN (1923, p. 190) concluded that the majority of Tegulorhynchia were "inhabitants of shallow to moderately deep water, probably ranging from shore line to several hundred fathoms". Deep water forms tended to be slightly thinner in build (ibid., p. 180).

The second infrabiotope is that of the Freilingen beds, and which may also be applied in part to the Frasnian Refrath beds of the Bensberg area. It marks the introduction into the Eifel area of strongly rheotropic brachiopods and also some traces of what may be hercynian faunal elements. The genera Kerpina and Carinatina are typical of the Freilingen beds. In the Frasnian, the place of these two appears to have been taken by a flat species of Spinatrypina, S. explanata (SCHLOTHEIM). Kerpina shows a noteworthy association with the small platy tabulate coral Alveolites and commonly moulded its shell to the surface of this coral (Pl. 38, fig. 5; Pl. 39, figs. 1-3) not vice versa. Twisting (not incurvature!) of the beak up to procline, excessive enlargement of the interarea, deformation of growth with geniculation and planations of the shell, all point to marked modifications of attachment. Kerpina appears to have had an obligate life cycle with its major host Alveolites. Kerpina is strongly homoeomorphic with another brachiopod Davidsonia (a genus placed in the Koninckinidae, a group of brachiopods of obscure origin sometimes designated as atrypids). Davidsonia is a cemented brachiopod which commonly also selected Alveolites as its host (STRUVE, 1964). Carinatina, a planate atrypid brachiopod which resembles spiriferids, but does not show the active morphological conformity and variation of Kerpina, is equally peculiar in that it is almost excessively flat (width/depth ratios are greater than 4:1). It has a wide, broad interarea and a carinate ridge. Carinatina probably lived free from hosts, although it may have been attached to elevated surfaces by its pedicle. Its hydrodynamic shape may have particularly suited elevation in a strong current (refer to Pl 57).

Other atrypid species groups, which probably were not native to this environment, but made morphological alterations to fit in are Spinatrypa aspera meridiana, Desquamatia iunctura and Atryparia stabilia. Each of these seems to have developed coarser, more deep-troughed ribs than normal. All three seem to have had functional pedicles, including Atryparia which almost consistently shows foraminal enlargement which does not appear to be caused by fracture. Each has developed characters which generally are not typical of the genus. For example, Atryparia tends to have a planate pedicle valve, Spinatrypa deeper ribs and a planate shell with a small area, Desquamatia lacks frills. These special variations cause some confusion in identification. Nevertheless the Freilingen beds mark a rare occasion when atrypids of many species-groups showed remarkable concurrence. The "Mühlwäldchen Mergel" of the Gerolstein syncline possibly shared ecological conditions.

The inferred invironment is that of well-aerated rather shallow marine waters with localized concentrations of corals, crinoids and brachiopods. The indigenous atrypids are adapted to an attached mode of life. The Thamnopora-dendroid coral subdivision of this biotope contains few faunal elements but the tabulate coral environment contains as many as 6 to 8 atrypid genera, usually not all in one population. Currents were probably strongly laminar, perhaps affected by waves sweeping over long stretches of partially exposed bank reefs and surging back towards their ocean source. The biotope probably well behind the reef-front, was sheltered from the worst turbulence. Argillaceous content of the limestones is already much lower in the tabulate zone than in the dendroid coral zone. Some shelter may have been given by large patches of crinoid growth. Depth was shallow, and probably less than 10 m.

### (7) Bank reef zone.

The mass reef environment, consisting of thick, pure limestones in Europe at Torquay, Devon and in Germany at Iserlohn, Frettertal and Waldgirmes, is typical of the upper Givetian of this area. Such reefs may reach a length of 100 kms and a thickness of up to 800 m in the German Devonian. Atrypida are scarce and are found only at a few localities, as at those above. Rich collections are found only occasionally. Monotypic faunas are characteristic. Comments about 'nest-like' concentrations of brachiopods were made by HOLZAPFEL (1908, pp. 113-114) when he was describing the Fretter Massenkalk faunas. The host sediment is pure limestone, frequently bioclastic but also cryptocrystalline. Whitish and pinkish colours for the massive, resistant weathering units make them readily indentifiable in the field. Bedding is poor. Dolomitization, in masses or even small patches, is common. Atrypids tend to be sorted out into two kinds : (1) very small, less than 15 mm wide, globose, rather smooth shells (Cryptatrypa, Punctatrypa, Glassia, Dubaria) which are hercynian elements and are not described in this study, and (2) large, up to 60 mm , variform atrypids such as Mimatrypa, Carinatina and Karpinskia. The latter is a Lower Devonian guide fossil and is absent in northwestern Europe. There is a tendency towards a loss of spiralia, which can partly be attributed to a phylogenetic rather than ecological cause. Frilled Atrypa (a good specimen is figured in WHIDBORNE, 1893, Pl. 13, fig. 10) are, surprisingly, not uncommon, although shell heaps of these forms are uncommon. Specimens of Atrypa tend to be isolated, rare occurrences. It is possible that some of these apparently delicate frilled Atrypa (found in very coarse matrices) were inhabitants of underwater caves, sheltered and surf-scour free. Caves are common morphological features in fore-reef areas, and such caves often yield delicate bryozoans and corals (STORR, p. 21). Atrypids are very rare in areas which have massive, laminar to pillow-like build-ups of stromatoporoids, some of which are bituminous and dark gray in colour. On the other hand, the non-stratified, light-coloured, coarsely crystalline zones are not uncommonly source beds for atrypid collections.

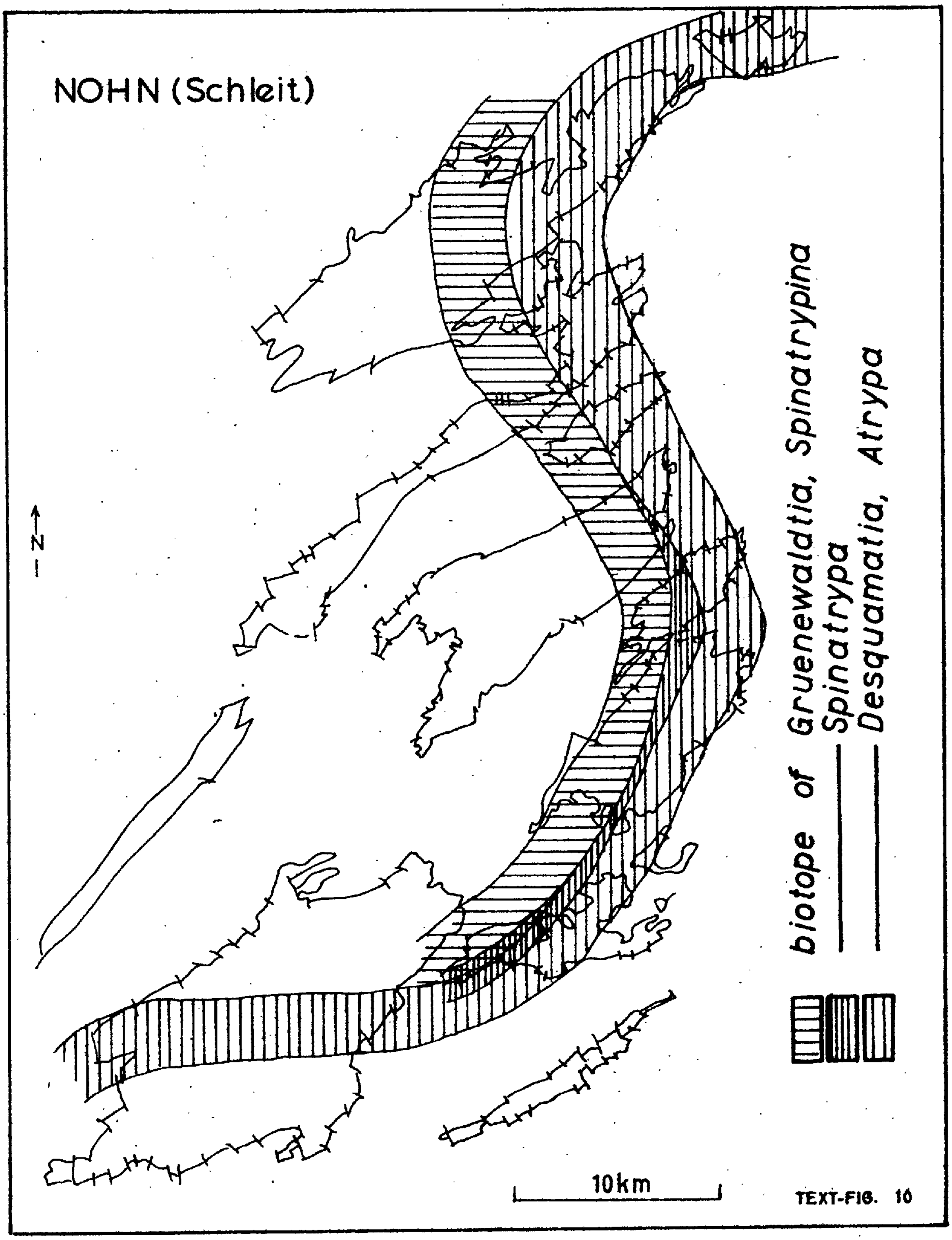
The biotope is probably close to being in the high-energy, turbulent zone which can be classified as fore-reef. The strong currents and waves appear to have caused the faunas to seek out more sheltered hollows in the reefs, and concentration in nests, crevices or caves resulted. Concentration by waves is possible but most nest-like faunas contain undamaged specimens of many sizes which would not be expected in wave-sorted zones. Intermittent sub-aerial erosion is feasible. Ammonoids are locally very rich for the first time.

## Distribution of the biotopes

The distribution of marine organisms is more or less predetermined by their tolerance to physical and biological factors. Outside certain sea limits, their mortality rate becomes very high. Once it can be determined that faunas collect at certain localities and that they show a high degree of specialization to particular sediments and fossil associations, it should also be possible to plot such faunas geograpically. An attempt was made for selected time intervals in the Eifel region of synnlines to plot the individual distribution of genera. The bio-facies maps in text-figs. 10-14 resulted.

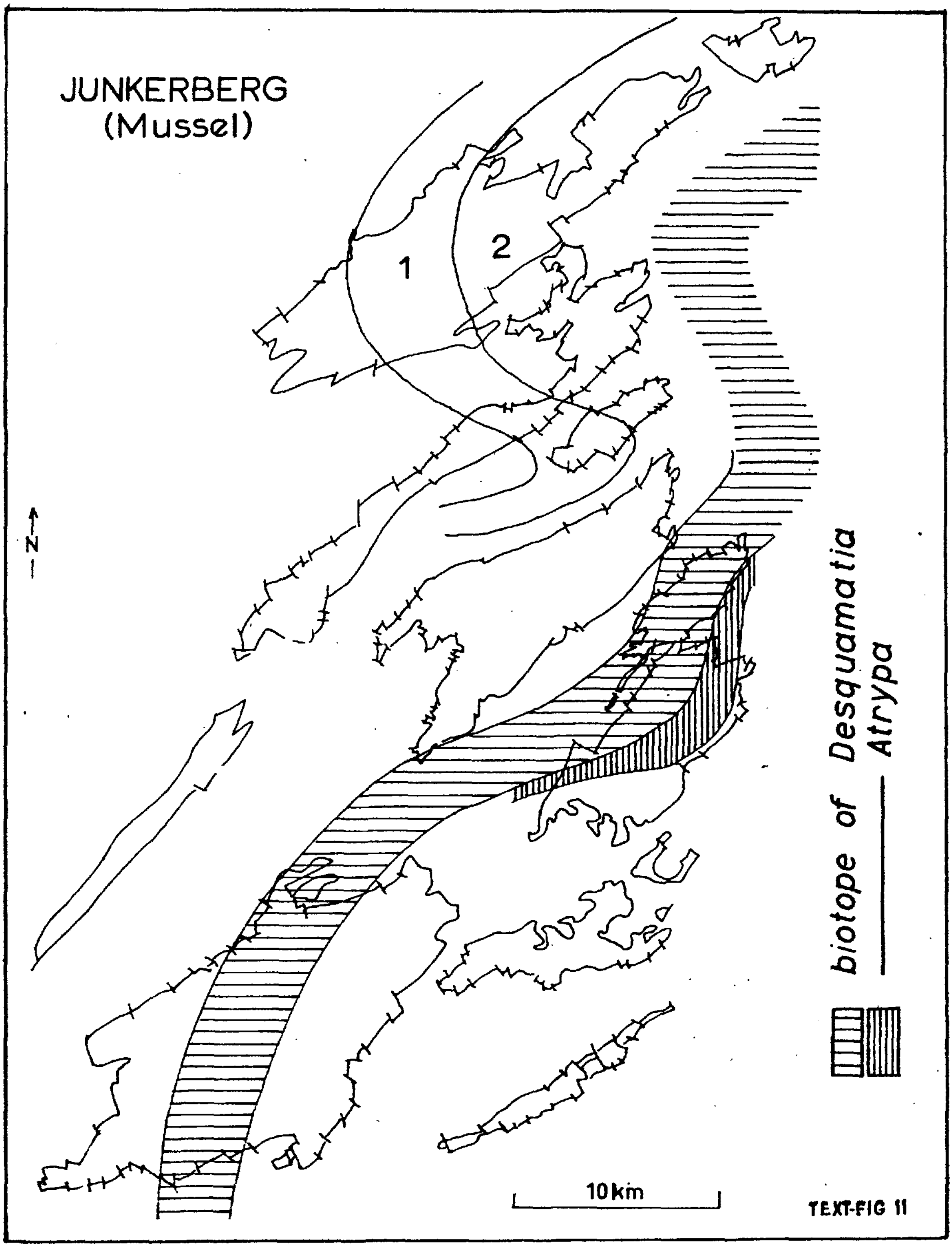
In the Eifel area and east of the Rhine, the abundance ot the atrypid brachiopods and their range through a number of biofacies in which other brachiopods are very scarce or even absent, makes them well suited for distribution pattern reconstructions. Their shells are relatively fixed to the substrate (there is no evidence that they may have been self-propelled by flapping their valves or by ejecting streams of water); they are classed as sessile benthos in contrast to vagarious benthos such as trilobites or worms. Many atrypids have lost their pedicle as a means of attachment, but substitute means of stability such as frills, spines or planate valves developed. Plotted as sessile benthos they probably quite accurately reflect facies patterns.

As stated previously most atrypid collections at single Eifel localities, appear to have been fair representatives of fossil communities. The criteria used for in situ populations were the presence of complete ontogenetic series in percentages nearly reflecting bell curves, lack of sedimentological evidence of current disturbance and lack of shell damage. In themselves these criteria probably are insufficient evidence to conclude that the collections represented biocoenoses, Text-figs. 10-14. Biotope patterns in the Eifel region during Middle Devonian time. Patterns are reconstructed from the known distribution of important, abundant and diagnostic atrypid genera. Isolated, rare occurences are disregarded. Fig. 11: 1, zone of spiriferids and schelwienellids. Schizophoria also abundant. Atrypids absent; 2, unfossiliferous limestones and shales. For distribution of individual species see the systematic descriptions.



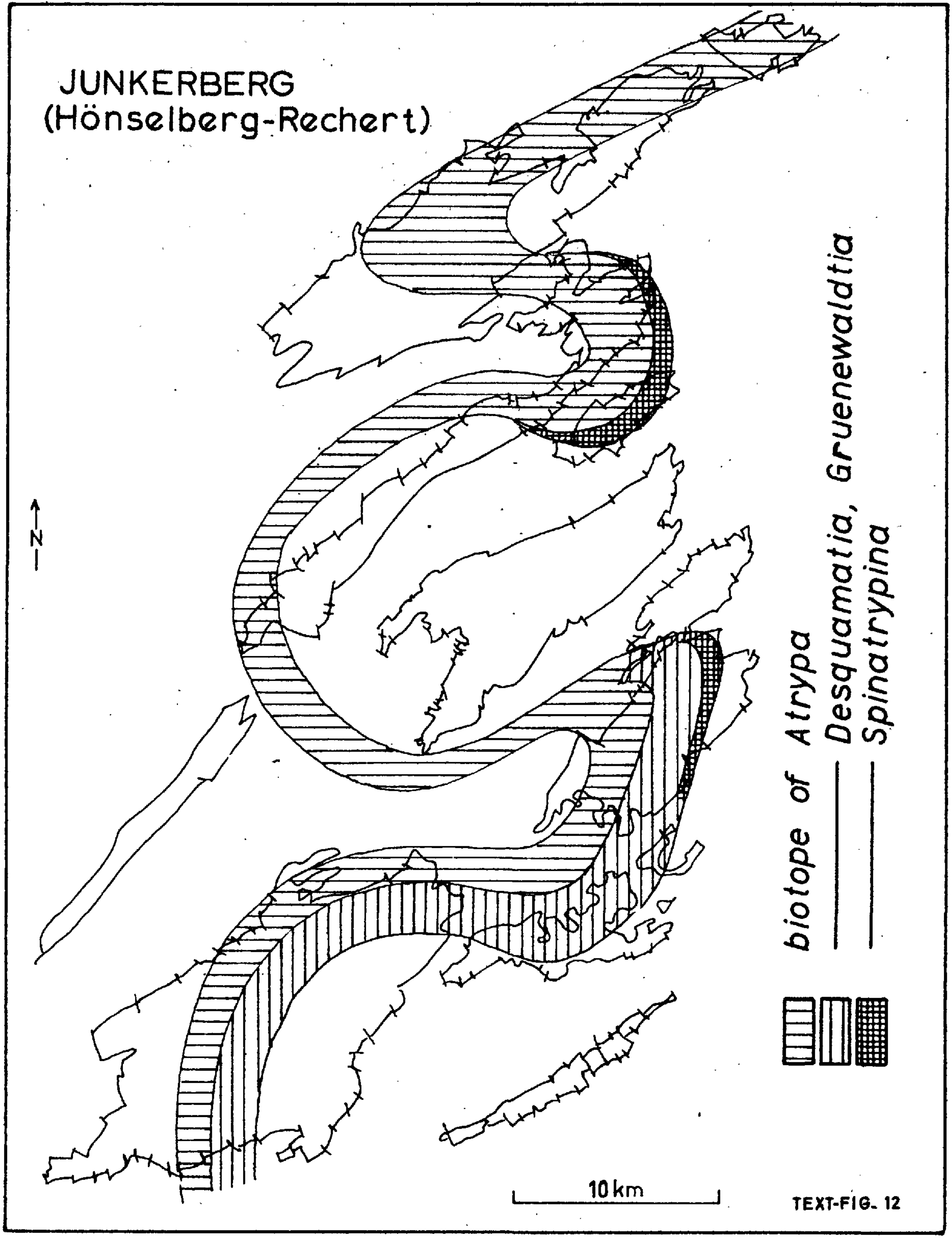
TEXT-FIG. 10

Biotope distributon in the Eifel region in Nohn (lower Eifelian) time.



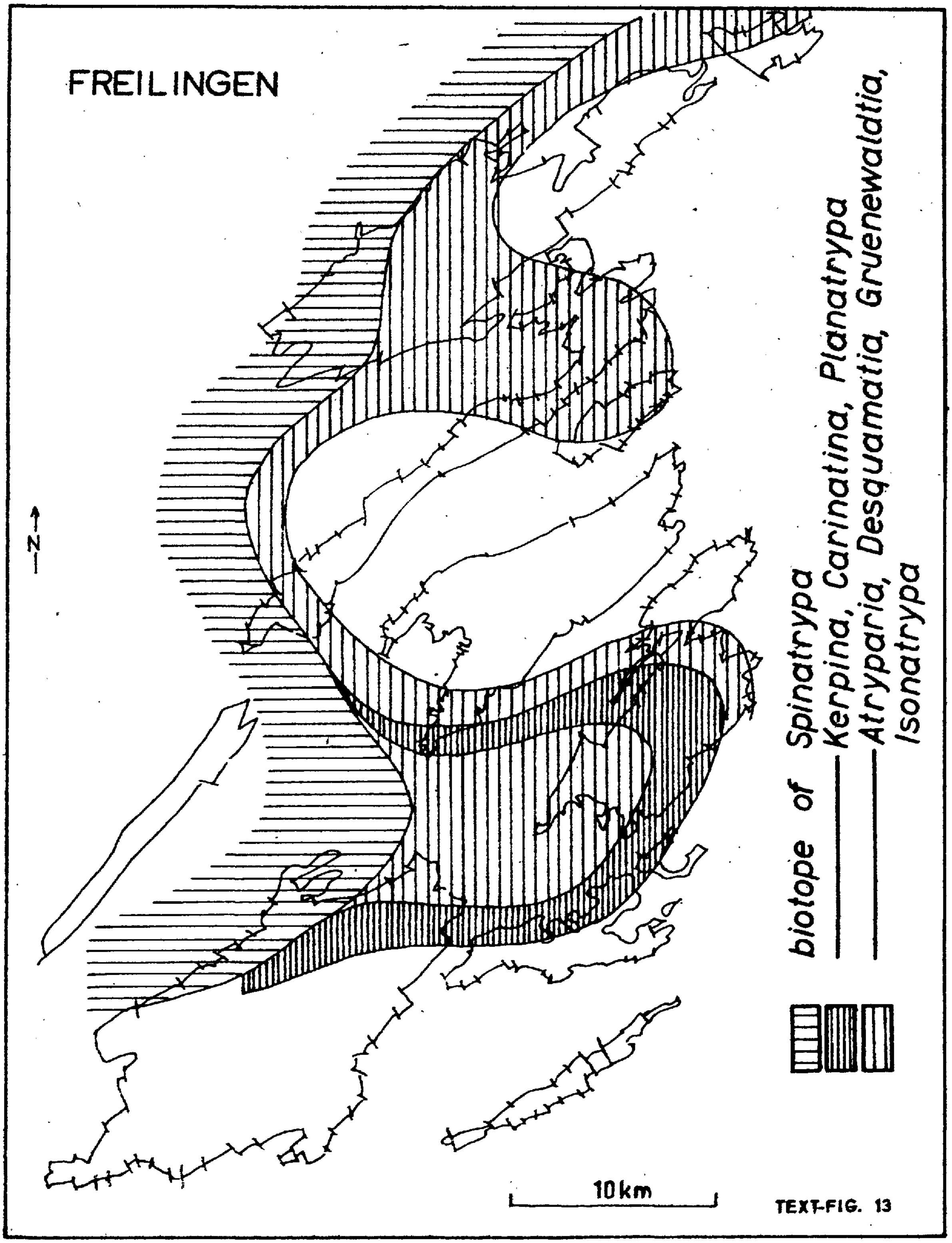
TEXT-FIG 11

Biotope distribution in the Eifel region in Junkerberg (middle Eifelian) time.



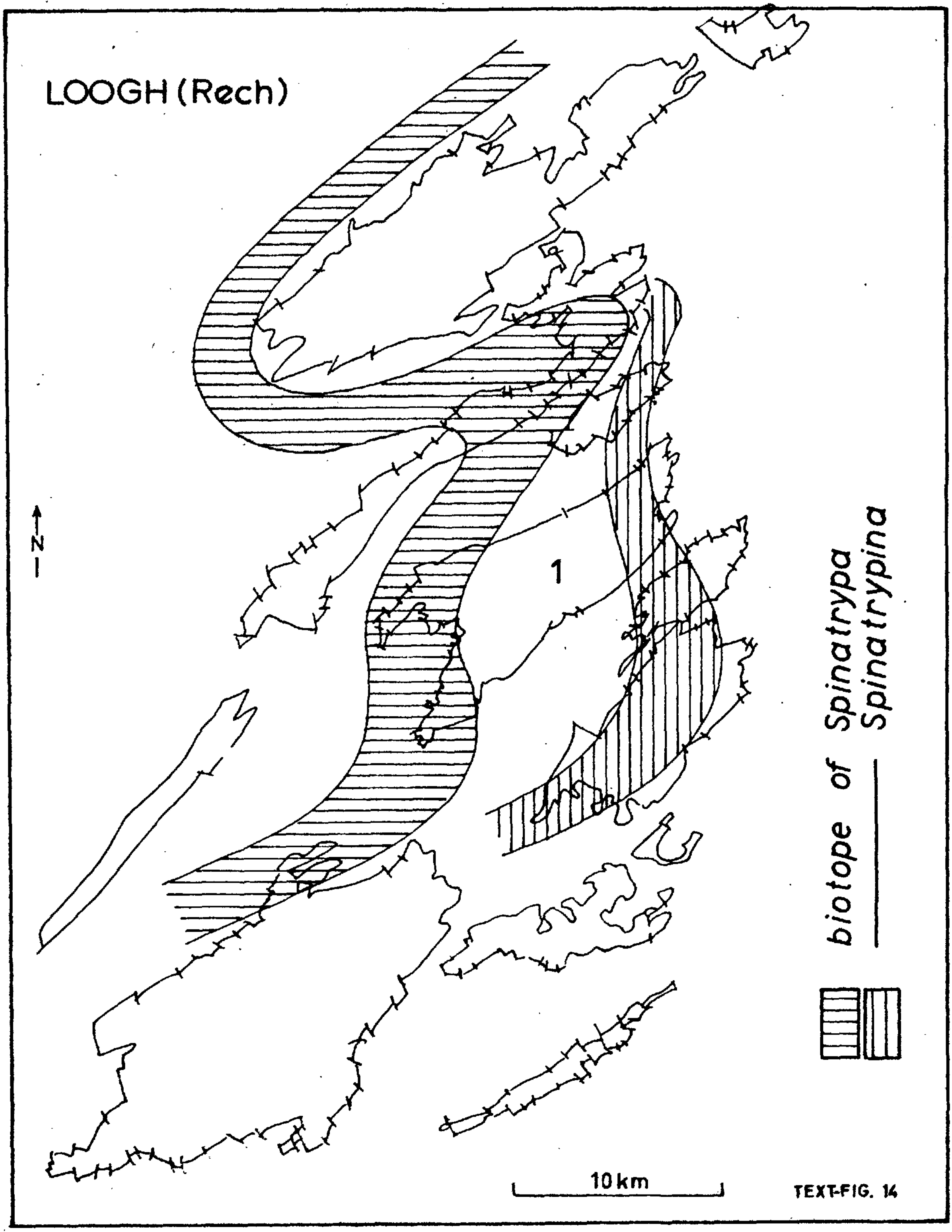
TEXT-FIG. 12

Biotope distribution in the Eifel region in Junkerberg (middle Eifelian) time.



TEXT-FIG. 13

Biotope distribution in the Eifel region in Freilingen (upper Eifelian) time.



TEXT-FIG. 14

Biotope distribution in the Eifel region during Loogh (lower Givetian) time.

rather than thanatocoenoses. The evidence is therefore largely negative. If numerous spearate valves were found, or valves of only one kind (dorsal or ventral), or only large valves, or whole shells oriented in parallel directions, the collection was taken as a current sorted one. Even the lack of damage may not point to undisturbed life assemblages, as MENARD & BOUCOT (1951) have shown. However, the fact that a population was current sorted probably had little effect on the final facies patterns plotted, since most of the biotopes are more than 1-2 km wide and currents do not seem to have spread over areas much wider than this (albeit that the longitudinal distribution may have been greater). In the Atrypida single pedicle valves are much more common than single brachial valves. The simple explanation is that the pedicle valve is usually thicker, reinforced with muscle callous, and also more planate and therefore less liable to crushing. Exceptionally, single brachial valves dominate : one of these exceptions occurred in the upper part of the Refrath beds (Frasnian). The Frasnian genus represented was Desquamatia: both valves are very thin, the shell dorsibiconvex, but the soft argillaceous limestones contain numerous separated brachial valves, in a position usually with concave side up. Loose ventral valves were rare. Brachial valves were (e.g. Spinatrypa fabaca n.sp.) also not uncommon in the Rechert horizon at Rohr.

Five different Eifelian and Givetian time intervals were selected for plotting : Schleit horizon (Nohn beds), Mussel horizon (Junkerberg beds), Hönselberg-Rechert horizon (Junkerberg beds), Eilenberg horizon and Rech horizon (Loogh beds) times. All but the last are in the Eifelian and only the Eifel region was selected for plotting. The biotopes probably ran parallel to shore-lines or to "Schwellen" on the ocean floor. Most of the biotopes are not wider than 5 km and ones narrower than 1 km do not have sufficiently numerous exposures to be worth plotting. The combined biofacies patterns are not much wider than 10 km , and this roughly is representative of the biotope cross-section shown in text-fig. 9. The biotope poor in atrypids (no. 1 in the scheme) may have been as wide as 30 or 40 km , but probably not more than that. The bank reef facies also is not fairly represented on the maps drawn, and in itself may have reached a width of up to 30 km (the Great Barrier Reef of the east coast of Australia may be much wider than this). The whole of the island Istaevonia (STRUVE 1961) may have been submerged and formed the axis around which massive reefs were built. Istaevonia does not appear to have contributed any sediment to the Eifel sea lane, and it may not even be necessary to postulate an island in its place.

The actual shoreline itself comes outside the study since it lacked atrypids. Erosional and shoreline morphology of the rhenish Devonian are treated by JUX in a number of fine papers (1963, 1964, 1965). The atrypid brachiopods also do not fall into the range of the "globithyrid" facies of BOUCOT (1963). Biotope no. 1, scarce in atrypids, may partly or wholly coincide with JUX's Hysterolites facies which was said to be accumulated in a "mostly calm, lagoonal environment" (JUX, 1965, p. 114), and which may be a sand bar-sand spit type of environment.

The exposures in the Eifel synclines are not known to show the complete, idealized facies scheme at any one time, and some of the information is vertical as well as horizontal or gergraphical. Vital links are sometimes missing because they are unfossiliferous or simply occur where there is no exposure. The schematic diagrams of text-figs. 10-14, were previously attempted in a similar fashion by STRUVE (Wotan time, 1961, p. 99; Rech time, 1963, p. 269; Giesdorf time, 1963, p. 267). The ones presented differ markedly in some aspects from those of STRUVE because there is no agreement on some of the critical correlations. The reconstruction of Giesdorf time by STRUVE (above), is incorrect because of invalid correlation of the Giesdorf with the Rohr horizon. The latter has been shown to be of Rechert age (COPPER 1965b) and is therefore younger than the Giesdorf horizon. Such changes in correlation can have drastic effects on palaeogeographical reconstructions.

IVANOVA (1962) made a summary of the chief biotic factors controlling brachiopod distribution : nature of the substrate, rate of sedimentation and hydrodynamic influence. IVANOVA thought that brachiopods were extremely sensitive to changes in salinity and this may have been so. But this cannot be measured in fossil populations and is not known to markedly affect the distribution of Recent brachiopods. IVANOVA, using this as a basis, divided brachiopods into euryhaline groups (highly tolerant) and stenohaline groups (restricted). How this can become a measurable criterion in brachiopod ecology and taxonomy is not specified. In the Eifel region, and also the rest of western Europe, it appears that the atrypid brachiopods were more influneced by the substrate, currents, and possibly temperature-depth controls.

DAY (1963, p. 34), writing about the effects of salinity in recent physical environments, stated that "major differences in salinity certainly limit distribution in faunas in estuaries and in the Baltic sea where the changes are very great, but in the open ocean, where the salinity range is less than 4 parts per thousand, the importance of salinity may be questioned"! The most important physical control listed by DAY is water temperature. The basic biotic controls were found by DAY to be trophic links, i.e. relationships of the organism to its basic plant food, to competing herbivores and to the carnivores which in turn fed upon them. Another interesting feature of DAY's research was that he found benthonic communities were far more complex than pelagic ones (ibid., p. 36). Speciation appeared to occur as a result of increasing complexity of the biotic environment alone! DAY's assumptions would account for many of the peculiarities of atrypid distribution.

No bathymetric scale was proposed. The deepest water may have been as much as 200 m (but more likely less than 50 m ) in the Eifel 'Mischfazies' zone and the shallowest probably was partially sub-aerial and intertidal. Relatively, the deepest atrypids may have been Spinatrypa, and the shallowest in the Mimatrypa group at the hercynian end and the primitive Atrypa at the rhenish end of the facies scale.

ELIAS (1937, fig. 3) identified a number of bathymetric zones in the Permian rocks of Kansas. The calcareous brachiopods, in ELIAS's scheme, occupied the 90 ft to 160 ft. depths (30 to 50 m ). ELIAS based these predictions on the work of SCHUCHERT (1911), who summarized the distribution of Recent Brachiopoda and calculations of the depth ranges showed that about 25% of Recent brachiopod species were collected at a depth of less than 50 m , and about 20% at depths between 50 and 150 m. That means that less than half of to-day's brachiopods live at a depth of less than 150 m (a figure which does not seem to agree with SCHUCHERT's calculations). Unfortunately the collecting depths may not always coincide with the actual site at which the brachiopods lived. WALTHER (1893, p. 347) misinterpreted DAVIDSON's statement that the recent Terebratulina septentrionalis lived in clear water, to mean in non-saline fresh water. Brachiopods are marine organisms. It is thought that the depths occupied by most European atrypids may have been considerably less than those expected by ELIAS (i.e. less than 30-50 m ).

The depth quoted by SCOTT (1940) for mud-flat (not tidal flat) environment which accommodated shallow, intermittent and widespread seas, was from low tide to 5-7 fathoms (about 10-15 m ). Such a depth may have been more realistic for the bulk of atrypid biotopes. SCOTT (1940, p. 299) remarked that "ammonoids do not occur in littoral, mud flat or reef deposits". The atrypids, which are found in such sediments, also are hardly ever accompanied by ammonoids.

This phenomenon of distribution, atrypids and ammonoids mutually excluded, is overlooked in Devonian faunal studies. Applying ammonoid zonations to rocks which do not contain them is impractical. HOUSE & PEDDER (1963, p. 503) reached the remarkable conclusion in their correlations of the Devonian of western Canada, that in the coral and brachiopod rich Hume Formation "surprisingly ammonoids have not been found". There is nothing surprising about such distribution. They are also very rare in the Eifel region.

The atrypid distribution in the Eifel clearly shows that the environmental tolerance of individual genera was rather narrow. The time intervals selected are arbitrary and depended on the more ideal brachiopod horizons. These selected time intervals were interrupted by several transgressions and regressions of the biofacies (see COPPER 1965c), but nevertheless show a gradual increase in faunal complexity up to Freilingen time and then a rapid retreat into monospecific or bispecific atrypid faunas. This increase in faunal complexity may have caused an increase in narrow adaptations and multiplication of new species.

In Nohn time (text-fig. 10) the arrangement of the biotopes suggests that deeper marine conditions are do be found to the east and southeast and that the shore line existed to the west. The Istaevonian high probably did not exist at that time, and fringe reefs are more likely to be found to the west. The biotope is in a very loose S-shape and is located on the eastern margins of the Eifel sigmoid.

The Mussel biotopes are restricted to the southern part of the sigmoid : their absence to the north is notable (text-fig. 11). Their presence to the north-east, outside the area of exposure, is postulated.

By Hönselberg time (text-fig. 12) the biotopes make a number of snake-like curves across the synclines and are also present on the western parts of the sigmoid. The 'Rasenriff' environment carrying Spinatrypina is only developed in the Rohr and Hillesheim synclines.

The Freilingen beds mark the most advanced stage of biotopes in the Eifel region. Spinatrypa is concentrated on the western margins, probably also marking the deepest marine channel. The Istaevonian 'Schwelle', although not contributing any sediment, may have caused a slope of shallow to deep from east to west which is opposite to that suggested for Nohn time. Faunal complexity was at its height (text-fig. 13).

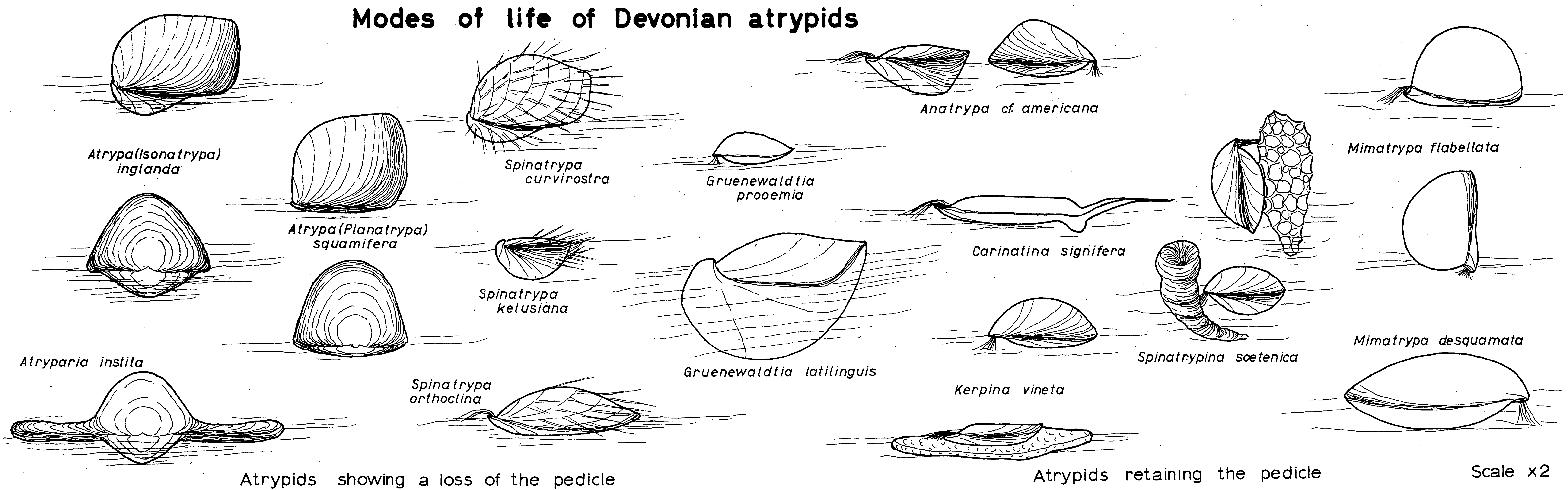
The Givetian, introduced by the Loogh beds, is richly fossiliferous but a number of previously abundant atrypid genera have vanished. Only Spinatrypa and Spinatrypina survive (text-fig. 14). At this time there was a migration of the atrypid biotopes from the southern to northern synclines. During the Eifelian only the area to the north was sparsely fossiliferous, to the south faunas were rich. The Givetian marks a near absence of faunas to the south and rich faunas to the north.

## Adaptation and mode of life

In each of the above mentioned biotopes different species of the same or different genera were adapted to their environment in individualistic, specialized ways. In one species it seems likely not only that there was a change in mode of life during ontogeny, but that different adult members of the one species may have had differing modes of life in the same environment (refer to Kerpina vineta).

The first paper dealing with the life habits of the Atrypida is the classical work of FENTON & FENTON (1932b). The FENTONs inferred that young atrypids were attached by means of a pedicle, and were positioned

TEXT-FIG. 15



Modes of life of Devonian atrypids

with their pedicle valve up, and that in adult atrypids the pedicle became non-functional with the shell coming to rest in a position with the pedicle valve down. This life position, although probably the most common in the Atrypida, has been applied rigorously to all atrypids whatever shape or sculpture.

A second paper by FENTON & FENTON (1932c) stated that most if not all atrypids were characterized by alate lamellae; that spines were constrictions of lamellae and that spinescence was a convergent character traceable in independent lineages. Furthermore, the FENTONs said that frills gave the atrypid shell stability and aided in lifting the shell margin from the substrate. No function for spines was suggested.

A different view of the mode of life of Atrypa was given by LAMONT (1934, p. 217, fig. 13). LAMONT believed that the uppermost valve of Atrypa reticularis (LINNE) from the Wenlock limestone, was the pedicle valve and that this valve 'may have served as a shovel cf. the modern lamellibranch Pecten maximum LINNAEUS'. He thought that the upper (pedicle) valve was used in mud removal and that silt particles on it would slide down the tongue towards the hinge margin. This unique mode of life does not seem to have been postulated by other geologists.

The adaptations to different modes of life are dealt with under four headings : shells with and without frills, shells with spines, shells with areas and the position of epifauna on shells. A diagrammatic outline of many shell changes is given in text-fig. 15.

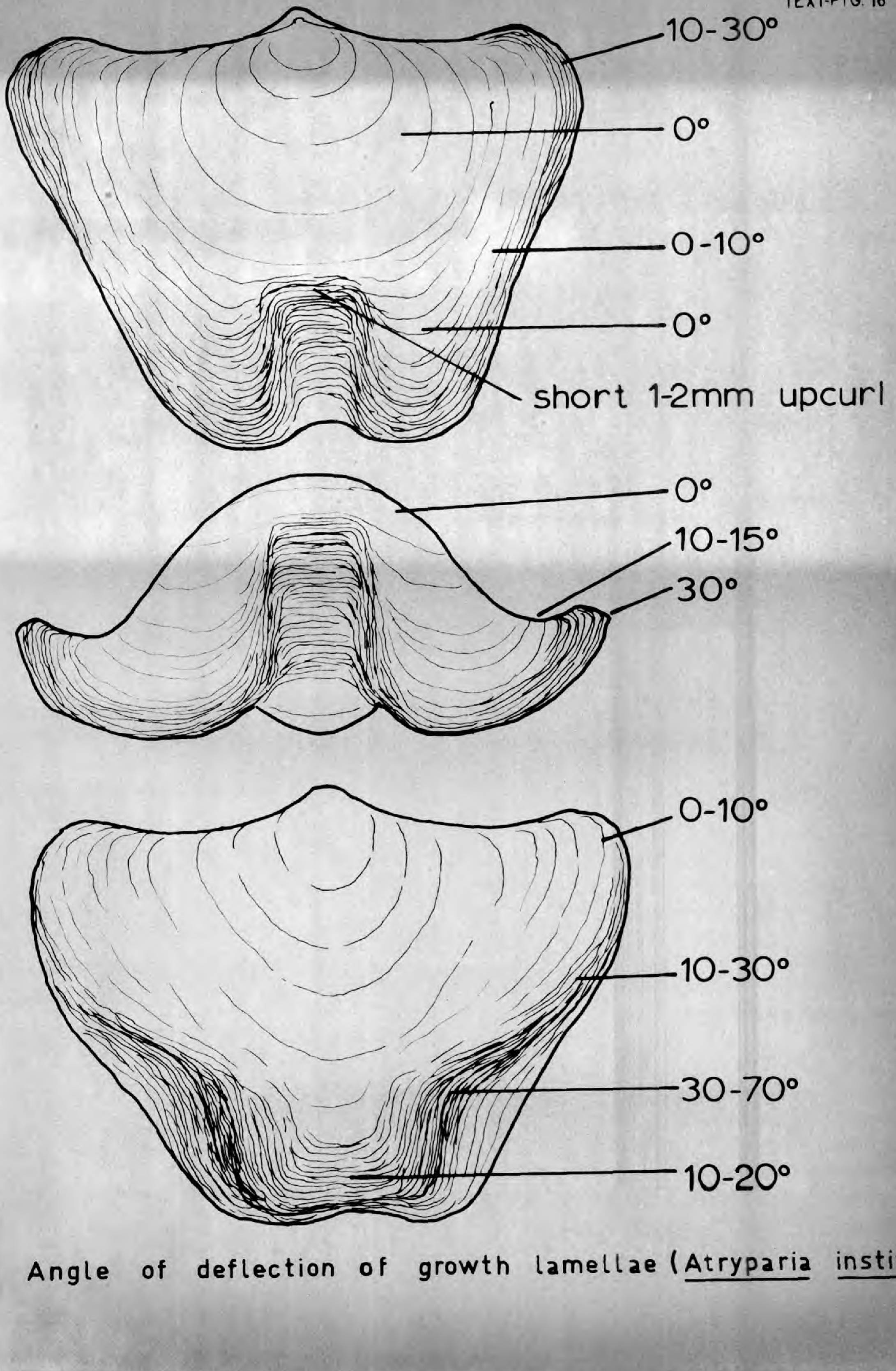
Frilled atrypids.

The first known figure of alate extensions on an atrypid shell is that of HISINGER (1837, Pl. 21, figs. 11d, e). DAVIDSON (1853, Pl. 7, fig. 87) also gave some early illustrations of this feature and remarked of Atrypa's surface lamellae, 'often considerably produced beyond the margin under the shape of tubular spines or foliaceous expansions' (ibid., p. 90). G. and F. SANDBERGER (1856, Pl. 33, fig. 1) quoted DAVIDSON and figured a rather alate specimen of their own. SCHRÖTER (1777, pp. 385-386) did not remark on frills, yet realized that the lamellae must have marked stages of growth. Findings of atrypids with long frills are abundantly listed in the literature. Huge frills found on an atrypid from Western Canada were drawn by WHITEAVES (1892, Pl. 37, fig. 8) and his sketch has been copied by many others. THOMAS (1916, Pl. 95, figs. 1-2) also figured an atrypid with enormous frilly extensions. LEITH read a paaer to a meeting of the Geological Society of America in 1951 describing frilled atrypids from Manitoba, Canada. The contents of this paper were never published, but the material dealt with is probably of the same age and source as that of WHITEAVES. Recently, IVANOVA (1962, Pl. 15, 16) figured frills for Atrypa vulgariformis from Siberia and concluded that these functioned in elevating shells from the oozy bottom. Underlying most of the recent research on atrypid frills are two associated ideas : that frills are only rarely found because rarely preserved and that frills replaced a pedicle as a stabilizing device. The first implies that frills are an essential element in atrypid morphology and the second leaves out the fact that other stabilizing devices were developed.

There is no evidence that the atrypid genera Gruenewaldtia, Mimatrypa or Karpinskia had frills during life or that in certain species-groups of Atrypa and Desquamatia frills were necessary to mode of life or were even developed. The suppression of frill development may have been as much a phylogenetic as ecological factor, and those forms without frills may have been preferentially selected in favoured environments. However, the absence of frills must be used with care as support for speciation. McCAMMON (1960, p. 22) may well be at least partially correct when she thought that alation in Atrypa was the cause of environmental stress, some species with the capability to develop alation perhaps doing this only when needed. McCAMMON found that in the stromatoporoid zone (usullly the fore-reef, high energy zones) there was a consistent lack of alations on specimens of 'Atrypa' independensis WEBSTER.

In the Eifel region and also at Refrath (Germany) calcareous shales contain frilled specimens of the genus Desquamatia (see Pl. 45, fig. 3). In the Müllert horizon of the Eifel the genus Atryparia also has magnificent frill development, again in calcareous shales. Frilled specimens are definitely lacking in more current moved and sorted sediments. A rare exception may be some of the late Givetian Atrypa found in the Massenkalk facies (?fore-reef) : a frilled specimen in this type of pure, coarsely bioclastic limestone is figured by WHIDBORNE (1893, Pl. 13, fig. 10). Desquamatia and Atryparia have frills of the type which hug the contours of the shell surface and are flared out laterally in thick, overlapping layers more or less parallel to the horizontal plane. This is rather different from the picture presented by FENTON & FENTON (1932c, figs. 1d, 1e) in which lamellae are sharply deflected. There is a broad correlation between the distance of separation of adjacent lamellar bases and the angle of deflection from the shell surface. With a slight deflection frills are more widely spaced and fewer in number and with a deflection greater than 10 degrees they are spaced at less than 5 mm. In a species with few, widely spaced lamellae (e,g, Desquamatia ajugata COPPER), frills are hardly developed in the true sense, but instead the whole shell becomes flat and wide-brimmed. In other words, the body cavity also increases in size, rather than merely the width and length. The word alation should strictly be applied only where the shell gains in width without gaining in body cavity size. Similarly the word frill is confined to the numerous overlapping layers which multiply shell width and not to individual growth lamellae with limited extent. FENTON & FENTON (1932c, p. 208) distinguished three types of alations :
(1) those curving freely away from the valve, leaving pronounced ridges, (2) those close to the shell surface, (3) those bending abruptly away

TEXT-FIG. 16



Angle of deflection of growth lamellae (Atryparia instita) without leaving scars. These distinctions appear to be difficult to identify clearly in specimens. For the last, the FENTONs may in fact have been describing non-frilled Spinatrypina. The only two end members identifiable in European material are those with rather close-spaced deflected frills, The former are characteristic of Desquamatia (Variatrypa), the latter of Atrypa (Isonatrypa).

A character which has not received any mention is the difference in deflection of surface lamellae from the pedicle and brachial valve. An example of this in Atryparia instita COPPER is given in text-fig. 16. The adult brachial valve of this specimen for most of its expanse except the margins, shows little lamellar warping. On the other side, the pedicle valve shows marked deflection of lamellae except apically and postero-medially. It is this variation in deflection on individual valves which makes the separation of frill types as in FENTON & FENTON (op. cit.) so difficult. Atryparia falls into the range of specimens with horizontally deflected frills.

The other type of frill growth is that of Atrypa (Isonatrypa) and is well displayed in the late Eifelian A. inglanda n.sp. Frills on such forms tend to be short (5-10 mm at most) and best developed about the anterior fold. Extensions at the hinge corners are rare. Lamellae are nearly always closely spaced and the shell itself is usually globular, rather strongly and equally biconvex. Deflections may be as much as 90 degrees in critical parts about the anterior fold. It is not improbable that the life position of such shells was with the umbones downwards and the commissural plane at a steep angle to the substrate.

## Spinose atrypids.

In some of the atrypid brachiopods the growth lamellae which project from the shell surface are funnelled distally into spines. STAINBROOK (1945, p. 49) grouped such atrypids into a new genus called Hystricina (Latin, covered with spines), which was later changed to Spinatrypa (STAINBROOK 1951). Two other spine-bearing genera are Punctatrypa HAVLICEK and Spinatrypina RZHONSNITSKAYA.

The problem of the appearance of spines has bedevilled many authors. Very often in the literature the origin and function of spines in one group of organisms has been used to explain the presence of spines in other unrelated groups. It is very likely, however, that the spines of the chonetid, the productid, the rhynchonellid and spiriferid brachiopods may each have had different origins, as well as functions. BEECHER (1898) tried to explain the appearance of spines in all organisms, plant and animal, as a feature of racial senescence. This is best summarized in his own words : "The species are small and unornamented. They increase in size, complexity and diversity, until the culmination, when most of the spinose forms begin to appear. During the decline, extravagant types are apt to develop..." BEECHER, 1898, p. 354). BEECHER selected, as one of his many examples (ibid. pp. 18-19) the development of the North American *Atrypa hystrix* HALL, a spinose atrypid, from a non-spinose ancestor *Atrypa reticularis* (LINNE). Though BEECHER's calculations that spinose forms evolved from non-spinose ones appears to be correct, it is doubted that spinescence can actually be said to be symptomatic of senescence or racial decline. It seems rather that spinescence in atrypid brachiopods is characteristic of increasing complexity, and marks the acme of their evolution.

DAQUE (1921, p. 642), who did a great deal of work on comparative morphology in primitive animals listed 8 functions of spines : protection, shell strengthening, suspension, anchoring, mimicry, sexual distinction, supporting, and elevating. Many of these functions had previously been discussed and interpreted by BEECHER in 1898.

In some Palaeozoic rhynchonellids, there are spines located on the shell commissure and HERTA SCHMIDT (1937, p. 34) concluded that these must have functioned as filter-feeding devices.

HERMANN SCHMIDT (1938, p. 307) suggested that spines may have had largely a respiratory function ('Hautatmung', transl. skin-breathing). He had noticed previously (HERMANN SCHMIDT, 1935, p. 143) that spinescence was often associated with dark gray or black shales presumably sedimented under unoxygenated, anaerobic conditions. In addition to mentioning the productid and chonetid brachiopods, he also listed the atrypids *Spinatrypina tubaecostata* (PAECKELMANN) and *Spinatrypa hystrix* (HALL). It is doubtful that the spinose atrypids used their spines for respiration as suggested by SCHMIDT.

It is possible that spines may have served as warning devices, and through their thinness and hollowness echoed subaquatic noises or sudden shock waves in the water generated by aprroaching predators or rapid changes in currents, and which caused it to close its valves. Spines may have been temperature sensors, though without the ability to move this would not have been of great value except again in shell closure. Another possible function of spines is as an aggressive rather than passive proctective device. In other words, by increasing its volume several times over by means of extruding spines it could have cleared away competition on the sea floor. This is not unrealistic because many rich collections of spinose atrypids afe virtually monotypic and show few associated fossils.

Spinosity is best developed in the chonetid and productid brachiopods, but also occurs in the rhynchonellids and spiriferids. GILL (1950, pp. 47-48) postulated that the function of spines in the chonetids was probably to fix the shell so that it could gain maximum benefit in respiration and nourishment, and that spines probably superseded the pedicle as an anchoring device. This is probably true of the spinose atrypids as well. Hollow spines are more advantageous than solid ones because of their greater resilience and strength. In the atrypids the major function of spines (as is that of frills and planoconvexity) was probably anchoring. Minor functions may have been as protective devices, perhaps in the shelter of spats. JUX (1962) believed that atrypids spines were filter-feeding devices, but since the peculiar spine direction shown by JUX has never been found on a specimen, not even topotypic material, this is doubtful.

The spines of atrypids do not suggest a pelagic mode of existence, i.e, it is doubtful if they were used in attachment to floating seaweed of the Sargassum type. Spinose atrypids are more frequent than other atrypids in black calcareous shales and limestones but there is no proof that such black Devonian shales carried rich pelagic faunas as did the black, graptolotic shales of Silurian age. RUEDEMANN (1934, pp. 33-34), who made an extensive study of Palaeozoic plankton found only small primitive inarticulate brachiopods associated with definite pelagic forms of life. Articulate brachiopods are extremely rare in graptolitic shales. Among pelagic trilobites, however, spinosity is a common feature (RUEDEMANN, 1934, p. 39). Atrypids, like other brachiopods, probably had a brief pelagic existence in larval stages, but by the life stage when a calcareous shell was developed probably became benthonic. Spines are not usually well developed on very small, young shells of spinose atrypids, and seem unlikely to have proved useful in attachment.

The presence of spines on atrypid shells was not recognized or discovered by early researchers. DAVIDSON (1853) mentioned, but never figured spine development. HALL (1867, Pl. 53a, figs. 8, 9, 15-17) was apparently the first to illustrate spinose forms. RIGAUX (1873, figs. 1a-b) figured a thickly spinose atrypid called Spinatrypa longispina (BOUCHARD). JUX (1962) made a special study of spinose atrypids from the Sötenich syncline of the Eifel (refer to S. curvirostra n.sp.). Spinosity seems to have been much more common in Devonian than Silurian atrypids, although Spinatrypa can probably be traced back to the Wenlockian. The only known figures of spines on Silurian atrypids are those of POULSEN (1943, Pl. 2, fig. 14) and CHAPMAN (1913, Pl. 11, fig. 15). DAVIDSON (1882, p. 112) described a Wenlockian atrypid, Atrypa asperula, which has strong spine bases and probably was an early Spinatrypa (a photograph of this species was sent by R. COWEN, Sedgwick Museum, Cambridge). Spinatrypa asperula (DAVIDSON) is very similar to Atrypa insolita BARRANDE (1879, Pl. 28, fig. 6).

FENTON & FENTON (1932c) believed that spines were due to iterative trends in the atrypid group, being evolved repeatedly in different species groups. None of the recent systematic studies have advanced evidence in favour of such a contention. No phylogenetic series between Atrypa (or any other genus) and spinose atrypids have yet been found in the

Devonian. It is possible that such a series may be found in Silurian sediments. The Spinatrypa stock seems to have been long lived. The origin of Spinatrypina is not clear : RZHONSNITSKAYA (1964, p. 94) extends the genus into upper Silurian. Possibly it was derived from Spinatrypa.

The most well-developed spines occur on more coarsely ribbed specimens of Spinatrypa. In a species such as Spinatrypa kelusiana STRUVE the ribs become so coarse that they almost disappear, yet spines are still present. On Spinatrypina on the other hand, which has sharply defined, deep troughed ribs, and where one would expect better spine development, spines have become almost obsolescent. Only one specimen of the Frasnian species had one or two thick short spines preserved. These two observations, that the best spines are present on the most coarsely ribbed forms, and that the shortest spines or non-spinose forms have the most deeply troughed ribs, appear to be contradictions to the postulated evolution of spines in FENTON & FENTON (1932c).

Several trends towards extreme coarsening of the ribs of spinose atrypids appear to have taken place. Such trends locally resulted in nearly complete flattening of the ribs and loss of radial ornament. One of these occurred in late Eifelian time and can be observed in Spinatrypa kelusiana STRUVE (see Pl, 20, figs. 4a-b). The second one known was present in the American Upper Devonian species Spinatrypa trulla (STAINBROOK, 1945, Pl. 5, figs. 2-10). A third possible cline towards rib flattening occurred in the late Givetian of Europe. This appears to have culminated in such forms as Spinatrypa squamosa (SOWERBY, as figured in DAVIDSON, 1865, Pl. 10, fig. 5) and Spinatrypa paffrathi (WEHRLI, 1931, figs. 3-4). Spinatrypa orthoclina n.sp also shows a marked tendency towards losing its ribs (see Pl. 26, figs. 2a-b).

When spines are developed, small extended fringes of the growth lamellae are often still retained, and where spines are broken off specimens may have the appearance of showing short, deflected frills. The rib structure and the nodose intersections of the ribs and growth lamellae distinguish such forms unmistakably from Atrypa. The spinose nature of the shell surface is evident without the presence of spines because at the point at which the rib meets a concentric lamella, the shell curves slightly upwards to form the node mentioned above. But in the more lammelose, thick shelled spinatrypids the swelling may be insignificant. The shortest, most sharply deflected spines appear to make the most marked nodules on the shell surface, while the longest, most weakly deflected spine makes hardly any swelling at all. In the latter the spine seems to have developed at a greater distance from the shell wall.

The growth of a spine is a simple process. FENTON & FENTON (1932c) have already demonstrated this growth. At a distance (1-2 mm) from the shell surface, the extended growth lamella begins to curl, much like a drying leaf, until it forms a hollow tube. This hollow tube tapers at the end to a solid point. The longest spines on the material studied were about 10 mm in length. In Pl. G, fig. 1 a cross-section of a spine is shown. The inner margin of the spine does not seem to fuse completely but is somewhat flared.

Not a great deal of work mas been done to show what directions the spines take on the shell surfaces. There is a great deal of variation from one shell to the next, from one species to the next, and also on different parts of either valve of one shell. This compares to the deflection variation of frills. JUX (1962, fig. 1) reconstructed the spine growth of Spinatrypa curvirostra n.sp. This reconstruction showed all the spines directed anteriorly and nearly parallel to the commissural plane. Topotypic material from the Wachtberg quarry was collected, and a collection included about 1000 specimens many with a full array of spines. Not a single specimen showed the spines in the position reconstructed by JUX (above). Spines were found to be multidirectional, dependent upon their position on either valve. On the fold and sinus spines were thickest, longest and directed anteriorly, sub-paralled to the commissural plane as JUX (ibid.) suggested. This conforms to the direction usually taken by frills at this point. On the shell margins, laterally and posteriorly, spines were deflected at up to 90 degrees but not anteriorly directed. The filtering function which JUX imputed to spines is unlikely. The spines on the pedicle valve appear to have been mainly anchoring devices and on the brachial valve probably proctective devices. The distance between the spines is so great that they could not effectively have stopped the most bothersome particles from entering the shell : particles greater in size than crinoid ossicles would probably not have been admitted since it is doubtful if the gape of the anterior commissure would have been greater than two or three millimeters.

Most spines are relatively straight. Those on Spinatrypa kelusiana STRUVE were rather flat-lying. Spinatrypa variaspina n.sp. is remarkable in that spines point in numerous cross directions and many spines are curled and twisted.

There appears to have been no acme in spine development, except in general that the longest and best developed spines are found on Givetian and Frasnian species of Spinatrypa. Spinosity as a whole appears to be more characteristic of Devonian atrypids. Spinosity is not the last stage in elaboration of surface morphology. This place is taken by those forms which have passed through the spinous stage and ribbed stage and have merely coarse, short lamellae on the shell surface. A similar morphogenetic trend is present on frilled forms : frills became more widely spaced until they disappeared altogether. These trends are not true of the whole group of Atrypida for the youngest Frasnian species have full arrays of spines or frills.

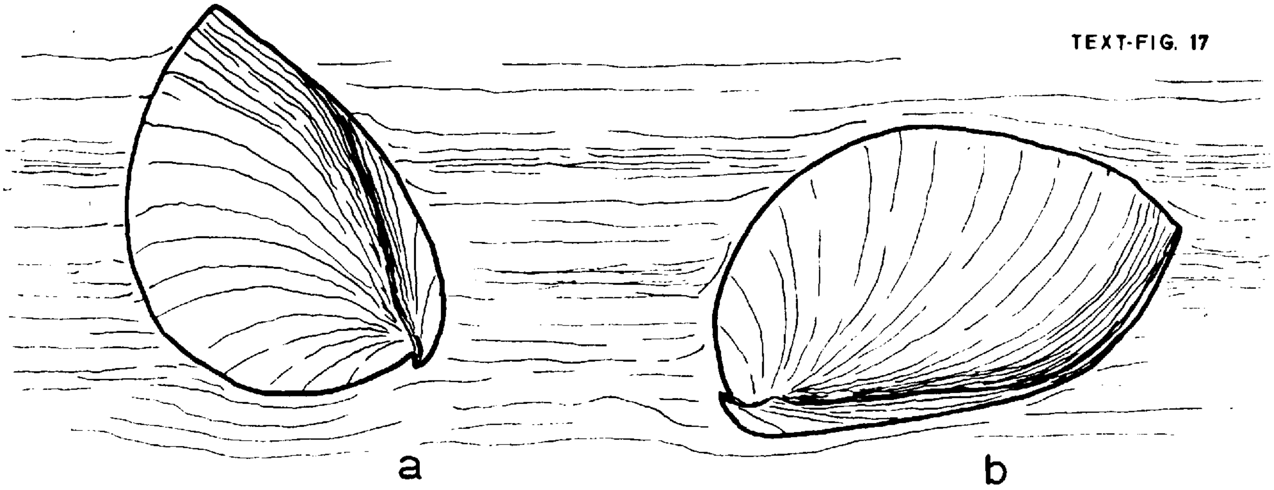
## Other orientational structures.

Some atrypids have neither frills nor spines. Numerous genera, even those still very close to Atrypa, appear to have developed alternative methods of stabilization and anchoring. Some are completely smooth (the family Lissatrypidae), some have large areas and pedicle openings, some have peculiar shell convexity.

Atrypa of the A. (Planatrypa) group have imbricate ribs and similar growth lamellae, but lack frills and show a planation of the pedicle valve which is far greater than that of normal dorsibiconvex Atrypa. This is seen in its extreme development in Atrypa (Planatrypa) petasa n.sp. The pedicle valve in these forms is even slightly concave. Most of the shells of Planatrypa have a foramen which has penetrated and resorbed part of the ventral umbo, and it is feasible that the pedicle may even have remained functional in late ontogenetic stages. The shell is stable in only one position, pedicle valve down. Except as weak auricular extensions, frills are completely lacking in this subgenus, and doubtlessly will not be found.

A richly fossiliferous locality in the Ahrdorf syncline (C325, MTB Dollendorf r5248:h8038) has yielded lower Eifelian atrypids which also have nearly planar pedicle valves. The majority of specimens at this locality are found in two positions in the sediment (silty calcareous, dark brown shales), roughly half fall in either category (see text-fig. 17). These two orientations correspond to those figured by FENTON & FENTON (1932b, figs. 6e, 7) though there is no deep sinuation of the commissure as in the American specimens. The great number of shells found in the two positions at this locality would point to a cause other than post-mortem sorting. One of the positions (text-fig. 17a), would not be expected from the shell convexity, which is convexoplanate. The second position, which shows the pedicle valve parallel to the substrate, is more natural. This position cannot always be assumed to be a life position because it is also the current stable situation. A curious mode of preservation would, nevertheless, confirm that these life positions were true. The shells are free of adhering sediment except in certain parts which are identical on all specimens showing one mode of preservation. For fig. 17a, clayey sediment is firmly fixed to the ventral umbo and a wide stretch of the dorsal umbo; for fig. 17b, clayey particles are firmly glued only to the pedicle valve, with the brachial free. This fixed clayey cement is difficult to remove without damaging the shell wall and its distribution appears to be not merely fortuitous.

TEXT-FIG. 17



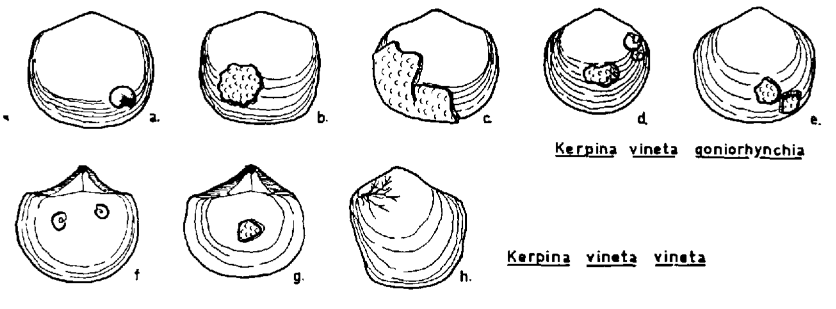
Orientation of *Atrypa* at fossil locality C325

The above species of *Atrypa* is associated most commonly with the large spirifer *Paraspirifer cultrijugatus* (ROEMER), and this association strikingly resembles the association of the convexoplanate *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR) with a similar large spiriferid *Cyrtospirifer ostiolatus* (SCHLOTHEIM). Both atrypid populations are monotypic at their localities, both have similar substrates, both have similar associates and the remaining fauna is sparse. The symbiotic association may have been mutualistic.

With its tubular-imbricate ribs, expansive interarea and highly variably inclined beak, the genus *Kerpina* STRUVE is a remarkable atrypid. It resembles the stropheodontic genus *Schuchertella* in its beak structure. Frills are lacking completely. The imbricate ribs are suggestive of *Spinatrypina*. The intraspecific variability in size, shape and beak structure are immense, wider than in any other known atrypid. Its variability is of the magnitude which has been used to separate whole families of atrypids. The changeable external morphology of *Kerpina vineta* STRUVE is probably due to marked adaptability to many different modes of life (text-figs. 153-161).

Beak incurvature in *Kerpina* ranges from epicline to orthocline, shell shape from wide and flat to narrow, thick and elongated, delthyria from small to large and convexity from biconvex to convexoplane all in the species *Kerpina vineta*. These features suggest a versatile mode of life and a short, probably broad pedicle, perhaps supplemented by ligaments attached to the interareas. The flat shelled subspecies *Kerpina vineta vineta*, which distantly resembles the atrypid genus *Carinatina*, probably lived with the ventral valve down. The anterior margin of these specimens is geniculated dorsally, presumably to elevate the inhalent-exhalent food currents from the substrate), the dorsal valve is nearly flat (more stable in laminar currents ), and the beaks often twisted, bent and warped, and in positions ranging from apsacline to procline ( a position expected if the pedicle were short and firmly held the umbo of the shell to the substrate or to an object on the sea floor). Some of these specimens were found almost cemented, at any rate firmly attached to small platy tabulate corals of the genus *Alveolites*. These platy corals are often wrinkled and warped : two of the specimens showed how the shell of *K. vineta vineta* conformed to the shape of the coral, rather than the reverse (if coral attached itself to the brachiopod). An illustration of this relationship with *Alveolites* is given in Pl. 39, figs. 1, 3. This mutualism is similar to that of the brachiopod *Davidsonia* which also is most commonly attached to *Alveolites*.

The subspecies *Kerpina vineta goniorhynchia* STRUVE has an inflated, globose pedicle valve, nearly flat brachial valve and narrow, elongated outline combined with a rather consistent orthocline, weakly apsacline beak incurvature, The mode of life was opposite to that of *K. vineta vineta*, i.e. the pedicle valve must have been up. The location of small epifauna such as *Spirorbis* and *Clionolithes* confirm this life position. A sketch of epifaunal location is given in text-fig. 18. The epifauna is



Epifauna location on *Kerpina vineta* STRUVE

TEXT-FIG. 18

always attached to the brachial valve in K. vineta vineta, on the pedicle valve in K. vineta goniorhynchia. The two opposed modes of life have led to complete dimorphism in morphology. Intermediates between the two morphologies occur only in neanic specimens in which the mode of life may have been identical. The smallest specimens of each subspecies are virtually indistinguishable. Such sharp intraspecific dimorphism may have led, if the Freilingen environment had continued, to complete speciation at a later stage. The Freilingen environment probably was ideal to the widest variation in atrypid morphology and seemed to some extent to be almost a laboratory in evolution. Almost every Eifelian atrypid genus managed to find a small niche in this environment, and although this led to some convergence in morphology (as well as the divergence intraspecifically), each genus retained its distinct identity. It was also during late Freilingen time that the transition between the atrypids Gruenewaldtia and Mimatrypa seems to have taken place. In these two species-groups, connecting members of which are difficult to separate on the basis of external morphology, there was an internal change from septally elevated muscle platforms to cemented muscle platforms, as well as some accompanying changes in shell wall structure, loss of lateral cavity and growth of unified collars and deltidial plates.

Carinatina NALIVKIN is a rare genus in the Devonian of northwestern Europe. Its origins are puzzling. Its morphology is unique. It is nearly flat and has a wide, spiriferoid interarea and large delthyrium. This genus developed a "skirt" around the margin of the shell. This skirt is thin and usually consists of only one growth lamella from each valve, and is not a frill consisting of numerous overlapping lamellae. Such a skirt is figured in Pl. 58. Another feature, seen only rarely in late mature specimens, is the growth of a curled margin (Pl. 57, figs. 2-3). On this margin, which appears to be typical of more than one species, the ribs show a sudden burst in multiplication, decreasing their wave length by as much as a third, and increasing the number of ribs correspondingly. The function of this curled margin probably was the same as that of the geniculated commissure of Kerpina, and may be analogous to the commissural fold of Atrypa. After its name, Carinatina has a strong mesial keel or carina. All these combined structures, the flatness of the shell, the horizontal thin frill, the carina, the wide interarea are features which would be expected as adaptions to fast laminar currents. The streamlining of shape caused some homoemorphy with Kerpina, present in the same stratum.

LAMONT (1934, pp. 217-218) suggestedthatin poorly oxygenated, muddy bottoms, brachiopods adapted themselves to use a minimum of oxygen by growing flat shells, and to collect as much oxygen as possible by extending the antero-lateral margins. He applied this argument particularly to strophomenids but it is doubtful if the flat, wide shell of Carinatina had the same adaptive origins.

Not all frilled atrypids have incurved or appressed beaks. Species of the subgenus Desquamatia (Variatrypa), with a small but marked interarea, exposed delthyrium, and orthocline-anacline beaks, also show extensive frills. A figure of such a form, Desquamatia zonata (SCHNUR) is given in COPPER (1965d). This species, showing the longest frills of any Eifelian species of Desquamatia, also has a more incurved beak than other Eifelian species. In addition, D. zonata has a pedicle collar, a rather late ontogenetic feature which appears to be coupled with beak incurvature and loss of pedicle. Frill development seems, at any rate, to have encouraged atrophy of the pedicle. The life position of Desquamatia (Variatrypa) may have been two-fold, pedicle valve down in frilled forms or in late ontogenetic stages, and pedicle valve up in neanic or non-frilled specimens.

Desquamatia triangulata COPPER has an extensive interarea which exceeds that of the other Eifel species. No frills have yet been found in collected specimens of this species. It is likely that specimens of D. triangulata have been mistaken for Carinatina, to which there is some resemblance. No frills have been found on specimens of Desquamatia iunctura n.sp. nor is there anything to indicate that these may have been present. Its interarea is relatively large, the ventral valve somewhat planate and the ribs tubular and deep-troughed. The early Givetian D. ajugata COPPER has a like development, except that the convexity is one stage further : the pedicle valve partially concave and the shell wide-brimmed. There probably was a minor trend in the Eifel region for Desquamatia (Variatrypa) to develop a larger interarea and to lose its frills. Desquamatia iunctura n.sp. and D. ajugata n.sp. probably had a mature mode of life with the pedicle valve down, but still with a functional pedicle. It is possible that in the genus Desquamatia only frills of the last stages of growth were preserved during life. many specimens, though well preserved, lack the ragged edges expected of broken frills. Such lamellae may have broken or been shed and the newly grown lamellae have replaced them in function. This may have been particularly true of Desquamatia.

There is a correlation between weakly sulcate-rectimarginate anterior commissures and an orthoclinal beak or large areas. The corollary, 'Large interarea, weak fold' is plain in the following species, Desquamatia ovata COPPER, D. subditiva COPPER, Gruenewaldtia spp., Mimatrypa spp., Spinatrypina spp., Carinatina spp., Kerpina spp. The assumption appears to be more valid for atrypid species-groups never known to have frills. Exceptions are inevitable : Desquamatia iunctura n.sp. and D. triangulata COPPER both have large areas and prominent folds on the commissure. A prominent fold is more typical of the frilled atrypids, Atrypa (Atrypa), Atrypa (Isonatrypa), Atrypa (Planatrypa), some Desquamatia. It is also very rare in Spinatrypina. The function of the fold no doubt was to elevate the central part of the anterior commissure from the substrate.

Alate extensions or elevated or deflected growth lamellae are unknown in Gruenewaldtia and Mimatrypa and since the skirt developed in Carinatina cannot be called a true frill, the absence of deflected lamellae or imbricate structure may be a biocharacter of family or subfamily importance. Such atrypids may be broadly grouped under SPRIESTERSBACH's Palaferellidae. None of the atrypids in this genus group show incurvature of the beak, all having marked interareas and delthyria. The ribs of most members also fall into the 'tubular' class, deep-troughed and uninterrupted.

Most of the Gruenewaldtia, if not all, probably had a strong supporting pedicle and ventral valve in the 'up' position. The life position of late ontogenetic specimens of Gruenewaldtia latilinguis (SCHNUR) may have been somewhat different. The incurvature of the beak, which is quite marked, as well as the strong convexity of the pedicle valve, possibly was typical of a brachial-valve-up position, with much of the ventral valve buried in the mud. The commissural fold is bent dorsally and most of the epifauna (see example on Pl. 48) is attached to the brachial valve. These two characters support such a postulated life position. Another atrypid, not in the family Palaferellidae, also shows a morphology similar to mature Gruenewaldtia latilinguis (SCHNUR). This is the late Eifelian Spinatrypa kelusiana STRUVE, with a plano-convex to ventribiconvex shell, dorsally turned commissure and dorsal epifauna. Its life position probably was identical to Gruenewaldtia latilinguis in maturity.

The most prominent commissural folds are established in atrypids adopting a ventral-valve-down position. Such a position necessitates elevation of the commissure to allow adequate respiration. Marked folds are also linked to marked globosity : the higher the arch, the older and more globose the specimen. The height of the fold may match the depth of the shell. Many species appear to reach a maximum length after which they begin to grow in depth. In grossly globose specimens, the rate of growth of the tongue on the pedicle valve exceeds the rate of the rest of the shell. The growth of the tongue pushes the successive layers of the brachial valve posteriorly. If the gape of the first five millimeters of shell growth on a globoss specimen is measured, it may exceed 180 degrees. In this way the ventral umbo is pressed against the dorsal umbo and the dorsal apex may be completely obscured. There are no adequate terms in the atrypid literature to cope with the barely measurable incurvature to the dorsal beak relative to the commissural plane.[1]

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[1] A distinction is made here between appressed and epicline beaks. An appressed ventral umbo is one which, relative to the commissural plane, has not been incurved but has remained in position. It is the dorsal umbo which has slowly been incurved and pressed against the ventral beak. An epicline beak is one which, relative to the commissural plane, has incurved sharply around the hinge axis to press against the dorsal valve. The former is typical of Atrypa (Planatrypa), the latter of Desquamatia and Spinatrypa.

The importance of the pedicle, or lack of it, in taxonomic studies of brachiopods, has drawn the attention of many researchers. One of the early and classical studies in this line, is a paper by YAKOVLEV (1908). YAKOVLEV picked his examples from a wide range of strata and placed the accent of his study on spiriferids and terebratulids. He stressed that the mode of attachment could lead to considerable differences in the shape of the cardinalia even in adjacently located specimens of one species, and that the type of substrate could lead to convergent pedicle development in synchronous but unrelated stocks. YAKOVLEV's observations can also be identified in atrypids from northwestern Europe.

The mode of life of most atrypid genera appears to have been fairly constant. An exception is the dimorphism of Kerpina vineta, which bears out well the first of YAKOVLEV's conclusions that the mode of attachment can lead to intraspecific variance in the beak structures. But the general pattern of growth of the beak appears to have been settled by latent capabilities to develop particular structures. For example, Atrypa will never develop the wide area, large delthyrium and foramen of Desquamatia. However, the more 'advanced' Desquamatia may still revert to an Atrypa-like state by completely obscuring the area and delthyrium. In this way the environment can have little influence on structures which a particular species-group could not develop in the first place. This is probably the fundamental reason why so many species-groups of atrypids have been misidentified, the authors simply assuming that the variation in such groups are an invironmental rather than hereditary cause. The background to a proper understanding of ecological variation in Atrypida must always remain correct identification and taxonomy.

YAKOVLEV's (ibid.) second premise, which can be summarized as 'similar sediment, similar morphology', is similarly true of a limited number of structures in Atrypida. The atrypids found in argillaceous, clayey sediments with few corals show strong beak incurvature or appression of the beak. The atrypids associated with coral-rich rocks are marked by large interareas. But there is no broad, phylogenetic separation of atrypids into reefal and areefal types, and their separation cannot be attributed to variation either. Most genera which are common to argillaceous rocks are hardly ever found in coral-rich rocks. When such an atrypid is outside its normal biotope, it tends not only to be very rare, but also shows minor adaptations. These adaptations are usually a change in the rib structure, in interarea and in the presence or absence of frills or spines. Because such forms appear to occur rather seldom, they are not a problem in identification. One instance is the species Spinatrypa aspera (SCHLOTHEIM). It reaches maximum abundance in clayey shales in which it tends to be coarse and shallow ribbed and globose, somewhat elongated. But, in the Hillesheim syncline it is also found in shales associated with corals. In this environment its shape changed to rather flat and broader, its area enlarged slightly and its ribs became more deeply troughed and marked. This appears to be a case of geographic separation, although the latter form is also slightly younger in age.

## Epifauna and mode of life

Atrypids are often abundant in biota which are also rich in other non-brachiopod constituents, some of which are attached to the atrypids, or vice versa, serve as points of attachment for atrypids. Dead atrypids frequently served as the central cores about which the corals Alveolites or Heliolites wrapped themselves. The coral may have settled on the atrypid while it was still living and subsequently stifled the atrypid by its weight and size. But in most instances, the colonization of the coral probably took place post-mortem; and post-mortem attachment is of little value in the determination of life positions, or symbiotic associations. It may indeed be difficult to decide whether the attachment took place before or after death, particularly when the side to which the organism is attached is also the side which is upturned in the stable shell position. For example, epifauna attached to the brachial valve of a convexoplane shell means little to accurate interpretation. The best way of deciding a 'during life' attachment is probably to observe patterns of distribution of the epifauna. If they are consistently attached to the hinge margin or to another special place, it is likely that this spot was favourable for its attachment, because of respiratory currents or shell movement.

A number of small organisms, like Aulopora, Spirorbis, the brachiopod Crania and some small spiriferids, were cemented to atrypid shells, and may have shared, contributed to or derived benefit from a common food supply, symbiotic associations respectively of mutualism, commensalism and parasitism.

Aulopora, a colonial tabulate coral consisting of a chain of trumpet-like calices (Pl. C, fig. 4), may have kept other pests away from atrypids by stinging cells (common protective cells in corals) and derived in turn some benefit from waste currents of the atrypid. On Atrypa squamifera (SCHNUR) it settled on the brachial valve, usually mid-anteriorly and on the fold. A large auloporid coral is figured on a specimen of Gruenewaldtia latilinguis (SCHNUR), again on the brachial valve (Pl. 48, fig. 4b). A specimen of the planoconvex Spinatrypa kelusiana STRUVE shows a crowded colony of auloporids located anteromarginally on the brachial valve. It has already been suggested that the life position of these two atrypids was brachial valve up. This position would not be expected because in a current the more stable position is the other way up.

The inarticulate brachiopod Crania, commonly an atrypid guest, reflects on its own shell surface an exact replica of the ribs of the host atrypid (Pl. 2, figs. 1a-b). The mimed surface sculpture is correct

## PLATE C

Fig. 1. Specimen of *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853) with borings of *Clionoides labyrintheus* n. sp. --Middle Eifelian, Giesdorf horizon, Junkerberg beds; Prüm syncline, MTB Schönecken r32200:h60330. -- HOLOTYPE PC225, oblique lateral view of the brachial valve. x2½.

Fig. 2. Specimen of *Atrypa* sp. with cemented inarticulate brachiopod near the dorsal umbo, *Crania* sp. -- Lower Eifelian, Wolfenbach horizon, Lauch beds; Ahrdorf syncline, MTB Dollendorf r52480:h80380. -- Specimen PC10 (refer to Pl. 2, figs. 1a-d), oblique postero-lateral view. x2.

Fig. 3. Specimen of *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853) with growth deformation. This type of deformation usually occurs along the plane of symmetry. -- Middle Eifelian, Giesdorf horizon, Junkerberg beds; Prüm syncline, MTB Schönecken r32200:h60330. -- Hypotype PC226, ventral view. x2½.

Fig. 4. A colony of "trumpet" corals, *Aulopora* sp., attached to a specimen of *Desquamatia* (*Variatrypa*) *zonata* (SCHNUR 1853). -- Middle Eifelian, Junkerberg beds; precise locality unknown, specimen labelled "Gondelsheim". Hypotype PC227, oblique lateral view. x2½.

C

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even to details of the rib direction and the concentric growth lamellae. Crania is located near the shell centre and also near the hinge margins, but rarely anteriorly. Usually it almost covers the dorsal umbo. It seems to be rare in atrypids with large interarea and pedicle openings.

Spirorbis, a small, gastropod-like worm with a calcareous test appears to have favoured a position on the flanks of the shell, towards the posterior margin.

Several boring organisms also attacked atrypid shells. The linear borings of Clionoides FENTON & FENTON and the dendritic borings of Clionolithes CLARKE often scar the shell walls of atrypids. FENTON & FENTON (1932a) attribute these borings to sponges.

BIERNAT (1961) described an 'annelid-like parasite' Diorygma atrypophylia which sent calcareous tubes into the central cavity of the spiral cones of Desquamatia subzonata (BIERNAT). Such organisms also have been found in a few specimens from the Sötenich syncline (in Atrypa (Isonatrypa) inglanda n.sp.), although the paired arrangements with one tube in each spiralium was not observed.

Recently a FENTON-like study of boring organisms was repeated by JUX (1964) in Frasnian atrypids from the famous locality at Refrath. JUX found a species of Clionoides on the dorsal valves of Atrypa (Devonatrypa) europeaea STRUVE and stated that they were commensal. The commensalism can be questioned, much as can the 'parasitic' worm tubes of BIERNAT (1961). Their symbiotic relationship must remain in doubt. For Clionoides and Clionolithes parasitism seems more probable since the multiple borings could hardly have left the shell unmaimed or unweakened. Clionoides seems to have preferentially selected only certain atrypid species. For example, on Spinatrypina explanata (SCHLOTHEIM) which accompanies the much bored Atrypa waterlooensis-like atrypid, there is no sign of any boring. The modern sponge Cliona selects lamellibranchs and bores into these for protection rather than for food (SHROCK & TWENHOFEL, 1953, p. 94) and its role is essentially parasitic. A like role was probably played by the Devonian Clionoides.

In the Eifelian atrypid Atrypa (Planatrypa) squamifera (SCHNUR) the borings of Clionoides are somewhat different in being wandering and often circular. The borings occasionally penetrate the shell wall but often remain inside the wall. A new species is described in a footnote (next page).

Clionolithes, a dendritic borer, is common on the convexiplane Atrypa (Planatrypa) petasa n.sp. and the planoconvex Kerpina vineta STRUVE (Pl. 7, fig. 3c; Pl. 39, fig. 5c). In several instances however, it bored into the planar pedicle valve which is usually down. This position is the reverse of that taken by Clionoides. In Eifelian sediments of Germany, Clionolithes is rather more abundant than Clionoides and also seems to have selected a wider range of hosts.

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## Order INCERTAE SEDIS

## Genus Clionoides FENTON & FENTON 1932

Type species: Clionoides thomasi FENTON & FENTON 1932, p. 47, Pl. 7, figs. 1-3.
Range: Middle to Upper Devonian.

### Clinoides labyrintheus n.sp.

**Pl. C, fig. 1**

Name: Latin, labyrintheus, a, um, labyrinthine, maze-like.
Type locality: Exposure on W. side of Giesdorf along road to Oberlauch, MTB Schönecken, r32200:h60330.
Stratum typicum: Giesdorf horizon, Junkerberg beds, Middle Eifelian.
Range: Mainly from the Giesdorf horizon, but scattered occurrences in the underlying Rechert-Nims horizons.

Diagnosis.-

Planar, winding and sinuous, non-branching, canal-like borings parallel to the shell surface, partly buried, partly open, partly through to the shell cavity. The 0.8 to 1.5 mm wide borings range to a depth of about 1 mm. Some canals are parallel to the ribs, but the majority varidirectional, sinuous, commonly in circles or loops completely reversing direction almost to the point of origin. Source or start of the borings usually at the shell margins. Most borings occur anterolaterally on the brachial valves of Atrypa (Planatrypa) squamifera (SCHNUR 1853).

Remarks.-

In width of boring this species is similar to the type Clionoides thomasi FENTON & FENTON. It also preferentially selected a large, convexoplane host atrypid. C. labyrintheus n.sp. differs in having sinuous, loop to whorl-like coils whereas those of the type species are straight and parallel to the shell ribs. These differences are consistent in all specimens.

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# IV MORPHOLOGY

## External form

Atrypa is usually described as having a dorsibiconvex, ovoid shell with a hidden pedicle opening, small area and radial and concentric sculpture. Under this simple guise a diverse, variegate group of brachiopods with complex external and internal morphology has been obscured in the past. For nearly a hundred years after its discovery, it was not even recognized as an independent genus. To-day DALMAN's original Atrypa-group contains some 65 genera of Silurian to Devonian age.

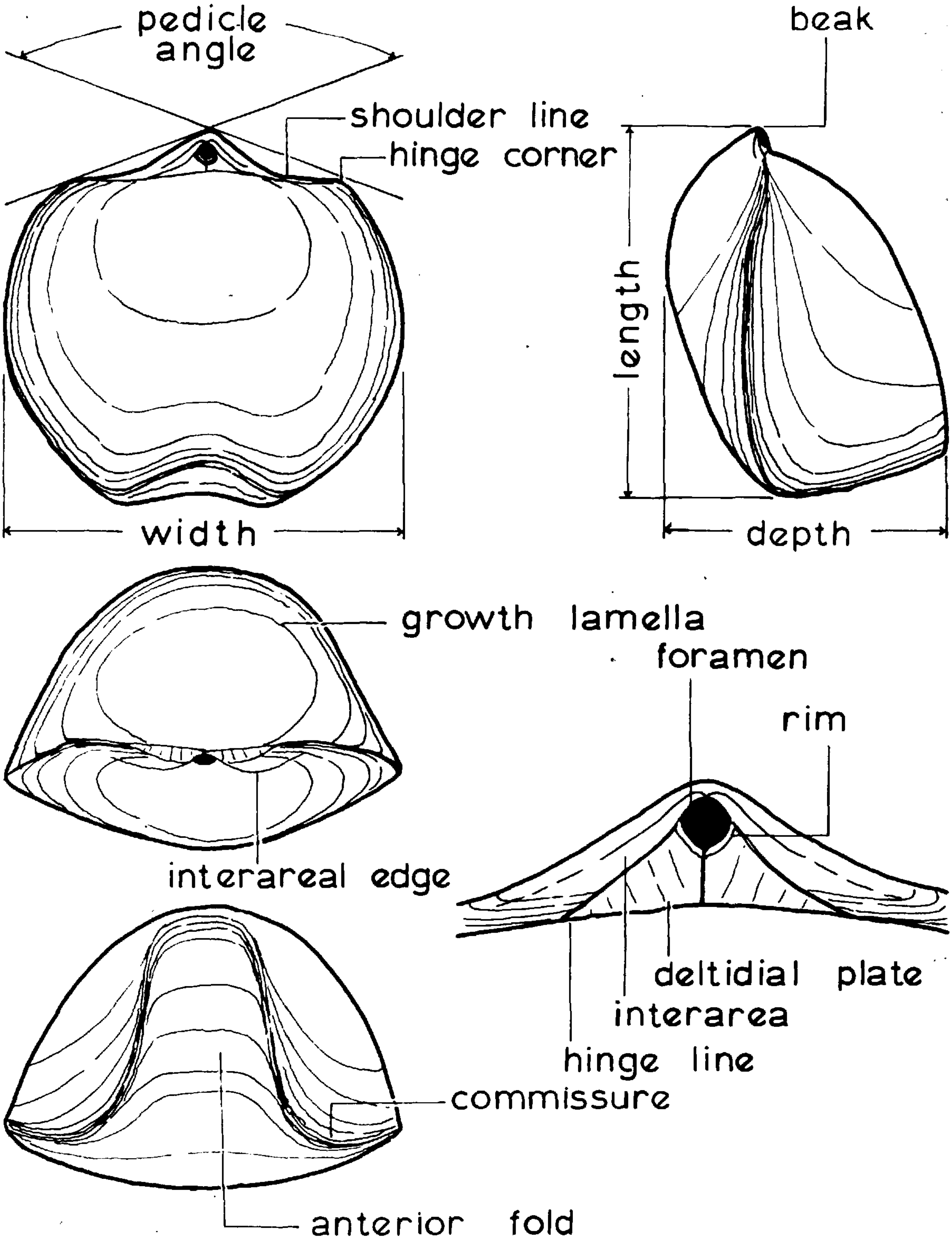
The Atrypacea are known to be homoeomorphic with nearly every major order of brachiopods, a diversity possibly unparalleled in the phylum. They have imitated the smooth athyrids and terebratulids, the marginate spiriferids, the costate rhynchonellids, the flattish schuchertellids and koninckinids, the rostrate pentamerids and the spinose productids. This wide diversification of morphology has simplified their separation, and a large number of biocharacters are available for comparison.

The most useful biocharacters in the distinction of atrypids are the external features of rib and growth lamellar patterns and their micromorphology, shell shape, shell convexity, and structure of the ventral umbo. The most useful internal features are the presence and structure of the deltidial plates and pedicle collars, the teeth, the crura and the structure of the jugal processes.

A basic outline of the morphological terms presently in use in atrypid studies is given in STRUVE (1955, p. 209) and SIEHL (1962, pp. 183-186); these are illustrated in text-fig. 19. They have been translated and modified for English usage. For the terminology of the foraminal positions and the plication of the anterior margin of the shell, the standard, classical reference of THOMSON (1927) was consulted. The terms used to describe the position of the beak and interarea follow the work of SCHUCHERT and COOPER (1932). COLEMAN (1951, p. 679) adapted some of THOMSON's terms for use in the atrypoid brachiopods, but these terms, 'inclined, subinclined' etc., have been abandoned. A graphic summary of some of these standard descriptive words is given in text-fig. 20. Slight changes have been made where they were felt necessary. There is, for example, no term to provide for the complete incurvature of the beak against the brachial valve; epicline is suggested. It was also necessary to distinguish between dorsiconvex and dorsibiconvex. The latter is less ambiguous. Because the former could refer also to a convexoplane or convexoconcave shell, it is dropped.

The terms interarea (or area, or cardinal area) and palintrope have been clearly defined in the literature, and, in theory, should be readily separable. An area (after BUCH, 1834, p. 37) is defined as a sharply

TEXT-FIG. 19



Shell morphology

bordered, even or curved surface on both sides of the delthyrium, and a palintrope as a convex, rounded surface of reflexed growth. Most atrypids have areas. In the atrypid group of brachiopods all gradations between terebratuloid areas and spiriferoid areas are found and a shapp definition, as it has been applied to other groups, is valueless. There fore the term area or interarea is used in its broadest sense to mean a planate surface, with or without sharp edges, in the same plane or tilted, on the reflexed portion of the ventral valve.

A complex argument has been advanced by RUDWICK (1959, p. 18) towards a basic separation of all brachiopods into strophic and non-strophic shells. This separation is based on idealized growth accretion parallel or non-parallel to a hinge axis. In practice, however, the atrypids appear to straddle the borderline between strophic and non-strophic shells. Carinatina plainly is strophic, but most other atrypid genera are non-strophic. A full cline is apparent between the two groups.

BUCKMAN (1919, p. 453) makes a further distinction in the rhynchonellid group of brachiopods of a planarea, areas which occur in pairs separated by a beak and not in the same plane. Again, in the atrypid brachiopods, there is a complete cline between areas in the same plane (interareas), and those not in the same plane(planareas). DAVIDSON astutely remarked (1853, p.91) that Atrypa seemed to be a morphological combination of Spirifer, Rhynchonella and Terebratula, the three brachiopod archetypes. In short, the 'area' of atrypids may occur in mirror-image, parallel or non-parallel pairs, may be partly round, partly sharp-edged, and a mixture of the three basic types or areas, interareas, planareas and palintropes. Accurate definitions of each are given by CLOUD (1942, pp. 8-17). The simplest solution lies in the use of the generalized term area.

In 1916 BUCKMAN proposed a standard terminology for the position of the pedicle opening in relation to the deltidium, and this terminology is widely accepted. The descriptive adjective hypothyrid was applied to the foramen 'when it is in the pseudo-area, and the apex is intact' (BUCKMAN 1916, p. 131). This is the traditional foraminal position in the Atrypida and Rhynchonellida. Unfortunately BUCKMAN's term is imprecise since it leaves open a number of possible positions inside the delthyrium. This inaccuracy is reflected in THOMSON's diagrammatic reconstruction of the BUCKMAN position (THOMSON 1927, fig. 20). This view shows the hypothyrid foramen completely surrounded by a deltidium, a situation which is not known to occur in either atrypid or rhynchonellid brachiopods for which it was obviously intended. As a result many palaeontologists have tended to select the submesothyrid illustrations of THOMSON (op. cit.) as being typical of the Atrypacea, although the description of the submesothyrid foramen specifies that the ventral apex is at least partly absorbed. It is recommended that BUCKMAN's terms hypothyrid either should be redefined to reflect the foraminal position in atrypids and rhynchonellids and THOMSON's diagram altered, or a new term in addition to the term hypothyrid selected to fit the foramen position in atrypids and rhynchonellids.

Some atrypid species-groups, notably *Atryparia* and *Atrypa* (*Planatrypa*), show a late ontogenetic enlargement of the foramen into the ventral umbo, to which the term submesothyrid could apply. This feature can, on occasion, be confused with fracture or ersoional damage of the umbo, and certainly most such specimens have this as a main cause. However, it is more predominant in some genera than others, particularly in those with appressed rather than orthocline to epicline beaks. It is possible that in *Atryparia* and *Atrypa* (*Planatrypa*) the pedicle remains functional much longer than was previously suspected, and that it needed an exit through the nearest available spot, the ventral umbo. Nevertheless, the submesothyrid foramen is not of taxonomic value since it appears to be mainly a pathological or simply gerontic character. Well-preserved material shows a slight rim around the anterior side foramen. This rim is formed by a slight thickening and curling of the deltidial plates.

STRUVE has accentuated the importance of valve convexity and erected a new genus *Invertrypa* (STRUVE 1961, p. 334) for a species of *Spinatrypa* STAINBROOK possessing a ventribiconvex shell. In a closely related species *Spinatrypa fasciplicata* (STRUVE) both valves are nearly equally convex. Numerous ventriconvex atrypid genera are known (*Gruenewaldtia* CHERNYSHEV, *Anatrypa* NALIVKIN, *Kerpina* STRUVE, *Spinatrypina* RZHONSNITSKAYA and *Carinatina* NALIVKIN), and what is more, all atrypids go through a ventriconvex neanic stage. It is doubtful that convexity is of great taxonomic importance on a level higher than specific, except in such genera where it is consistently developed in all species. An atrypid genus based solely on shell convexity is as untenable as the convexity classification of McEWAN (1939, p. 620). McEWAN divided the atrypid brachiopods into two families, the Atrypidae with dorsibiconvex-dorsiconvex shells and the Atrypinidae with ventribiconvex-ventriconvex shells. No one has ever adopted this unrealistic grouping.

STRUVE (1956) has also attempted to elevate the importance of the 'Doppelkiel' or 'mittleren Rippen-Paar', a crest developed along the apex of the ventral valve, beyond specific bounds. This keel-like ventral elevation is matched by a dorsal depression, and is common to all atrypids, particularly in early ontogenetic stages. In *Plectatrypa* SCHUCHERT & COOPER and *Spirigerina* ORBIGNY, two Silurian atrypids, such a keel is a prominent shell feature. In *Carinatina* NALIVKIN, a Devonian genus probably unrelated to the above, a keel also figures prominently except apparently in early Devonian specimens of *C. salairica* (PEETZ) and an atrypid incorrectly identified in Russia as *C. signifera* (SCHNUR) (in ALEKSEEVA, 1962, Pl. 9, figs. 3, 7). But in other atrypid species-groups a strong middle rib pair is developed in numerous unrelated species.

## Ribs and growth lamellae

Atrypids belonging to the families Atrypidae and Palaferellidae have shells with a radial sculpture of ribs and a concentric sculpture of growth lamellae. The variations in rib structure and growth lamellae are important diagnostic characters which can be used in the field as simple and ready identifications of different genera. Several distinctive types or rib-lamellae patterns can be identified. These types range between two extremes ; tubular, highly arched ribs which grade into undulose, flat, almost vanishing ribs, and strongly deflected, closely spaced growth lamellae which grade into shell-hugging, distally spaced lamellae, or no lamellae at all.

Six main types are listed :

a) imbricate : Atrypa, Anatrypa (partim), Pseudogruenewaldtia.
b) tubular -imbricate: Spinatrypina, Kerpina, Plectatrypa.
c) tubular-lamellar: Desquamatia.
d) tubular: Gruenewaldtia, Carinatina, Mimatrypa.
e) undulose-interrupted: Spinatrypa.
f) undulose: Atryparia.

Some of these are represented on Pl. D. Under a section on ecology it is explained how the growth lamellae may be extended as frills or spines. Spines appear to have developed mainly from an undulose-interrupted pattern (exception Punctatrypa) and frills mainly from undulose, imbricate or tubular-lamellar patterns.

## Shell micromorphology

The radial and concentric surface sculpture of the Atrypidae and Palaferellidae is covered by a thin, crypto-crystalline calcite film which is characterised by fine, microscopic, concentric growth lines. The relief, shape and separation of these lines appears to be markedly different in some genera and may be used in systematic studies (Plate D). Micromorphology has long been an important diagnostic biocharacter in other brachiopod groups, particularly the spiriferids. Atrypids do not have microspinosity and their shell is impunctate. Since they lack such distinctive features, little attention has been paid to their micromorphology.

RZHONSNITSKAYA (1960, Pl. 1, fig. 1e; same illustration repeated in RZHONSNITSKAYA, 1964, Pl. 2, fig. 3), innovated the study of the micromorphology in Atrypacea by comparing a species of Gruenewaldtia with a species of her new genus Pseudogruenewaldtia. She failed to recognize the significance of this microsculpture and classified both genera in the Palaferellidae on the basis of possessing a pedicle collar. Micro-growth lines similar to those on Gruenewaldtia are present in the

# PLATE D

Figs. 1-4. Rib and growth lamellae patterns of four different atrypid genera. The fine concentric growth lines of fig. 1 are typical of the atrypid family Palaferellidae, and the remainder of the family Atrypidae. All x8.

1. *Carinatina plana* (KAYSER 1871). Growth lamellae have retreated to minor and few interruptions but growth lines are accentuated. In between each visible growth line there are 8-10 smaller lines of microscopic size.

2. *Spinatrypa curvirostra* n.sp. Radial ribs are raised and depressed at each growth lamella and arranged in rib "rows". At the lower side some spine bases and broken spines are present.

3. *Atrypa* sp. (Lauch beds, lower Eifelian). The shell surface is marked by an imbricate pattern. Growth lamellae are abundant and closely spaced.

4. *Atryparia instita* COPPER 1965. Ribs have become very broad-crested and narrow-troughed as well as shallow. Growth lamellae hug the surface and are widely spaced.

D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subgenus Desquamatia (Variatrypa) and have been illustrated in COPPER (1965b, Pl. 1, fig. 4). They were also observed in Desquamatia (Variatrypa) zonata (SCHNUR), and D. triangulata COPPER. It is not certain that they are present in the lower Eifelian species D. ovata COPPER and are still to be found in the smaller subgenus Desquamatia (Synatrypa).

The diversity in micromorphology is shown in Plate D. The resemblance between the microscopic growth lines (abbrev. : microlines) of Desquamatia (which have so far been found only in rib troughs) and the microlines of Gruenewaldtia (according to STRUVE also present on rib crests; person. commun.), is puzzling. There are a number of similarities between these genera which need still be explained in terms other than morphological iteration.

In Mimatrypa STRUVE the lines become quite coarse and also extend over the rib crests. The microlines of Carinatina NALIVKIN contain two sets, a coarser set spaced at about a millimeter, and a finer set at 10 per millimeter (Pl. D. fig. 1). This is also not uncommon in Desquamatia ALEKSEEVA.

In Atrypa, Anatrypa, Kerpina and Spinatrypina lines are shallow, more irregular and indistinct, but still somewhat closer packed than in Spinatrypa and Atryparia.

Micromorphology can be a useful asset in determining the genus of specimens, but it seems doubtful at present that it can be used as a familiar or subfamiliar character. Clearly, it destroys the affinity between Kerpina and Carinatina which BOUCOT, JOHNSON & STATON (1964, p. 810) assumed, and seems to draw a closer link between Kerpina and Spinatrypina. The Desquamatia which are abundant in the Frasnian of the famous Bensberg fossil locality, although well-preserved, do not have the microlines that the Eifelian Desquamatia (Variatrypa) species group shows. It is even possible that Desquamatia (Neatrypa) europaea STRUVE 1964 is an end member of the Atryparia species group, to judge on the basis of micromorphology.

## Inner shell surfaces

Most of the palaeontological texts of the last decade have relied on the terminology of the inner atrypid shell surface which was supplied by ALEXANDER (1949, pp. 210-211) in her revision of the genus Atrypa DALMAN. Her figures have become classical and have been repeated in European, American and Russian treatises and text-books. A more up to date version is supplied by VANDERCAMMEN & LAMBIOTTE (1962).

DAVIDSON (1853, Pl. 7, fig. 90) pioneered the study of the muscle scars, the vascular markings and the ovarian pits in the Atrypida. He illustrated a pedicle valve of Atrypa (ibid.), a figure which was imitated in many of the early zoological texts much as ALEXANDER's is in recent literature. DAVIDSON (1853) was able to distinguish, next to the 'cardinal muscles', a set of 'pedicle muscles' (which he believed to correspond to the 'retractor superior' and 'retractor inferior' of OWEN, 1853, p. 8). DAVIDSON probably intended to replace the names 'adductor brevis' and 'cardinalis' of OWEN (ibid.) with his own 'cardinal muscles', but he probably did this incorrectly for the 'cardinalis' is a muscle set located near the hinge line (OWEN 1853, fig. 2). The 'adductor brevis' and the 'cardinalis' are respectively equal to the 'diducture principal' and the 'diducture accessoire' of the modern work of VANDERCAMMEN & LAMBIOTTE (1962, fig, 3). The 'adductor' muscles of DAVIDSON (1853) corresponded to the 'adductor anticus' and adductor longus posticus' of OWEN (1853, pp. 8-9). DAVIDSON's 'cardinal' muscles are the same as VANDERCAMMEN & LAMBIOTTE(s 'diducteur principale' and DAVIDSON's 'pedicle' muscles identical to 'pedenculaire ventral'. The chief muscle patterns which VANDERCAMMEN & LAMBIOTTE designate are easy to recognize, but the minute apical scars are so thinly impressed that they could not be identified even in the best Eifel material.

The terminological confusion became even greater when DAVIDSON renamed many of his muscle terms in 1865. For example, the old cardinal muscles were replaced by 'ventral adjustor' muscle scars (1865, Pl. 11) in a figure, and in the text of a later work (1893, p. 55) called divaricator muscles as was the custom on the continent. In modern usage the term divaricators is changed to diductors.

VANDERCAMMEN & LAMBIOTTE (1962) retained the Davidsonian interpretation that the muscle field lateral to the diductors, was occupied by pedicle muscles. But such a division certainly is not clear in most atrypids, and there is no direct evidence that the pedicle muscles occupied more than a small part of the delthyrial cavity. It seems more likely that the whole field was occupied by the diductors. This was also the the interpretation of ALEXANDER (1949, fig. 1), although ALEXANDER seems not to have paid any attention to DAVIDSON's work along this line. In one specimen of <u>Gruenewaldtia</u> (see Pl. 48, fig. 1) the pedicle muscle has left a clear, circular depression at the base of the delthyrial cavity and does not seem to have extended further than this. It also seems unlikely that <u>Atrypa</u> sensu lato made much use of a pedicle during life and would not require the large scars postulated by DAVIDSON and others. ALEKSEEVA (1962) surmised that the dental plates served as places for the attachment of pedicle muscles, but no markings were observed on these although they would be expected. The most probable place of pedicle attachment must be that of the 'pendonculaire median' (VANDERCAMMEN & LAMBIOTTE 1962, fig. 3), and the 'pendonculaire ventral' is rejected as a possible pedicle attachment.

# PLATE E

Figs. 1-3. The inner shell markings of Devonian atrypids.

1. *Desquamatia* (*Variatrypa*) *zonata* (SCHNUR 1853).

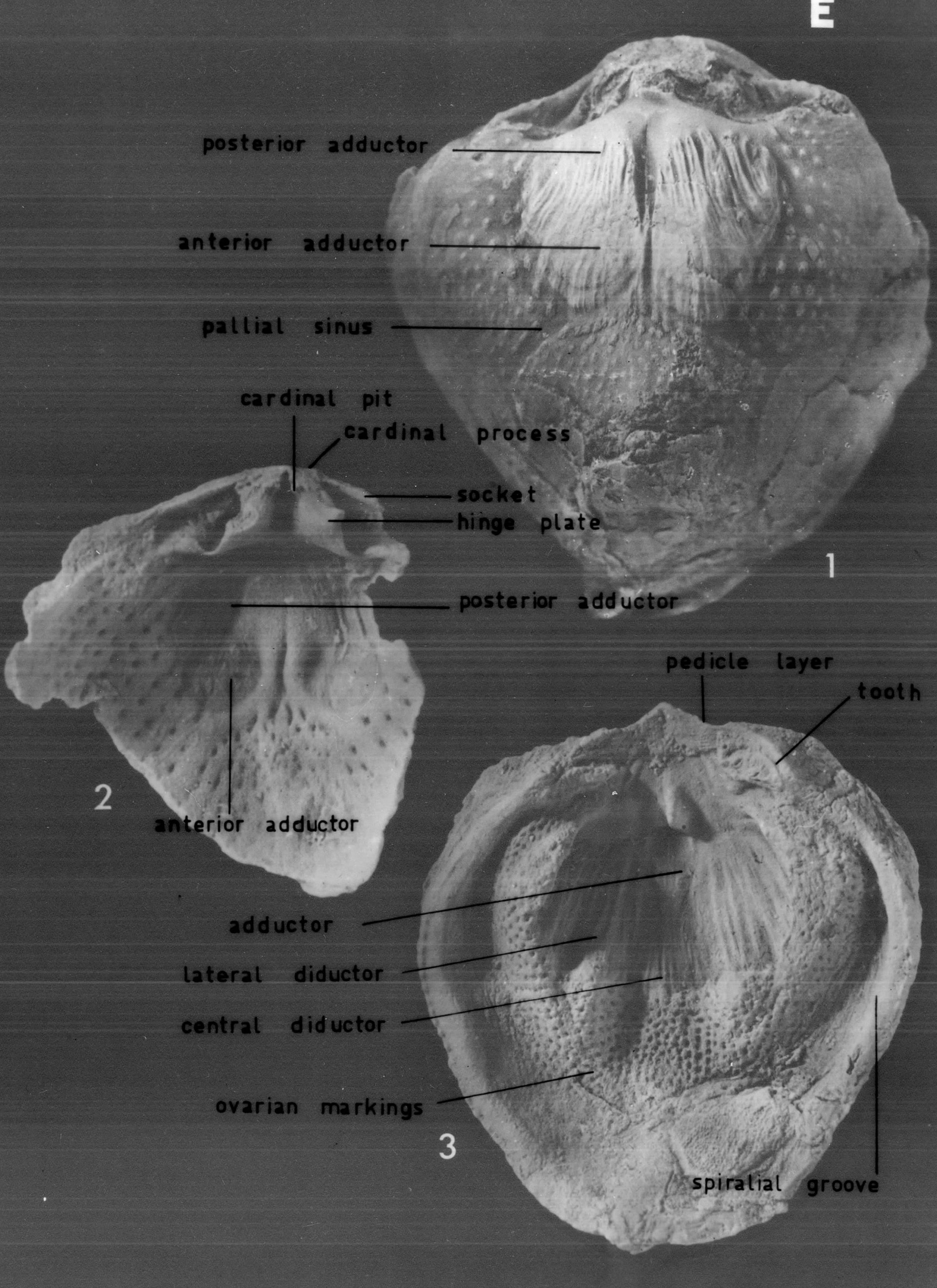
Dorsal view of a decorticated specimen. x3.

2. *Atrypa* (*Planatrypa*) *petasa* n.sp.

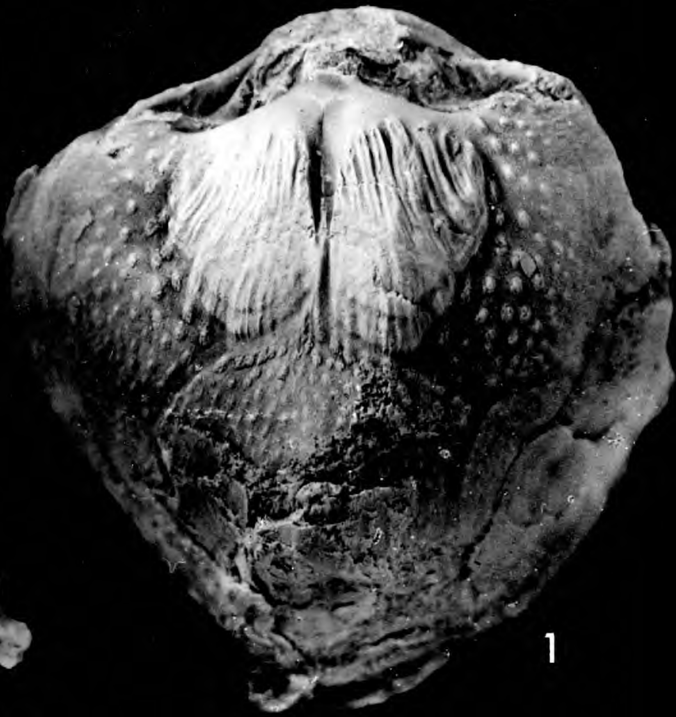
Dorsal valve, loose. x4.

3. *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853).

Ventral valve, loose. x3.


E
posterior adductor
anterior adductor
pallial sinus
cardinal pit
cardinal process
socket
hinge plate
1
posterior adductor
2
anterior adductor
pedicle layer
tooth
adductor
lateral diductor
central diductor
ovarian markings
3
spiralial groove

**E**



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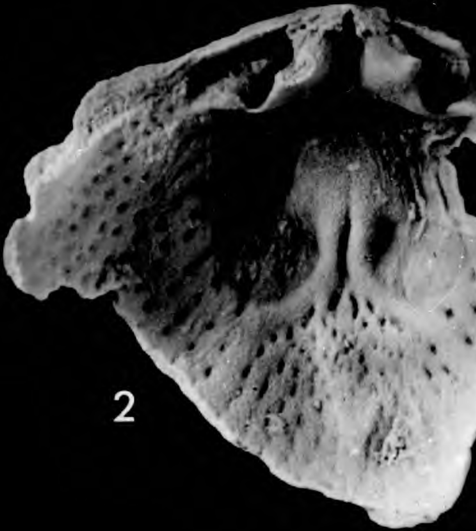

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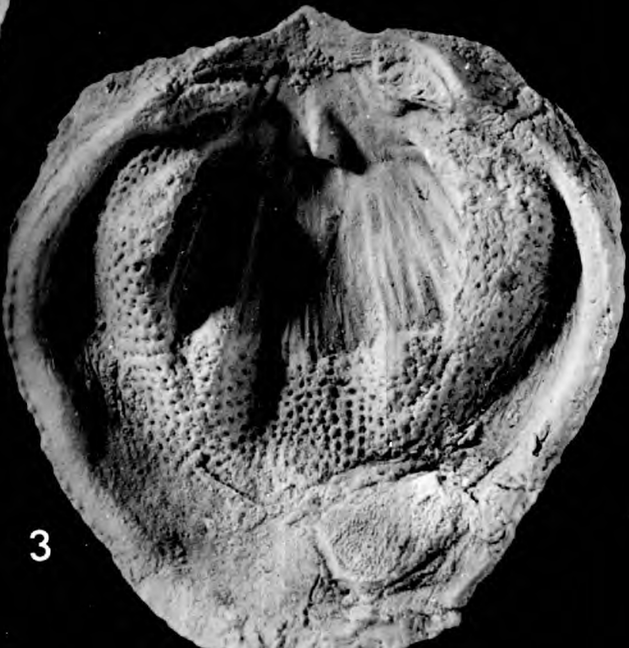


3

The muscle pattern of the brachial valve is not as muddled in the literature. There is general agreement. DAVIDSON (1853, Pl. 7, fig. 91) recognized that the dorsal muscle was divided in two, the posterior and anterior adductors (adductor longus anticus, adductor longus posticus in OWEN 1853, p.8). It was also realized that the diductors were attached to the dorsal apex. ALEXANDER regarded the dorsal adductors as a single scar (1948, p. 212). VANDERCAMMEN & LAMBIOTTE (1962) were able, in addition, to recognize precisely where the diductors were attached on the dorsal apex and even identified pedicle muscles in the dorsal valve. No such scars have been found in Eifel material and the identifications are treated with some skepticism.

The pallial arteries, vascula myaria and vascula media are not always well marked. The latter particularly are not always present, e.g. in Atrypa (Planatrypa) they are wholly obscured. The vascula media, the smooth arterial ridges flanking the muscle field and extended toward the anterior margin, are best seen in species of Desquamatia (Pl. E, fig. 1). It is probably characteristic of that genus. VANDERCAMMEN & LAMBIOTTE (1962) have given a combined name for the pallial arteries and vascular systems, and called them angioglyphes, and have grouped ovarian markings under the term sarcoglyphes. The terminology suggested by WILLIAMS (1956), vascula media, gonadal sacs, vascula genitalia and vascula myaria, is difficult to apply to the atrypid brachiopods. No attempt is made, other than a generalized one, to map in detail the pattern of pallial sinuses and ovarian markings. This is to be left for later study. At present they do not appear to be very useful in diagnosing atrypid genera.

It is possible that Silurian and Devonian, at least Middle and Upper Devonian, atrypids may be separated by differences in angioglyphes. The Devonian species, except those belonging to Desqua matia, and some of the Spinatrypa, show suppression of the angioglyphes and a thickening and enlargement of sarcoglyphes.

The dorsal adductor impressions are divided by a weak ridge stretching from the cardinal pit to tha anterior margin of the muscle field. Where the adductors become more widely separated from each other the septum bifurcates. The septum (Latin, barrier, partition) hasbeen given various names in atrypid brachiopods. ALEXANDER (1949, p. 211) called it a pseudoseptum, but made no attempt to distinguish if from a real septum. CLOUD (1942, p.. 7, 14), in his study of Devonian terebratuloids coined two new terms for such dividing structures. The first, breviseptum, was applied to a short partition independent of the muscle scars. The second, myophragm, was proposed for a median ridge dividing the muscle field of the brachial valve. CLOUD (ibid., p. 13) restricted the term median septum to mean a prominent median plate in either valve. The basic difference between the last two terms appears to lie in their function, the one merely dividing a muscle field, the other acting as a support for a cruralium or septalium or to serve as a muscle attachment.

There is no doubt that CLOUD' myophragm is the term which applies strictly to the dorsal partition in atrypids and is more accurate. Unfortunately its application has been abused in atrypoid systematics, with some authors claiming to have found true middle septa in atrypids, and others equally staunchly refuting these and substituting myophragms. POULSEN (1943) has even erected subfamilies and families for atrypoids with median septa and without. VEEVERS (1959, p. 119) did not separate a myophragm from a median septum, but nevertheless attached great significance to rather minor differences in the size of septa. VEEVERS (ibid.) believed that 'the broad median ridge of the dorsal valve is found only in forms of *A. reticularis*'. This is not the case. All the atrypid brachiopods of northwestern Europe examined in this study had developed septa to a greater or lesser degree. It can be safely asserted that no major groupings of the atrypids, into those with median septa and those with myophragms, is possible and that this structure is of little taxonomic value on higher levels. The word myophragm (Greek, myos, muscle; phragmos, partition) appears to be unnecessary as it is applied to the atrypids, and also rather ambiguous since it implies a particular function. The term median septum is simple and descriptive, in itself implying no function, and therefore wholly adequate. It has been used throughout the thesis.

## Shell wall structure

The wall of the atrypid shell, excluding the parts which make up the cardinalia and brachidia, is composed of three separate units, an outer layer, a fibrous layer and a columnar layer (see Pl. F). The wall is impunctate.

Some confusion exists in the terminology used to identify the shell layers, and such terms as prismatic, fibrous, lamellar and columnar have been employed interchangeably, and not always for the same layer. The outer layer is very thin (usually less than 0.1 mm) and crypto-crystalline. It covers the whole shell surface except the deltidium, and varies slightly in thickness at the shell margins and on the rib crests and tib troughs. This layer is rather rarely preserved. *Mimatrypa flabellata* C.F. ROEMER) shows a thickening of up to 1 mm of this layer at the margins, but this is remarkable. ALEXANDER (1949, p. 212) failed to find this outer layer in *Atrypa*, although in her revision of *Conchidium*, a pentamerid brachiopod, she described it as 'the outer shell layer' (1948, fig. 3). VEEVERS (1959, pp. 119, 123, figs. 72-75) confused the outer layer with the next, lamellar layer : in *Spinatrypa* he correctly named the outer layer, but in *Atrypa* he failed to find the true outer layer and called the lamellar layer the outer layer. However, VEEVERS appears to have been the first author to recognize the layer at all in atrypaceids. Its thinness has accounted for the fact that it is often overlooked. ALEKSEEVA (1962) also failed to find it. DUNLOP (1962) described the same layer in her study of *Spirifer trigonalis* and called it the lamellar

# PLATE F

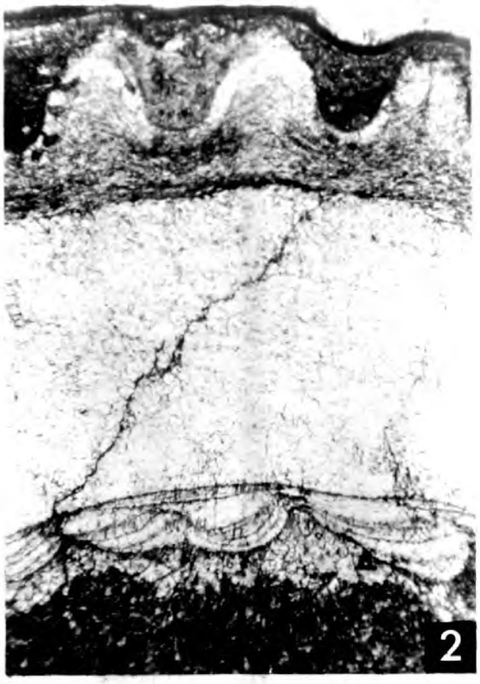
Fig. 1. <u>Kerpina vineta goniorhynchia</u> STRUVE 1961.
Transverse section of the ventral wall. Thin outer layer (dark) visible on rib crests. Thick fibrous layer and equally thick columnar layer. Serial acetate peel at 3.5 mm. x50.

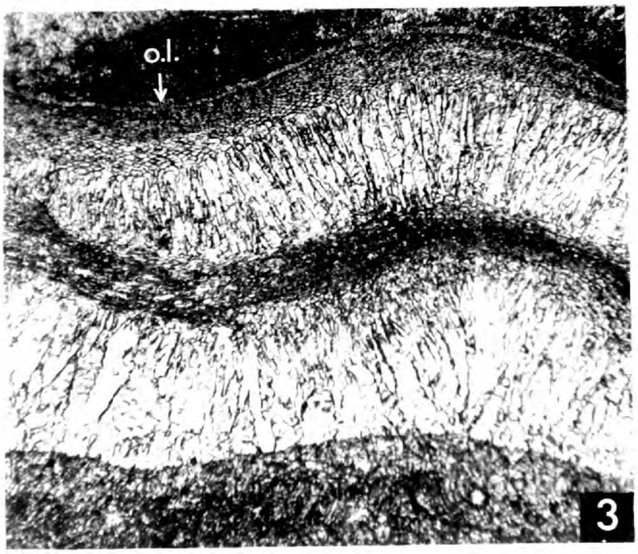
Fig. 2. <u>Mimatrypa flabellata</u> (C.F. ROEMER 1844).
Transverse section of the dorsal wall. Thick outer layer, thin fibrous layer, thick columnar layer. Serial acetate peel at 4.6 mm. x50.

Fig. 3. <u>Spinatrypa curvirostra</u> n.sp.
Transverse section of the wall. Thin outer layer (o.l.), two successive fibrous and columnar layers. Serial acetate peel at 4.7 mm. x50.

Fig. 4. <u>Gruenewaldtia latilinguis</u> (SCHNUR 1851).
Transverse section of the ventral valve. Arrow pointed at the supporting septum of the muscle platform. Columnar layer thickens the platform. Serial acetate peel at 3.6 mm. x50.

**F**





layer. It is not truly lamellar however because it consists of a single crystal sheet, and the term lamellar is preferred for the next shell layer which is composed of true lamellae. Tme outer layer corresponds to the primary layer of WILLIAMS (1956, p. 249). A chitinous periostracum, a layer which forms the outermost covering of Recent impunctate brachiopods, has never been found preserved in Atrypida.

The second, fibrous layer, consists of numerous acicular calcite crystals which are arranged in radial lines and form thin lamellae which overlap each other. In transverse section these crystals are diamond shaped. The frills and growth lamellae are mainly composed of these crystals, each layer being deposited underneath and slightly anterior to an older layer. The diameter and size of the crystals varies from species to species although Gruenewaldtia, Mimatrypa and Spinatrypa have consistently larger crystals. ALEXANDER (1948, p. 149, fig. 3c), again in describing Conchidium, has called this layer the 'inner shell layer' and for Atrypa (1949, p. 212) the 'outer layer', although structurally these layers are the same in both genera. The fibrous layer forms only a part of the 'secondary shell layer' of WILLIAMS (1956). WILLIAMS rightly referred to the fact that among some fossil brachiopods, including atrypids, a third calcareous shell layer is found which 'although distinctive in appearance, is simply a modification of the secondary layer' (WILLIAMS, 1956, pp. 249, 250). Each prism in the fibrous layer does in fact coincide with a crystal in the columnar layer, but the shape, size and distribution of these layers is so different that a distinction must be made. DUNLOP (1962, p. 483) also called this layer the fibrous layer. SCHROCK & TWENHOFEL (1953, p. 266) have called the layer 'prismatic'; MOORE, LALLICKER & FISCHER (1952, p. 204) called if 'fibrous'.

The third, columnar layer1 consists of thick, short and coarse columns of crystals normal to the shell wall and always located inside the fibrous layer. The crystals are structurally continuous with the fibrous layers' crystals but nearly at right angles to these. The columnar layer is only thinly spread at the shell margins : its maximum thickness is attained underneath and around the muscle bases, and usually it is much thicker on the pedicle valve. This layer is the 'inner layer' of ALEXANDER's Atrypa (1949, p. 212), and VEEVER's Atrypa (1959, p. 118, text-fig. 72), although the latter author also called the fibrous layer by this name (ibid,. p. 123) in a species ascribed to Spinatrypa. In Conchidium ALEXANDER (1948, p. 149) referred to it as prismatic.

Each of the layers described by DUNLOP for Spirifer trigonalis is typical of the atrypids under study and such development features as interfingering, interlayering and growth discontinuities of the fibrous and columnar layers are present. There are some differences from one atrypid genus to the next in the distribution and size of the fibrous-columnar layers. In Gruenewaldtia and Mimatrypa the lamellar layer thins our considerably and the columnar layer becomes massive. These two genera also show little of no interlayering of fibrous and columnar crystals. The disappearance of numerous interlayers is also typical of Spinatrypa, Desquamatia and Spinatrypina, but the early Devonian species of Desquamatia still show quite a few layers. This is possibly a phylogenetic trend in off-shoots from the main Atrypa stock. It should be noted also that Gruenewaldtia and Mimatrypa (and it appears in the genera Karpinskia, Vagrania as well) the loss of numerous interlayers and thinning of the fibrous layer is accompanied by a complete reduction of frills.

Examples of the different shell layers are given in Pl. F, figs. 1-4. As many as six or seven columnar layers may interfinger with lamellar layers. It is difficult to show so many layers in the drawings of serial peels. Usually the columnar layers are much thicker and these are then shown as one. The initial columnar layer at the apex appears to be deposited rapidly since it is thick and uninterrupted. Later layers tend to be thinner. The muscle platform of Gruenewaldtia (Pl. F, fig. 4) is strengthened by columnar crystals, but the muscle plate itself is only a thin, monocrystalline sheet. The major septa have a spine which is connected directly to the muscle plate, but minor septa lack this stiffening although they may still be quite prominent. Remnant septa are very short, discontinuous and not regular throughout one species. The origin of the muscle plate in Gruenewalatia remains obscure. The linings of the lateral cavities and the dental nuclei also are lined by columnar crystals.

## Internal shell structures

Very little is known about the structure and composition of the inner parts of the atrypoid shell and a major portion of the study was absorbed in a re-examination and redefinition of all the inner parts in order to determine their structure and origin. It became clear from the beginning that a number of misconceptions exist and that these had to be clarified. In spite of the long history of research into this extinct branch of brachiopods, it was not until 1962 (SIEHL) that the growth and structure of some atrypoid shells was demonstrated in serial sections.

The first descriptions of the calcareous spires is that of DEFRANCE (1827, p. 295), who promptly referred the atrypid in his collection to a new species Spirifer sowerbyi. The plates to the 'Dictionnaire' in which DEFRANCE's species appeared were prepared by BLAINVILLE and are also the first illustrations of the calcareous spires in an atrypid. The same plates also were published in BLAINVILLE's 'Manuel de Malacologie et Conchyologie' (1827, P. 54). ORBIGNY (1847, p. 268) grouped all the spire-bearers into the Spiriferidae, a classification which has survived to the present day.

WHITFIELD in 1867 described the discovery of a loop which he alleged connected the spiral cones of Atrypa. Ih nis figures there is no doubt that this loop referred to the jugal processes. GINLEY (1878, quoted incorrectly by DAVIDSON & DALTON as GURLEY) questioned that these processes actually were connected, and gave correct illustrations of the disconnected jugal processes in Atrypa (GINLEY , Pl. 14, figs. 1-4). Subsequent authors have shown processes connected or disjunct (sometimes in the same species!) or showed some connected but others apart. WOODWARD (1856) was the first skeptic of the popular assumption that Atrypa belonged to the Spiriferidae because of its spiralia, stating, 'The shells of this genus differ from Rhynchonella chiefly in the calcification of the oral supports, a character of uncertain value' (WOODWARD, 1856, p. 299). Accordingly he grouped Atrypa in his Rhynchonellidae

The shell components can be divided into three parts, each part identified by its own calcite structure. These three parts are :

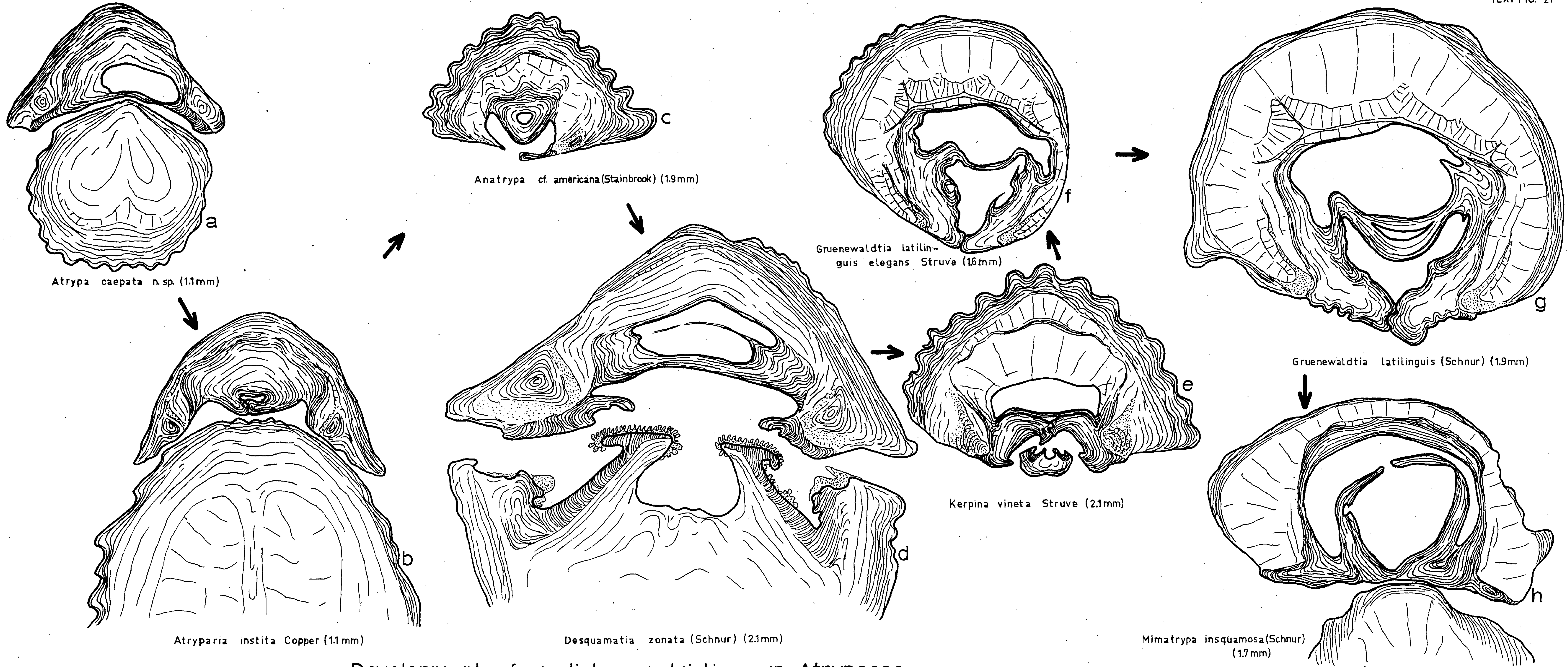
(1) umbonal structures - pedicle layer, pedicle collar, deltidial plates and cardinal process.
(2) hinge structures - teeth, dental pads, dental ridges, dental nuclei and lateral cavities, dental plates and the corresponding hinge plates, hinge pads, socket plates and socket ridges and crural bases (refer to text-fig. 22).
(3) brachial structures - crura, jugal processes, jugal plates and spiralia.

The umbonal structures must have had a common origin for they consist of thinly layered, cryptocrystalline calcite. Mostly the pedicle layer, pedicle collar and cardinal process are irregularly and often asymmetrically distributed abcut the umbones. They are inconsistently developed even within one species. The deltidial plates are more permanent, regular structures and only rarely asymmetric. Nevertheless the deltidial plates must be closely linked to the remaining umbonal structures because they form unified structures in some atrypoid genera.

The parts of the pedicle valve which served to restrict or constrain the pedicle muscle are variably developed in different atrypid taxons and may be a valuable criterion in the separation of genera. An outline of the phylogenetic cline is given in text-fig. 21.

In Atrypa and Atryparia the delthryial cavity is lined by a thin tissue of calcite in the form of a tapering pipe closed at the foraminal end or open on the dorsal side (Pl. H, fig. 3; text-fig. 21). This pipe is not freed from the ventral side of the cavity. The name pedicle collar is not used because either the end of the pipe is blocked (with no pedicle exit) or the dorsal side is open and the term collar cannot be strictly applied. JACKSON (1916, p. 24) introduced the term pedicle collar as 'a kind of continuation of the deltidial plates, ....free in front and separated from the shell by a narrow cavity'. Deltidial plates

TEXT-FIG. 21



Atrypa caepata n. sp. (1.1 mm)

Atryparia instita Copper (1.1 mm)

Anatrypa cf. americana (Stainbrook) (1.9 mm)

Desquamatia zonata (Schnur) (2.1 mm)

Kerpina vineta Struve (2.1 mm)

Gruenewaldtia latilinguis elegans Struve (1.6 mm)

Gruenewaldtia latilinguis (Schnur) (1.9 mm)

Mimatrypa insquamosa (Schnur) (1.7 mm)

Development of pedicle constrictions in Atrypacea

×16

are primitive or absent in Atrypa-Atryparia group and since there is no cavity to separate the layer from the shell wall, JACKSON's term is inapplicable. JACKSON (ibid., p. 25) mentions that the discovery of this structure can be attributed to FISCHER & OEHLERT (1891). THOMSON (1927, pp. 73-74, fig. 21) adopted JACKSON's definition and illustrated the pedicle collar. THOMSON, in saying that the pedicle collar 'is commonly free anteriorly' (ibid., p. 74), did not therefore preclude the possibility that it might also be attached for its length. The term pedicle layer is here defined as any calcite layer, excluding the well-developed structures of the deltidial plates, which lines the delthyrial cavity and is not freed for any part of its length or which does not lead to a foramen. This leaves the term collar for a strict application of a pipe-like structure freed from the shell wall for a whole or part of its length and leading to a pedicle opening. The latter structure is common to Desquamatia zonata (SCHNUR), Anatrypa spp., Kerpina spp., Mimatrypa insquamosa (SCHNUR), Gruenewaldtia latilinguis (SCHNUR), G. apsaklina STRUVE. Phylogenetically, the Atrypa-Atryparia like pedicle layer is believed to be the most primitive and stable type of deltidial structure. It is developed only in atrypids which lack an area or exposed deltidium. From this type of pedicle layer it is probable that deltidial plates evolved through a thinning of the ventral portions of the pedicle layer and division and separation of the dorsal portion.

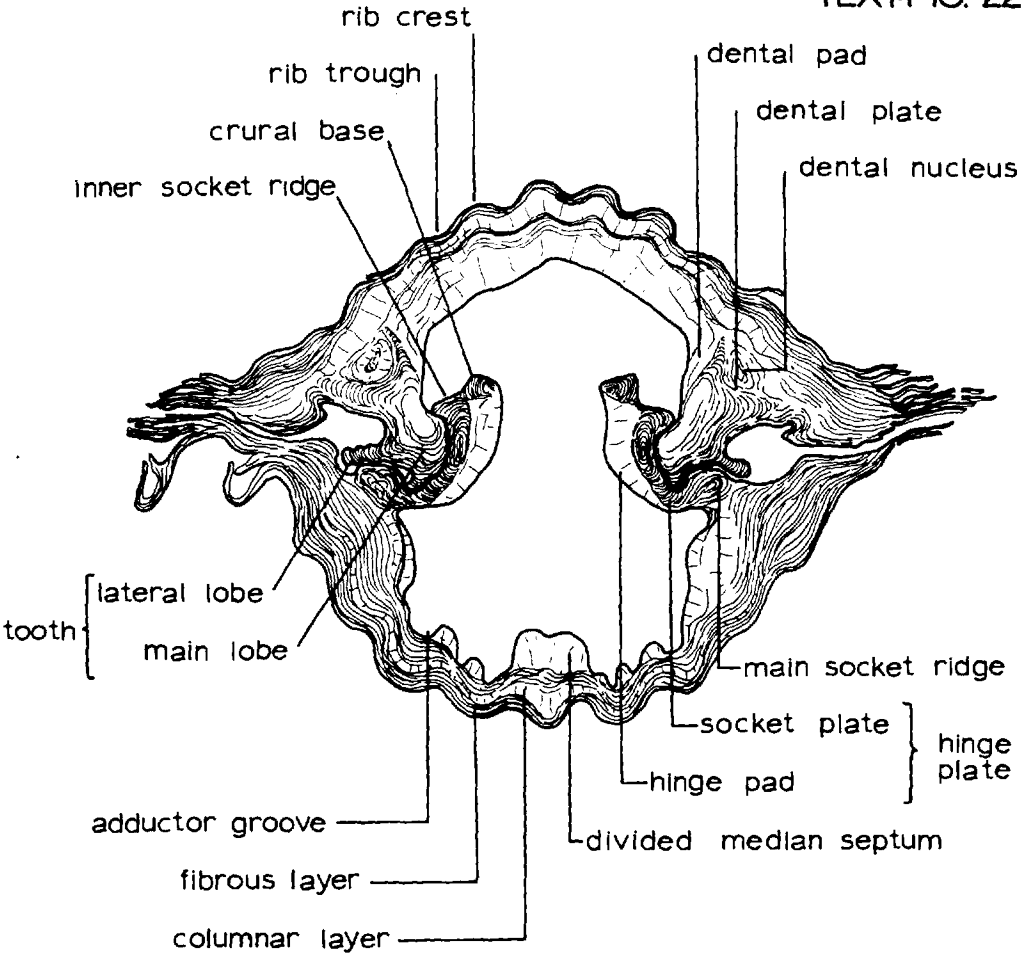
In Spinatrypa, Spinatrypina and Desquamatia many species have well developed deltidial plates (hollow) but lack a pedicle collar. The delthyrial cavity in such species is constricted by thick columnar shell layers, often rather asymmetrical and with a deep median groove. Two lateral grooves are not uncommon. This type of delthyrial infilling is not a true pedicle layer because a few species, e.g. Desquamatia zonata (SCHNUR) and Spinatrypa coriacea CRICKMAY also show the development of a collar. These collars are separated from the deltidial plates (text-fig. 21). The disappearance of a pedicle layer and accentuatuon of deltidial plates appears to be a more progressive character.

Kerpina has a complete, attached pedicle collar which touches and supports the inner side of the deltidial plates. A suture between the collar and deltidial plates is visible. It is thought to be a rather advanced stage of development, preceding a complete fusion of collar and deltidium. Anatrypa, although it is a much younger atrypid than Kerpina, has a more 'primitive' development of a free, or partly attached collar with very short and primitive deltidial plates. But there are strong similarities between these two genera.

The origin of pedicle collars is uncertain. They are present in a number of unrelated atrypid genera. They are yet to be found in Spinatrypina and Carinatina. The first published account of pedicle collars in the atrypid brachiopod group,is that of RZHONSNITSKAYA (1960, Pl. 2, figs. 1a-e). Her drawings tell us little about the origin and development of this structure. RZHONSNITSKAYA (1964) repeated her illustrations four years later and also described the discovery of a pedicle collar in her genus *Pseudogruenewaldtia* in which she had not previously noticed it. IVANOVA (1962, fig. 31) also observed a pedicle collar in the genus *Gruenewaldtia* CHERNYSHEV. Unfortunately RZHONSNITSKAYA attached great significance to the presence of a collar even though it is quite clear that the genus *Pseudogruenewaldtia* RZHONSNITSKAYA is not at all related to *Gruenewaldtia* CHERNYSHEV. Pedicle collars were described and figured in COPPER (1965a, figs. 3-8; 1965b, fig. 34). They are now known to occur in a wide range of unrelated atrypid genera. In general they appear to be late ontogenetic, late phylogenetic features, but they may not even appear in all specimens of a single species with a collar. The earliest species of *Desquamatia* and *Spinatrypa* are without collars, but youngest species are just as barren. Collars are absent in *Atrypa* and *Atryparia* from the Eifel region, and appear to be developed only in specimens which have areas and exposed deltidial plates. It is rather striking that two Eifelian species with pedicle collars, *Desquamatia zonata* (SCHNUR) and *Gruenewaldtia latilinguis elegans* STRUVE, also should have more strongly incurved beaks than other Eifelina species of the same genera. It seems that the orthocline, weakly anacline beak positions of deltidiate atrypids are not conducive to collar development. This would suggest that collars are more prominent when the pedicle begins to lose its function, and that calcification is mainly a gerontic feature. This does not apply to all the Atrypida for in *Kerpina*, *Mimatrypa* and Eifelian *Gruenewaldtia* the associated collars and deltidial plates are integral characteristics.

It is in *Mimatrypa* and *Gruenewaldtia* that the common origin of collars and deltidia is seen clearly in the atrypids. The intergrading, overlapping species series leading from *Gruenewaldtia* to *Mimatrypa*, which was demonstrated in COPPER (1964), convincingly shows the evolution of a fused, monostructural collar-deltidium. An illustration of the end-product is in text-fig. 21. Not all species of these two genera show specialized collar-deltidia, but a peculiar incurvature of the deltidial plates is consistently developed in the group. It is obvious that this structure is related to the presence of a collar and that it is not merely the fault of inwardly twisted deltidial plates. The crude figures of RZHONSNITSKAYA (1960, Pl.22) probably are related in function except that these are directed outwards from a collar rather than inwards from deltidia. The umbonal structures in the *Gruenewaldtia*-*Mimatrypa* group, and particularly the deltidial plates are very firm, solid crystalline structures, which lack growth lines excpet on outer layers, (Pl. G, fig. 3). In *Mimatrypa* the deltidial plates are completely fused near the dorsal umbo and no suture line is visible. The German term for deltidial plates which have medially grown together into a single plate is *syndeltarium* (see STRUVE, 1964, p. 434). but it should be remarked that this term is apparently not always used correctly. *Gruenewaldtia* is said to have a

TEXT-FIG. 22



*Spinatrypa curvirostra* n.sp.
(x6; 3.3mm)

# TERMINOLOGY OF INTERNAL PARTS

syndeltarium (Pl. H, fig. 1) when clearly in sectioning it is seen that it does not (STRUVE 1955, 1964).

The later Givetian Mimatrypa show a retreat of the pedicle collar, although the fused deltidial plates remain. In Mimatrypa flabellata (C.F. ROEMER), M. desquamata (SOWERBY) and M. fretterensis n.sp. the collar has become a thin circular layer on the ventral side of the delthyrial cavity or has gone entirely.

Hollow deltidial plates, as compared to solid ones, appear to mark 'advanced' stages in atrypid development. Thin, delicate hollow plates do not appear until late Eifelian-early Givetian time in Desquamatia of the Eifel, and until middle Givetian time in Spinatrypa of that area. The earliest plates are rather short, stubby and solid. Although no one has described hollow plates in Silurian atrypid genera, it is likely that they are less frequently present in rocks of that age. Sections of the deltidial plates indicate that hollow plates become thicker by accretion of calcite on their inner rather than outer margins. The function of this hollow groove is not understood.

A tightly crenulated pattern may mark the outer surface of the deltidial plates. In section it is seen that these crenulations are only 'skin-deep' and scar only the outermost layer (Pl. G, fig. 3). Crenulations are common to all the deltidiate atrypoids.

Deltidial plates show a complex lock medially. They may touch along a straight line, overlap or join each other by means of ball and socket, mortice, mitre or rabbet joints (Pl. G. fig. 3). There is no consistent locking structure developed for any genera (Pl. H, figs. 1, 2, 4).

The pedicle valve is fitted with teeth which form part of the articulatory device of the shell (see text-fig. 22). The tooth, consisting of a main and a lateral lobe, is supported by a dental plate which commonly straddles a dental nucleus or lateral cavity. The correct usage of the term dental plate is discussed in COPPER (1965b). Much of the misunderstanding about the dental plate arises from inadequate knowledge of its structure. In the literature it is a common argument to state that an atrypid lacks a dental plate if there is no lateral cavity to separate it from the shell wall. In other words, the absence of a lateral cavity has come to mean the absence of a dental plate, a corollary which is false. The dental plate may be solid, as in many Atrypa, as in Karpina and Mimatrypa, or it may have a nucleus of circular growth lines (a dental nucleus) as in Atryparia, some Atrypa and Anatrypa (possibly Atrypa (Devonatrypa). The nucleus may expand and become a lateral cavity : such is the case in Spinatrypa, Spinatrypina and Desquamatia and in some, but not all Carinatina. Lateral cavities do not appear to be useful in defining taxa larger than genera, although they may be a help in fixing the generic status of species. Lateral cavities are developed independently in several species-groups. The species-groups Spinatrypa, Spinatrypina, Desquamatia and possibly Carinatina have a development history showing a gradual expansion and widening of lateral cavities with time. The full development of lateral cavities was accomplished at different times in these groups. In Spinatrypina lateral cavities developed very early and are present in even the lower Eifelian species. But the thin and long dental plates of other genera are absent. In Spinatrypa the first full-fledged, wide lateral cavities are found in the lower-middle Givetian species S. orthoclina n.sp. Not a single Eifelian Spinatrypa has more than a minute hole. Lateral cavities in European Spinatrypa tend to be rather elongated parallel to the shell wall. In Desquamatia the first large lateral cavities are not found until late Eifelian time. The youngest Desquamatia from the Eifel (COPPER 1965b) shows remarkably thin dental plates and large triangular cavities. Middle and lower Eifelian species including D. zonata (SCHNUR) show a marked tendency towards infilling of the cavities, mainly with columnar calcite. These phylogenetic trends in European atrypids may reflect world-wide trends, and if this is so, the lateral cavities may serve to date species of these genera. Frasnian species appear to show a return to a small nucleus or loss of cavity. Pl. J shows a few of the variations in lateral cavities.

ALEKSEEVA (1962, p. 22) asserted that a study of Russian atrypids clearly indicated that 'dental plates' (in the old usage) were developed in all atrypids with a marked area and orthocline beak. The internal structure of Gruenewaldtia, Mimatrypa, Carinatina and Kerpina contradicts this statement . Moreover, on the basis of this constant parallelism in Russian atrypids, ALEKSEEVA claimed that dental plates must have served as attachment for the pedicle muscles. There is no longer any evidence to support this theory and a great deal to contradict it. The function of the dental plates appears to be clear - they must have supported the teeth. This function is clearly implied in a literal translation of the German term for dental plates, 'Zahnstütze' (KELUS 1939, p. 15; STRUVE 1956, p. 394). ALEKSEEVA (1962, p. 22) also argued that there was only one place for the pedicle muscles to be fastened to, the dental plates, since the rest of the delthyrial cavity was occupied by diductor and adductor muscles. But loose valves show that the adductor muscles of the pedicle valve are small and medial and the diductors large and anterior, and that both left prominent scars nowhere near the delthyrial cavity. In Gruenewaldtia (Pl. 48, fig. 1) the pedicle muscle has left a large circular scar at the base of the delthyrial cavity (at present the only atrypid genus to show this scar). There seems to be no valid reason or justification for assuming dental plate attachment of the pedicle muscles when these muscles have left no indications of their presence on the dental plates but have left clear and identifiable traces on other parts of the shell. The thin pedicle layer near the ventral apex of Atrypa (Planatrypa) (Pl. E, fig. 3) as well as in other genera (Pl. 10, fig. 2; Pl. 9, figs. 1-4) is the most likely point of attachment for the pedicle. Studies of recent brachiopods (viz. WILLIAMS 1956) support this view.

Various authors have stressed differently the value of 'dental plates' (read lateral cavities) in taxonomy of the atrypids. RZHONSNITSKAYA (1959) thinks it diagnostic of one atrypid subfamily.

There is a broad correlation between orthoclination of the beak and the presence of lateral cavities, and also the more coral-rich or multispecific brachiopod rich facies. For example, the Givetian Spinatrypa orthoclina is commonly associated with the coral colonies of Hexagonaria but evidence is lacking that this association was due to direct attachment of the brachiopod on the coral, with the deduction that the pedicle remained functional and hence the lateral cavities were useful in pedicle attachment. This chain of arguement is too indirect and unsatisfactory. It is repeatedly argued that a functional pedicle would keep the beak from curving inwards, and that therefore specimens with incurved beaks had nonfunctional pedicles. Since there are now several genera known which have marked interareas and large pedicle openings and deltidial plates, but still lack lateral cavities (or dental plates in the old sense), the association of orthoclination and lateral cavities must be ruled out.

The dental plate and tooth are composed of finely layered, minute fibrous crystals (about one tenth the diameter of fibrous layer crystals). Apically these crystals appear as a slender stalk with a bulbous end about which the deltidial plates or pedicle layer is wrapped (in transverse section), but distally they broaden out to include all of the tooth and dental plate. It is difficult to show these apical sections except by means of dots in drawings. The dental plate is built around the dental nucleus (in genera which have such nuclei), which lies at the base next to the shell wall. Flanking the inner margin of apical portions of the dental plate is a thick bulging layer called the dental pad. Where the dental pad is sufficiently thickened and angular it forms a ridge against which possibly the crura found a resting place. The dental pad seems to consist of columnar crystals which are oriented at a different angle to the main body of columnar layer. A corresponding structure on the brachial valve is the hinge pad which seems to have strengthened the socket plate. It should be noted that the teeth and socket plates are composed of identical shell material.

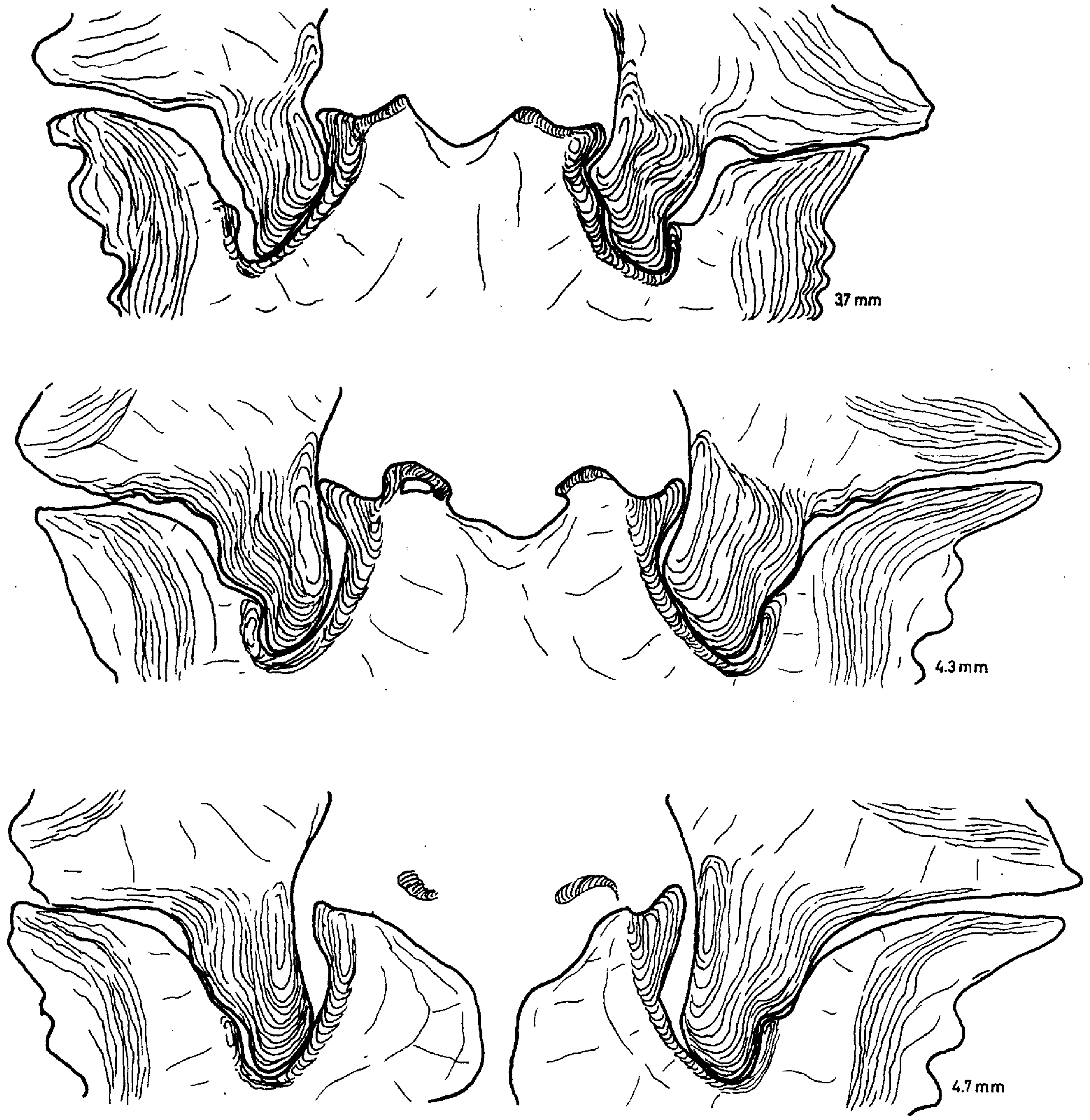
The direction of the tooth is variable, although quite consistent infraspecifically. It is not greatly affected by shell convexity. If an axis is drawn through the centre of the dental plate and the main lobe the globose convexoplane Mimatrypa flabellata (C.F. ROEMER) has nearly vertical teeth and the planar Carinatina plana (KAYSER) has sub-horizontal teeth. But the ventribiconvex Gruenewaldtia latilinguis (SCHNUR) also has subvertical teeth and the planoconvex Kerpina vineta goniorhynchia STRUVE sub-horizontal teeth. The direction of the teeth appears hardly to be influenced by convexity of the pedicle valve. Most biconvex shells have obliquely directed teeth.

The main tooth lobe may be geniculated in respect to the dental plate. Geniculation is more marked in somewhat flattened species. Species with nearly vertical teeth rarely have well developed lateral lobes. The best lateral lobes are seen in Spinatrypa and Desquamatia. The margin of the pedicle valve which lies outside the tooth may serve as an accessory hinge device. This margin often is flattened and may even hold a notch which fits into a groove on the opposite valve. This type of accessory hinge device is called a denticulum in rhynchonellids, and is present in Atrypa (Planatrypa) and some Spinatrypa and may also function in the emarginate Desquamatia triangulata COPPER. It is not a diagnostic feature.

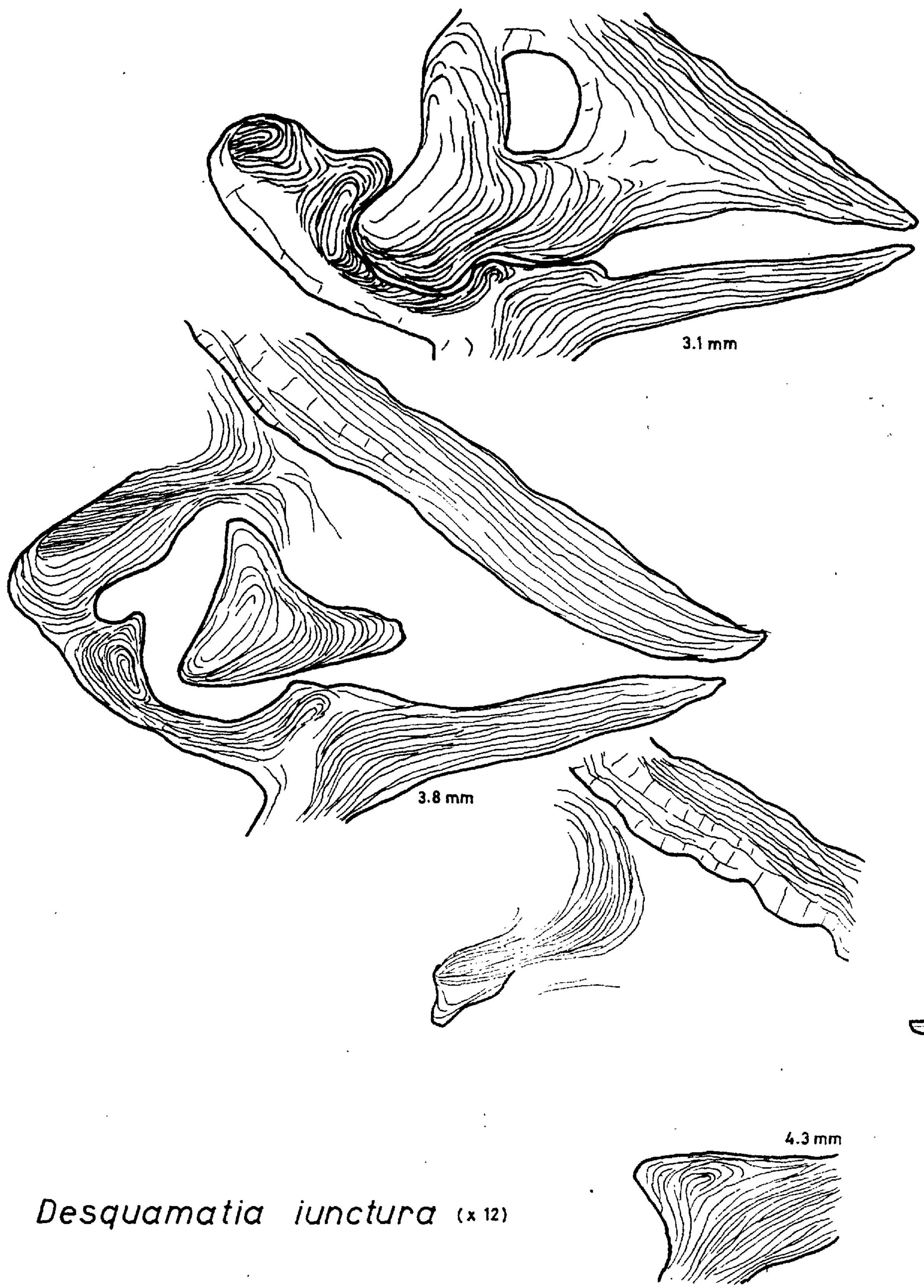
The presence of a cardinal process, a pad to which the diductor muscles were attached on the brachial valve, has long been overlooked in atrypid studies. As late as 1949 ALEXANDER (p. 208) said that Atrypa had no cardinal process, although she noted that a space for the diductor muscles existed between the crural bases (ibid., p. 212). VANDERCAMMEN & LAMBIOTTE (1962, p. 12) were the first to examine a cardinal process in the Atrypa group. Subsequently they were also found by BIERNAT (1964), BOWEN (1964) and COPPER (1964, 1965a, b, c, d). The cardinal process consists of a bushy, mushroom-like growth of cryptocrystalline calcite in the notothyrial pit and overlapping the apices of the hinge plates (Pl. I, figs. 1, 4). Not uncommonly the cardinal process grows even further and spreads along the dorsal hinge **margin** into the socket cavities. The apices of these socket cavities are unoccupied in mature stages. The source of the cardinal process is possibly the same kind of epithelial layer that deposited the ventral umbonal structures.

The notothyrial pit is a small pocket which occupies the point where the hinge plates join. The word was coined by STAINBROOK (1954, p. 49); its German equivalent, 'Notothyrialrinne' (SIEHL 1962, p. 185) means notothyrial trough. The septalium of other brachiopods possibly is a distant homologue or analogue, whether it corresponds in structure or origin is uncertain. If transverse serial sections are taken of globose specimens or specimens oriented more obliquely to the brachial valve, the misleading appearance of a full 'septalium' may be simulated (text-fig . 83-84). Similarly ,a 'strong' or 'weak' median septum can be artificially created by differing orientations of the shell. POULSEN (1943, p. 40) attached great importance to the notothyrial pit in his classicication (calling it a 'narrow fissure') and used it in separating two new subfamilies, the Clintonellinae and Lissatrypinae. POULSEN (ibid., p. 41) also argued that in some genera the hinge plate was 'supported' by a median septum. POULSEN thereby fell into the two main pitfalls of serial sectioning, describing sections in two dimensions and misinterpreting differently oriented specimens. Although in transverse section the septum looks as if it supports the hinge plate, it does in fact do no such thing. Indeed the septum at the dorsal apex is so slight that 'supporting' is an impossible function. Such hallucinatory structures should be

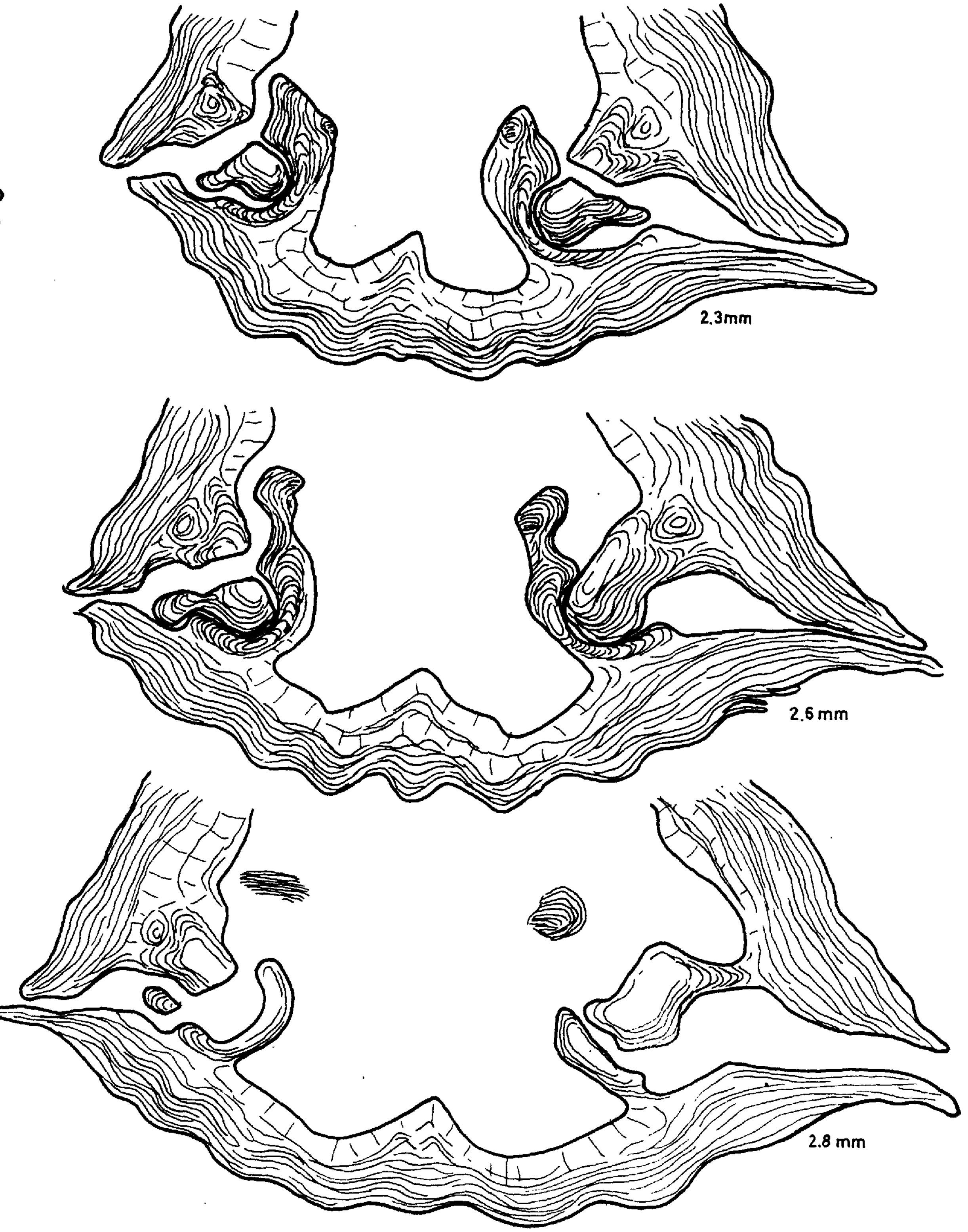
# Development of crural structures in Atrypida



*Mimatrypa flabellata* (x 12)



*Desquamatia iunctura* (x 12)



*Spinatrypa kelusiana* (x 16)

eliminated from atrypid systematics. It is encouraging that nearly all of POULSEN's subfamilies have been removed or else redefined on more suitable bases.

SIEHL (1962, p. 185) has introduced the term cardinal block for the thick columnar layers which usually fill in the notothyrial cavity. The hinge pad (new term) which forms the inner part of the hinge plates, can be distinguished from the cardinal block in more anterior sections but is also clear in the apical sections. The normal orientation of columnar crystals is missing and the hinge pads flank only the hinge plates. The columnar layer commonly overlaps the hinge pad apically to form the thick cardinal block of SIEHL. The hinge plate itself is composed of hinge pad and socket plates. The socket plates stand out from the hinge pad by their minutely fibrous crystals and the orientation of these fibres. Their crystal strucutre is comparable to that of the teeth.

The tips of the socket plates give rise to the crural bases and crura, which are structurally continuous with it. The finely fibrous, compact, crural bases are bulky and knob-like in most Atrypacea, but in some, e.g. Desquamatia, Gruenewaldtia and Mimatrypa they tend to be thin, long and sub-horizontal. The hair-like, feather-like fibres of the crura are directed ventro-laterally, swinging about the anterior margins of the teeth and dental plates to the lateral commissure. HALL (1894, Pl. 55, figs. 15, 17) has given some accurate figures of the junction between spiralia and crura. The crural fibres are closely sompacted at the crural base, but distally there is a trend for the fibres to part and flare out in elaborate patterns. This is particularly true of some Atrypa, Desquamatia and Spinatrypa. The cause of such flaring is uncertain and has been speculated (COPPER, 1965b), to add to greater flexibility of movement of the spiralium. In Mimatrypa the crura become minute and vestigial (e.g. text-figs. 193-194). The term 'primary lamellae' is abandoned : ALEXANDER (1949, p. 211) introduced it to refer to the connecting fibres between crura and jugal processes. However, no distinction can be made between crura and 'primary lamellae' and it appears that in the literature there is some confusion. Quite commonly the term lamellae has been applied to what can only be crura. STRUVE (1956, p. 396) confused the crura with the socket plates and primary lamellae with crura.

ALEKSEEVA (1962, p. 24) described two kinds of crura : 1) elongate, broadly diverging laterally, 2) short, hardly diverging at all. She regarded these two types of crura as being diagnostic of subfamilies. The dividing line between the two types of crura of ALEKSEEVA was not observed in European genera, and since the divergence of the crura appeared to depend largely on the shape of the shell, it has not been used as a criterion in systematics.

The microstructure of the junction between the crura and socket plates is interesting since it sheds light on how the crura originated and how considerable variations in the early stages of the crura can occur. Several variant types of crural attachment are shown in text-fig. 23. The type of attachment may be diagnostic of genera. The fibres of the socket plates are recurved 360 degrees from ventro-laterally to dorso-inwardly. This recurvature usually takes place at the crural base but also occurs much more anteriorly when the base of the crus is already quite long.

Dissident views on the nature of the jugum of atrypid brachiopods are also rife. Most authors have accepted without question that the spiralia were connected by a jugum. As mentioned previously the 'connecting' loop was discovered by WHITFIELD in 1867. QUENSTEDT (1852, p. 461) appears to have recognized two 'horns' or 'feelers', as he called them, but did not think that these connected the spiralia. DAVIDSON (1853, Pl. 7, fig. 91) had a similar view. GINLEY (1878, p.337) became skeptical of the idea held since WHITFIELD's discovery of a connecting loop, and remarked that in his material there was no connection between the jugal processes. DAVIDSON (1882, p. 110) was later infected by GINLEY's view and began also to 'question whether they formed always a continuous band.' ALEKSEEVA (1962) insisted that the jugum could be either separated or united. STRUVE (1955, p. 219, fig. 2) showed a figure of Gruenewaldtia with a united jugum and for Spinatrypa noted 'die beiden Äste des Jugums ......vereinigen' (STRUVE, 1956, p. 396). Sectioning of topotypic Eifel material has shown that STRUVE was incorrect. It has already been pointed out that DAVIDSON figured both connected and disjunct jugal processes (COPPER 1965a, p. 368) in the same species. HALL (1867, Pl. 53a, figs. 22-25) corrected a jugum which he showed originally to be united, to a disjunct jugum (HALL, 1894, Pl. 55, figs. 10, 20, 24). The different views reflect the doubt and uncertainty which exists about the jugum.

Not a single atrypid specimen from the Eifel region had a united jugum : all specimens were carefully sectioned completely through the jugal processes at intervals of less than 0.1 mm and the sections recorded by means of peels. Each peel was magnified at up to 80 times. In addition to disproving united juga, the sectioning showed that the jugal processed were extremely elaborate in development, some with structures completely unknown in the atrypoids. Some of these are of taxonomic importance,

The jugal processes are directed inwards from their point of attachment to the crura, at right angles to the plane of symmetry. Near the centre, they begin to curve anteriorly and dorsally, often rather sharply. They terminate in small jugal plates. Processes are three-layered. a thin, finely fibroua compact dorsal layer, a coarsely cyrstalline middle layer, and a fibrous ventral layer. The dorsal and middle layers probably also form the bulk of the ribbons of the spiralia, the thick, middle layer possibly acting as a rigidifying spine for the basal whorls. A row of nodules or short spines marks the central, ventral layer of the jugal processes. In Gruenewaldtia the spines are not arranged in a row, but project from a bulbous growth. This bulbous, or boss-like growth marks the tip of the jugal process in Carinatina and Gruenewaldtia, possibly also Mimatrypa (Pl. K, fig. 2; Pl. L, fig. 1). The middle layer reached its greatest thickness in the juga of the last two genera. In others it is rather irregular, or even suppressed. The jugal spines were present in all genera, but more abundantly in some than others. In Atrypa they are present as small nodules only (Pl. L, fig. 4). In COPPER (1965b), a new structure is described which also is of taxonomic value. This is the jugal plate, a short, monocrystalline plate devoid of nodules or spines which is attached to the end of the jugal processes. In Desquamatia the characteristic form of the plate is hook-like; in Atrypa is is rather straight; in Spinatrypa it is shaped in section like a boomerang; in Spinatrypina it is minute, also somewhat hook-like. The jugal plates never join. Usually they are in mirror-image positions and may come as close as touching, but no fusion was seen to occur. There was no evidence in any material that possibly the plates may have broken apart after death.

The popular view that jugal processes connected the spiralia and held them more firmly together must be rejected. If this had been their function they would hardly have evolved the elaborate and delicate structures with which they are provided. A simple, straight plate would have pefformed this function much better. Two alternatives are feasible : 1) jugal processes supported a mouth or some sort of digestive-alimentary system, 2) jugal processes served as levering devices to lift or raise the spiralia during respiration, and may have been attached to muscles performing this function. There is more evidence for the latter. The jugal plates are made up of finely crystalline, non-fibrous calcite which is similar in structure to the calcite of the pediculate epithelium. They were a likely place of muscle attachment. The nodules and spines, as well as the boss of Carinatina and Gruenewaldtia would have been ideal for muscle attachment.

The calcite ribbons of the spiralia are wound tightly in the form of two dorsally-directed, mirror-image cones. The plane of the whorls is not horizontal but slanted towards the cone apices. Basal whorls are in the form of a D with flat side facing inwardly. Cone apices are central and sometimes touch each other. Monstrous cones are common : one cone may be larger than another, cones may interlock, one cone may enlarge to take up the complete body space when another atrophies or is destroyed. The number of whorls in a cone may vary with each genus, although in the superfamily Atrypacea this variation is slight. The maximum number of whorls counted was 30 (Spinatrypa). The genus Atryparia, mature specimens of which can attain a very large size, has rather few, widely-spaced whorls (1 to 1.5 mm). Carinatina, with a body cavity height of less than 5 mm, has up to 10 whorls in a cone (0.5 mm spaced). The usual spacing is 0.7 to 0.9 mm.

In Atrypa and Spinatrypa the spiral ribbons tend to be thicker and less planar. The outer side of the ribbons is extended by a thin flange the width of which can double the normal width of the spiral ribbon (viz. COPPER 1965b, fig. 3), The function of this flange probably was to canalize the food currents as drawn by RUDWICK (1960, fig. 7).

The direction of the cone axes does not vary greatly in the Atrypacea, in spite of the strong variation in shell convexity which might be thought to affect the orientation of the cones. The planoconvex or ventribiconvex shell of Anatrypa spp., Spinatrypa kelusiana STRUVE, Kerpina spp. and Gruenewaldtia have not had any major effect on cone direction. GRABAU (1931, p. 202), who described Spinatrypina sinensis (KAYSER 1883) thought that the remarkable planoconvexity of that shell 'implies a distinct rearrangement of the brachidia'. That this is not so has already been demonstrated by STRUVE (1956, p. 397). ALEKSEEVA (1962, p. 25) used the direction of the cone axes as a subfamily characteristic and the number of spiral whorls as a family generic biocharacter.

In a number of different publications there have been reports that the spiral ribbons of different Atrypida were equipped with rows of spines. Although nodules and spines were observed on the jugal processes of the material under study, no spines were seen on the spiralia. The Rev. N. GLASS, who prepared a special technique to expose the spiralia in calcareous matrices, demonstrated that the Wenlockian atrypid Plectatrypa marginalis (DALMAN) had spines on the outer margins of the spiralia (in DAVIDSON, 1881, p. 9, fig. 8; 1882, Pl. 7, fig. 8, p. 113). The Ludlovian atrypid Dayia navicula(SOWERBY) apperently also displays spines (DAVIDSON, 1882, Pl. 5, figs. 2a-c). HALL & CLARKE (1894, p. 166, Pl. 5, figs. 13, 14) made similar discoveriss. More recently it has been STRUVE (1956, Pl. 2, fig. 13) who figured spines on the spiralia of Spinatrypa. Unfortunately similar preparations of well preserved topotypic Eifel material has failed to confirm STRUVE's findings. The lamellae of Spinatrypa were found to be smooth. It is possible that the spinosity figured by STRUVE (ibid.) was due to the post-mortem growth of small calcite crystals on the whorls, a feature which is very common in such material where spiralia are not wholly embedded in matrix. Detailed peels also failed to disclose spinosity in the material examined. The discovery of spines is treated with some doubt.

The ontogenetic development and growth of spires is a new field of study. Not sufficient material was studied in neanic stages of growth and no conclusions can be presented. It would be valuable to know the position and extent of the jugal processes and spiralia in small specimens. GLASS (in DAVIDSON 1882, p. 111) studied some Silurian Atrypa and concluded that the number of coils increased with age (as would be expected)

# PLATE G

Fig. 1. <u>Spinatrypa</u> <u>curvirostra</u> n.sp.

Transverse section of a spine and rib crest. The inner surface of the spine is not fused. It consists of a fibrous and outer layer. Serial acetate peel at 1.8 mm. x 50.

Fig. 2. <u>Atrypa</u> (<u>Atrypa</u>) <u>caepata</u> n.sp.

Transverse section of the ventral and dorsal wall at the lateral commissure showing a curious inward projection of the shell layer, possibly a filter. Serial acetate peel at 4.1 mm. x50

Fig. 3. <u>Gruenewaldtia</u> <u>latilinguis</u> (SCHNUR 1853).

Transverse section through the locking device of the deltidial plates, anterior to the foramen. Serial acetate peel at 2.4 mm. x50.

Fig. 4. <u>Gruenewaldtia</u> cf. <u>apsaklina</u> STRUVE 1961.

Transverse section of the deltidial plates. The plates have an inward projection,possibly an incipient or remnant pedicle collar. Serial acetate peel at 1.1 mm. x50.

G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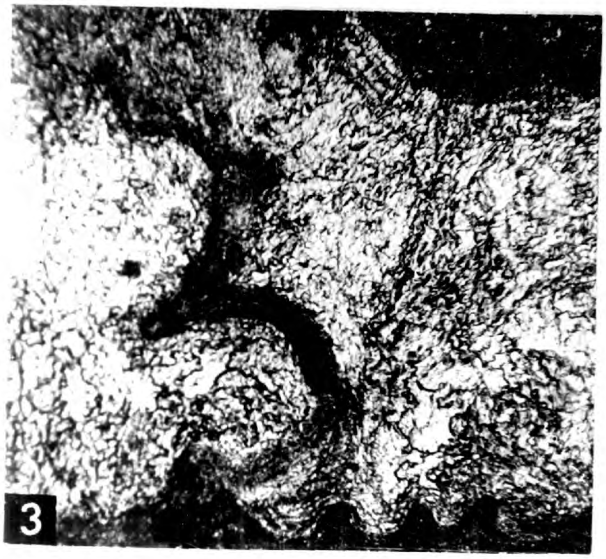
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# PLATE H

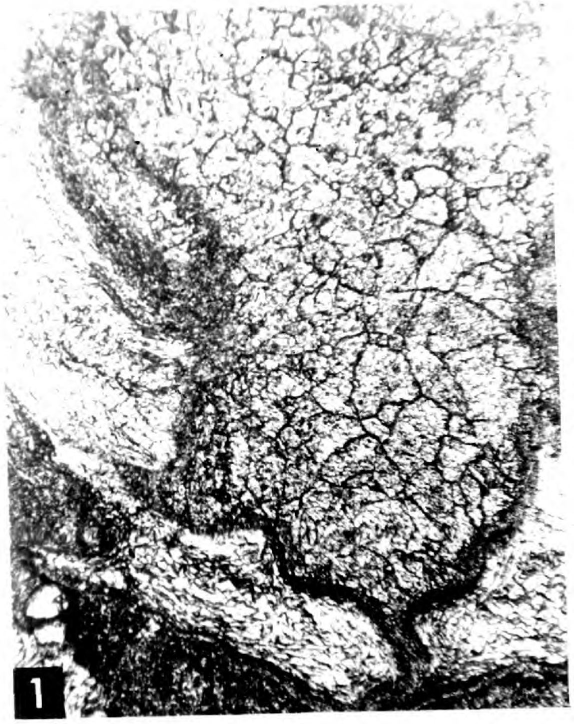
Fig. 1. *Gruenewaldtia latilinguis elegans* STRUVE 1961.
Transverse section of the deltidial plates and part of the pedicle collar (thin, wavy dark line of calcite). Serial acetate peel at 1.5 mm. x50.

Fig. 2. *Kerpina vineta goniorhynchia* STRUVE 1961.
Transverse section of the pedicle collar, the deltidial plates and the apex of the brachial valve. Serial acetate peel at 2.1 mm. x50.

Fig. 3. *Atryparia instita* COPPER 1965.
Transverse section through the pedicle constriction in the delthyrial cavity. The lack of deltidial plates is notable. Serial acetate peel at 1.3 mm. x50.

Fig. 4. *Kerpina vineta vineta* STRUVE 1961.
Transverse section through the hollow deltidial plates and the thin lining of the pedicle collar next to the plates. Serial acetate peel at 0.8 mm. x50.

H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# PLATE I

Fig. 1. Carinatina plana (KAYSER 1871).

Transverse section of the dorsal apex. The cardinal process (large and bushy) is attached to the cardinal block (a notothyrial cavity is absent). Serial acetate peel at 1.4 mm. x50.

Fig. 2. Spinatrypa fasciplicata (STRUVE 1961).

Transverse section of the socket plate, the inner socket ridge is extended to support the crus, and the beginning of the crus. Serial acetate at 2.2 mm. x50.

Fig. 3. Kerpina vineta goniorhynchia STRUVE 1961.

Transverse section of part of the tooth, the socket plate, the inner socket ridge and the inception of the crus. A lateral cavity is lacking. Serial acetate peel at 3.5 mm. x50.

Fig. 4. Atrypa (Planatrypa) squamifera (SCHNUR 1853).

Transverse section of the dorsal apex, revealing a distinct, pronged cardinal process in the notothyrial pit. Serial acetate peel at 2.1 mm. x50.

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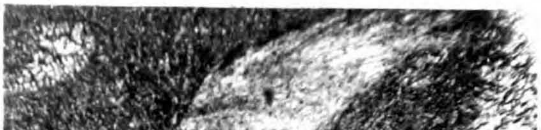
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## PLATE J

Fig. 1. Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)
Transverse section of the ventral valve near the apex. The elongated dental nucleus, the dental pad which lines it and the pedicle layer towards the ventral side of the cavity, all are present. Serial acetate peel at 1.0 mm. x50.

Fig. 2. Mimatrypa flabellata (C.F. ROEMER 1844).
Transverse section through the base of the tooth, the deltidial plate and the pedicle collar. There is a lack of dental nucleus. Serial acetate peel at 2.3 mm. x50.

Fig. 3. Spinatrypina explanata (SCHLOTHEIM 1820).
Transverse section through the base of the tooth, the hollow deltidial plate (open) and the socket cavity with serration caused by the middle socket ridges. Serial acetate peel at 1.3 mm. x50.

Fig. 4. Gruenewaldtia prooemia n.sp.
Tramsverse section through the base of the tooth and remnants of the deltidial plate. Note the large lateral cavity. Serial acetate peel at 2.0 mm. x50.

J


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# PLATE K

Fig. 1. <u>Atrypa</u> (<u>Planatrypa</u>) <u>petasa</u> n.sp.

Transverse section through a thickly layered tooth and a socket plate with distal, tightly wound crural base and proximal two ridges of the serrated middle socket ridges. Serial acetate peel at 2.5 mm. x50.

Fig. 2. <u>Carinatina</u> <u>plana</u> (KAYSER 1871).

Transverse section through the right jugal process (photograph to belined horizontally). Note the striking, projected boss on the ventral side of the jugal process. Serial acetate peel at 3.8 mm. x50.

Fig. 3. <u>Gruenewaldtia</u> <u>latilinguis</u> (SCHNUR 1851).

Transverse section theough the jugal process at a point near the lateral commissure. Note the feathery crural support on the dorsal side, and the thick, coarsely crystalline ventral layer of the process. Serial acetate peel at 4.9 mm. x50.

Fig. 4. <u>Mimatrypa</u> <u>flabellata</u> (C.F. ROEMER 1844).

Transverse section of the hinge plate and the crus, which already has separated from its base in this section. Serial acetate peel at 4.7 mm. x50½

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# PLATE L

Fig. 1. *Gruenewaldtia* cf. *apoaklina* STRUVE 1961.
Transverse section of the jugal process with a spine covered boss. Serial acetate peel at 8.1 m. x50.

Fig. 2. *Desquamatia* (*Seratrypa*) *pectinata* (SCHRÖTER 1777).
Transverse section of the hook-like jugal plate characteristic of *Desquamatia* (orient figure horizontally). Serial acetate peel at 6.8 mm. x50.

Fig. 3. *Spinatrypa* *orthoclina* n.sp.
Transverse section of the jugal plate, which is remarkable in *Spinatrypa* for its massivity. Serial acetate peel at 5.8 mm. x50.

Fig. 4. *Atrypa* (*Planatrypa*) *petasa* n.sp.
Transverse section through the ends of jugal processes and the jugal plates : the ventral margins of the jugal processes are lined by nodules. The jugal plates form a U-shaped trough in section. Serial acetate peel at 6.6 mm. x50.

Fig. 5. *Atryparia* *stabilia* COPPER 1965.
Transverse section of the jugal plate and jugal process, the latter lined by a ventral margin of nodules. Compare to fig. 5. Serial acetate peel at 9.3 mm. x50.

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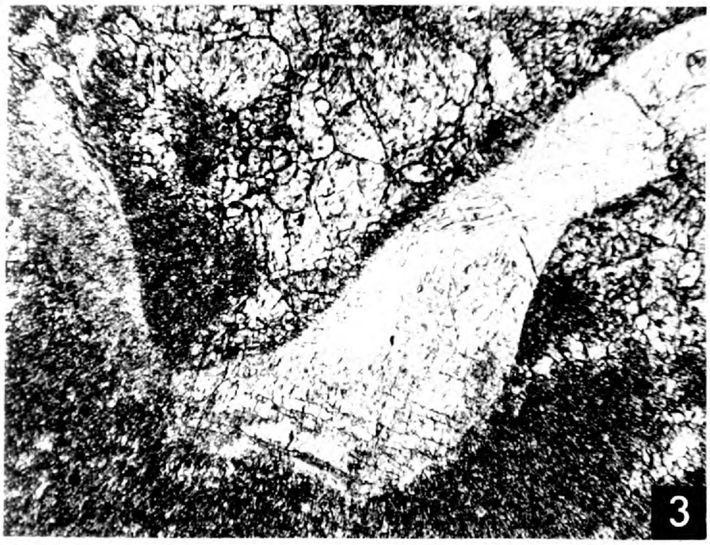
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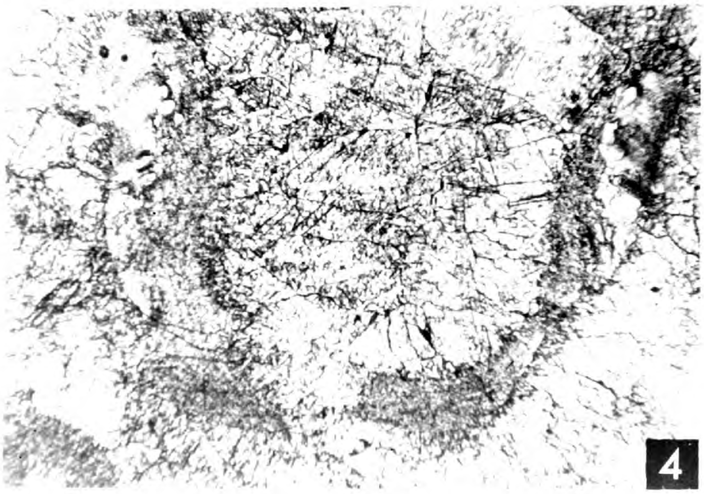
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and that the bases of the coils were levelled in maturity. It would be valuable also to know how the coils grew, whether they were continually enlarged by resorbtion or by simply upward projection of the oldest coils. The spiralia generally take advantage of the full body cavity available. This is especially remarkable in the flat shell of Carinatina where the coils have a very wide base but are low and short in extent.

## Ontogeny

In the systematic descriptions of species a great deal of attention was paid to distinguishing 'young', neanic specimens from 'old', gerontic specimens and to distinguish small species of one genus from a small specimen of a larger species. It was found necessary to establish criteria to separate stunted or dwarfed species from merely immature forms, although this turned out to be difficult.

Wherever possible the ontogenetic variation in width/depth and width/length ratios was plotted on scatter diagrams. Bell curves for these ratios were prepared for several species of Desquamatia. Simple graphs of the size distribution were also plotted for several species. Such information was not used in distinguishing species.

Neanic specimens of co-existent atrypid genera and subgenera usually were readily separated, often more easily than mature specimens of wider ranges of size and shape. This is because the coarse, undulating ribbing of Spinatrypa, the wide interarea and fine ribs of Desquamatia, the minute area and finely squamose ribs of Atrypa are distinctive at a very early stage. The separation of synchronous Givetian Spinatrypa and Spinatrypina also presented no problem.

Although they remain distinctive of their genera, most atrypid species go through similar elementary stages of shape. Neanic specimens are all ventribiconvex or planoconvex, and most have a somewhat circular outline. A slightly elevated mid-rib pair and corresponding weak dorsal groove are common. Commissures are rectimarginate or weakly plicate.

The neanic differences usually are most clearly expressed in the size of the area and the position of the beak. Rib shape and size also become characteristic early. The early ontogenetic area of Desquamatia is several times the size of that of Atrypa.

In 1882 DAVIDSON (pp. 110-111) initiated the first known study of a growth series in the atrypid brachiopods. WHITFIELD (1867, p. 269) made a brief note of studying the age variation of Atrypa, but did not go into much detail. BEECHER & CLARKE (1889) elaborated DAVIDSON's study into a single memoir devoted to an ontogenetic variation study of 25 Silurian brachiopod species, including Atrypa. The work of BEECHER & CLARKE has become almost classical. The most notable aspect of their work was the changes they described in the position of the foramen, the fold on the anterior commissure and the incurvature of the beak in Atrypa. Their conclusions are still valid to-day, although they apply only to the genus Atrypa and not to the wide number of genera aslo included under that name in the previous century.

There are not many other studies devoted to the ageing of brachiopods. One of the few is the study of old age in brachiopods by SHIMER (1906). SHIMER stated that senility was expressed by lamellosity of growth lines, changes in the curvature of apical portions resulting in a groove at the commissures, rotation of the umbos, flattening of plications (i.e. ribs), disappearance of the median sinus and fold, reduction of the width/length ratio, modification of the pedicle (enlargement or obscurement), disappearance of spines, and thickening of the valves. SHIMER selected several specimens of atrypids to demonstrate these features (ibid., figs. 3, 4, 20, 27, 28).

Many of the features mentioned by SHIMER can be observed, although some appear to contradict SHIMER's conclusions. For example, many atrypids show a marked increase in the size and definition of the anterior fold, spines are best seen on large mature specimens, and often, the width/length ratio shows an increase rather than decrease in old age. Nevertheless, a study of the kind which SHIMER attempted needs still to be done for the atrypids. It would be of particular interest to discover the internal modifications with age, the changes in the jugal processes, spiralia and crura.

The influence of environment in causing mass gigantism or stunting is difficult to assess in fossil populations. Physical environment can usually be eliminated as a cause of anomalies in size whan many of the brachiopods in a population are of uniform and normal size and only a few remain small, or when the host sediment is such that faunas are very richly developed. Atrypids appear to be highly intolerant of even small changes in the texture and composition of sediment (as seen in its colour, for example), and it is difficult to visualize how they could thrive at a normal size in conditions in which other brachiopods could not survive. For example, the Lower Devonian rocks in Europe, particularly in the type areas of the Gedinnian, Siegenian and Emsian, are predominantly sandstones, siltstones, which locally display rich faunas of chonetids, stropheodontids, rhynchonellids and spiriferids, but almost never atrypids. This shows rather limited adaption and tolerance. On the other hand, atrypids, more than other brachiopods, appear to have adapted themselves well to coral-rich environments where others failed to establish.

There appears to be only one instance in the Eifel region of possible stunting of the atrypid fauna. This is in the brachiopod rich Bildstock horizon of the Ahrdorf beds. The atrypids in this horizon are small, rarely reaching a width greater than 25 mm. Only a few Desquamatia are of larger size. The remaining fauna, mainly athyrids, meristellids and rhynchonellids, is also small sized. An orthoid, Schizophoria pygmaea STRUVE, is typical of the horizon. The underlying beds are sandstones. The most abundant atrypid, Atrypa (Planatrypa) sp. M. does not have much in common with older or younger Atrypa in shape and rib structure and the problem of distinguishing it from small, young specimens of another species does not really arise.

It is more difficult to judge the influence of the biological environment, i.e. competition from other associated fauna. It is possible to visualize that of two associated, unrelated species, one may become stunted because it is less successful or because it is more successful in its smaller size. The clayey, calcareous shale environment of the upper Eifelian Müllert horizon contains, for example, two major atrypid elements (and almost nothing else). These are very large Atryparia instita COPPER (c. 15%) and small, 10-20 mm wide Spinatrypa kelusiana STRUVE (c. 85%). Both appear to be equally successful, and the small size of S. kelusiana cannot be attributed to stunting. Spinatrypa does not attain large size until the Givetian. In the Eifelian, specimens of greater width than 30 mm are unknown.

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Stunting is here distinguished from dwarfing to mean environmental size restriction, and dwarfing is specified as being due to genetic causes.

# V EVOLUTION

The evolution and classification of genera and species of atrypid brachiopods is closely linked. At the present time, very few developmental series have been established and many postulated generic links are weakened because of the lack of knowledge of internal structure. A number of gradations from one type of external morphology to the next can be outlined in the Eifel region. In the Eifel region alone one genus may repeat the same trend several times over. A prime example of this type of iteration is the change in rib structure of Spinatrypa. During the Eifelian there is a cline towards coarser and shallower ribs culminating in Spinatrypa kelusiana STRUVE, in which specimens with almost no ribs are found (Pl. 20, figs. 4a-b). After a return (?) to a more undulating rib structure in the lower Givetian, the middle Givetian saw a repetition of the rib shallowing in Spinatrypa orthoclina n.sp. and the upper Givetian S. paffrathi (WEHRLI). In the Frasnian of North America, a similar trend is again repeated and ends in Spinatrypa trulla STAINBROOK, an atrypid with ribs so flattened as to be nearly indistinguishable. This is possibly an example of zig-zag evolution as explained by HENNINGSMOEN (1964).

There are also trends shown by the same shell structure which may be 'progressive' (complex) in one group and 'regressive' (simple) in another (it is difficult to decide which is which!). An example of this is the expansion and contraction of the lateral cavities, small cavities which form the nuclei of teeth. In Desquamatia, Spinatrypa and Spinatrypina the lateral cavities become progressively larger, though at different times and different rates. In Desquamatia (Variatrypa) large cavities first appear in late middle Eifelian species, in Spinatrypa they appear during the middle Givetian and in Spinatrypina wide cavities are present in the Lower Devonian. In the last genus, there appears also to be a reverse or perhaps stationary cline of a small lateral cavity in the Frasnian species. In Gruenewaldtia the opposite, a change towards reduction and complete loss of a lateral cavity, is noticed. Late Eifelian species of this genus show a closing of the lateral cavity, but early species have a wide and expanded lateral cavity.

One of the most evident changes is one of size. Though this character may be strongly influenced by environment and may differ during growth stages, it is remarkable that the earliest species of nearly every atrypid genus are small. Size change may be also a measure of their phylogenetic development. It is possible that size can be used for correlation purposes. In Spinatrypa all the Eifelian species in north-western Europe, and, as far as could be ascertained also in the Ural mountains and the Kutznetsk basin of Russia, were small, i.e. with a width rarely greater than 20 mm and on average much less. The first large Spinatrypa in western Europe occur in the lower Givetian (Cürten beds) in the form of Spinatrypa curvirostra n.sp. the average size of which exceeds 25.mm. For atrypid brachiopods this is relatively a large change in size. If large Spinatrypa (greater than 25 mm) are found elsewhere it probably indicates that they are younger than the lower Givetian. However, this method is limited because there are also numerous small species of Givetian and Frasnian Spinatrypa, and therefore it is not axiomatic that small size is indicative of Eifelian or older age.

An 'evolutionary' pattern which may be of some value is the development in the different layers of the shell wall. There is some indication that numerous interlayers of fibrous and columnar layers are a primitive characteristic in atrypids and that development of a thick, even, uninterrupted columnar layer and a thin, outer fibrous layer is an advanced characteristic. This is, for example, noticeable in the more advanced atrypids Desquamatia (Variatrypa), Spinatrypina, Atryparia and Gruenewaldtia (leading to Mimatrypa). The youngest species of these seem frequently to have fewer interlayers and thicker columnar shell layers.

There are signs that the development of deltidial plates and pedicle collars also mark an advance in atrypid morphology, Pedicle collars first appear in the younger Desquamatia in the Eifel region and are absent in the older. Similarly the only known pedicle collar in Spinatrypa (S. coriacea CRICKMAY) is in a Givetian rather than Eifelian species. Both Kerpina and Anatrypa (partim) which appear to be specialized off-shoots of Atrypa have deltidial plates and pedicle collars which Atrypa itself lacks. In Atryparia, which lacks deltidial plates, there is a development of an elevated collar in the late Eifelian A. instita COPPER which is not evident in older species.

In Gruenewaldtia the pedicle collar and deltidial plates unify into a single structure (text-fig. 21). The unification is completed in Mimatrypa insquamosa (SCHNUR) in which the inner part of the deltidial plate-pedicle collar structure is completely fused anterior to the foramen. This advanced stage of deltidial structure is presently not known in other atrypids.

The growth and change in jugal processes cannot be evaluated because not every species was serially sectioned and specimens of sectioned species not always had these structures developed. The oldest , lower Eifelian members of the long-ranging Atrypa group to be examined, appear to have had rather simple, long, slightly curved jugal plates and slightly nodular, aspinose jugal processes, which in transverse section take a U-shaped outline. In Desquamatia there is a broad change towards greater incurvature of the ends of the jugal processes until they eventually have curved round completely and face outwards and laterally. The development of a boss or spinose base on the jugal processes also appears to mark an advanced stage. At no time were the brachiopods from northwestern Europe found to have fused or joined jugal processes.

There are several additional iterative trends which are complex and, under present knowledge, not well understood. One is the development of a large interarea, with expanded deltidial plates, usually an advanced feature. It is one of the typical characters of *Desquamatia* and *Spinatrypina* to have a prominent interarea, but at different positions in the stratigraphic column there has been expansion and reduction of the areas. Another complex and poorly understood feature is the presence of a strong middle rib pair, frequently resulting in a keel or carina on the ventral valve and a depression on the dorsal valve. It is present in *Carinatina* and *Plectatrypa* and to a much lesser extent in other atrypids. It may be a primitive rather than advanced feature because the Silurian *Protatrypa*, a keeled atrypid, appears to have given way to *Atrypa*, which does not have a marked keel (BOUCOT & JOHNSON 1964).

The thick growth of the spines and frills appear to be much more characteristic of Devonian than Silurian atrypid genera. But in Devonian atrypids individually there is, at present, no trend marked out towards an increasing complexity of frill and spine patterns. Again a reverse trend may have set in in the palaferellid group in which growth lamellae show a major decline, become more and more widely spaced and rarely form into frills, and never into thick *Atrypa*- or *Desquamatia*-like frills.

There are some characters, such as changes in convexity and in the shape and size of the anterior field which appear to have ontogenetic rather than phylogenetic importance. *Spinatrypa kelusiana* STRUVE shows a short cline towards ventribiconvexity, opposed to the normal atrypid dorsibiconvexity, but ventribiconvexity is characteristic also of neanic atrypid specimens and it may be that *S. kelusiana* has retained such features into a late ontogenetic stage. The retention of ventribiconvexity is also common to other genera such as *Anatrypa*, *Atrypina*, *Gruenewaldtia* and *Spinatrypina*.

More details are given of the phylogenetic sequence sketched in COPPER (1964) for the change from *Gruenewaldtia* to *Mimatrypa* (*Desatrypa* is a junior synonym of *Mimatrypa*).

The first Eifel *Gruenewaldtia* (*G. prooemia* n.sp.) appeared in late Weilersbach time (lower Eifelian, Nohn beds)) It is a small, coarsely ribbed, biconvex form with, internally, several major septa supporting each muscle platform. It was followed by the more finely ribbed *G. matutina* STRUVE of Schleit age (Nohn beds). The shell of this species remained small, the beak ortholline to anacline, and internally there was a loss of asymmetrical septa, and detachment of minor septa from the muscle plate. During Ahrdorf time, *G. rhenana* SPRIESTERSBACH kept the finer ribbing of *G. matutina* but appears to have lost the two outside septa to two major and one strong central minor septum. The peak of distribution of Gruenewaldtia in the Eifel region was reached in late Junkerberg time with the Hönselberg horizon (middle Eifelian). Specimens of G. latilinguis (SCHNUR) were large, gibbous and showed strong beak incurvature. Muscle platforms were highly elevated by two high major septa and a remnant or ephemeral median septum in each valve. Pedicle collars were developed in the younger subspecies G. latilinguis elegans STRUVE, and also the collars began to show fusion with the deltidial plates (text-fig. 21). The last appearance of Gruenewaldtia in the Eifel region was probably in late Hallert, early Lahr time (upper Eifelian) Ahbach beds). The definition of the last species, G. apsaklina STRUVE, is not sharp since the last surviving specimens show a marked variation in shape and size. Internally, however, the specimens of Freilingen age, appear to be very similar. Minor septa appear to have gone completely and the platforms themselves appear to have rested on the shell floor, or even fused with the shell floor. The columnar calcite of the platforms is extremely thick. Pedicle collars are rare, but deltidial plates have thickened and grown coarse, though they have not fused medially. Externally, specimens of Freilingen age show such strong similarity to Mimatrypa that most specimens cannot be separated unless sectioned. In the Senckenberg collections some specimens identified as 'Atrypa' desquaatia turned out to be Gruenewaldtia.

In summary, most morphological trends are difficult to unravel. Some trends repeat themselves, others show a return to a previous condition of morphology. A great deal more about the internal structure of the oldest species of many atrypid genera must be discovered.

## VI CLASSIFICATION

Atrypid classification is, at present, in a fluid and chaotic state. No remedies are proposed until more is known about the internal structure of some of the earliest Silurian and Ordovician genera. However, the unsettled state of systematics is encouraging because basically very little has changed since ORBIGNY (1847) assigned Spirigerina (in part a junior synonym of Atrypa DALMAN) to the family Spiriferidae. In 1871 GILL recognized the individuality of the atrypid brachiopods and united them under the Atrypidae. MOORE (1952) raised the atrypids to the level of a sub-order, while retaining its union with the spire-bearers. In 1960 RZHONSNITSKAYA justifiably severed the atrypid-spiriferid union by making the atrypids into an order.

The atrypids have a great deal more in common as a group with the rhynchonellids than spiriferid brachiopods. For the past 100 or more years the atrypids have consistently been joined to the spire-bearing or Spirifer group of brachiopods because the presence of a calcified spiralium was thought to be of great significance. But there are repeated instances in the atrypid stock of genera and species lacking the dorsally directed spiralia which make them so distinctive. Some have been pointed out previously e.g. in BOUCOT, JOHNSON & STATON (1964, p. 807) and COPPER (1965a, p. 360). Furthermore, studies of Recent rhynchonellid brachiopods have shown repeatedly the presence of a dorsally directed fleshy lophophore, which is, more or less, the 'soft-part' counterpart of the calcified atrypoid spiralium (e.g. RUDWICK 1960). Some of the more convincing evidence of a rhynchonellid-atrypid relationship appears to lie in the oldest, Ordovician representatives of these stocks, many of which are virtually indistinguishable on the basis of external morphology, and indeed difficult to assign specifically to one or the other groups. Examples of these are the early genera Idiospira, Protozyga and Hallina (see COOPER 1956), the internal strucutre of which is poorly known and little understood. Even during the Devonian, confusion of external form can arise, as for example in the genus Rhynchatrypa SIEHL or in some species of Mimatrypa STRUVE (refer to Pl. 51, figs, 6a-e). The relationship of the cardinal structures of atrypids and rhynchonellids also is striking : both groups have similar, if not identical, deltidial structures and foramina, and likenesses in their dentition and septal structure. Both groups also lack the straight hinge lines and the expansive planar interareas typical of the Spirifer-group.

The idea that the atrypids and rhynchonellids are phylogenetically linked is by no means new. WOODWARD (1856) was one of its first proponents when he grouped Atrypa, together with Pentamerus, under the Rhynchonellidae, and remarked (ibid., p. 229), 'The shells of this genus differ from Rhynchonella chiefly in the calcification of oral supports, a character of uncertain value.' QUENSTEDT (1871, p. 208) became a firm supporter of WOODWARD's idea and tried to recapture for *Atrypa* a place in the rhynchonellids. QUENSTEDT underlined the similarities between the two groups, though he hoped, in vain, to find calcified atrypid-like lophophore supports in the Jurassic rhynchonellid *Acanthothiris spinosa* (QUENSTEDT 1871, p. 209). The idea that the rhynchonellids and spiriferids were related does not seem to have taken root and is not favoured in modern research. In modern western palaeontological literature, the atrypids are assigned, almost invariably, to the order Spiriferida, with the exception of COOPER (1956, pp. x-xi) who encompassed the Atrypacea, Pentameracea, Rhynchonellacea and Spiriferacea, by the sub-order Pentameroidea. The Russian literature has accepted the order Atrypida for the past five years.

In 1964, three new and markedly different classifications were proposed by BOUCOT, JOHNSON & STATON, RZHONSNITSKAYA and STRUVE for the atrypid group. These are reviewed briefly and particular attention is given to the family Atrypidae.

Under the sub-order Atrypoidea (MOORE 1952, emend), BOUCOT, JOHNSON & STATON listed two superfamilies, firstly the Atrypacea with the families Atrypidae and Lissatrypidae, and secondly the Dayiacea, with the families Dayiidae, Kayseriidae, Anoplothecidae and Leptocoeliidae. Under the family Atrypidae, BOUCOT *et al*, listed six sub-families.

The system propounded by RZHONSNITSKAYA (1964) differs strongly from the above. Four superfamilies were included under the heading order Atrypida : (1) the Atrypacea, with 2 families, (2) the Cyclospiracea, with 2 families, (3) the Coelospiracea, and (4) the Dayiacea. The family Atrypidae contained six sub-familes, but not the same families of BOUCOT *et al* (1964). Under RZHONSNITSKAYA's system there are, in effect, four subfamilies each of which has only one genus that can be assigned to it with any degree of certainty.

SRTUVE (1964) proposed a simpler taxonomic scale which is accepted in principle. The classification of STRUVE eliminated the Carinatininae and Karspinskiinae and reduced them to members of the subfamily Palaferellidae.

The division of the family Atrypidae is summarized as follows :

| BOUCOT, JOHNSON & STATON | RZHONSNITSKAYA | STRUVE (partim) |
|---|---|---|
| Subfamily Atrypinae | Atrypinae | Atrypinae |
| Subfamily Zygospirinae | Septatrypinae | Zygospirinae |
| Subfamily Karpinskiinae | Carinatinae | Palaferellinae |
| Subfamily Carinatininae | Karpinskiinae | Atrypininae |
| Subfamily Palaferellinae | Punctatrypinae | |
| Subfamily Atrypininae | Palaferellinae | |

STRUVE (1964) in fact only reduced three families to one, and it is not known if the families of BOUCOT, JOHNSON & STATON were accepted intact.

COPPER (1965e) proposed again a different classification based essentially on that of STRUVE (1964). The superfamily Atrypacea was divided into four families : the Lissatrypidae, the Zygospiridae, the Palaferellidae and the Atrypidae. The Palaferellidae include the subfamilies Palaferellinae, Carinatininae and Karpinskiinae; the Atrypidae include the Atrypinae, the Zygospirinae and possibly the Atrypininae (the last family is of questionable status). In addition, some of the generic assignations of BOUCOT, JOHNSON & STATON (1964) are changed : Kerpina is not a carinatininid, and the genus Notoconchidium GILL 1950 is not accepted as a junior synonym of Karpinskia CHERNYSHEV, but is returned to the pentamerids where it is judged to belong in its rightful place and to which it was assigned by the original author. BOUCOT, JOHNSON & STATON also identified Vagrania ALEKSEEVA from the Canadian Arctic, but the specimen in question probably belongs to Gruenewaldtia or Mimatrypa (BOUCOT et al, 1964, Pl. 128, figs. 10-12).

It will be some time before a satisfactory classification may be worked out. At present all systems proposed remain tentative. The answer lies in more detailed studies of internal structures, and the establishment of phylogenetic series of species between one genus and the next. One of such series is the transformation of the genus Gruenewaldtia into the genus Mimatrypa which can be successfully established in the Eifel region. With the establishment of phylogenetic links between species groups and a systematics based on phylogeny rather than straight morphology, it may become impossible, paradoxically, to define distinctions between groups of family size or greater. This is the case, for example, in the definition of the two families Atrypidae and Palaferellidae. In the Atrypidae, the species group Desquamatia (Variatrypa) begins to approach, in its end-numbers, a morphology of the ribs and growth lamellae which is strongly reminiscent of the genus Gruenewaldtia of the Palaferellinae.

# VII SYSTEMATIC DESCRIPTIONS

## Order Atrypida RZHONSNITSKAYA 1960

## Superfamily Atrypacea GILL 1871

## Family Atrypidae GILL 1871

## Genus Atrypa DALMAN 1828

Type species: Anomia reticularis LINNE 1758, p. 702
(refer to LECTOTYPE Pl. 1, figs. 1a-e).
Range: Upper Llandoverian (Silurian) to Frasnian (Upper Devonian).
BOUCOT, JOHNSON & STATON, 1964, pp. 809-810.
Distribution: World-wide. Presently not reported from South America and the Antarctic.

Diagnosis.-

Convexoplane to dorsibiconvex shells with an ovoid to shield-shaped outline and small, appressed or epicline beak. Interarea minute or obscured, foramen minute, deltidial plates absent or very primitive. Commissure variably folded. Ribs are shallow, imbricate, and growth lamellae close-spaced (usually less than 1 mm). Growth lamellae are projected as short frills rarely more than 10 mm long.

Internally, pedicle layers fill much of the delthyrial cavity and may form a primitive collar. Deltidial plates usually absent, otherwise solid, lacking in growth lines and minute. Lateral cavities never developed : dental nuclei insignificant or absent. Cardinal process bushy, irregular and expansive, covering apical portions of dental sockets. Socket plates, excluding middle socket ridges, are corrugated. Hinge plates thick, crural bases massive and bulbous. Crura compact or slightly feathered distally. Disjunct jugal plates appear U- or V-shaped in transverse section. Whorls of spiralium spaced at about 1 mm. Shell wall with numerous interlayers of fibrous and columnar test.

Remarks.-

The name Atrypa has been applied, at one time, to nearly all species of the family Atrypidae. The shell structure of Silurian members of the genus has never been investigated, It is, therefore, difficult at the present time to make reliable distinction between Silurian and Devonian species. A revision of the type species Anomia reticularis LINNE 1758, based on topotypic material from the island of Gotland, Sweden, has never been attempted. This is urgently needed. ALEXANDER (1949) selected a lectotype from specimens deposited in the Linnaean Society collections.

In the Eifelian rocks of Germany, the genus Atrypa can be divided into two synchronous, but generally not associated, species-groups, which have been called Atrypa (Isonatrypa) and Atrypa (Planatrypa). It is not known if this distinction can be applied to Silurian species.

## Atrypa (Atrypa) DALMAN 1828

Type Species: As for the genus.
Range: Upper Llandoverian (Silurian) to lower Eifelian (?), (Devonian).

Diagnosis.-

Weakly to strongly dorsibiconvex shells with a moderately convex pedicle valve and commonly deeply arched brachial valve. Beak incurvature from appressed to epicline. Ribs imbricate, fine to coarse. Growth lamellae deflected. Frills short.

Remarks.-

There are no clearly defined borders between Atrypa (Atrypa), sensu restricto, and the two Eifelian subgenera Planatrypa and Isonatrypa. In a general sense, Atrypa (Atrypa) spans the whole range of variation of the two Eifelian subgenera. The type species of Atrypa is not dissimilar to the Eifelian Atrypa (Planatrypa) squamifera (SCHNUR 1853); both shells are somewhat convexoplanate (compare Pl. 1, fig. 1 and Pl. 5, figs. 1-2). It is possible that the subgenera Planatrypa and Isonatrypa are distinguishable only in the Eifel region, Germany, but this is unlikely because comparative collections from Poland indicate that these two groups also are definable in that region.

Atrypa can be distinguished from Isonatrypa by its more dorsibiconvex shells, less incurved beak, and usually also by its smaller size, and from Planatrypa.

Planatrypa differs in having a consistently convexoplane shell, lacking frills of any kind, and in possessing growth lamellae which hug the shell surface and give the ribs a more continuous appearance. Planatrypa rarely shows an incurved beak; it is nearly always appressed.

The Eifelian species attain a greater size than their Silurian counterparts.

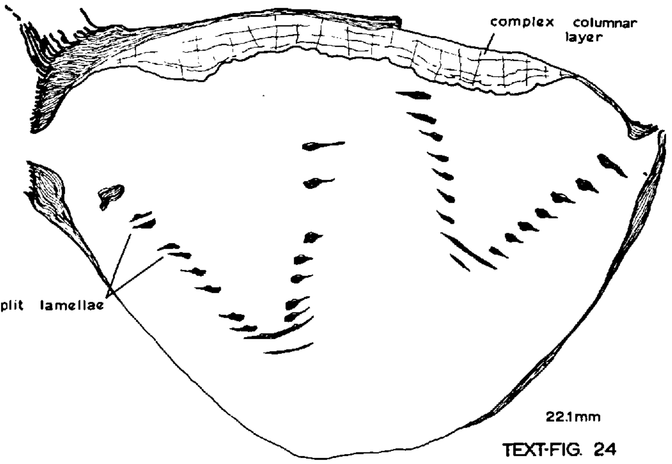
## Atrypa (Atrypa?) sp.

Pl.1, figs. 2-4; Pl.2, figs. 1a-d; text-fig. 24

Diagnosis.-

Large, convexoplane Atrypa up to 50 mm wide with a deeply arched brachial valve, almost planar pedicle valve. Short "ears" are typical. Brachial apex is strongly incurved, ventral apex appressed, not epicline. Ribs are relatively fine, about 14-16 per millimeter, interrupted by frequent short lamellae spaced at about 1 mm, and more closely spaced at the margins. Anterior fold is moderate.

Internally (text-fig. 24) spiralia appear to be rather small with up to nearly 10 whorls. Whorls are rather narrow and thick.



Text-fig. 24. Transverse section of Atrypa sp. from locality C325. At 22.10 mm. x 2½.

Remarks.-

Only a brief description of this early Eifelian atrypid is given. No serial sections were made. This large atrypid is characteristic of the Wolfenbach horizon (Lauch beds) and is locally quite abundant. It is easy to distinguish from the smaller and more finely ribbed Atrypa (Atrypa?) caepata n.sp. of the overlying Nohn beds. Atrypa sp. is more highly arched and finely ribbed than a similar convexoplane atrypid Atrypa (Planatrypa) squamifera (SCHNUR 1853). In its rib structure it is also different : Atrypa sp. is strongly interrupted surficially by slightly projecting, broken growth lamellae, whereas Atrypa squamifera (SCHNUR) shows complete degeneration of projecting lamellae and few breaking edges.

The orientation of the shells of Atrypa sp. at one locality (C325, MTB Dollendorf r5248:h8038) shows a two fold separation, already discussed under Ecology.

In one orientation the planar pedicle valve is down and parallel to the bedding plane, in the other the commissural plane is sub-vertical, usually tilted in a dorsal direction (see text-fig. 17). The adhering sediment is also fixed firmly to the shells in two positions corresponding to the observed orientations.

Material.-

Total 396 specimens from the Lauch beds.

C255(20); C262(3); C325(184); C369(14); C396(101); C403(28); H21(1); H76(5); St296(13); St709(18); St710(6); St878(1); RW74(1); BP246(1);

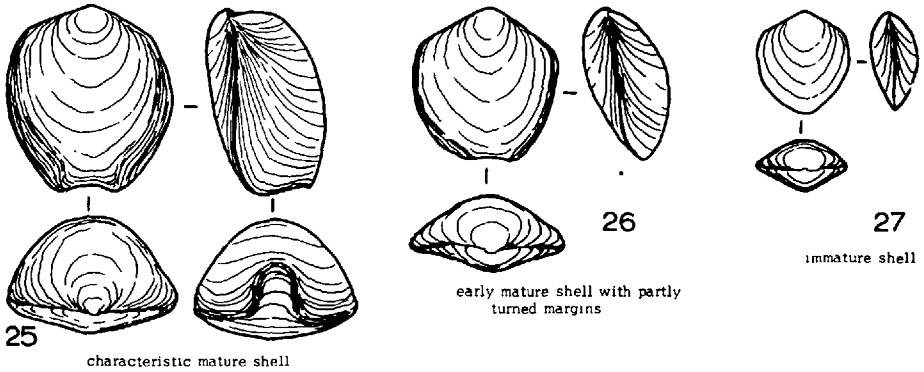
## Atrypa (Atrypa?) caepata n.sp.

Pl. 2, figs. 2a-d; Pl. 3, figs. 1-4; text-figs. 25-28.

Name: Latin, caepa, onion. The somewhat bulbous posterior and tapering anterior gives the shell an onion shape.
Locus typicus: Also the type locality of the Schleit horizon, i.e. brachiopod rich layers on the S-slope of Kirberg, Hillesheim syncline, MTB Dollendorf r54330:h74110.
Stratum typicum: Schleit horizon, Nohn beds, lower Eifelian.
Range: Chiefly in the Kirberg sequence of the Nohn beds, but the species is arbitrarily extended to the top of the Nohn beds, where it is, in the Hillesheim syncline, very rare.
Source sediment: Brownish-green, dark brown silty, calcareous shales with thin limestone interbands.
Associated fauna: Desquamatia (Variatrypa) ovata COPPER, rare Spinatrypa variaspina n.sp., rare rhynchonellids, common spiriferids, and gypidulis. Atrypa dominant. Horn corals scarce, tabulates absent.

Diagnosis.-

Medium sized, dorsibiconvex onion-shaped Atrypa. Ribs are fine (20-25 per 10 mm of arc at 15 mm from the apex), shallow; growth lamellae abundant at less than 2 mm spacing. Frills are short (less than 5 mm ), projected ventrally from the antero-lateral margin of the pedicle valve. Hinge angles 130-145 degrees, shoulder line weakly indented. Hinge corners well-rounded, swept forward. Pedicle valve weakly convex, brachial strongly convex. Globosity not uncommon. Anterior fold small, sharp and U-shaped (text-figs. 25-27).



Text-figs. 25-27. Shell variation in *Atrypa* (*Atrypa*) *caepata* n.sp. from the type locality. x1.

Interiorly, a primitive pedicle layer and deltidial plates close the delthyrial cavity. A dental nucleus is present apically. Teeth have wide bases, narrowed main lobes, weak lateral alobes. Cardinal processes short, wide apart; jugal plates small. Spiralia with up to 15 whorls (text-fig. 28).

Remarks.-

This species is similar to one described as *Atrypa subtrigonalis* BIERNAT 1964, which is said to occur with *Spinatrypa fasciplicata* STRUVE (an upper Eifelian fossil) in Poland. *Atrypa caepata* n.sp. appears to be somewhat larger, thicker and more tapering in outline anteriorly. It is restricted to the lower Eifelian.

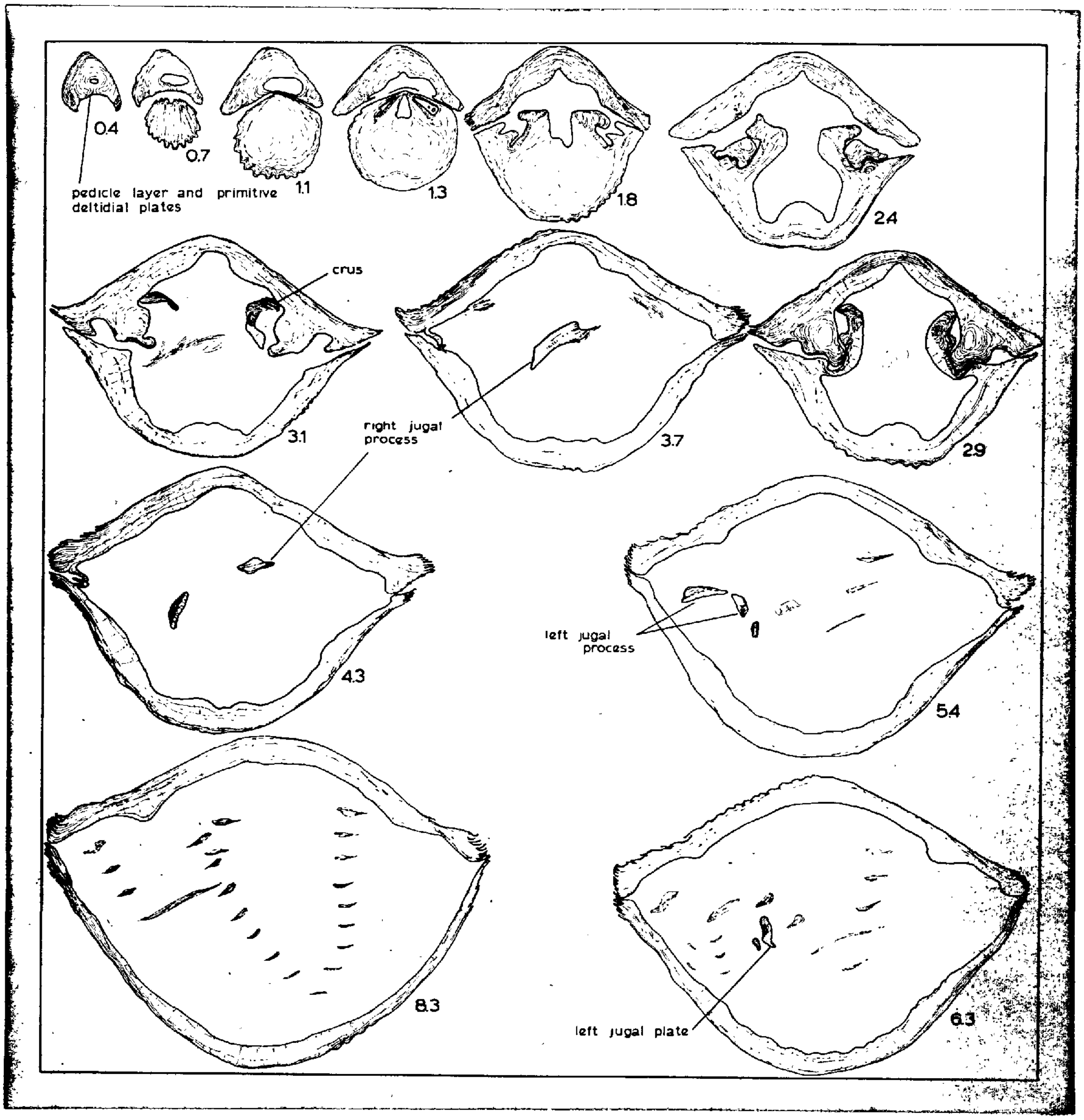
*Atrypa tenuicostata* ALEKSEEVA 1962, from the Kutznetsk basin in Russia has less resemblance to *A. caepata* n.sp. because it is more roundish in outline, with widely and evenly spaced growth lamellae. Internal structures in the Russian species are unknown.

*Atrypa caepata* n.sp. includes biconvex specimens which resemble some of those from the Ahrdorf beds, *Atrypa* (*Isonatrypa*) sp. X, but *A. caepata* does not contain a clear-cut division between biconvex and planoconvex *Atrypa* as is evident in younger Eifelian species. It was thought better to leave the Nohn species undivided. Furthermore, in the Nohn beds the two morphological types convexoplane and biconvex occur together at the same localities and a separation is not possible.

Material.-

Total 1821 specimens

C261(27); C274a(77); C274b(73); C276(22); C277(136); C283(2); C284a(4); C284b(28); C284c(19); C285(4); C287(92); C288(3); C324(1); C367(4); C368(6); C384(145); C397(29); C398)33); C440(2); H1(81); H33(2); H75(3);



Text-fig. 28. Transverse serial sections of Atrypa (Atrypa) caepata n.sp. Schleit horizon, Nohn beds; MTB Dollendorf r54320:h79070. x3.

H77(19); H78(141); H87(58); H99(25); H121(12); H139(21); H252(13); H256(41); AG22(1); BP49(4); BP80(1); St1(15); St2(1); St3(1); St13(57); St19(11); St101(14); St297(3); St298(5); St304(25); St307(14); St308(1); St343(3); St428(9); St511(11); St559(2); St711(92); St712(41); St713(21); St714(6); St715(79); St716(13); St830(1); St965(11); St966(4); St967(4); Fp1261(8); Fp1262(70); Fp1263(7); Fp1264(174).

## *Atrypa* (*Isonatrypa*) n. subgen.

Name: Latin, *iso*, the same, equal. This refers to the predominantly equally convex nature of the shell.
Type species: *Atrypa* (*Isonatrypa*) *inglanda* n.sp.
Range: Middle Devonian, chiefly Eifelian. Possibly present in the Upper Devonian.
Distribution: Probably world-wide.

Diagnosis.-

*Atrypa* with consistently equally convex, or weakly dorsibiconvex valves, commonly with the pedicle valve strongly globose, and beak incurved to epicline rather than appressed. Frills are often sharply deflected and show a lesser tendency to overlap in thick layers at the margins.

Remarks.-

The first indications of divergence in the morphology of *Atrypa* appear in specimens of *Atrypa* (*Atrypa*?) *caepata* n.sp. However in the Eifel region it can be distinguished clearly from other *Atrypa*, only for the first time in the Ahrdorf deds. It is abundant where *Atrypa* (*Planatrypa*) is rare and vice versa. The species groups are mainly allopatric. A few intermediates occur in each species, but these are rare. It is already distinct from *Atrypa* (*Planatrypa*) in neanic stages when its shells are much more globose, ovoid and pointed. It can also be distinguished from *Planatrypa* n.subg. by its ribs, which are more sharply crested, narrower and often finer and by growth lamellae which are more closely packed. The incurvature of the beak is also a diagnostic character : in *Isonatrypa* it is epicline, in *Planatrypa* appressed. There is not a marked borderline between *Isonatrypa* and *Atrypa* (*Atrypa*) and the subgenera obviously intergrade. They may be distinguishable only in the Eifel region.

Member species: *Atrypa* (*Isonatrypa*) sp. X, *Atrypa inglanda* n.sp., *Atrypa verneuiliana* (BARRANDE)?

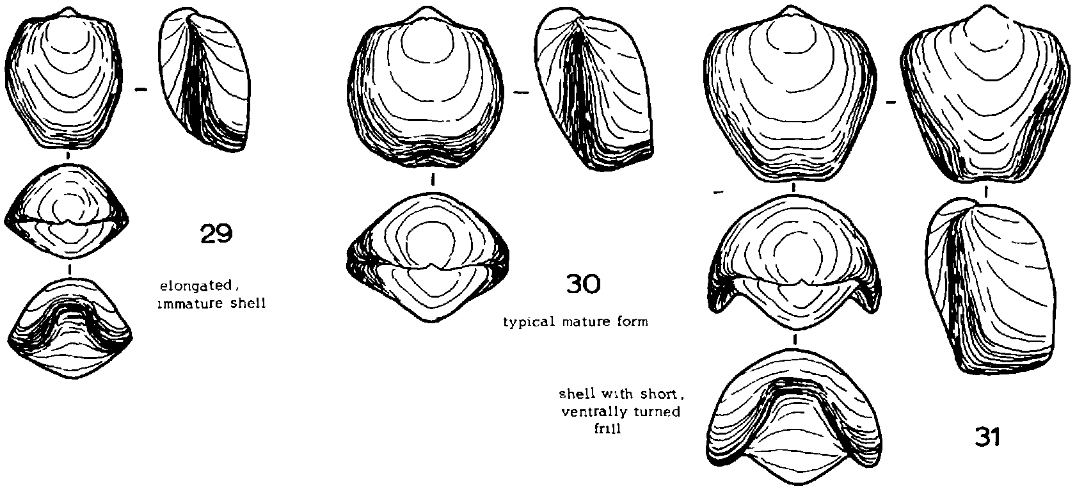
## Atrypa (Isonatrypa) sp. X

Pl. 4, figs. 4-5; text-figs. 29-31

Type locality: N flank of small hill WNW of Nohn (Pt. 439,0) Hillesheim syncline, MTB Dollendorf r55790-6110:h78000-78090.
Type stratum: Niederehe horizon, Ahrdorf beds, middle Eifelian.

Diagnosis.-

Small to medium sized, sharp beaked, pointed, often rather globose shells with strongly incurved beaks. Short 5 mm marginal frills not uncommon. Ribs are fine, 18-22 ribs per 10 mm of arc, and growth lamellae are short and numerous, spaced closely at less than 1 mm., even 10-15 per mm.



29 elongated, immature shell

30 typical mature form

31 shell with short, ventrally turned frill

Text-figs. 29-31. Shell variation of Atrypa (Isonatrypa) sp. X from the type locality. x1.

Remarks.-

The ribbing, growth lamellae and convexity of the shell appear to mark this atrypid as a forerunner of Atrypa (Isonatrypa) inglanda n.sp. Neverless it is different in being much finer ribbed, almost half the wave length of its descendant. It is much smaller, more biconvex and has shorter frills some of which tend to concentrate on the margins rather than being more widespread about the shell. The fold and hinge corners are rather sharp and tend to give some shells a hexagonal outline.

Material.-

Total 209 specimens

C240(1); C242(7); C244(1); C247(1); C248(1); C256(3); C258(6); C272(7); C290(1); C297a(3); C365(4); C399(1); C411(2); H28(11); H215(1); AG305(1); RW246(1); St10(1); St20(2); St30(2); St32(11); St50(3) St52(3); St54(5); St54a(1); St57(7); St58(1); St60(3); St61(2); St62(4); St65(1); St98(13); St104(1); St109(36); St180(4); St182(1); St393(2); St394(2); St430(1); St442(1); St446(9); St447(1); St459(1); St460(7); St476(2); St503(1); St679(10); St717(2); St814(7); St831(3); Fp1280(4).

### *Atrypa* (*Isonatrypa*) *inglanda* n.sp.

Pl. 8, figs. 1-2; Pl. 9, figs. 1-5; text-figs. 32-34.

Name: Latin, *inglanda*, a walnut. The shell is nearly the size and shape of a walnut.

Type locality: Quarry on Steinberg, 1500 m. N Kerpen, Hillesheim syncline, MTB Dollendorf r5218:h7636.

Type stratum: Eilenberg horizon, Freilingen beds, upper Eifelian.

Range: Junkerberg beds to Ahbach beds, Eifelian.

Source sediment: Dark to brownish green calcareous shales, rich in brachiopods.

Associated fauna: *Spinatrypa aspera aspera* (SCHLOTHEIM) to the north, *Kerpina vineta*. STRUVE to the south; *Atrypa* (*Planatrypa*) *petasa* n.sp. *Atryparia stabilia* COPPER. These are associated atrypids of the Freilingen beds.

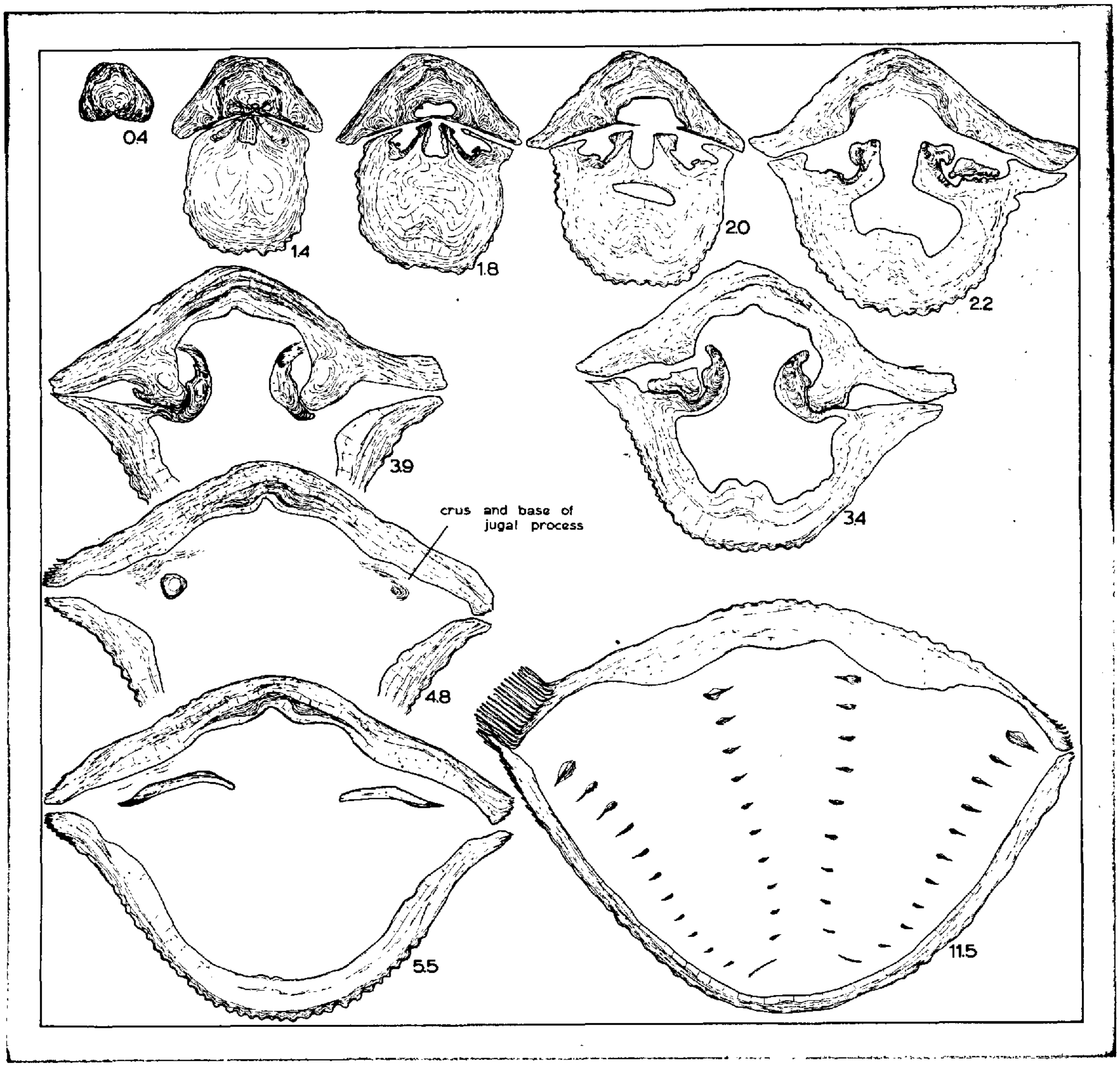
Diagnosis.-

Medium sized, globose biconvex atrypids with numerous coarse growth lamellae. Ribs are medium sized (12-13 per 10 mm.). Beaks are pointed, apical angles acute. The commissure is moderately folded.

Internally, deltidial plates are absent, deltidial layers form a pedicle constriction (text-fig. 32). Teeth are short, blunt. Cardinal process thick. Strong inner socket ridges, thick crural supports and crural bases. Jugal processes short. Jugal plates meet at a V- ngle, are not connected.

Remarks.-

The species is most abundantly developed in the Hillesheim syncline. Specimens of Junkerberg age are somewhat smaller, slightly more finely ribbed and with less deflected lamellae. In the Junkerberg and Freilingen beds specimens of the new subgenus *Isonatrypa* are difficult to confuse with the flat-shelled specimens of *Planatrypa*. The Junkerberg forms grade into *Atrypa* (*Isonatrypa*) sp. X in their finer ribbing, smaller size and more pointed, sharp-ridged mid-fields.



Text-fig. 32. Transverse serial section of Atrypa (Isonatrypa) inglanda n.sp. Eilenberg horizon, Freilingen beds; MTB Dollendorf r53870:h74680. x3.

HAVLICEK (1955, Pl. 3, figs. 1-7, 16) figures specimens of Atrypa verneuiliana (BARRANDE), from the Devonian of Prague, which share a similar type of rib construction as Isonatrypa inglanda n.sp. But the Czech form is flatter ventrally, and appears to possess fewer concentric lamellae. It is also evidently much smaller than the specimens occurring in the type stratum (Eilenberg horizon) of the Eifel area.

In the northern Eifel the Junkerberg beds contain very few specimens of this new species; in the Prüm syncline, to the southwest, they also are not as frequent. It may be feasible to separate the Junkerberg forms from those which occur in the Freilingen beds, possibly as a subspecies. The specimens which are found (more rarely) in the Ahbach beds also are smaller and in some aspects come closes to the type figured by HAVLICEK (see above).

It is possible that an atrypid illustrated by QUENSTEDT (1871, Pl. 42, fig. 103) is a specimen of *Atrypa inglanda* n.sp., but this cannot be verified because QUENSTEDT left specimens undescribed under the encompassing name *Terebratula prisca* SCHLOTHEIM. The atrypid figured by QUENSTEDT could belong to *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR) although it is somewhat too finely ribbed for that species.

The specimen figured by SCHNUR (1853, Pl. 24, fig. 4a-b) may belong to *Atrypa* (*Isonatrypa*) *inglanda* n.sp. It has stronger affinities with Junkerberg specimens which are usually smaller and have the marginal curl shown in SCHNUR's figure. SCHNUR's specimen is too flattened at the sides to belong to *A.* (*I.*) sp. X and lacks the stronger, angular median mid-field.

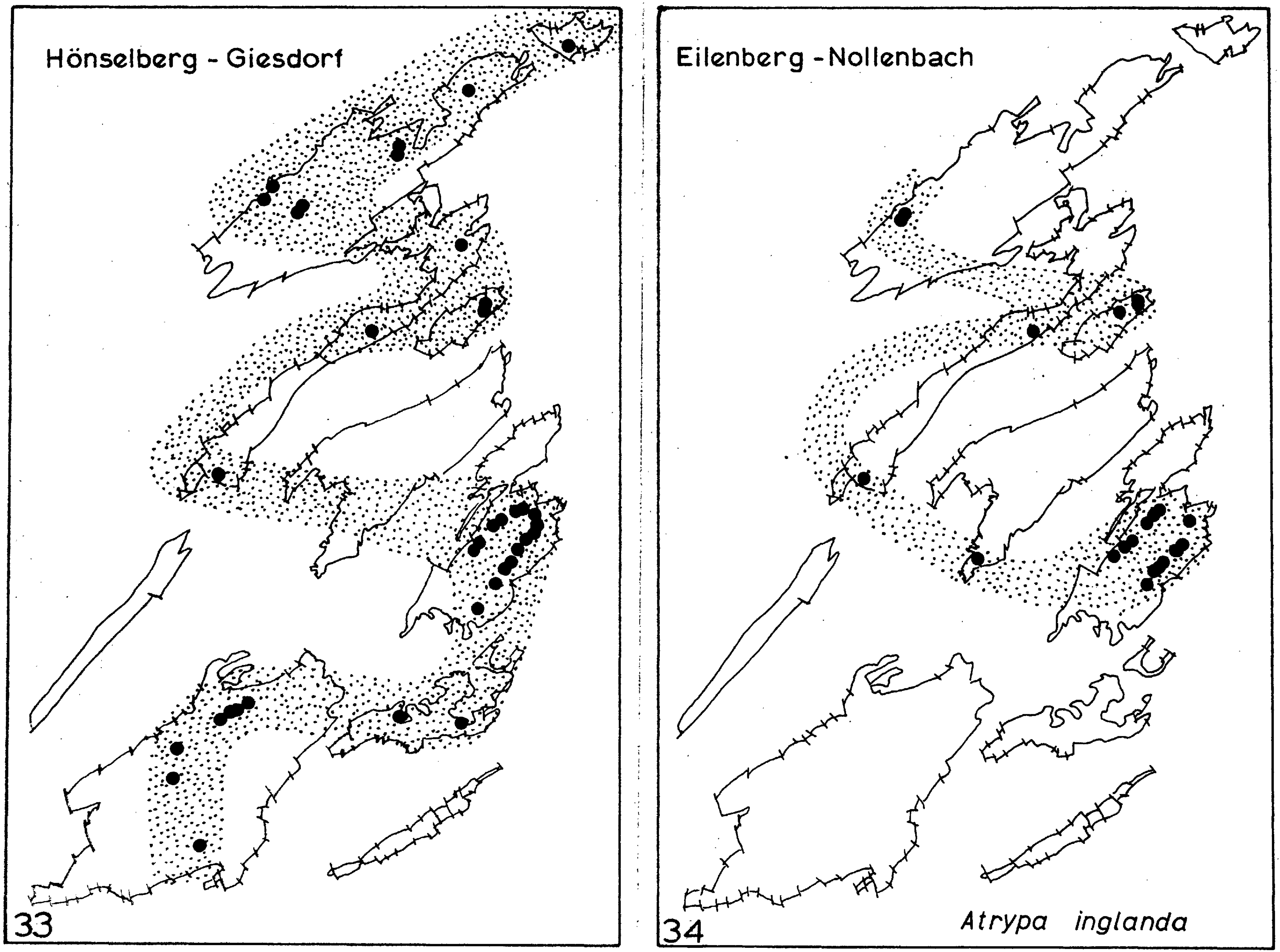
An examination of the syntypes of *Terebratula squamifera* SCHNUR 1853, revealed that under this name were a few specimens belonging to *Atrypa inglanda* n.sp. It may have been SCHNUR's original intention to call the biconvex forms *squamifera*. One of the convexoplanate shells, however, was selected as lectotype, leaving the biconvex forms under *Atrypa inglanda* n.sp.

*Material*.-

Total 2084 specimens

*Junkerberg beds*: C294(1); C295(28); C300(17); C302(33); C303(28); C304(6); C326(2); C350(4); C352(2); C356(6); C357(18); C374(7); C376(1); C379(7); C381(1); C388(3); C389(1); C390(2); C394(17); C395(5); C409(2); C438(2); C450(3); C455(6); C457(8); C466(4); C477(3); C508(5); C511(12); C513(11)=C394; St7(1); St21(5); St23(2); St40(3); St67(12); St41(9); St68(7); St69(1); St72(4); St73(4); St75(2); St76(1); St78(1); St79)33): St83(2); St100(25); St107(1); St114(1); St183(1); St184(1); St246(1); St252(5); St274(2); St275(3); St336(1); St356(1); St362(7); St438(1); St441(1); St449(8); St450(2); St451(1); St491(3); St252(15); St593(1); St604(1); St620(1); St624(7); St630(7); St633(58); St637(54); St638(4); St736(263); St737(82); St738(36); St741(29); St742(39); St743(144); St744(1); St745(2); St758(6); St821(5); St824(1); St825(1); St287(1); St959(2); St960(3); Fp1304(6); RW45(1); BP161(1); BP242(1); BP262(1); AG82(1); AG170(2); AG291(1); AG33(2).

*Freilingen beds*: C279c(1); C298(27); C299(19); C301(8); C316(22); C317(27); C318(10); C343(2); C344(2); C345(20); C346(4); C347(7); C353(14); C354(8); C355(3); C358(17); C359(105); C360(21); C361(15); C364(8); C414(6); C468(19); C475(27); C507(19); C512(62); St8(2); St43(18); St44(9); St70(25); St71(19); St77(4);St78(7); St80(2); St99(2); St591(6); St600(2); St614(2); St618(10); St619(17); St626(4); St639(2);



Distribution of *Atrypa* (*Isonatrypa*) *inglanda* n.sp. in the Eifel.

St672(60); St673(22); St674(24); St707(1); St723a(1); St724(2); St728(12); St731(7); St732(1); St734(6); St735(5); St752(2); St766(1); St771(2); St810(24); St811(2); St868(1); AG6(4); AG33(2); AG77(4); AG82(1); AG297(6); AG313(2); Fp1193(7);BP273(8); S8t40(15)=BP273; BP94(2).

Ahbach beds: C279fa(16); C279fb(3); C279e(7); St739(2); St961(5); St190(6); St640(2); St651(1); St765(1); St950(29).

## Atrypa (Planatrypa) n. subgen.

Type species: Atrypa (Planatrypa) petasa n.sp.
Range: Ahrdorf beds to Ahbach beds, Eifelian, Middle Devonian.
Distribution: At present known mainly from Germany. Also present in the Skaly beds, Poland.

Diagnosis.-

Convexoplane, medium to coarsely ribbed Atrypa lacking deflected growth lamellae and frills. Beaks appressed not incurved. Young specimens planar; pedicle valve commonly marginally concave in maturity.

Remarks.-

As early as Ahrdorf time two independent distinct "varieties" or species groups of Atrypa are discernible in the Eifel region. This is the variation with consistently flat pedicle valves.

It is distinguishable from synchronous Isonatrypa in being more coarsely ribbed, and with rather strong growth ridges at each concentric lamellae base. Growth lamellae leave few breaking edges and are only slightly, if at all, deflected. Frills are completely absent. Even early ontogenetic stages are clearly differentiated.

Planatrypa is not easy to distinguish from the type species of Atrypa, i.e. Atrypa reticularis (LINNE), which is also strongly convexoplane and has similar rib structure. Planatrypa is separated purely on the basis of material from the Eifel region, where clear distinctions exist. Elsewhere Planatrypa may completely intergrade with Atrypa, and may in fact form a single morphological group. Internally, there is at the moment not sufficient evidence to separate these two subgenera.

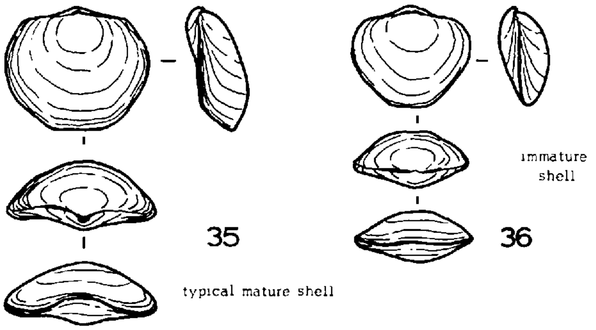
## *Atrypa* (*Planatrypa*) sp. M.

Pl. 4, figs. 1-3; text-figs. 35-36.

Type locality: S slope of Betterberg, Hillesheim syncline, MTB Dollendorf r5448:h7473.
Type stratum: Flesten horizon, Ahrdorf beds, middle Eifelian.
Range: Ahrdorf beds, Eifelian.

Diagnosis.-

Small, planar *Atrypa* with weakly corrugated ribs severely interrupted by growth lamellae. Anterior margin curved ventrally. Brachial valve not highly arched, pedicle valve planar to weakly concave. Obtuse hinge angle. Beaks appressed, blunt. Hinge margin gently folded. Outline subquadrate. Weak anterior fold (text-figs. 35-36).



Text-figs. 35-36. Shell variation of *Atrypa* (*Planatrypa*) sp. M. Flesten horizon. x1.

Remarks.-

The species is much smaller (about $\frac{1}{3}$), more planar, and weakly ribbed than the younger *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR). The same features distinguish it from the Nohn atrypid *Atrypa* (*Atrypa*?) *caepata* n. sp. *Atrypa* (*Planatrypa*) sp. M. can be used in conjunction with (*Isonatrypa*) sp. X to give a more precise age to the upper parts of the Ahrdorf beds. *Planatrypa* is more richly developed than *Isonatrypa* in the Flesten horizon and is absent higher up the sequence where *Isonatrypa* begins to reach it acme. This correlation also holds for the Ahrdorf beds in the Gerolstein syncline. The internal structure of *Atrypa* (*Planatrypa*) sp. M. still needs examination.

*Material*.-

Total 381 specimens

C241(4); C244(4); C248(59); C253(1); C290(10); C291(5); C297c(6); C399(1); C406(2); C408(5); St31b(8); St32(15); St50(5); St54a(3); St54(51); St57(1); St58(5); St60(9); St62(10); St90(1); St109a(29); St180(3); St182(2); St394(5); St396(9); St430(2); St440(4); St447(5); St461(5); St471(3); St503(5); St535(2); St662(4); St679(12); St717(27); St802(4); St813(2); St814(26); St831(17); St879(2); Fp1279(1); Fp1280(5); H28(11); H83(4); H100(4); H216(1); H236(1); AG25(3); AG26(1); AG234(1); AG305(2); Lehmen 1(27); Ge22(7); Ge20(3); Ge24(6); St15(18).

## *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853)

Pl. 5, figs. 1-2; Pl. 6, figs. 1-3; text-figs. 37-38.

1853 *Terebratula squamifera* SCHNUR (partim), pp. 181-182, 242.

*Type locality*: "allenthalben im Kalk, hin und wieder in der Grauwacke z.B. Daleiden" (SCHNUR, 1853, p. 234). Other than Daleiden, where the species does not occur, SCHNUR did not name any type localities.

*Locus typicus restrictus*: A small excavation at Giesdorf, Prüm syncline, MTB Schönecken r32200:h60330 is designated as type locality.

*Stratum typicum*: SCHNUR (1853, p. 182) gave the species a long and wide range through the whole Devonian sequence and in all types of strata "Im Kalk und in der Grauwacke". The type stratum, in which the SCHNUR species sensu restricto, is abundant, is confined to the Giesdorf horizon, Junkerberg beds, Eifelian.

*Range*: Junkerberg beds, middle Eifelian. The species is replaced in the Freilingen beds by *Atrypa* (*Planatrypa*) *petasa* n.sp. It is an index fossil of the Junkerberg beds. *Atrypa squamifera* (SCHNUR) is most abundant in the upper parts of the Junkerberg beds, especially the Nims-Giesdorf horizons. It becomes smaller in the Hönselberg horizon and ia rare in the Klausbach-Mussel horizons.

*Source sediment*: Typically in dark brownish clayey or crumbly calcareous shales. Calcareous debris is lacking.

*Associated fauna*: *Spinocyrtia ostiolata* SCHLOTHEIM), *Schizophoria schnuri* STRUVE. The fauna is mainly bitypic, consisting of *Spinocyrtia* (70%) and *Atrypa* squamifera (25%). Most shells of *Atrypa* show borings of *Clionoides* (see Ecology, p. ). *Crania* and Aulopora are common epifauna.

*Diagnosis*.-

Large, convexoplane shells, with flattened, appressed beaks and a strong anterior fold. Ribs are coarse, about 10 per 10 mm; growth lamellae are fairly evenly spaced at about 1 mm. except at the margins. Frills or ears lacking. The ventral valve is weakly convex or plane and only rarely concave.

Long, inwardly directed teeth are typical (text-fig. 37). Deltidial plates lacking. Delthyrial cavity with lining to form a pedicle constriction. The cardinal process is thick, and consists of 4 to 6 main strands in the notothyrial cavity, but also spreads widely over the socket plates (Pl. I, fig. 4). Crura are short, thick. Jugal processes are straight, terminate in sub-vertical jugal plates with bulbous tips.

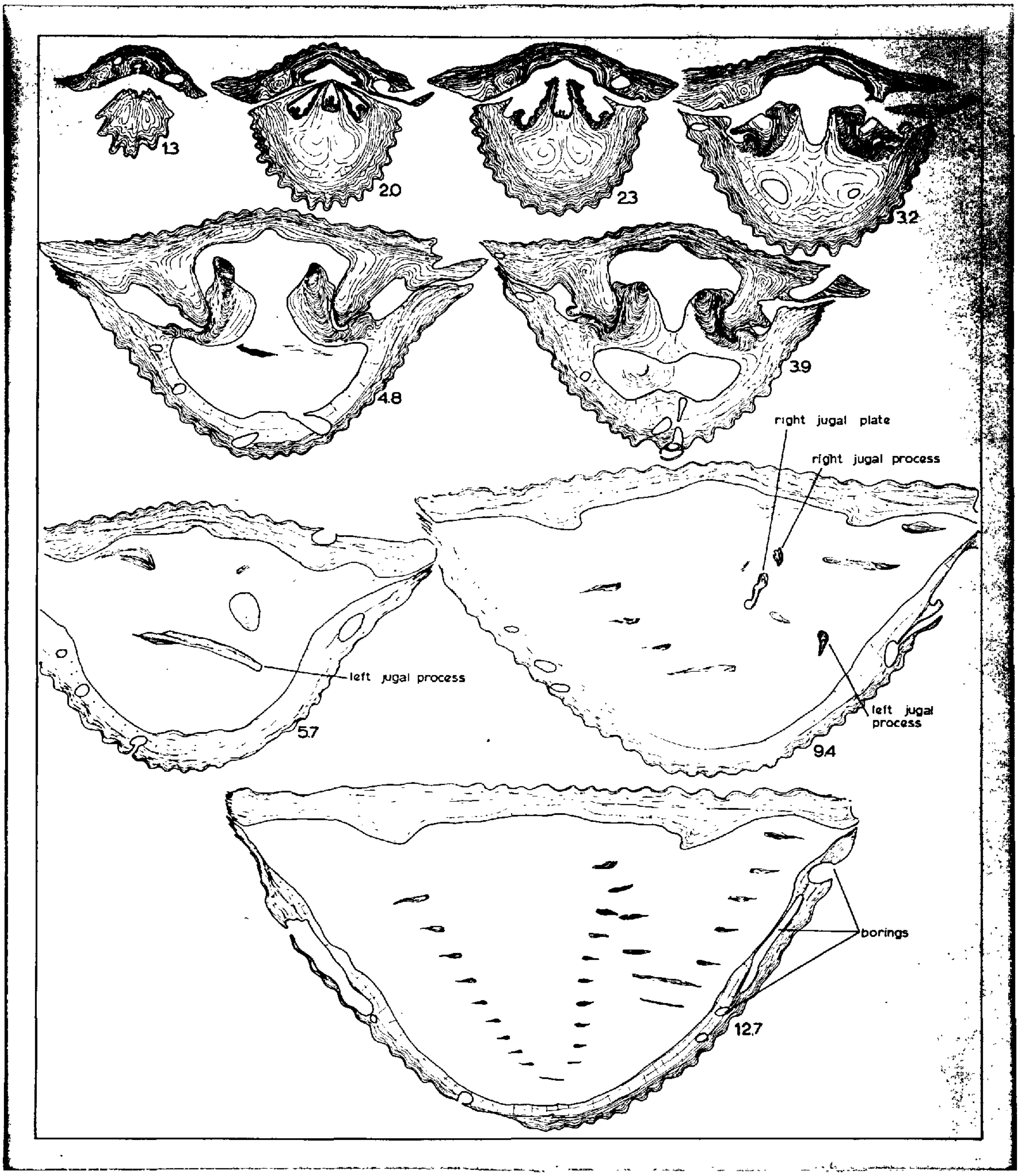
Remarks.-

Atrypa squamifera (SCHNUR) is as distinctive of upper Junkerberg beds as the guide fossil of the southern synclines, Spinocyrtia ostiolata (SCHLOTHEIM), but it reaches a much wider distribution and may be more useful. It differs from the younger Atrypa (Planatrypa) petasa n.sp. in its much larger size (nearly x2), coarser ribs, lack of ventrally turned margins, and wider spaced growth lamellae. Young specimens are equally distinctive and cannot be mistaken for the smaller mature form of A. petasa.

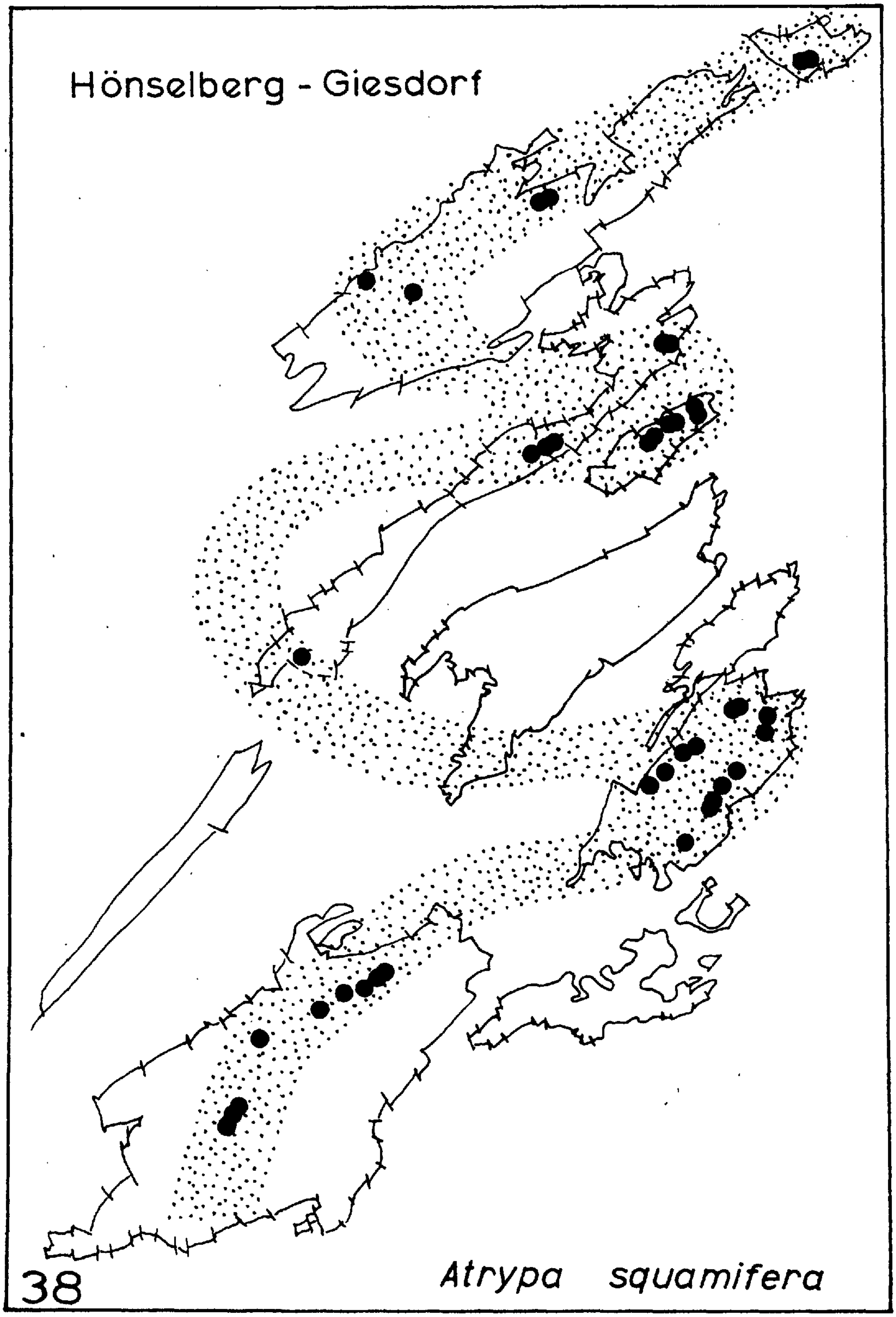
SCHNUR (1853) obviously intended to group all of the Devonian atrypids roughly equivalent to the old Atrypa reticularis in his own species squamifera, much as SCHLOTHEIM (1820) probably intended to regroup all reticularis-like atrypids under Terebratula prisca. SCHNUR (1853, p. 181) apparently did not think that squamifera was identical to SCHLOTHEIM's prisca for he stated "Terebratulites priscus Schloth zum Theil". SCHNUR (ibid.) also referred to DAVIDSON's redescription of LAMARCK's atrypids in which a figure is given which SCHNUR thought was a good illustration of the Eifel species (DAVIDSON, 1850, Pl. 14, fig. 55). This figure of DAVIDSON's seems however to be more like Desquamatia pectinata (SCHRÖTER 1777) from the classical Frasnian locality at Refrath. The evidence for this lies in a clear view of a small area and foramen, characteristics which SCHNUR did not recognize in Atrypa squamifera.

There is some difficulty in reconciling this revised version of Atrypa squamifera (SCHNUR) with the convexity description given by SCHNUR (1853, p. 181, "Die Ventralschale viel stärker gewolbt"). This convexity applies more suitably to associated specimens of Atrypa (Isonatrypa). The flat ventrally valved atrypid was chosen as type of Atrypa squamifera because it was most easily definable, and known to be stratigraphically more restricted.

None of SCHNUR's figures can be attributed definitely to the redefined Atrypa squamifera. SCHNUR's collection contained three specimens only one of which corresponded to a figure (SCHNUR, 1853, Pl. 24, figs. 4a-b). This one was not elected as lectotype. One of SCHNUR's unillustrated specimens is identical to the atrypid so common in the Giesdorf horizon. This flat form was designated as lectotype. It is not illustrated, SCHNUR's figures (except possibly fig. 4c) cannot be attributed to Atrypa squamifera and are partly part of the



Text-fig. 37. Transverse serial sections of *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853). Giesdorf horizon, Junkerberg beds; MTB Schönecken r32200: h60330. x2.



Distribution of Atrypa (Planatrypa) squamifera (SCHNUR 1853).

genus *Spinatrypa* and perhaps *Atryparia*.

No foreign convexoplane atrypids of identical size and shape are known. The most similar atrypid appears to be *Atrypa vulgaris* LJASHENKO, as it is figured in ALEKSEEVA (1962, Pl. 2, figs. 2a-c). This shell has a more acute apical angle and is more shield-shaped and biconvex than the Eifel species.

*Material*.-

Total 1697 specimens. Old collections, precise localities of which are not known, have not been listed.

The species is relatively rare in the Hillesheim syncline, and more abundant in the Prüm syncline and to the north.

C300(5); C302(6); C303(11); C326(16); C341(9); C356(15); C357(10); C370(93); C376(1); C381(4); C382(5); C383(10); C388(3); C389(3); C390(5); C393(4); C394(167); C395(40); C408(14); C409(5); C438(3); C450(14); C455(172); C457(41); C458(18); C466(31); C508(29); C513(133); AG6(10); AG7(3 ); AG32(21); AG33(15); AG43(3); AG52(12); AG82(4); AG82a(1); AG170(5); AG177(1); AG239(6); AG239a(12); AG245a(1); AG256(1); AG267(1); AG264(16); AG265(2); AG268(7); AG270(3); AG276(10); AG279(1); AG281(3); AG283(3); AG287(3); AG289(3); AG298(3); RW23(1); RW24(1); RW226(2); Söt19(37); KoBaasem(13); St7(2); St23(1); St40(5); St68(3); St69(2); St71(7); St72(14); St73(5); St75(2); St77(1); St79(78); St80(1); St83(1); St86(2); St100(2); St275(1); St324(2); St356(1); St362(6); St449(5); St451(11); St453(1); St525(5); St526(5); St591(3); St620(1); St624(4); St630(17); St633(18); St637(15); St638(2); St655(3); St736(38); St737(12); St738(2); St741(5); St743(26); St758(5); St809(1); St821(4); St822(3); St960(3).

### *Atrypa* (*Planatrypa*) *petasa* n.sp.

Pl. 6, figs. 4-12; Pl. 7, figs. 1-3; text-figs. 39-40.

*Name*: Latin, *petasa*, a hat, cap. With its convexoplane, highly arched shell it resembles a small hat.

*Type locality*: Road cut along field road, N Niederehe creek, approximately 500 m ENE Niederehe, Hillesheim syncline, MTB Dollendorf r5453:h7559.

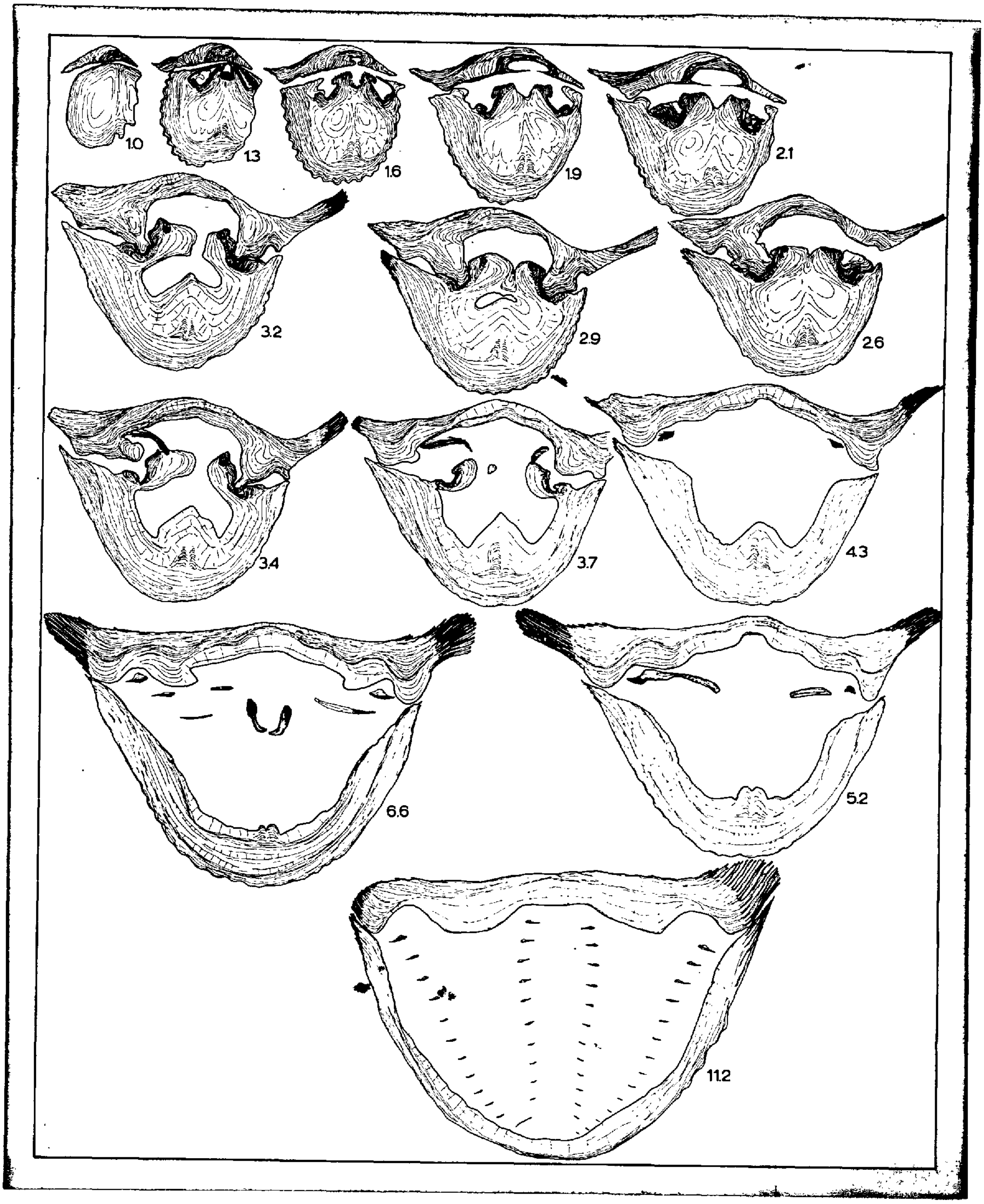
*Type stratum*: Nollenbach horizon, Freilingen beds, upper Eifelian.

*Range*: Freilingen beds to Ahbach beds, Eifelian.

*Associated fauna and sediment*: See *Kerpina*. .

*Diagnosis*.-

Small, convexoplane, longer than wide shells with short, ventrally turned margins and weak anterior fold. Beak flattish, blunt, appressed. Ribs fine (11-14 per 10 mm.); growth lamellae spaced at less than 1 mm.



Text-fig. 39. Transverse serial sections of *Atrypa* (*Planatrypa*) *petasa* n.sp. Eilenberg horizon, Freilingen beds, upper Eifelian; MTB Dollendorf r54330:h75590.

Brachial valves highly arched with steeply dropping sides.

Internally (text-fig. 39) deltidial plates are completely lacking but a thick pedicle constriction is present. Teeth are short, blunt, with 3-4 crenulations and an indistinct lateral lobe. Hinge plates thick, bulbous. Crura thin, unfeathered, connected to short jugal processes with numerous nodules terminally. Jugal plates slightly bent, opposed in a U-shape. Nearly 15 whorls form a mature spiral cone.

Remarks.-

Among the specimens in the original collection of SCHNUR there is one which corresponds to *Atrypa* (*Planatrypa*) *petasa* n.sp. and SCHNUR probably meant to include this specimen in his *Terebratula squamifera* (SCHNUR, 1853, p. 181-182). Under the latter name SCHNUR did however include a number of species only one of which was selected as lectotype of *Terebratula squamifera*, the remainder not belonging to the same species. It is doubtful if the specimen figured by SCHNUR (1853, Pl. 24, fig. 4a-b) can be attributed to *Atrypa* (*Planatrypa*) *petasa* n.sp.

*Atrypa petasa* n.sp. is an index fossil of the upper Eifelian. Extremely few specimens gradational with *Atrypa squamifera* (SCHNUR) were found at this level. The rather sharp transition from one to the other seems to have occurred at the boundary between the Giesdorf and Eilenberg horizons. It can be distinguished from *A. squamifera* (SCHNUR) by its smaller size (about one half to one third), finer ribs, more closely spaced growth lamellae and internally by less accentuated margins around the ventral diductors.

Where the *Spinocyrtia ostiolata* fauna, marking the Giesdorf horizon, is absent, the change from *Atrypa* (*Planatrypa*) *squamifera* to *Atrypa* (*Planatrypa*) *petasa* n.sp. can be equally indicative of stratigraphic horizon. The well known *Spinatrypa aspera* horizon of the Sötenich syncline contains a few somewhat large *Atrypa petasa* n.sp. This is a valid independent check on the placement of the *aspera* horizon directly above the Giesdorf horizon.

A similar foreign species is an atrypid described and figured by McCAMMON (1960, p. 51-52, Pl. 8, figs. 10-12) as *Atrypa bremerensis* STAINBROOK, from Manitoba in western Canada. The Manitoba atrypid is more coarsely ribbed but in general is close enough morphologically to *Atrypa petasa* as to suggest a similar stratigraphic position. The age of the Canadian species is said to be lower Givetian; the Eifel species is upper Eifelian. The species described by McCAMMON has little in common with the atrypid originally described as *Atrypa bremerensis* by STAINBROOK (1938, p. 231, Pl. 31, figs. 11-14), *Atrypa petasa* n.sp. also is dissimilar to STAINBROOK's species, being less rounded, more angular, more convexoplane and even concave on the pedicle valve.

LJASHENKO (1959, Pl. 24, figs. 1-4) figured a Frasnian species which is very similar in its shape to *Atrypa petasa* n.sp. The name given was *Atrypa richthofeni* KAYSER. The pedicle valve of *Atrypa petasa* is not quite as concave, and the ribs are coarser than the Russian species of LJASHENKO. GRABAU (1931, Pl. 21, figs. 7-11) figured a species which he called *Atrypa richthofeni* KAYSER from the Middle Devonian of China, but from GRABAU's illustration it seems likely that the Chinese species belongs to *Desquamatia ajugata* COPPER 1965. The original "*Orthis richthofeni*" described by KAYSER (1883, p. 92, Pl. 13, figs. 2, 2a-c) probably also belongs to *Desquamatia*.

*Material*.-

*Atrypa* (*Planatrypa*) *petasa* n.sp. is rare in the northern synclines including the Sötenich, Blankenheim, Rohr and Dollendorf synclines (text-fig. 40).

Total 1037 specimens: 820 Of Freilingen age.

C279b(72); C279c(19); C279d(19); C299(2); C305(4); C315(16); C316(59); C318(4); C343(15); C344(5); C345(18); C346(3); C347(2); C350(8); C351(5); C352(5); C353(38); C354(4); C355(4); C357(2); C358(20); C359(49); C360(18); C361(18); C362(6); C382(52); C388(24); C392(2); C468(2); C512(38); C519(8); St41(4); St43(26); St44(21); St8(3); St67(1); St70(60); St76(4); St77(6); St78(13); St80(8); St274(8); St439(3); St589(6); St592(3); St600(6); St618(10); St619(6 ); St620(3); St621a(2); St621(4); St623(5); St625(1); St626(10); St623a(7); St639(3); St665(3); St672(38); St673(23); St674(38); St675(1); St708(3); St720(1); St723a(5); St724(1); St728(2); St731(2); St732(2); St734(3); St735(4); St752(40); St767(9); St770(3); St772(2); St810(14); St811(8).

*Ahbach beds*.-

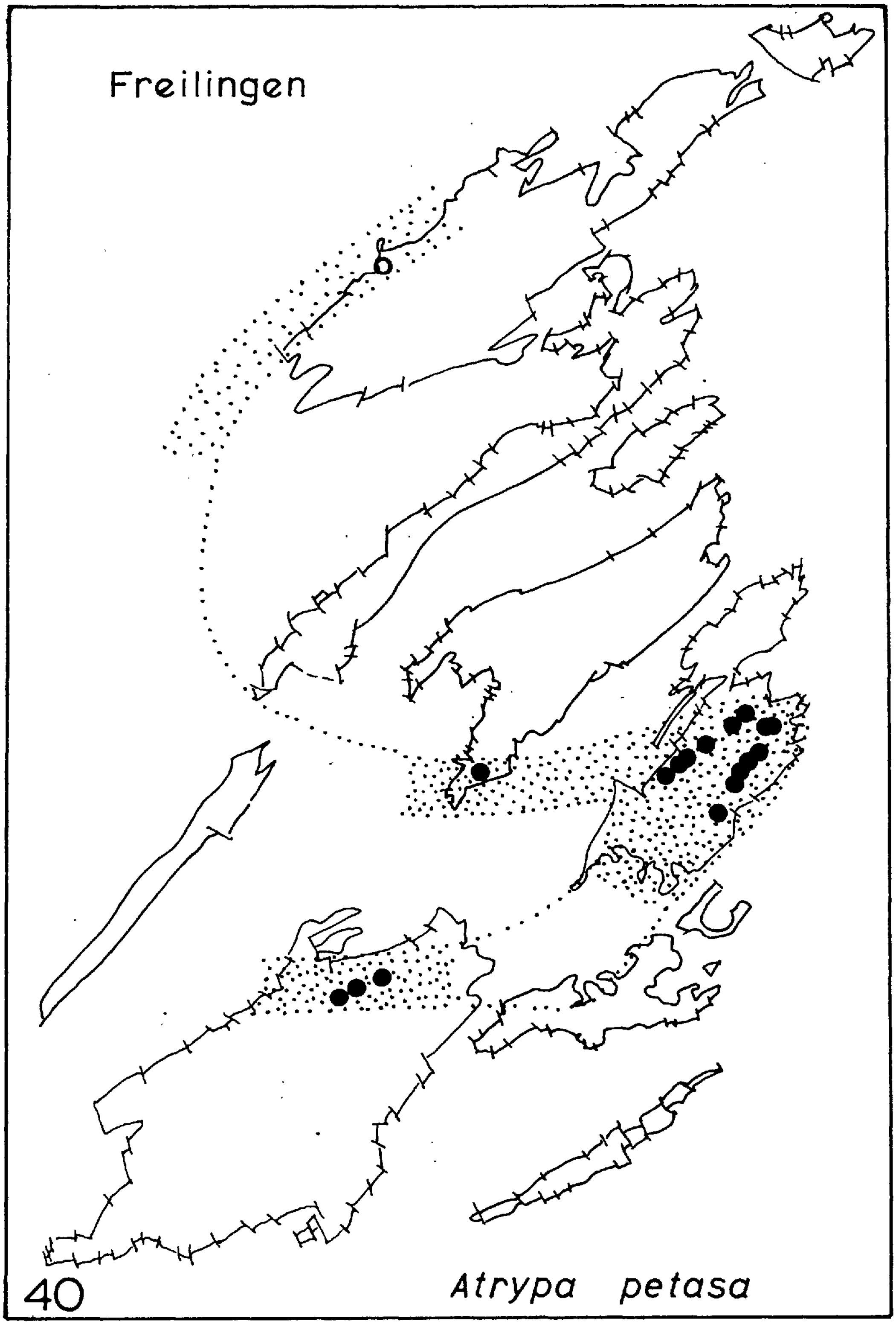
Specimens from the Ahbach beds are rare, particularly in the upper Müllert horizon. They are somewhat larger with wider margins and more deflected growth lamellae and appear to show trends away from *Atrypa* (*Planatrypa*) towards *Atrypa* (*Isonatrypa*).

C279e(9); C279fa(11); C279fb(5); C279fc(4); C279f(4); C279h(3); C279i(16); C279j(6); C279ja(1); C412(2); St190(25); St191(1); St193(43); St193-R(78) as St193; St623(5); St640(5); St647(10); St650(48); St651(19); St764(9); St765(7).

*Freilingen beds*.-

A list of a number of localities with material of doubtful affinity is given. These are mainly from the northern synclines.

C438b(6); AG77(2) Arem; AG263(1) Mech; AG125(1); AG297(1); BP273(7).



Distribution of Atrypa (Planatrypa) petasa n.sp. in the Eifel.

## Atrypa (Isonatrypa) cf. varicostata STAINBROOK 1945

Text-figs. 41-49.

Associated fauna: Small, globose Schizophoria excisa (SCHLOTHEIM), rare Aulacella sp., Douvillina sp., Hypothryidina cf. cuboides (SOWERBY), Cyrtospirifer cf. verneuili (MURCHISON), Anatrypa sp., Spinatrypa sp. The age of the source beds is undoubtedly Frasnian, but a more precise date fails because the exact locality and stratum of the main collection (Berlin Museum) is unknown.

Source sediment: Moderate to dark brown or dark grey shales, somewhat nodular and calcareous. Small patches of crinoidal debris are common.

Range: Frasnian, Upper Devonian.

### Diagnosis.-

Small to medium sized Atrypa with short "ears" at the hinge corners or extended frills along the hinge margin but not laterally and anteriorly. Beak epicline; foramen small, obscured. Outline is shield-like. No deltidial plates were found. Teeth with strong lateral lobes. Small distinctive cardinal process present. Columnar test thick.

## Description

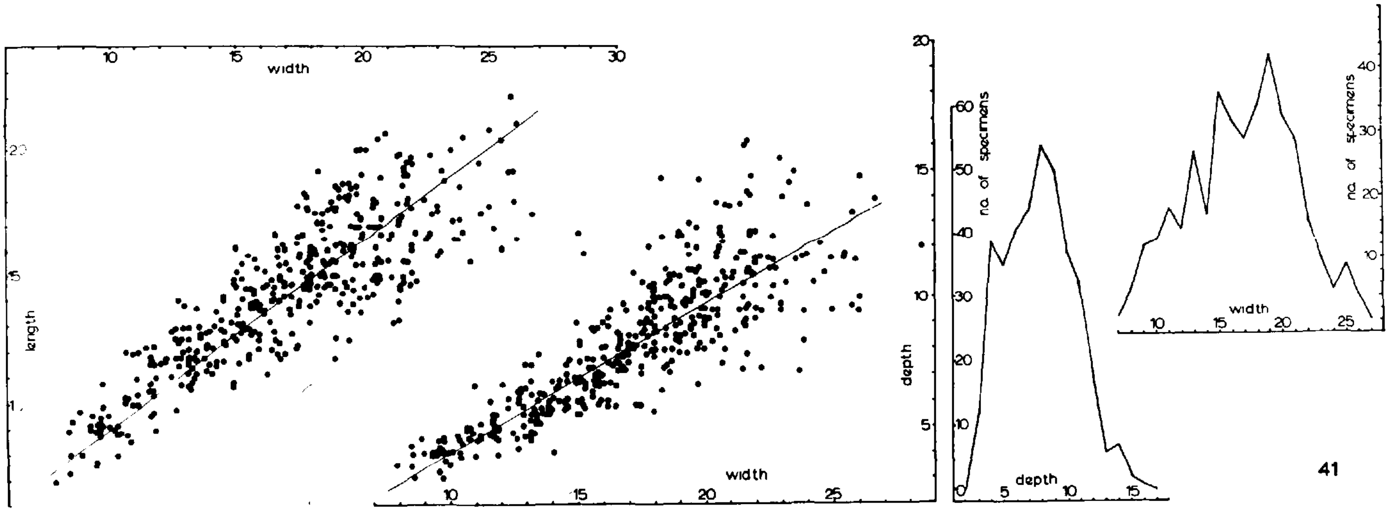
### External form.-

Most specimens are rather small, average width reached at 10 mm and maximum at about 28 mm. Width exceeds length (w/l ratio 1.2 in maturity) and the width/depth ratio 2.1. There is some disparity in the measurements when frills are broken (text-fig. 41). Maximum depth is near or slightly posterior to mid-length. The shell is shield-shaped in outline, particularly in early stages. The brachial valve is slightly more convex. An angular, but not strongly marked fold occurs on the anterior commissure.

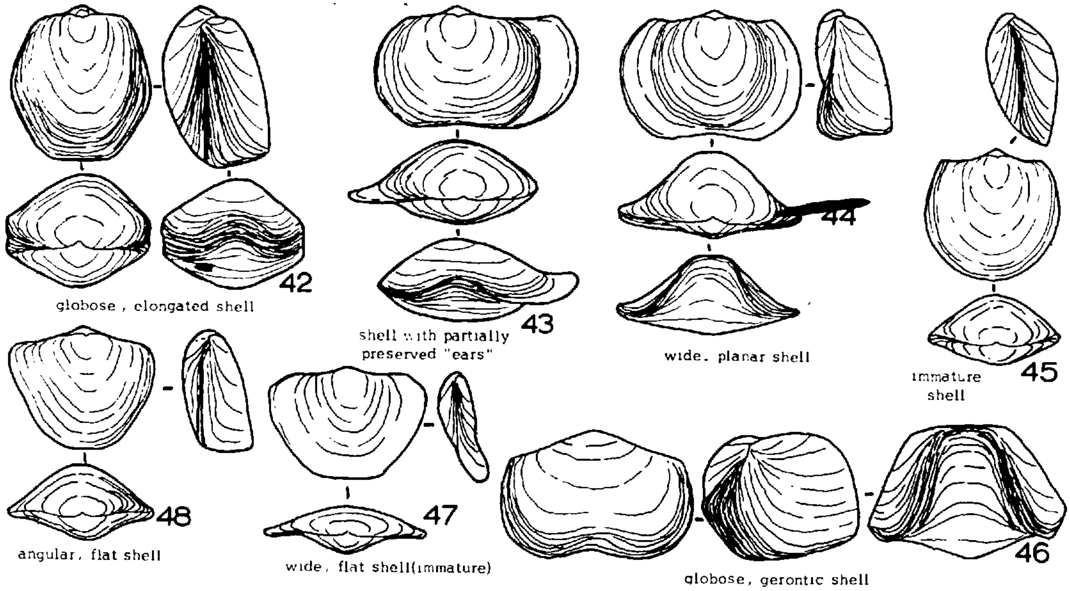
The pedicle valve is angularly convex at the apex but more weakly and roundly convex anteriorly. Margins are silghtly curled ventrally. The small beak covers about 1 mm of the dorsal apex; it is epicline. No area or delthyrium is exposed. The umbo is flattened. The brachial valve is broadly convex with gently sloping sides and a planar crest. Margins curl ventrally but not sharply. The dorsal apex is covered by the protruding, epicline beak.

### Ribs.-

Rib coarseness is not variable posteriorly to anteriorly : it levels at nearly 12-13 ribs per 10 mm. Ribs are sharper, better defined apically where there are fewer growth lamellae. Apically (on the pedicle valve) a single, strong, elevated mid-rib is flanked by two or three side ribs. The mid-rib bifurcates at about 2 mm from the apex, and each fork bifurcates once more at about 4 mm from the apex. Insertion is rare



Text-fig. 41. Scatter diagrams and frequency curves of the main dimensions of Atrypa cf. varicostata STAINBROOK. Locality BMB11, "Breinigerberg"; Frasnian.



Text-figs. 42-48. Shell variation of Atrypa cf. varicostata STAINBROOK. Locality BMB11. x1.

and more restricted to hinge corners. On the brachial valve, three side ribs flank a depressed central rib. The inner side rib is thicker. The central rib is inserted at 1-2 mm from the apex. Lateral ribs tend to curve.

Growth lamellae.-
Mature specimens show extension of the lamellae at the hinge corners into short "ears" or more extensive frills. Growth lamellae are weakly deflected at 10-20 degrees from the shell surface, more at the margins and less posteriorly. The first lamellae occurs at 4-5 mm from the apex, and is followed by several spaced at 1-2 mm. Marginally lamellae are crowded and overlapping.

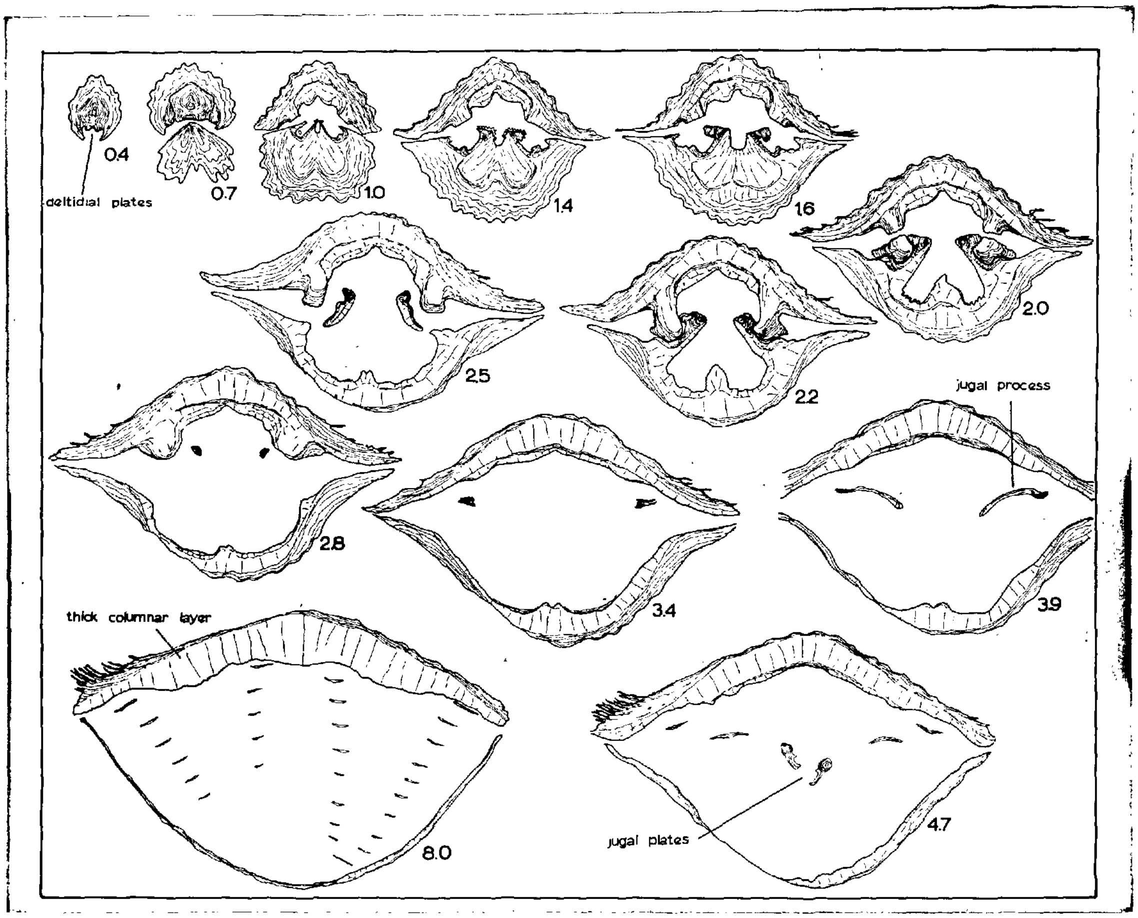
Growth of lamellae is less around the anterior fold and on the anterior commissure than it is postero-laterally. This considerably increases width as compared to length of shell.

Internal structure.-
No deltidial plates are present, but a pedicle laver forms a constriction (text-fig. 49). Adductor impressions appear narrow and deep. A dental nucleus is lacking. Teeth are strong, stubby, near-vertical with a squared main lobe and strong lateral lobe at right angles to it.

The brachial valve has a minute, tear-shaped notothyrial pit with a marked, linear cardinal process, which spreads over the hinge plate. Inner socket ridges are thick, crural bases small and spherical. Crura are rather short, slightly bent and compact. Jugal processes strong, slightly convex ventrally and terminate in long, straight jugal plates distally opposed in a V-shape. Jugal plates thicken at their ends.

Remarks.-
This small, globose species with frills extended along the hinge axis differs from Atrypa boussuensis n.sp. in its smaller size, finer ribs, strongly incurved beak, and tendency towards globosity rather than planarity. It probably is younger (F3?) than A. boussuensis n.sp. from which it may have been derived.

At present it is not believed that substantial differences exist between the atrypids from Breinigerberg, near Aachen, and those described by STAINBROOK (1945, p. 47, Pl. 5, figs. 13-17). These atrypids are nearly alike in shape rib coarseness and size. Atrypa varicostata STAINBROOK was found in the Independence Shale of Iowa, North America, and STAINBROOK himself (ibid., p. 3) already pointed out the strong similarity of the Independence fauna with that of the calcareous and nodular limestone of Aachen. This correlation is so striking that it would not be surprising if many German and American orms were indeed conspecific. Such faunal similarities do not exist for earlier Devonian strata.



Text-fig. 49. Transverse serial sections of Atrypa cf. varicostata STAINBROOK. Frasnian. "Breinigerberg". Locality BMB11. x3.

The trend in Frasnian Atrypa appears to be towards thickening and coarsening of the columnar shell layer with fewer interlayers of fibrous test.

Material.-

BMB11(215); BMB13(87); BMB14(48); BMB15(118). The Berlin Museum localities are all labelled "Breinigerberg", a locality about 10 km SE Aachen, Germany. The likely source of the collections is a sequence of nodular shales of Frasnian age (F3 in the Belgian standard sequence?). Total number of specimens 468. No similar atrypids were found in the Frasnian sediments of Westfalen and Bergisches Land, which probably are largely unfossiliferous black nodular shales.

## Atrypa (Isonatrypa?) boussuensis n.sp.

Pl. 13, figs. 1-2; Pl. 14, figs. 1-3, text-figs. 50-56.

Name: After Boussu-en-Fagne, near Couvin and Frasne, Dinant basin, Belgium.
Type locality: Carriere du Cimetière, Boussu-en-Fagne, Belgium.
Type stratum: Uppermost 5 m of the F2i shales in the Cimetière quarry, Boussu.
Range: Restricted to F2i (?), Frasnian, Upper Devonian.
Associated fauna: See LECOMPTE, 1960, p. 71. In a large collection from the type locality no other atrypids were found. The atrypids "Atrypa reticularis, Atrypa squamifera and Atrypa tubaecostata" which LECOMPTE (ibid.) listed, were not observed. Other brachiopods include Schizophoria striatula (SCHLOTHEIM) Athyris sp., Euryspirifer sp. Rhynchonellids were absent.
Sediment: Moderate brown, clayey shales, nearly devoid of bioclastic debris such as corals and crinoids.

Diagnosis.-

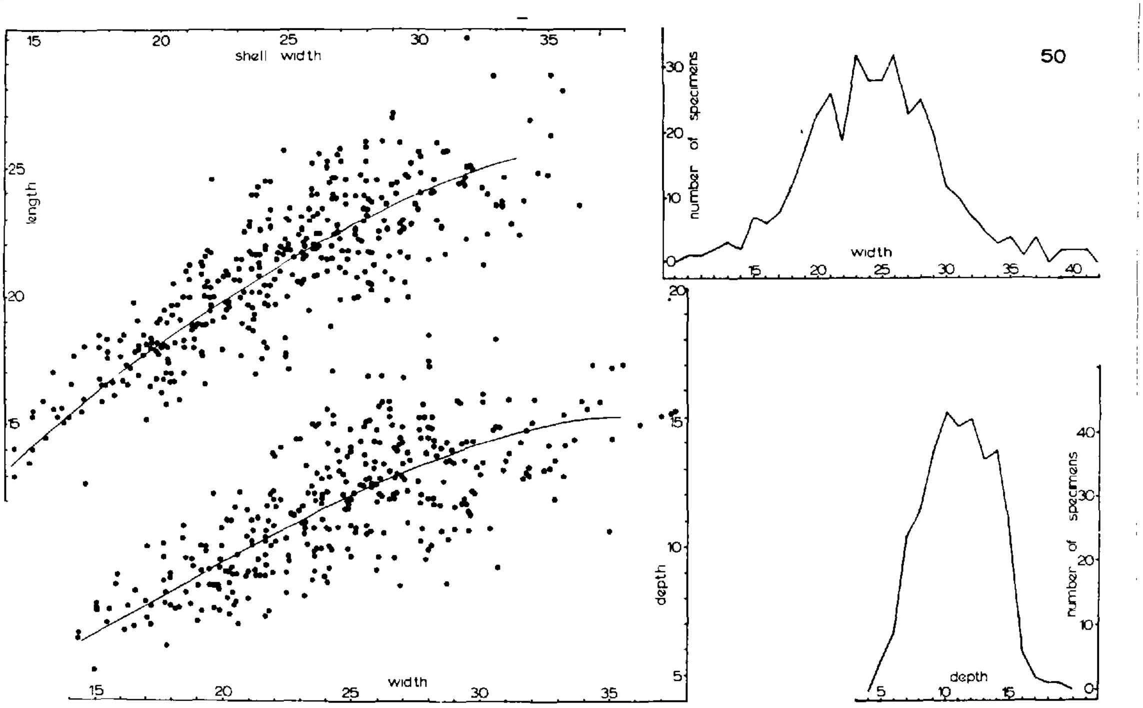
Medium to large, biconvex-dorsibiconvex atrypids, subtriangular in outline and marked by a relatively straight hinge line. Frills large and expansive (Pl. 13, fig. 1a). Ribs coarse. Internally a dental nucleus is present, teeth are short, hinge plates thin.

### Description

External form.-

Maximum total width observed (in a frilled specimen) 45 mm. Average mature width between 23 and 26 mm. Optimum depth 11 mm. In maturity the width/length ratio is about 1.15, the width/depth ratio 2.08 (text-fig. 50). Accurate measurement of width is difficult because of frill growth. Shell outline is near-triangular or shield-shaped. Maximum width is near the hinge axis. The shell is dorsibiconvex. A well-defined U-shaped fold marks the anterior margin.

The pedicle valve is weakly convex. The umbo is flattened and the mid-field planar. A weak ridge may mark apical portions. The sides are curved ventrally, but only briefly, then flatten distally with projected frills. Frilled specimens may mark slight marginal concavity. The beak is epicline, sharp, and its incurvature completely obscures foramen and area. The apical angle of 160-175 degrees is more typical of frilled specimens; it is less in those without frills. Shoulder lines are deeply indented, hinge corners sharp, but lateral margins well-rounded apically and straightening distally. The tongue is marked by steeply sloping sides with angular corners.



Text-fig. 50. Scatter diagrams and frequency curves of Atrypa boussuensis n.sp. Frasnian F2i; locality Boussu-en-Fagne, Belgium.

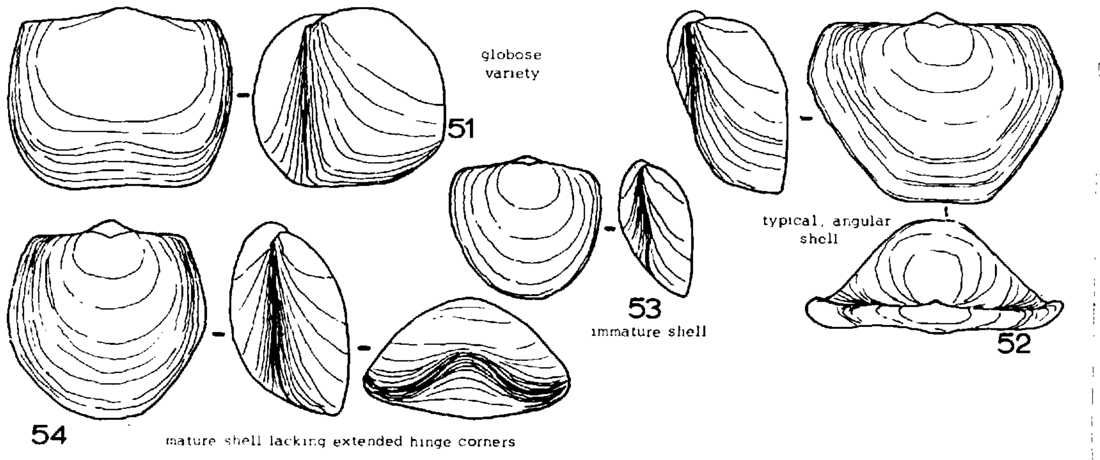
The brachial apex is covered, and valve smoothly and broadly rounded, rarely deeply arched. Apical portions are sub-vertical in globose forms. Postero-laterally, frilled forms show slight dorsal curling. The mid-field is planar, and commonly shows strong wear or erosion on specimens.

Ribs.-

Ribs are moderate to coarse, spaced at 10-12 per 10 mm. They have broad, somewhat weakly convex, well-rounded crests with narrow and slightly thinner troughs. There is no strong interruption by growth lamellae. Lateral and apical ribs are curved. There is a small difference in wave length posteriorly to anteriorly ranging from 10 ribs per 10 mm to 12 ribs per 10 mm (therefore some distal crowding). On the growth lamellae, distal portions may have very coarse ribs spaced at 4 per 10 mm because there appears to be little bifurcation on deflected lamellae. Such distal coarse ribs become narrow and high-crested and only the troughs broaden and expand (see Pl. 13, fig. 1a).

Growth lamellae.-

Flat and planar specimens are more usually frilled. Globose specimens appear to lose their frills. The longest recorded frill was 14 mm , which added some 28 mm to shell width (i.e. nearly doubled shell width). The frills are nearly horizontal, parallel to the commissural plane. On the pedicle valve, growth lamellae are initially sharply deflected and then flatten out laterally and distally. On the brachial valve there is a slight distal, dorsal curl. The first 15 mm of shell growth is marked by little or no frill development, and early deflected growth lamellae of frilled specimens appear to have broken. Growth lamellae are slightly deflected at 10-30 degrees on the pedicle valve and hug the shell rather tightly on the brachial valve. Overlapping distal lamellae are rarely layered.



Text-figs. 51-54. Shell variation of Atrypa boussuensis n.sp. Frasnian F2i. Type locality

Growth and variation.-

Two intergrading varieties are present. One, a globose form lacking frills (eroded?) and with strong anterior fold, and two, a broad, laterally extended flattish form with strong frills. The first form is rare (less than 10%), and possibly is a senile feature in many specimens. Some young specimens, however, show an early trend to globosity. Beaks are strongly incurved in all forms (text-figs. 51-54).

In young specimens the area and delthyrium are not visible : the beak is already pressed to the brachial valve in early stages. Neanic specimens tend to be flat, and have a slightly more convex ventral than brachial valve.

Internal structure.-

Shell layers are not thick (text-figs. 55-56). Embryonic deltidial plates appear to be separated from the pedicle layers, and are retracted inwards. Teeth are stubby; lateral lobes short, wrinkled; main lobe directed inwards at 20-30 degrees to the symmetry plane. Cardinal process with 6 strands in notothyrial pit, overlapping to socket plates. Inner socket ridge long, middle socket ridge high. Hinge plates thin to moderate, socket plates delicate. Crural bases small. Crura about 3 mm long, mainly unfeathered, though slight feathering takes place near the jugal process. Jugal plates long, slightly curved and thickened distally, Spiralia with about 13 whorls.

Remarks.-

Atrypa boussuensis n.sp. is distinct from A. varicostata STAINBROOK 1945 in its coarser, flatter ribs, larger size, more acutely arched anterior fold, and its form and wider frills.

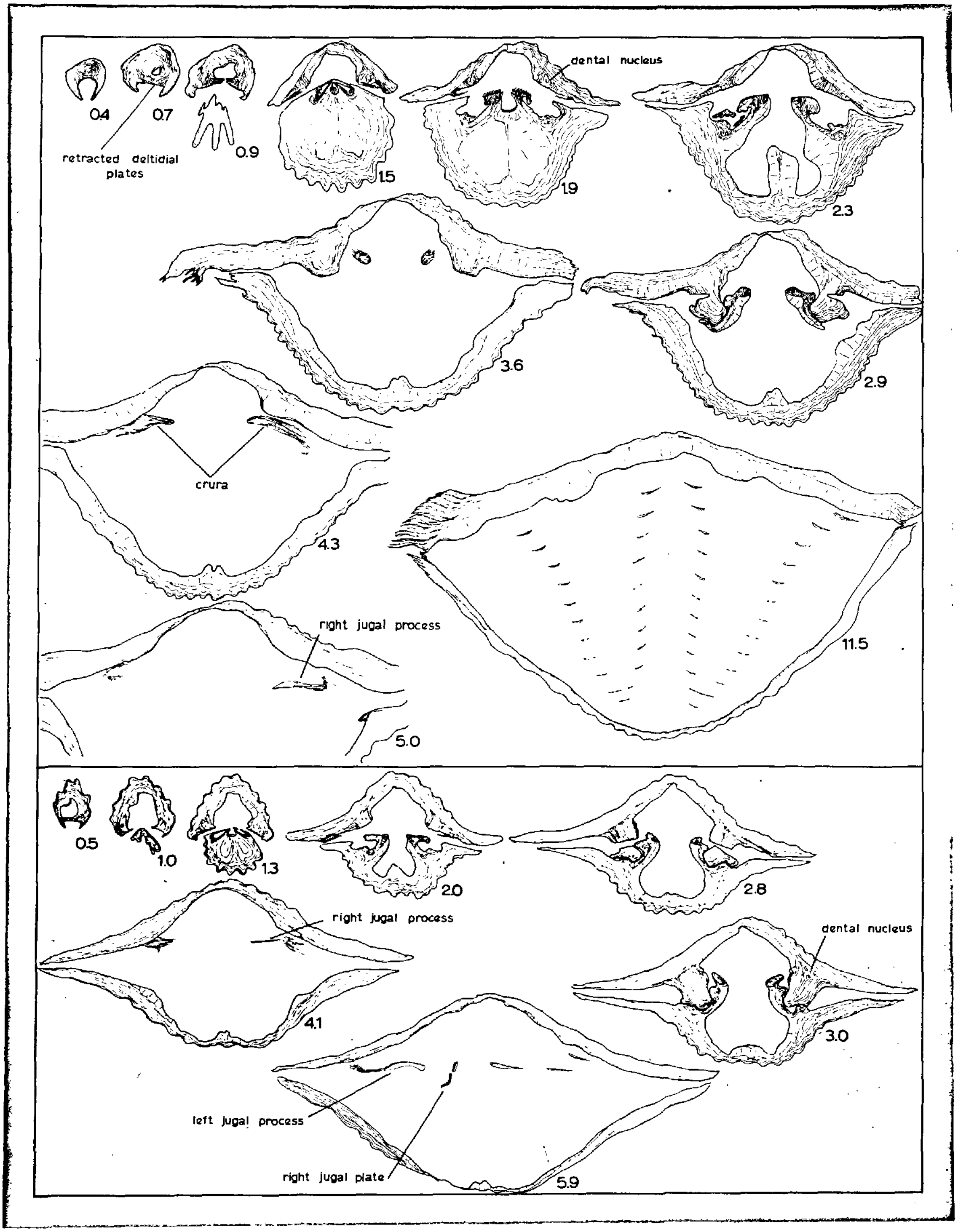
Two small collections were made at quarries in Germany, one at Breinigerberg, near Aachen, and one at Gruiten, near Düsseldorf. Both localities yielded an Atrypa fauna which was similar to the Boussu collection of Belgium. The specimens from Gruiten, which were collected in a black nodular shale above a dark, slabby limestone, were more concave and slightly coarser ribbed than the Boussu specimens and may be a different variety or species. A section of the sequence at Gruiten is given by BRINCKMANN (1962, p. 121) : the atrypids collected probably were derived from probe 20 of this section, or slightly above it. A similar section at Gruiten is given in text-fig. 8.

It is possible that A. boussuensis and its Aachen and rhenish equivalents are typical Atrypa of high F2 Frasnian, most likely F2h to F2j. In Germany, Atrypa does not return in the stratigraphic sequence until the Frasnian, after an absence in the Givetian. It is not likely to have made this return before F2c time.

Atrypa nefedovae LJASHENKO 1950 (as illustrated in LJASHENKO 1959, Pl.15, figs. 9-11) is also similar to Atrypa boussuensis n.sp. although it is smaller and has more closely spaced frills and strongly deflected growth lamellae.

Material.-

C498(545) type locality, Boussu; C481(34) Gruiten; C417(78) Breinigerberg.



Text-figs. 55 -56. Transverse serial sections of *Atrypa boussuensis* n. sp. Frasnian F2i; type locality Boussu-en-Fagne. x3.

## Subgenus *Atrypa*? (*Devonatrypa*) RZONSNITSKAYA

*Type species*: *Atrypa waterlooensis* WEBSTER 1921 (partim). A revision of *A. waterlooensis* by FENTON & FENTON 1935, pp. 370-374 recognized seven divisions of this species, including *A. waterlooensis* Form A, B, C, "variant", sp. cf., A. *waterlooensis canadensis*, *A. waterlooensis websteri*. RZHONSNITSKAYA (1964, footnote p. 93) did not specify any particular one as type, and the status of this species remains in doubt. As types it may be preferable to select STAINBROOK's specimens (STAINBROOK, 1938, Pl. 30, figs. 1, 4). The problem must remain unsettled until a second revision is made.

*Range*: Upper Devonian, Frasnian (F2-F3?).

*Distribution*: North America, Europe, Russia.

*Diagnosis*.-

Coarsely-ribbed, convexoplane atrypids with widely spaced growth lamellae (probably not developed into frills). Beak appressed or incurved, area not known, delthyrium not exposed. Foramen commonly enlarged into ventral umbo. Ribs undulating, non-interrupted, round-crested, round-troughed. Fold usually large.

Internally, deltidial plates minute, primitive. A dental nucleus is present, lateral cavities absent. Jugal process and spiralium still unknown.

*Remarks*.-

Shortly after RZHONSNITSKAYA's establishment of the subgenus *Atrypa* (*Devonatrypa*) (1964, p. 93), in a footnote on a major paper on atrypid classification, STRUVE (1964, p. 526) also proposed a new subgenus *Desquamatia* (*Neatrypa*). The second became a junior synonym of RZHONSNITSKAYA's *Devonatrypa* although they were assigned to different genera. ALEKSEEVA (1962) assigned Russian specimens by the name of *Atrypa waterlooensis* WEBSTER to the genus *Spinatrypa* STAINBROOK. This means that *A. waterlooensis* has been referred to 3 different genera by 3 different authors. It is possible that none of these are correct.

The internal structure of the type species of *Atrypa* (*Devonatrypa*), from the North American Devonian, has never been examined. It is possible that *A. Devonatrypa* is more closely related to *Atryparia* COPPER 1965, than to *Atrypa*. This comparison is based partly on external morphology : both species-groups have coarse, divergent ribs, widely spaced growth lamellae, obscured areas and dental nuclei. On the basis of tooth structure, *A.* (*Devonatrypa*) *europaea* STRUVE is difficult to assign to *Desquamatia*, and on the basis of rib structure it cannot be placed in *Atrypa*. The alternative would be to elevate *Devonatrypa* to generic status, but this is postponed until a re-examination of the type species is completed.

## Atrypa? (Devonatrypa) europaea STRUVE 1964

Pl. 29, figs. 1a-d; text-fig. 57.

1935 Atrypa cf. A. waterlooensis WEBSTER, FENTON & FENTON, Pl. 41, figs. 1-3.
1964 Atrypa waterlooensis WEBSTER, JUX, figs. 1-4.
1964 Desquamatia (Neatrypa) europaea STRUVE, pp. 526-527, figs. 1a-c.

Diagnosis, type locality: See STRUVE (op. cit.)

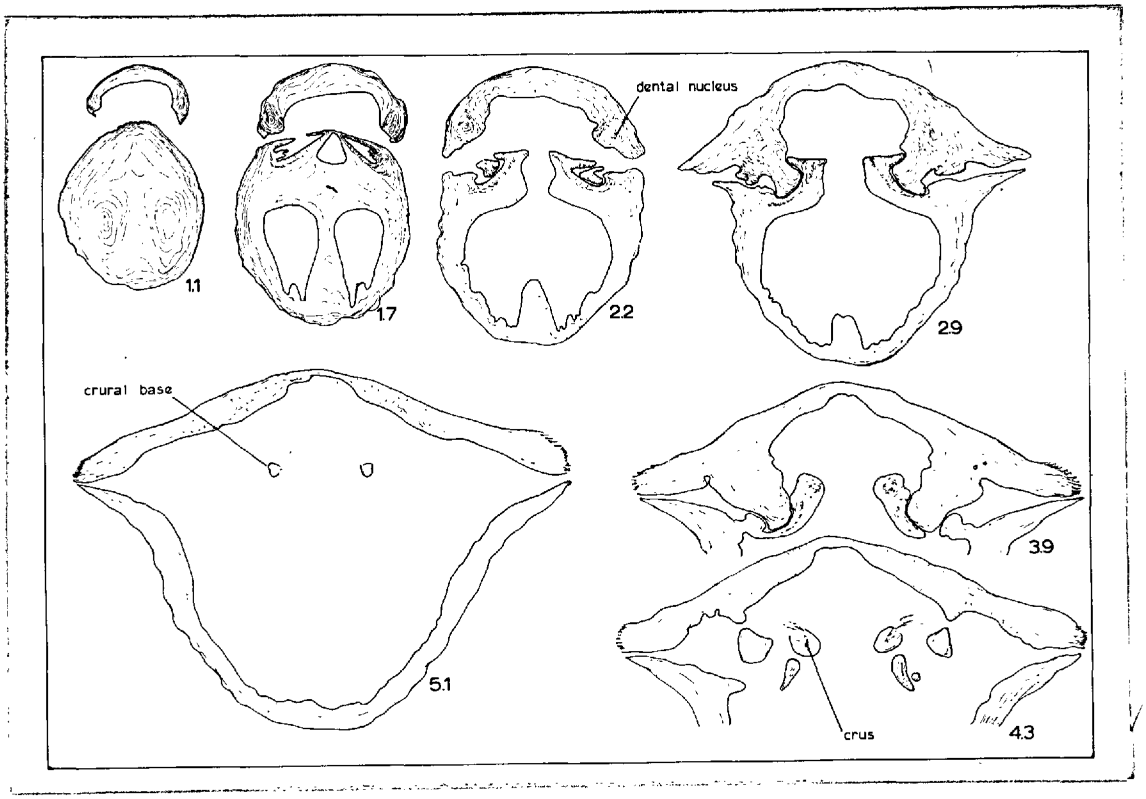
Type stratum: Steinbreche horizon, Refrath beds (beds rich in tabulate corals, cerioid rugose corals and disphyllid corals). The species is absent in the overlying calcareous shales and argillaceous limestones with Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777). The Steinbreche horizon correlates with the F2a, "Zone des Monstres", of the Frasnian of the Dinant basin, but possible is slightly younger and may even be sot in F2b. JUX (1964, p. 171) places the Refrath beds in F2a, but STRUVE (1964, p. 232) states them to be younger, "Besondere Ähnlichkeit besteht zum belgischen Frasnium F2c".

Remarks.-

This history of this species in the Paffrath region is complex. The first known figure of a European specimen of Atrypa (Devonatrypa) europaea STRUVE is probably given by DESHAYES (1827, Pl. 242, figs. 4a-c) in the Encyclopédie Methodique atlas. DESHAYES makes no reference in the text of the Encyclopédie Methodique (published later in 1832) to the figures given in the Atlas. This may be an oversight. The history of this confusion is given under Historical background.

When he described "Terebratulites priscus" SCHLOTHEIM (1820, p. 262) gave no figures but referred to the above mentioned Pl. 242, fig. 4 of the Encyclopédie Methodique as the only correct illustration of his new species. He stated, "Die einzige mir bekannt gewordene ziemlich richtige Abbildung dieses Terebratuliten ist in der Encyclop. T. 242, f. 4.a.b.c. befindlich". This illustration is most likely of an Atrypa waterlooensis-like brachiopod from a well-known locality at Refrath. STRUVE (1964, p. 526) designated this brachiopod as a new species, but it should have been referred to "Terebratulites prisca" SCHLOTHEIM 1820. The source of this error lies in the literature. Atrypa prisca SCHLOTHEIM was not a widely accepted species. When it was in use, the finely ribbed Desquamatia of Refrath or even all Devonian atrypids in general, were referred to it. The confusion was compounded by SCHLOTHEIM himself in 1822 when he figured for the first time an atrypid under the name prisca which in appearance did not coincide with the originally intentioned figures of the Encyclopédie. It is evident that under the name prisca, SCHLOTHEIM included a number of atrypid species which to-day can no longer be referred to it. Since STRUVE (1964) has renamed the original, "Encyclopédie", prisca of SCHLOTHEIM as Desquamatia (Neatrypa) europaea, the name prisca becomes a nomen nudum unless STRUVE's name is rejected.

Serial sections of Atrypa? (Devonatrypa) europaea (STRUVE 1964) are given in text-fig. 57.



Text-fig. 57. Transverse serial sections of Atrypa? (Devonatrypa) europaea (STRUVE 1964). Locality unknown. Probably Refrath; Frasnian.

## Genus Atryparia COPPER 1965

Type species: Atryparia instita COPPER 1965, p.
Range: Eifelian, Middle Devonian.
Distribution: Europe, North Africa.

Diagnosis.-
See COPPER 1965b., p.

Two additional diagnostic characters of the genus are the advanced shell structure with separation of a thick, single columnar layer (instead of numerous fibrous and columnar interlayers) and also the rather wide spacing of the spiral whorls as compared to Atrypa. These two features appear to be consistently developed over the full range of species.

Remarks.-

No more detailed description is given at the present time of the two species previously described when the genus was established. Extra figures of serial sections are included. Three additional, albeit still nameless species are separated. These fill out the quota of species of this genus in the Eifel region, and extend its range down to lower Eifelian (Nohn) beds. Detailed work is left for a future study.

### *Atryparia* sp. C.

Text-fig. 58-59.

Range: Nohn beds, lower Eifelian. Concentrated in the Schleit horizon, and not yet known lower than the Schmitzbach horizon.

Remarks.-

The genus is scarce in the lower Eifelian, but already typical in its morphology and separable from the genus *Atrypa*. Most specimens are large, up to 40 mm wide, and flattened. Ribs are finer than on younger species of the genus in the Eifel region. Growth lamellae are not raised above 10 degrees from the shell, and are wide spaced at 2-4 mm. Frills are still short, but the shell is planar and margins are thin knife-edged. Outline is elongated, shield-shaped. The pedicle valve is normally convex for the genus, i.e. somewhat angular and expanded apically and more flattened distally. The brachial valve is also rather flat medially.

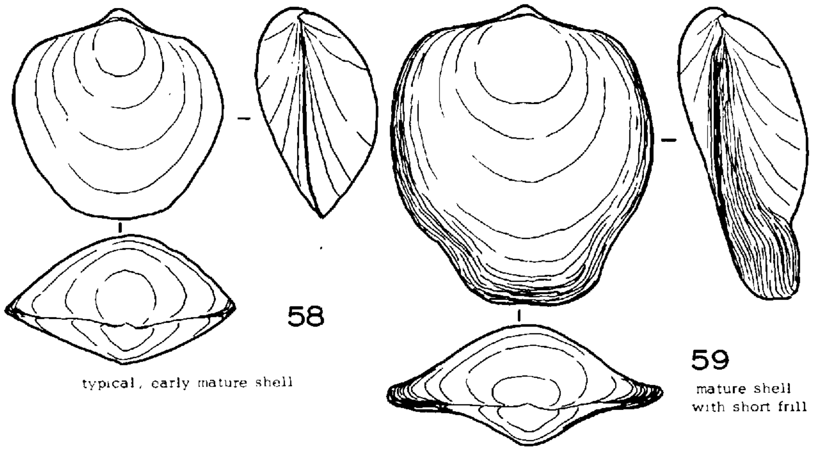
These specimens can be set apart from the *Atryparia* sp. B at the Ahrdorf beds in their flatter shells, knife-edged margins and generally larger and broader shells.

No specimens were sectioned.

Material.-

Total 51 specimens. All specimens stem from the Ahrdorf and Hillesheim synclines. They have not been found to the north of the Eifel synclines, nor to the south and southwest.

C274a(2); C284a(1); C384b(3); C287(1); C384(9); C398(2); H1(1); H78(1); H87(1); H107(1); H254(1); St13(3); St19(2); St101(4); St304(1); St711(10); St712(1); St713(1); St714(1); Fp1262(1); Fp1263(1).



Text-figs. 58-59. Shell variation of Atryparia sp. C, Schleit horizon, Nohn beds; locality random. x1.

Atryparia sp. B.

Pl. 9, figs. 6a-d; text-figs. 60-64.

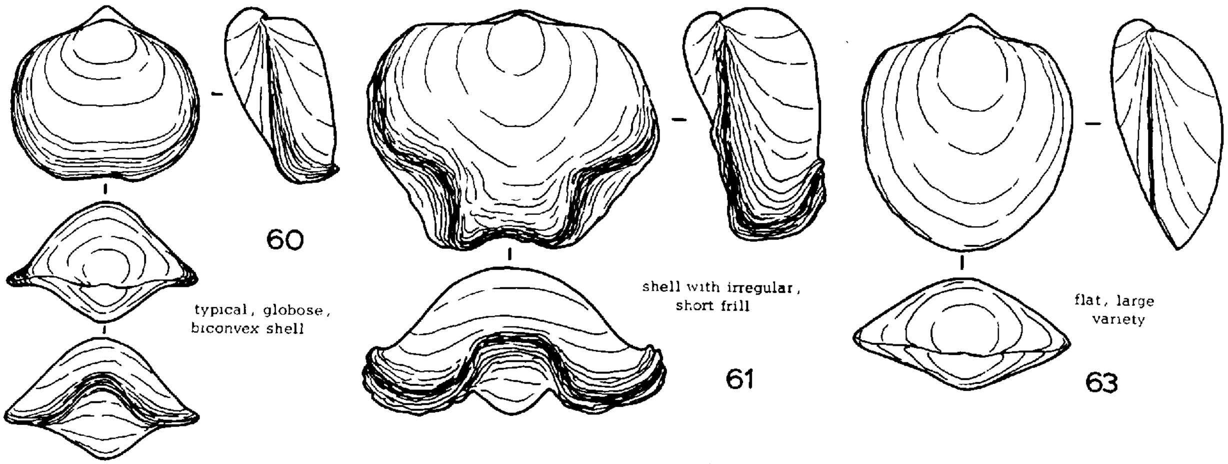
Range: Ahrdorf beds; mainly Flesten-Niederehe horizons.

Remarks.-

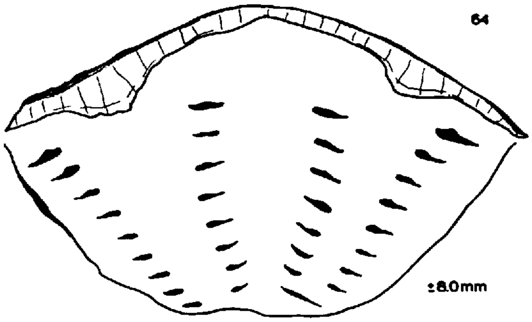
The second acme of Atryparia development in the Eifel region is reached in the Niederehe horizon which contains medium sized, globose (almost globular), strongly biconvex-dorsibiconvex specimens with short, frilly, deflected margins. The brachial valve is well rounded and deep, but on the ventral valve apical portions are acutely and angularly convex, almost keel-like. This strong ventral convexity is not matched by other Eifel material of the same genus.

Specimens in the underlying Flesten horizon tend to be larger and more planate like Atryparia sp. C. The Junkerberg specimens of Atryparia sp. A. are also larger, have coarser ribs, a more shield-shaped outline and lack the irregular, frilly lamellae, which are typical of Atryparia sp. B.

The Ahrdorf specimens reach a wider distribution than the Nohn specimens of Atryparia sp. C, and can be found in the Gerolstein and Prüm synclines though not north of the Ahrdorf syncline.



Text-figs. 60-63. Shell variation in Atryparia sp. B. 60-61, Niederehe horizon, 63, Flesten horizon. Random localities. x1. (Addendum: 62 not present).



Text-fig. 64. Transverse serial section of Atryparia sp. B. Niederehe horizon, Ahrdorf beds; MTB Dollendorf r56930:h78180. x3.

Material still needs to be serially sectioned to determine internal structure, and the full gradation with younger and older forms established.

Material.-

Total 247 specimens

C242(3); C256(2); C257(5); C289(88); C356(3); C366(3); C399(3); C406(1); H28(5); H236(1 ); Ge20(1); Munterley(1); St32(1); St52(1); St54(4); St57(5); St58(4); St61(7); St62 (2); St66(1); St88a(1); St91(1); St98(7); St102(8); St104(4); St109(19); St161(20); St186(3); St316(1); St393(2); St394(5); St395(1); St434(1); St440(1); St446(8); St447(6); St454(5); St460(5); St476(3); St527(1); St535(1); St658(2); St679(1); St813(1); St816(1); St874(1).

## Atryparia sp. A.

Pl. 10, figs. 1-3; text-fig. 65.

Range: Rare in the Klausbach and Mussel horizons at the base, common to abundant in the Hönselberg to Nims horizons of the Junkerberg beds. Peak probably at Nims-Giesdorf time.

Remarks.-

Medium to large-sized, dorsibiconvex shells of this species are marked by 8-10 ribs per 10 mm at the margins and even, 3-4 mm spaced growth lamellae. The ventral mid-area is strongly convex but not as angular and carinate as on Atryparia sp. B. Outline is ovoid, hinge corners are well-rounded. The beak is rather sharp, epicline. The shell may be elongated by an extension of the fold and a vertical sharp curl of the marginal growth lamellae.

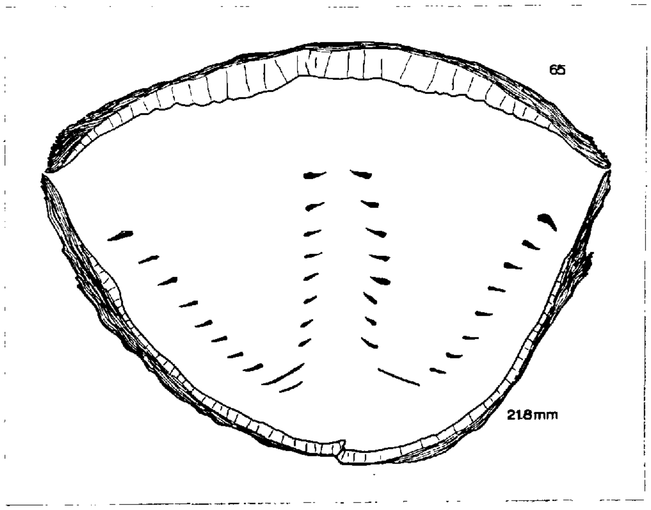
The specimens which come from critical Junkerberg-Freilingen border localities show a flattening of the ventral valve, a blunt beak and rounded rather than sharp edged commissure. These are characteristics which are more fully developed in Freilingen specimens.

This form, Atryparia sp. A., can be defined in its size, ovoid outline, less globose ventral valve and more evenly spaced frills from older specimens of Atryparia sp. B. It grades into Atryparia stabilia COPPER of the overlying Freilingen beds by expansion of size, flattening of the ventral valve, shortening of beak incurvature and deepening of the rib troughs.

Material.-

Total 269 specimens

C296(8); C302(5); C319(1); C352(1); C356(3); C357(7); C370(3); C374(2); C389(1); C390(2); C394(3); C413(3); C438(13); C438b(14); C450(4); C455(10); C457(2); C466(1); C477(6); C508(1); C511(1); C513(1); AG7(1); AG32(21); AG33(8); AG43(1); AG52(3); AG82(2); AG82a(1); AG85a(1); AG177(2); AG216(2); AG256(1); AG280(3); AG289(1); Os3b(2); S8t19(6); St40(3);



Text-fig. 65. Transverse section of *Atryparia* sp. A, Giesdorf-Nims horizon; Junkerberg beds; MTB Aremberg r50760:h90220. x2$\frac{1}{2}$.

St40(3); St67(18); St68(1); St72(3); St73(1); St74(1); St76(1); St79(5); St83(1); St110(3); St114(1); St184(1); St240(2); St324(3); St362(5); St438(4); St441(1); St449(4); St450(1); St541(1); St453(1); St525(1); St593(1); St597(1); St624(3); St630(3); St633(7); St639(1); St655(2); St736(8); St737(4); St738(3); St742(5); St743(7); St751(1); St758(1); St822(1); St825(1); Fp1304(1).

## *Atryparia stabilia* COPPER 1965

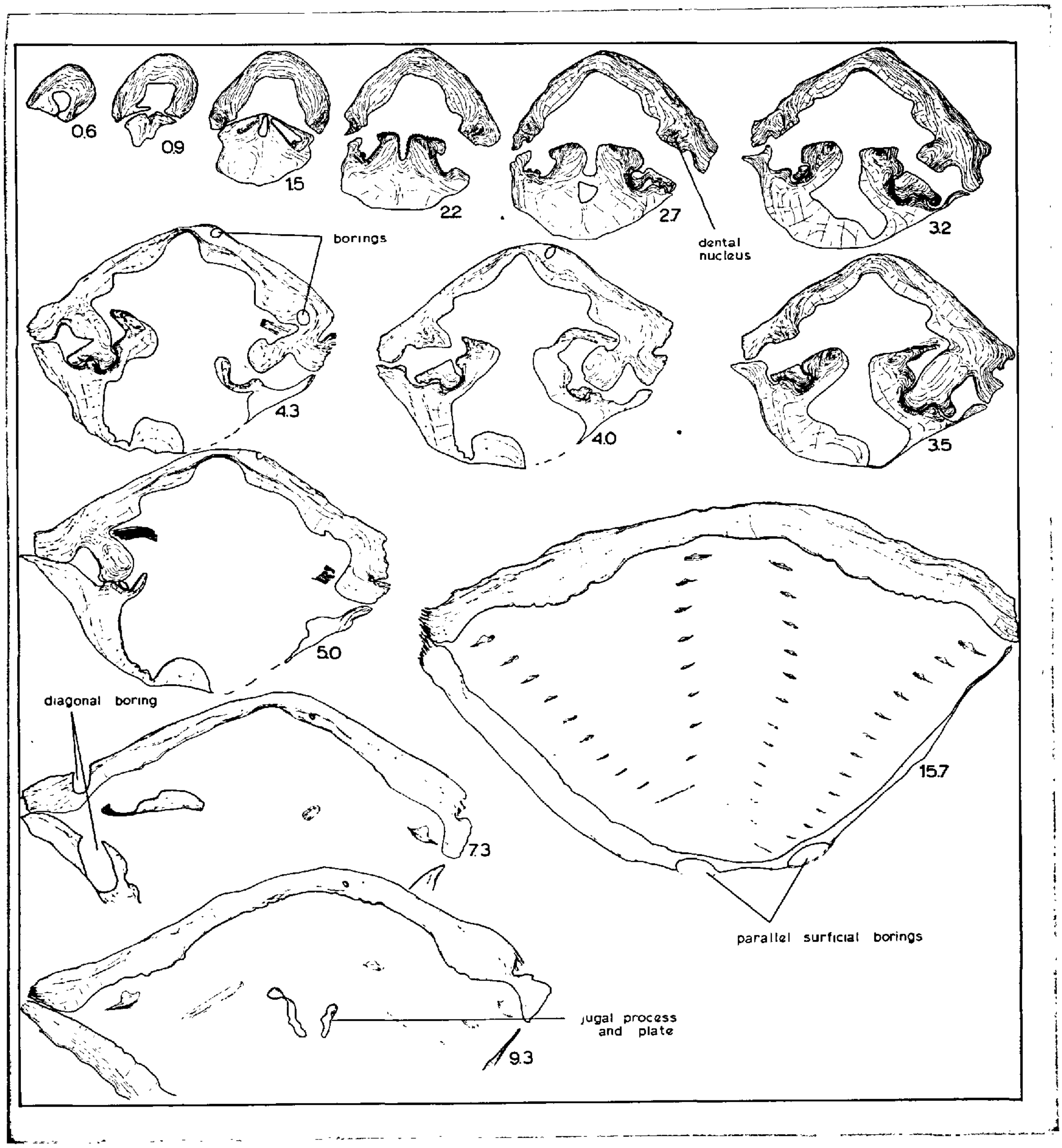
Pl. 11, figs. 1-3; text-figs. 66-67.

Range: Eilenberg horizon to Bohnert sub-horizon, Freilingen beds.

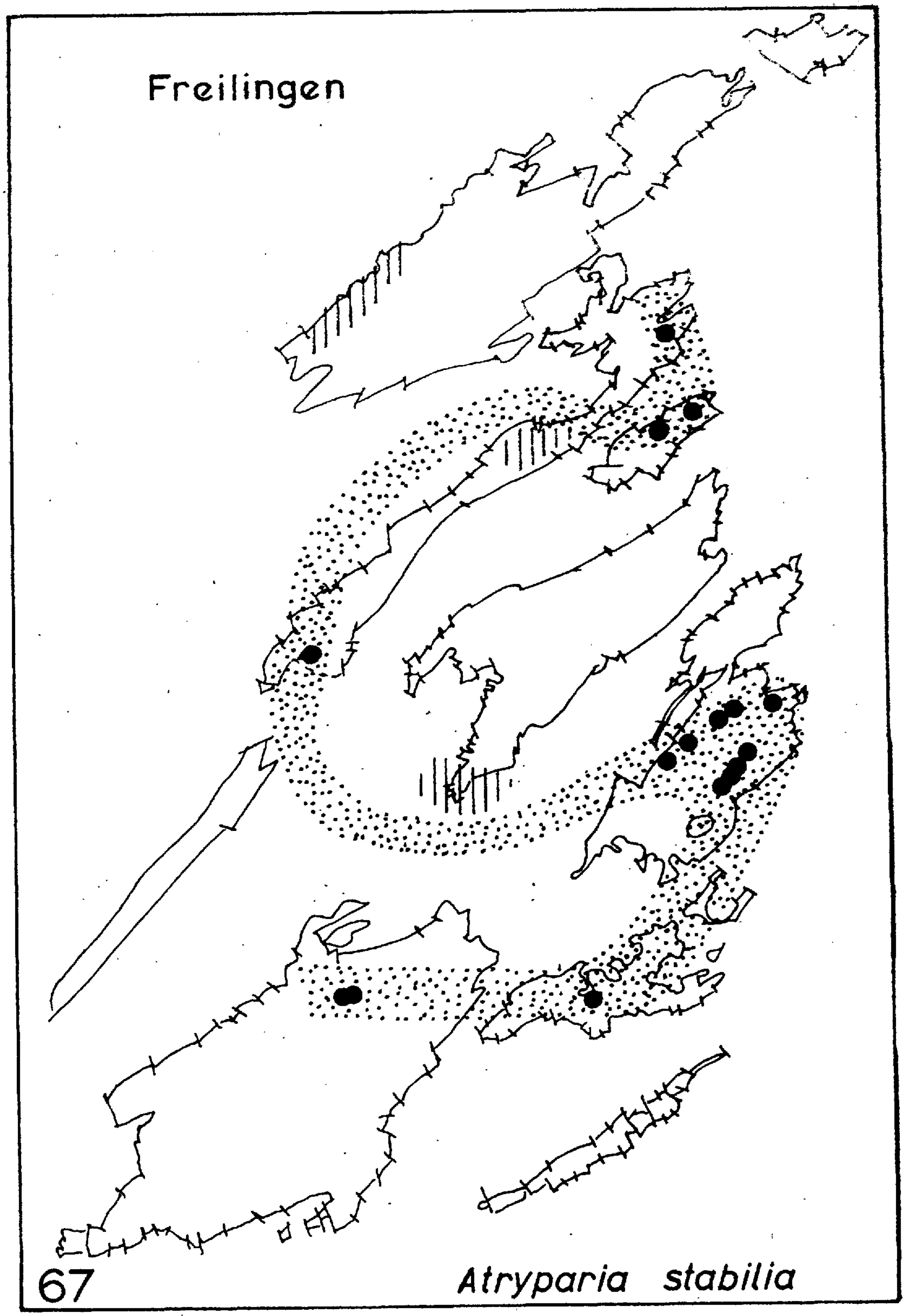
Remarks.-

A diagnosis of this species has already been given in COPPER 1965c, p. . The description is supplemented by serial sections (text-fig. 66). A list of material is given for the first time.

This species can be differentiated from other *Atryparia* by its rather planate pedicle valve, and more deeply grooved and better defined ribs. Growth lamellae do not appear to have been massed into marginal frills.



Text-fig. 66. Transverse serial section of Atryparia stabilia COPPER, 1965. Nollenbach horizon, Freilingen beds; MTB Dollendorf r56980:h75720. x2½.



Distribution of Atryparia stabilia COPPER 1965 in the Eifel.

Material.-

Total 418 specimens (text-fig. 67).

C279b(1); C278(4); C299(8); C301(4); C305(2); C316(6); C317(5); C335(4); C343(18); C344(68); C345(37); C353(4); C354(9); C355(1); C358(4); C359(37); C360(7 ); C361(7); C362(1); C382(4); C388(1); C512(24); RW4(1); AG276(2); AG6(2); AG77(2); St8(1); St41(5); St43(3); St69(4); St70(15); St71(6); St74(1); St76(5); St77(4); St78(7); St80(3); St274(5); St591(11); St592(3); St614(3); St618(5); St619(5); St621(3); St623(6); St626(2); St632a(6); St639(4); St655(16); St672(7); St673(2); St674(3); St707(2); St728(1); St752(1); St770(4); St810(1); St869(1).

## Atryparia instita COPPER 1965

Pl. 12, figs. 1-2; text-figs. 68-69.

Range: Ahbach beds, upper Eifelian. Chiefly in the Müllert horizon in which it is locally abundant.

Remarks.-

A diagnosis, type locality and stratum, and associated fauna and sediment are given in COPPER 1965c. A serial section previously published is repeated in an expanded form (text-fig. 68).

This late Eifelian species, the last one known to occur in the Eifel region, it the largest in size and shows the most elaborate frills.

Material.-

Total 252 specimens (text-fig. 69).

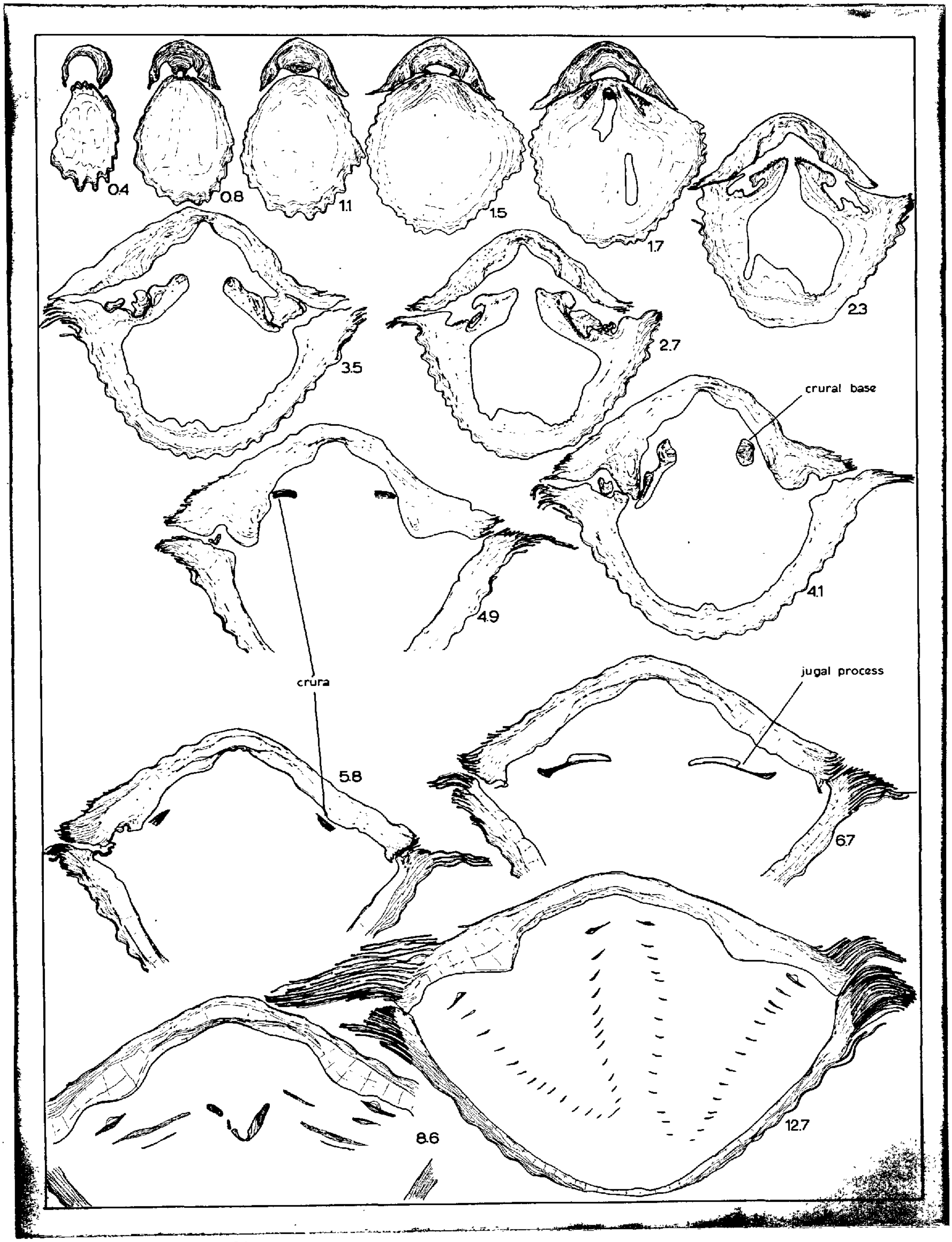
C279i(24); C279j(13); C279ja(5); C279jb(2); C320(41); C321(22); St190(8); St193(24); St193-R(12); St319(6); St333(2); St465(2); St622(1); St623(1); St640(8); St647(2); St647c(1); St648(1); St649(1); St650(12); St651(30); St764(1); St927(1); St950(23); Fp1269(3).

## Genus Anatrypa NALIVKIN 1941

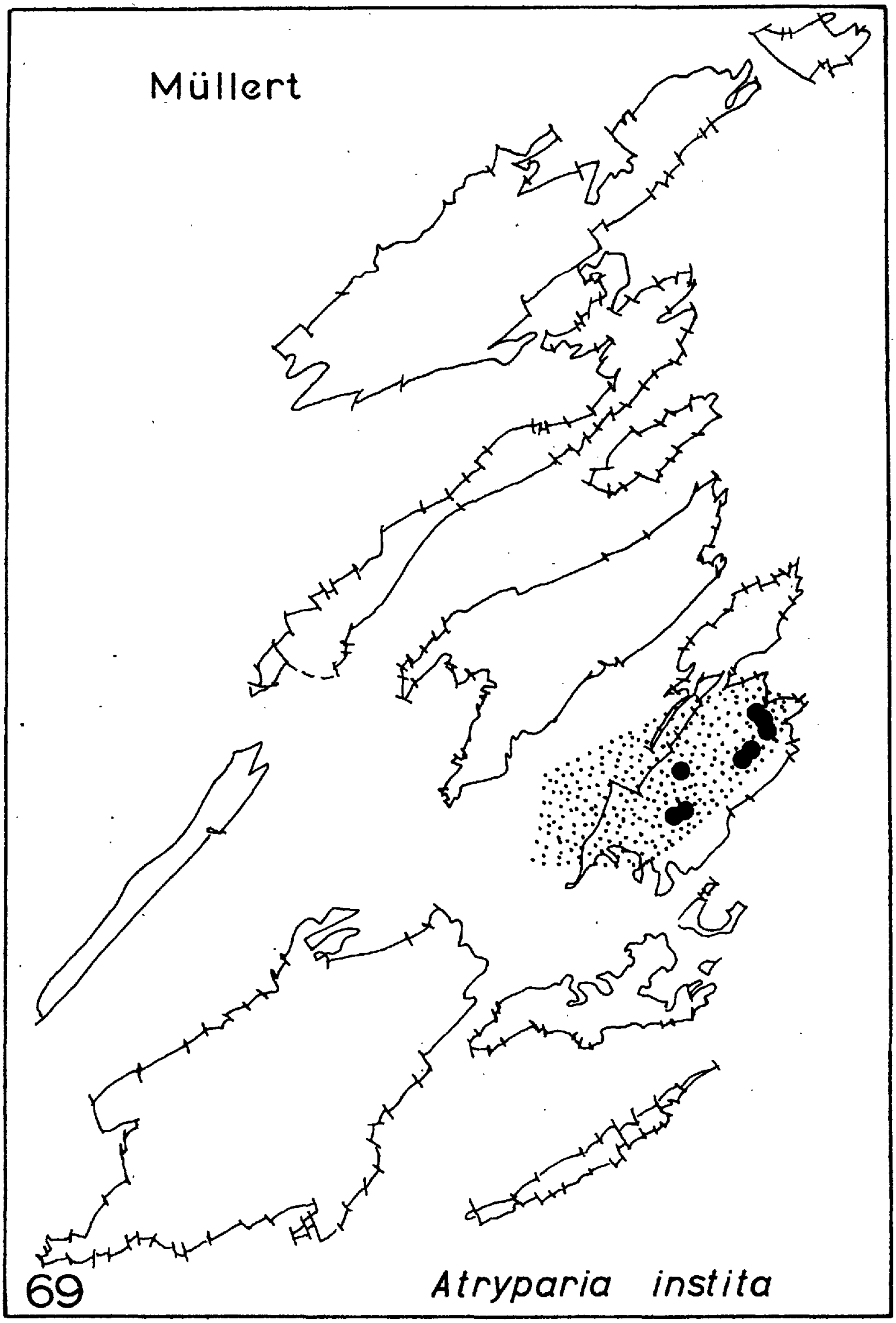
Type species: Orthis micans BUCH 1840, p. 56.
Range: Frasnian, Upper Devonian.
Distribution: Russia, ?Europe, ?North America.

Diagnosis (Anatrypa americana STAINBROOK species-group).-

As it presently stands, the definition of Anatrypa NALIVKIN is not at all clear, and seems to include two conflicting species-groups. The shell morphology portrayed by an alleged specimen of Anatrypa micans



Text-fig. 68. Transverse serial section of Atryparia instita COPPER 1965. Müllert horizon, Ahbach beds; MTB Dollendorf r55480:h77390. x2½.



Distribution of Atryparia instita COPPER 1965 in the Eifel.

(BUCH) in RZHONSNITSKAYA (1960, Pl. 55, figs. 7a-d) would relate that specimen to the palaferellid or possibly the *Desquamatia* group of atrypids. But in ALEKSEEVA (1962, Pl. 8, figs. 6,7) and LJASHENKO (1959, Pl. 26, figs. 1-6) two species, *Anatrypa timanica* MARKOVSKY and *Anatrypa kadzielniae* (GÜRICH), are illustrated which are more closely related to the *Atrypa* group and hence also the group from the Aachen area here described (see below). The differences between these groups is of familiar importance. Until the internal structure of the type species of *Anatrypa*, *A. micans* (BUCH), is determined, the question remains unsettled.

Another unsettled question is the relationship of RZHONSNITSKAYA's genus *Pseudogruenewaldtia* 1960. This genus is undoubdedly closely related to *Anatrypa* and *Atrypa* and has nothing to do with the palaferellid brachiopod *Gruenewaldtia* CHERNYSHEW 1885 as RZHONSNITSKAYA suggests both in her descriptions and name. The illustrations of sections and the micromorphology of the shell surface make this clear. The '*Atrypa zonata*' of DAMES (1868, p. 497, Pl. 11, fig. 1a-c) are closely related to *Pseudogruenewaldtia* RZHONSNITSKAYA and may be assigned to it.

ALEKSEEVA (1962, p. 144) stated that the *Anatrypa* she had examined had dental plates. i.e. they had lateral cavities. These are pointed out in her sketches of serial sections. The *Anatrypa* of the Aachen area do not have lateral cavities, but a dental nucleus is present. Similar dental nuclei and even slit-like lateral cavities are shown by RZHONSNITSKAYA (1964, p. 105, fig. 5). This is not evidence that these *Anatrypa* belong to or are related to the *Desquamatia* group. STAINBROOK (1945, p.48, figs. 6a-g), described an atrypid, "*Gruenewaldtia americana*", which probably belongs to Anatrypa sensu MARKOVSKY and GÜRICH, but for which no lateral cavities were shown.

*Member species*.-

?*Anatrypa micans* (BUCH), *A. americana* (STAINBROOK), *A. timanica* MARKOVSKY, *A. kadzielniae* (GÜRICH), *A. sigasa* NALIVKIN, *A. heckeri* NALIVKIN.

## *Anatrypa* cf. *americana* (STAINBROOK 1945)

Pl. 15, figs. 1-4; text-figs. 70-79.

1945. *Gruenewaldtia americana* STAINBROOK, p. 52, Pl. 5, figs. 18-23, 27-28, p. 48, figs. 6a-e.

*Range*: Frasnian (F3 most likely).

*Host sediment*: Thin bedded, nodular, moderate brown, argillaceous limestones and shales.

*Associated fauna*: Small spiriferids, athrrids, *Schizophoria*, *Aulacella* sp.

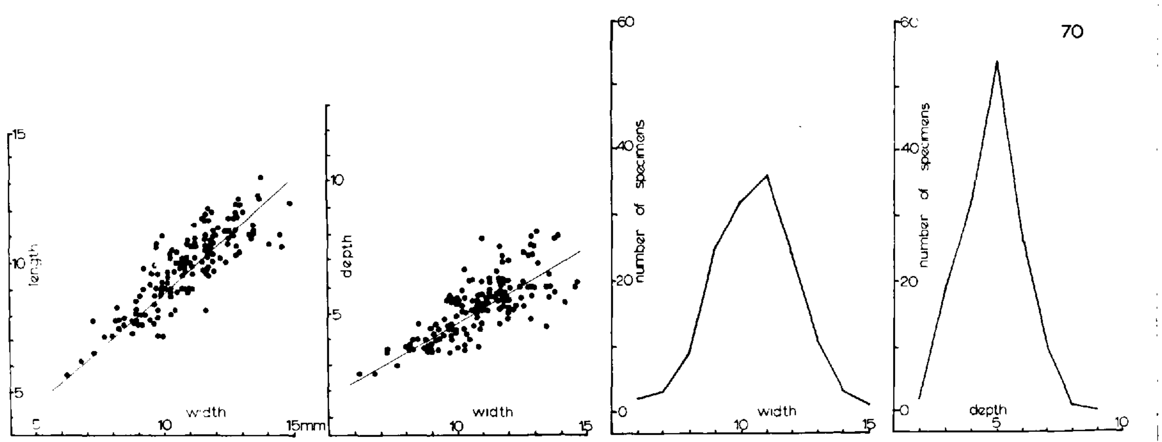
Diagnosis.-

Small ventribiconvex-planoconvex (even slightly concave dorsally) atrypids, with a nearly straight hinge margin, weakly developed ears. Ribs are fine. A small delthyrium and foramen are located in a small area.

## Description

External form.-

Specimens are marked by their small size; most are within a range of 9-12 mm wide (text-fig. 70), and are about 5 mm thick. Width slightly exceeds length, changing from a width/length ratio of 1.09 to 1.15 and a width/depth ratio of 2.41 to 1.15 from early to mature stages of growth. The shell outline is subquadrate to subcircular. The pedicle valve is much more convex than the brachial valve. Maximum width is about mid-length, maximum depth towards the anterior commissure. Folds on the commissure are weak.



Text-fig. 70. Scatter diagrams and frequency curves of the main dimensions of Anatrypa cf. americana (STAINBROOK). Frasnian "Kramenzel über Molocrinus Schichten", BMB10.

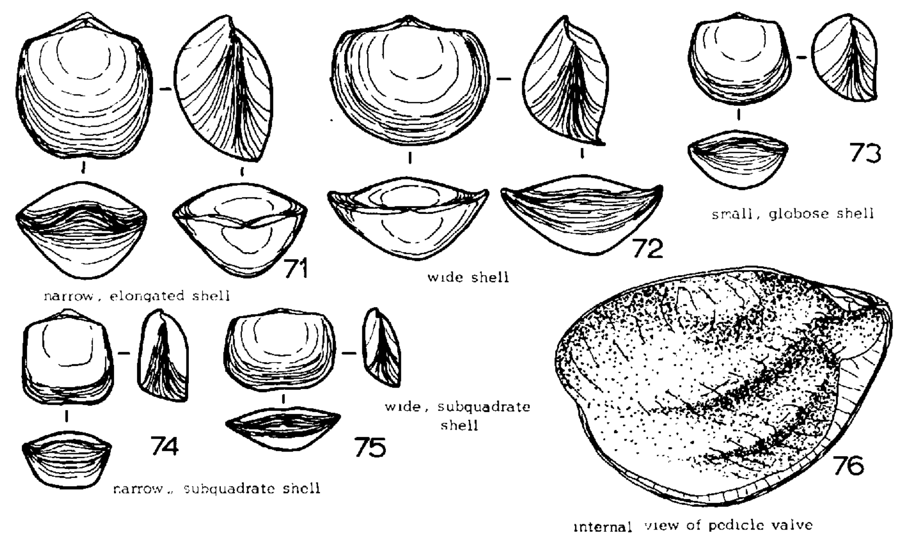
The strongly convex pedicle valve is geniculated at about $\frac{3}{4}$ of its mature length. A small, pointed but flattened beak varies from orthocline to epicline in position. The narrow and short area is sharp-edged, and contains a minute delthyrium with two tiny separated deltidial plates and a foramen. The apical angle is 120-170 degrees but most frequently fluctuates between 130 and 145 degrees. The convexity of the pedicle valve is mainly due to geniculations : the apical mid-fields tend to be flat and it is only the anterior portion which drops steeply. The brachial valve is weakly convex, partly concave at the margins. The apex may be slightly obscured by the ventral beak. The apical mid-field is weakly depressed and planar.

Ribs.-

Ribs are fine, ranging from 16-25 per 10 mm , but averaging at nearly 22. Ribs are Atrypa-like. Bifurcations occur gradually and are barely noticeable. The ventral mid-ribs spring fom a strong, apical mid-rib, and at the apex may be flanked by 2 or 3 side ribs. The dorsal valve has 3 lateral ribs and a depressed median rib at the apex.

Growth lamellae.-

The first marked lamellae appear at 5-7 mm from the apex and are followed by rapid and close-spaced insertion of less than 1 mm. The most rapid insertion of lamellae begins at the point of geniculation on the pedicle valve (which is unmarked, except by close lamellae, on the brachial valve). The lamellae hug the shell surface and are not deflected. They may extend slightly around the margins of large specimens to form a rim. A frill is not developed. This rim is gently curved in a dorsal direction.



Text-figs. 71-76. Shell variation of Anatrypa cf. americana (STAINBROOK). Randomly selected from "Breinigerberg" localities. x1.

Growth and variation.-

Small circular specimens are planoconvex and have a rectimarginate commissure. There is little increase in the size of the area with age, but some incurvature. The commissure becomes weakly flexed or remains straight. Variation is shown in text-figs. 71-76. Forms with rather long rectilinear hinge margins and wide apical angles are nearly as abundant as the narrow elongated forms.

Internal structure.-

A resume of three serially sectioned specimens is given in text-figs. 77-79. In the largest of the three specimens a pedicle collar was present (shown in greater detail in text-fig. 21). Apically this collar is free, distally it is attached. The dental nucleus does not broaden into a cavity. Short teeth with long lateral lobes are heavily supported by columnar calcite.

A small cardinal process, bearing 7-8 strands, fills the notothyrial pit. Inner socket ridges long, forming crural support. Crural bases are roundish, crura thick, solid. Jugal processes are curved, short, and terminate in small, tapering jugal plates which are off-set laterally from the direction of the jugal processes. Jugal plates are V-directed, disjunct. Spiralia with up to 8 whorls were counted, inner whorls resting in the mesial trough and outer whorls 3-4 mm higher along the shell sides.

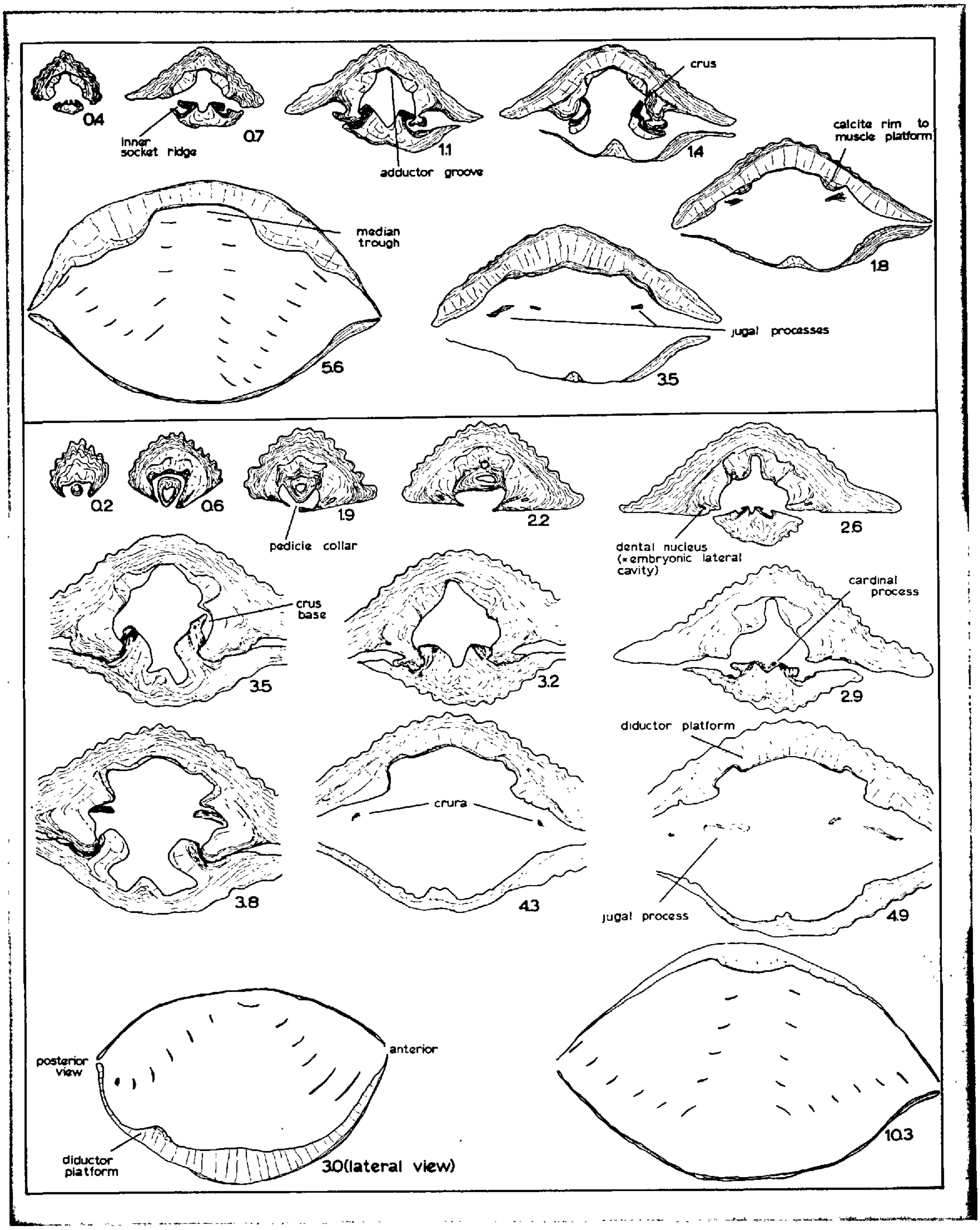
Internal markings.-

The shell wall was peeled wway from three specimens and reconstructed. No brachial valves were prepared in this way. On the pedicle valve, the small, single diductor scar is elevated by a supporting anterior ridge which resembles a platform when horizontally oriented. The diductor length is less than 3 mm (see text-fig. 78). Directly in front of the diductor scar is a deep, mesial trough which appears to accommodate the inner spiralial whorls, The sides of the valve, at mid-length, are bulged out or thickened to form a support for the outer whorls. The anterior portion of the mesial trough may contain a single, low ridge. From the sides of the diductor scar, running anteriorly, are two weak or moderately thick ridges which probably represented the swellings of the pallial sinuses.

Remarks.-

The strongest resemblance of this atrypid from the Aachen area (this is the first report of Anatrypa in Europe), is the "Gruenewaldtia" americana STAINBROOK 1945. STAINBROOK (Pl. 5, figs. 21, 28) already figured and discussed the unusual internal structure of free pedicle valves, but due to lack of comparative literature, did not realize how this type of shell differed internally from Atrypa. The free pedicle valves shown by STAINBROOK (op. cit.) are very similar to those of the German species. Externally these two, the American and German atrypids, also are similar.: in size, in shape and outline, and in rib structure. A re-examination of STAINBROOK's material may show that they are conspecific.

GÜRICH (1896, p. 272) described unfigured specimens of "Atrypa desquamata var. Kadzielniae" which ALEKSEEVA (1962) attributed to the genus Anatrypa. The specimens figured by ALEKSEEVA (1962, Pl. 8, figs. 6a-c) are nearly equally convex and half to two thirds circular in outline. This convexity and circularity makes it different from the German species.



Text-figs. 77-79. Transverse and longitudinal serial sections of *Anatrypa* cf. *americana* (STAINBROOK). 77-78, locality BMB10; 79, locality BMB9, "Breinigerberg"; Frasnian F3. 78 at about 3.0 mm from the plane of symmetry. x4.

Anatrypa timanica MARKOVSKY 1950 (as shown in LJASHENKO, 1959, Pl. 26, figs. 3-5) has a weak median trough on the brachial valve which is not observed in any German specimens, but its shape and size are comparable. The Russian form also differs in lacking the sudden marginal increases in growth lamellae.

The specimens from the Aachen area, Germany are of two types : one, very small forms which form the bulk of the collection and which probably were collected in F3 strata, and two, the rare large forms which occur as isolated specimens with Atrypa cf. varicostata STAINBROOK. The second type may be slightly higher in the sequence. The two, which are here jointly described, may belong to different species.

Material.-

BMB10(168) "Kramenzel über den Melicrinus Schichten"; BMB(16) "Breinigerberg"; BMB11(3) "Breinigerberg". The first two localities contain the small variety, the last two the large variety. Total number of specimens 373.

According to KLÄHN (1912, p. 4) the Melocrinus beds would correlate with Matagne beds (F3) of Belgium for the stated "Es entsprechen...... die Schichten b, c, d (with Melocrinus) der Schichtenfolge 5 des Walheimer Profiles." There is some contradiction here for KLÄHN (1912, p. 5) stated that Matagne beds with Buchiola retrostriata (F3) were also found at Breinigerberg. At present Anatrypa has been found only at Breinigerberg in Germany. It has never been reported elsewhere in Europe.

## Anatrypa? sp.

Pl. 15, figs. 5-7.

Remarks.-

A collection from the "Bodensteiner Ley, Villmar", which is east of the Rhine, contained 33 specimens which could not be assigned to Anatrypa cf. americana STAINBROOK from the Aachen area. They were highly variable in size and shape. All had much larger areas and foramina and had long, straight ribs with practically no interrupting lamellae. This type of rib and interarea structure is typical of the Anatrypa micans (BUCH) variation as shown by RZHONSNITSKAYA (1960), and already mentioned before. No serial sections were made of any specimens and identifications are delayed until their inner structure becomes known.

## Genus *Spinatrypa* STAINBROOK 1951

1945 *Hystricina* STAINBROOK, pp. 49-50.
1951 *Spinatrypa* STAINBROOK, p. 196.

*Type species*: *Atrypa aspera* var. *occidentalis* HALL 1858, p. 515, Pl. 6, figs. 3a-d.
*Range*: Wenlockian (Silurian) to Frasnian (Upper Devonian).
*Distribution*: Worldwide.

*Diagnosis*.-

Biconvex through dorsibiconvex and planoconvex spinose atrypids with small interareas and small deltidial plates, orthocline to epicline beaks. Ribs are coarse, undulose and raised at each growth lamella. Internally, thick pedicle layers are absent; deltidial plates are small, undeveloped and rarely hollow. Teeth bear dental nuclei or lateral cavities. Cardinal process small, amorphous. Crural bases round; crura frequently feathered. Jugal plates straight, long, V-directed.

*Remarks*.-

The preoccupied name *Hystricina*, which STAINBROOK nominated for a select group of spinose atrypids in 1945, was subsequently replaced by *Spinatrypa* by the same author in 1951. STAINBROOK's definition of the genus is still valid to-day.

*Spinatrypa* is easily distinguishable from *Atrypa* DALMAN by its undulose ribs arranged in interrupted rows. Internally *Spinatrypa* lacks the numerous interlayers of columnar and fibrous shell, the thick pedicle constrictions and the solid teeth of *Atrypa*. The jugal plates also are distinct : in *Atrypa* they are bent and more U-shaped, in *Spinatrypa* they are thick and straight.

The diagnostic characters of the genus *Invertrypa* STRUVE (1961, p. 33 which are a ventribiconvex shell, small area, and loss of ribs, are judged not to be of sufficient value to warrant separate generic status. Furthermore, the phylogenetic series *Spinatrypa*-*Invertrypa*-*Spinatrypa* is difficult to explain. Only one species can strictly be included in *Invertrypa*, the type species *kelusiana* STRUVE. BIERNAT (1964, p.315) also disputed the importance of the diagnostic characters proposed by STRUVE, and similarly chose to return *Invertrypa fasciplicata* STRUVE to the genus *Spinatrypa*. The diagnostic characters of *Invertrypa* are repeated several times in the spinose atrypids, at different times during the Devonian.

*Spinatrypa* STAINBROOK differs from *Spinatrypina* RZHONSNITSKAYA in its undulose, instead of tubular-imbricate ribs, in its minute area and small deltidial plates rather than relatively large area and deltidial plates, and in its development of spines, which are common and abundant *Spinatrypa* also reached a far greater size than even the largest known **Spinatrypina.**

## *Spinatrypa variaspina* n.sp.

Pl. 16, figs. 1-3.

*Name*: Latin, *varius*, *a*, *um*, variable, changeable; *spina*, *ae*, a thorn, spine. The spines are variable in direction.
*Type locality*: Road cut Lissingen-Büdesheim, Gerolstein syncline, MTB Gerolstein r44890:h64630.
*Type stratum*: Schleit horizon or slightly higher, Nohn beds, lower Eifelian.
*Range*: Nohn beds, Eifelian.
*Associated fauna*: *Atrypa* (*Atrypa*?) *caepata* n.sp., *Desquamatia ovata* COPPER, *Gruenewaldtia prooemia* n.sp. Corals are rare, mainly brachiopod biotope.
*Source sediment*: Brownish green to dark brownish gray calcareous shales and thin limestone interbeds, rich in bioclastic debris.

*Diagnosis*.-

Small, rather wider than long, flattish *Spinatrypa*. Beaks protruding, orthocline, small and blunted. Interareal edge sharp. Brachial valve only slightly more convex than a weakly angular pedicle valve. Ribs spaced at 9-11 per 10 mm., terminating at each growth lamella intersection in twisted, deflected, disarrayed spines about 5 mm. long. Growth lamellae spaced at about 1 mm.

*Remarks*.-

*Spinatrypa dorsata* BIERNAT (1964, pp. 307-309) from the Devonian of Poland, and also present in the Eifel in slightly younger beds than *S. variaspina* n.sp., is narrower, somewhat thicker and has coarser, deeper-troughed ribs and has a smaller area. *S. variaspina* appears to be highly variable in form and the number of varieties are more numerous than in other *Spinatrypina* from the Eifel. Some of these shape differences are illustrated in Pl. 16, figs. 1-3.

No material had been sectioned. The internal structure is still unknown. The presence of spines simplified generic identification.

*Material*.-

The species is scarce and makes up only a small fraction of the fauna at any locality. Total 103 specimens.

C274a(1); C274b(1); C277(1); C287(3); C288(1); C292(2); C398(9); C440(1); C451(4); C452(2); H33(2); H34(1); H77(1); H87(1); H99(5); H107(1); H221(1); H252(2); H256(1); St13(3); St19(20); St85(1); St101(1); St304(5); St307(1); St428(1); St711(6); St713(2); St715(3); St973(1); Fp1262(4); Fp1264(7); RW40(1); RW16(1); BP9(5).

## *Spinatrypa* cf. *dorsata* BIERNAT 1964

Pl. 16, figs. 4-6; text-figs 80.

1964 *Spinatrypa dorsata* BIERNAT, pp. 307-309, Pl. 3, figs. 1-8.

*Remarks*.-

In the Bildstock horizon of the Eifel, the lowermost part of the Ahrdorf beds, *Spinatrypa* becomes common for the first time. It dominates *Atrypa* in numbers, but does not reach a size greater than 15 mm. The identification with *Spinatrypa dorsata* BIERNAT is still not certain, though it has greater affinities with this Polish species than with others. Higher up in the Ahrdorf beds, specimens are larger by nearly one third, and also more globose and expanded. By Niederehe time *Spinatrypa* becomes rather rare and is taken over by *Atrypa* (*Isonatrypa*).

The crude serial sections figured by BIERNAT (1964, p. 309) are of little value in comparison. BIERNAT shows the delthyrial cavity plugged by solid calcite, a feature absent in the Eifel specimens, and certainly not diagnostic of *Spinatrypa* as a whole. BIERNAT also shows remarkable joined jugal plates which were not present in Eifel specimens (refer to text-fig. 80).

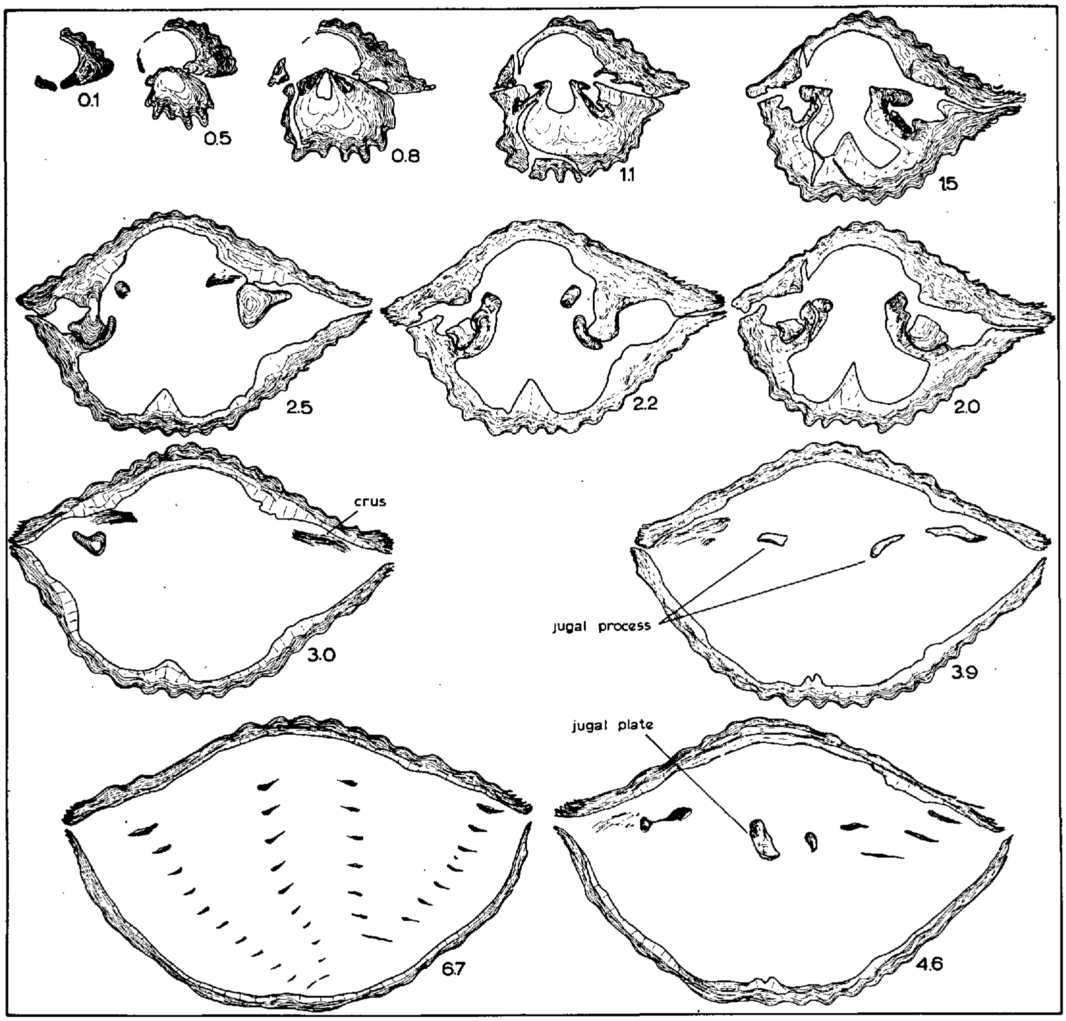
*Spinatrypa* cf. *dorsata* BIERNAT can be distinguished from *S. variaspina* in its more convex shells, its epicline rather than orthocline beaks, and its more undulose, flatter almost *Atrypa* (*Planatrypa*)-like ribs.

One specimen from the Bildstock horizon (Ahrdorf beds) was sectioned (text-fig 80); It shows the presence of very small deltidial plates, an elongated dental nucleus but no distinct cavity, short, stubby teeth, a prominent inner socket ridge, slightly feathered crura, a thick jugal plate and spiralia with about 10 whorls.

*Material*.-

Copper coll. not listed. Remainder 126 specimens. Total about 250 specimens.

St30(52); St32(2); St35(1); St54(3); St60(1); St66(1); St87(1); St109(8); St447(1); St460(1); St503(2); St658(1); St679(6); St717(2); H3(1); H121(3); H148(3); Fp1279(4); Ge22(15); Ge25(2); AG41(5); AG234(2); BP54(7); RW31(1).



Text-fig. 80. Transverse serial sections of Spinatrypa cf. dorsata BIERNAT. Bildstock horizon, Ahrdorf beds; MTB Dollendorf r54800:h79180. x4.

## Spinatrypa aspera aspera (SCHLOTHEIM 1813)

Pl. 17, figs. 1-7; Pl. 18, figs. 2-3, 5-11; text-figs. 81-85

1813 Anom. Terebratulit. asper SCHLOTHEIM, Pl. 1, figs. 7a-c.
1820 Terebratulites asper SCHLOTHEIM, p. 363.
1822 Terebratulites asper SCHLOTHEIM, Pl. 18, figs. 3a-b.
1825 Terebratula aspera SCHLOTHEIM, KOENIG, p. 3, Pl. 4, fig. 44.
1956 Spinatrypa aspera aspera (SCHLOTHEIM), STRUVE (partim), p. 387, Pl. 1, figs. 2a-c.
1964 Spinatrypa aspera (SCHLOTHEIM), BIERNAT, pp. 309-312, Pl. 4, figs. 1-5, Pl. 5, figs. 1-12.
1964 Spinatrypa aspera aspera (SCHLOTHEIM), STRUVE (partim), pp. 527-529, figs. 4a-c.

Stratum typicum (revised): Low Eilenberg horizon, Freilingen beds, upper Eifelian.
Range: Eilenberg horizon to lower Nollenbach horizon, Freilingen beds, Eifelian.

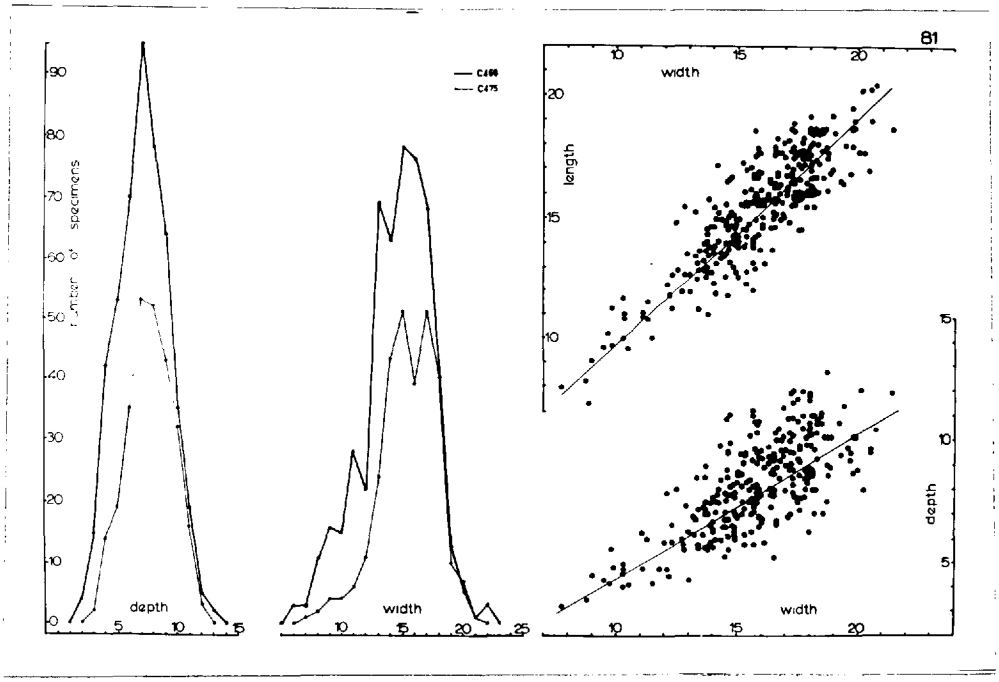
Diagnosis.-
A full diagnosis is given in STRUVE 1956, p. 387.

### Description

External form.-
Specimens are small, maximum observed width is 22 mm and maximum depth 13 mm. Average width falls between 15 and 17 mm , average depth 7 mm (text-fig. 81). Shell valves are nearly equally convex. The anterior fold is weak

The pedicle valve is slightly less convex and a bit flatter than the brachial valve. Shoulder lines straight. Lateral margins are subparallel, hinge corners may be marked and angular. Hinge angles range through 125-140 degrees. A blunt, anacline beak normally stays free from the brachial umbo. A foramen and small triangular delthyrium are exposed. The brachial valve is more rounded and more convex, but not gibbous. The apex is rounded and not exposed.

Ribs.-
The coarse, undulose ribs already show advanced disintegration and planation. Spacing at the margins is at 5-6 ribs per 10 mm., favouring 5. Distally, growth lamellae are thick and crowded and tend to blot out the rib structure. Rib plans were tabulated by STRUVE (1956, p. 387). The ribs do not show much bifurcation and intercalation because they taper from fine to coarse instead of maintaining an even width.



Text-fig. 81. Scatter diagrams and frequency curves of the main dimensions of *Spinatrypa aspera aspera* (SCHLOTHEIM). Scatter diagrams locality C475, MTB Mechernich r37910:h96450. Locality C468 r38020: h96980. About Eilenberg horizon, Freilingen beds.

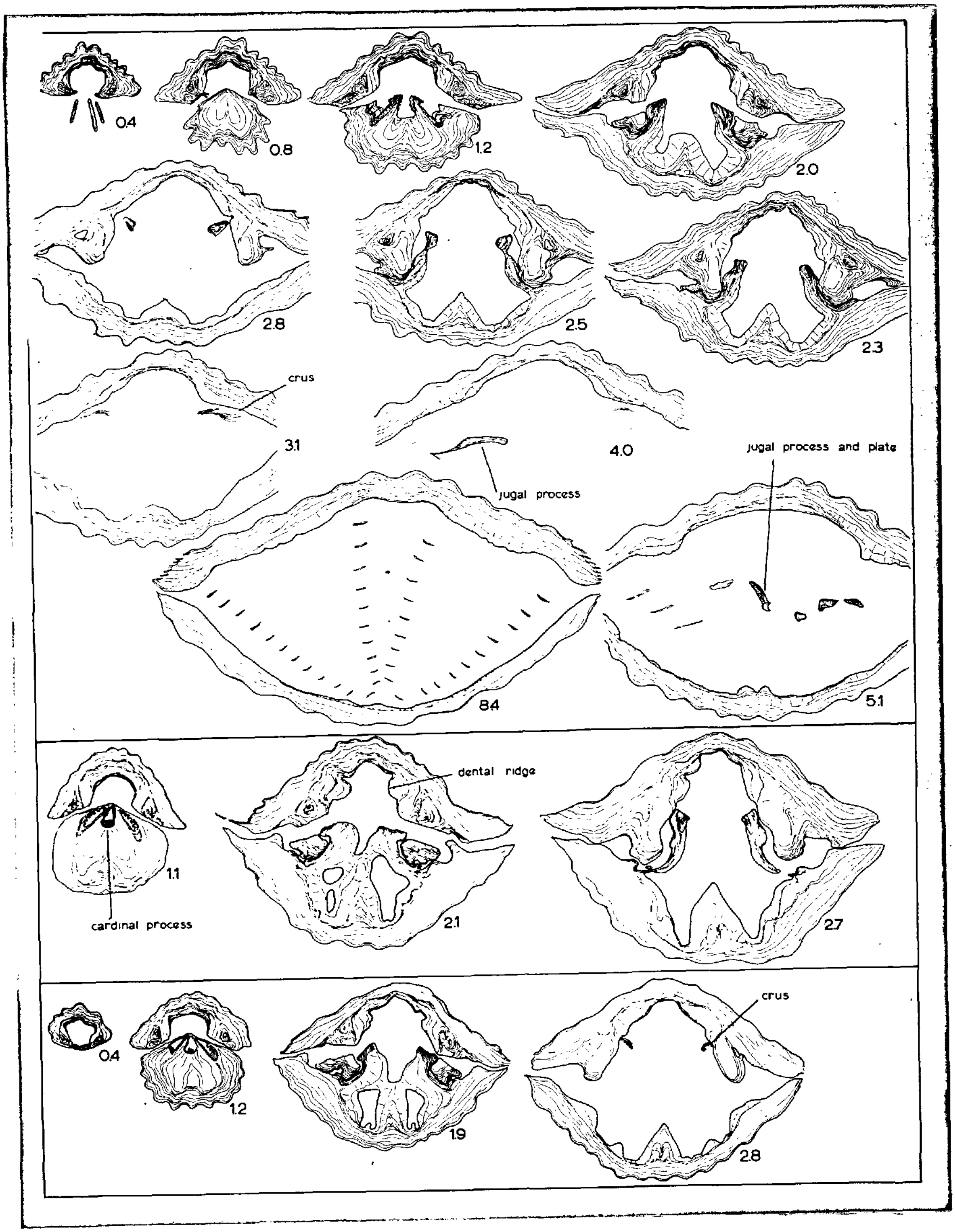
### Growth lamellae.-

Maximum space between lamellae in coarsely ribbed specimens is about 2 mm , but average is about 1.5 mm. Distal crowding of lamellae is characteristic. No spines were found even on well preserved material.

### Growth and variation.-

BIERNAT (1964, p. 312) found that Polish specimens of the species showed only limited variation. This was not true of the specimens from the type locality, where a broad dichotomy into wide and narrow forms seems to exist (though this did not show in scatter diagrams). Wide forms have longer, thinner areas, more orthocline than anacline beaks and generally lack globosity. Narrow forms have short areas and are gibbous in late growth stages. There is complete gradation between the two. This dichotomy is absent in higher beds of the Freilingen sequence, and is completely missing in *Spinatrypa aspera meridiana* n.ssp. The sub-species *meridiana* may have derived from the wide variation of *Spinatrypa aspera aspera*.

Growth changes show neanic, shield-shaped specimens with marked hinge corners, orthocline beaks, and ventri-biconvexity, giving way to the two variations described above.



Text-figs. 82-84. Transverse serial sections of *Spinatrypa aspera aspera* (SCHLOTHEIM. About Eilenberg horizon. Freilingen beds; MTB Mechernian r37910:h96450. x4.

Internal structure.-

BIERNAT (1964, p. 310, fig. 12) was the first and only author to illustrate the internal shell structure. Several specimens from the Eifel region are now sectioned for the first time (text-figs. 82-84).

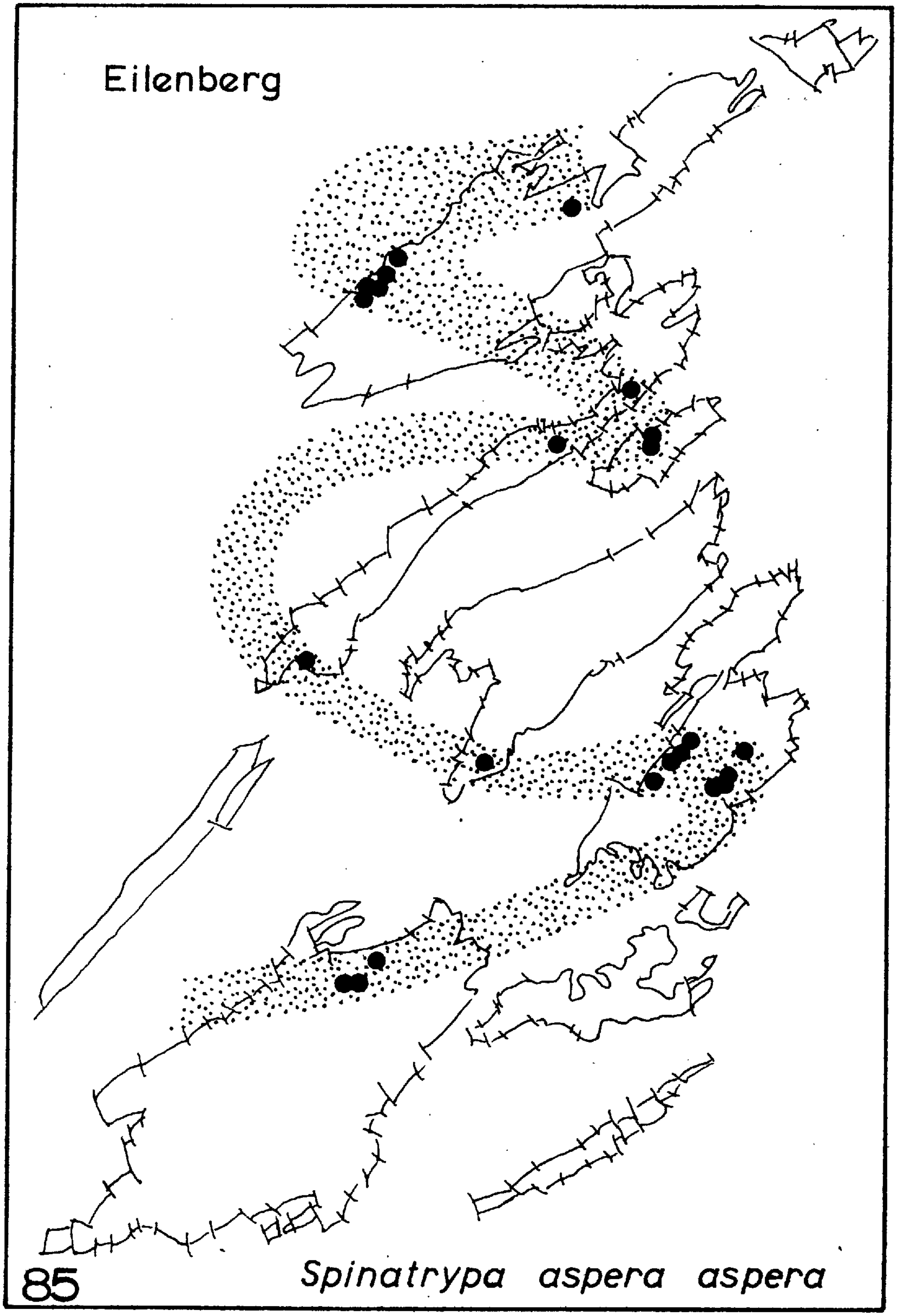
Minute, solid deltidial plates are preserved near the borders of the delthyrial cavity. Rare distal sections of the plates show that they may be at least partially hollow at their tips. The delthyrial cavity is lined by rather thick columnar calcite. A dental nucleus broadens out into a small, minute lateral cavity in some specimens. Teeth are stubby, short with the main lobe twisted inwardly and the outer lobe strongly crenulated. A 4-5 stranded cardinal process caps the notothyrial cavity and part of the hinge plate. Socket plates are moderately thick. Outer socket ridges are well marked. Thick crural bases give strong support to small delicate crura which are partially feathered distally. Jugal processes are thick and distally contain nodules or small spine bases. Jugal plates are short, thick, with small distal hooks. Spiralia with some 10 whorls.

Remarks.-

Like Atrypa reticularis (LINNE), Spinatrypa aspera (SCHLOTHEIM) has gained a reputation as a catch-all species. It seems to have been found everywhere. The name aspera was even applied by KOENIG (1825, fig. 219) to a species of Acanthothiris, a Jurassic rhynchonellid brachiopod. However, KOENIG (1825, fig. 44) was also among the first to recognize the validity of the Eifel species and repeated SCHLOTHEIM's figures.

The vertical, stratigraphic distribution of Spinatrypa aspera aspera us revised and re-interpreted on the basis of fresh evidence. This re-interpretation is vital to a key portion of Eifel biostratigraphy. STRUVE (1961, pp. 310-311) is of the opinion that the lower horizon of the Freilingen beds does not contain Spinatrypa aspera aspera and in order to explain the distribution of other species assumed stratigraphic hiatuses at several localities. With a revision of Spinatrypa aspera aspera (sensu STRUVE) into two sub-species, one aspera aspera (chiefly distributed in the Sötenich and Prüm synclines) and the other aspera meridiana (chiefly in the Hillesheim and Rohr synclines), the stratigraphic position of the critical Eilenberg horizon also can be determined. A detail of sections is given under Stratigraphy, and the problem is explained in detail there.

The revised Spinatrypa aspera aspera is rare in the Hillesheim syncline, and has been found in field localities in two places, at the base of the Eilenberg horizon near Hönselberg and to the north of the Weinberg quarry. It is abundant to the north and southwest, i.e. the Sötenich and Prüm synclines and also the southwest portion of the Blankenheim syncline.



Distribution of Spinatrypa aspera aspera (SCHLOTHEIM 1813).

At the type locality the species is extremely abundant and can be collected in thousands. Other brachiopods are scarce, a few *Atrypa* (*Isonatrypa*) and rare, rather large *Atrypa* (*Planatrypa*). STRUVE (1964, p. 529) places the species (tota species), in the Rasenriff, Crinoidenwald, Knollenblockriff milieu, but this applies only to *S. aspera meridiana*. *S. aspera aspera* occupies a wholly different environment, biotope 5 of this thesis. The substrate is clayey and at the type locality *no* crinoids, rugose corals or cerioid corals are nowhere to be found!

In the Eifelian of the Prague area (Czechoslovakia), spinatrypids are present which bear a likeness to some specimens of *Spinatrypa aspera aspera* from the type area Sötenich. These Czech spinatrypids, *S. semiorbis* (BARRANDE 1847) and *S. semiorbis latecostata* HAVLICEK 1955, show rather coarse, flattened growth lamellae which also are figured here in Pl. 18, fig. 2. But such specimens appear to be only rare varieties of the typical *Spinatrypa aspera aspera* (SCHLOTHEIM).

*Material*.-

Total 2536 specimens

C298(1); C316(2); C346(6); C352(2); C359(4); C360(3); C361(1); C382(73); C388(5); S392(34); C468(1002); C475(354); C506(155); C507(67); C508(2); RW55(1); )s3(3); BP94(5); BP137(4); BP273(241); Söt4(177); Söt15(104); Sot40(208); AG6(11); AG32(1); AG263(38); AG313(6); St44(1); St70(1); St591(10); St614(2); St772(10); st868(2).

## *Spinatrypa aspera meridiana* n.ssp.

Pl. 18, figs. 1-4; text-fig. 86

*Name*: Latin, *meridianus, a, um*, southern. This refers to the abundance of the sub-species to the south of the Eifel synclines.

*Type locality*: Weinberg quarry near Kerpen, Hillesheim syncline, MTB Dollendorf r53030:h77310.

*Type stratum*: Bohnert sub-horizon (A2), Nollenbach horizon, Freilingen beds, upper Eifelian (consult STRUVE, 1961, p. 313).

*Range*: Freilingen beds, mainly Nollenbach horizon.

*Associated fauna*: *Atrypa* (*Planatrypa*) *petasa* n.sp., *Kerpina vineta* STRUVE, *Atryparia stabilia* COPPER, *Carinatina plana* (KAYSER), *Atrypa* (*Isonatrypa*) *inglanda* n.sp. Many tabulate corals, crinoid remains.

*Source sediment*: Pale green to yellowish brown calcareous shales and thin interbeds of argillaceous limestones.

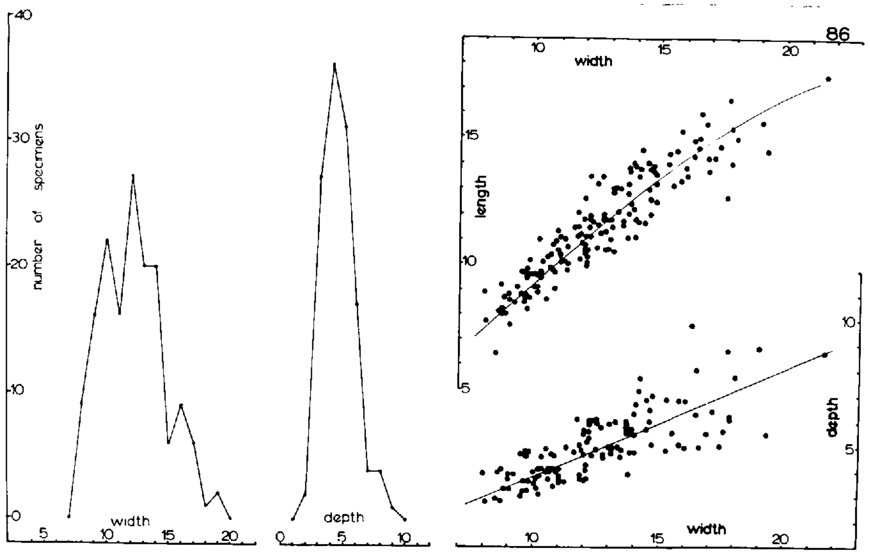
Diagnosis.-

Small, flattish, strongly ribbed Spinatrypa with well-rounded outline and a wider than long shell. Beaks orthocline, areas small, triangular but well exposed and marked by two small deltidial plates and a foramen. Ribs are coarse (6-7 per 10 mm. marginally), imbricate and interrupted by more deflected lamellae with less concentric thickening and thinning. The anterior fold is weak.

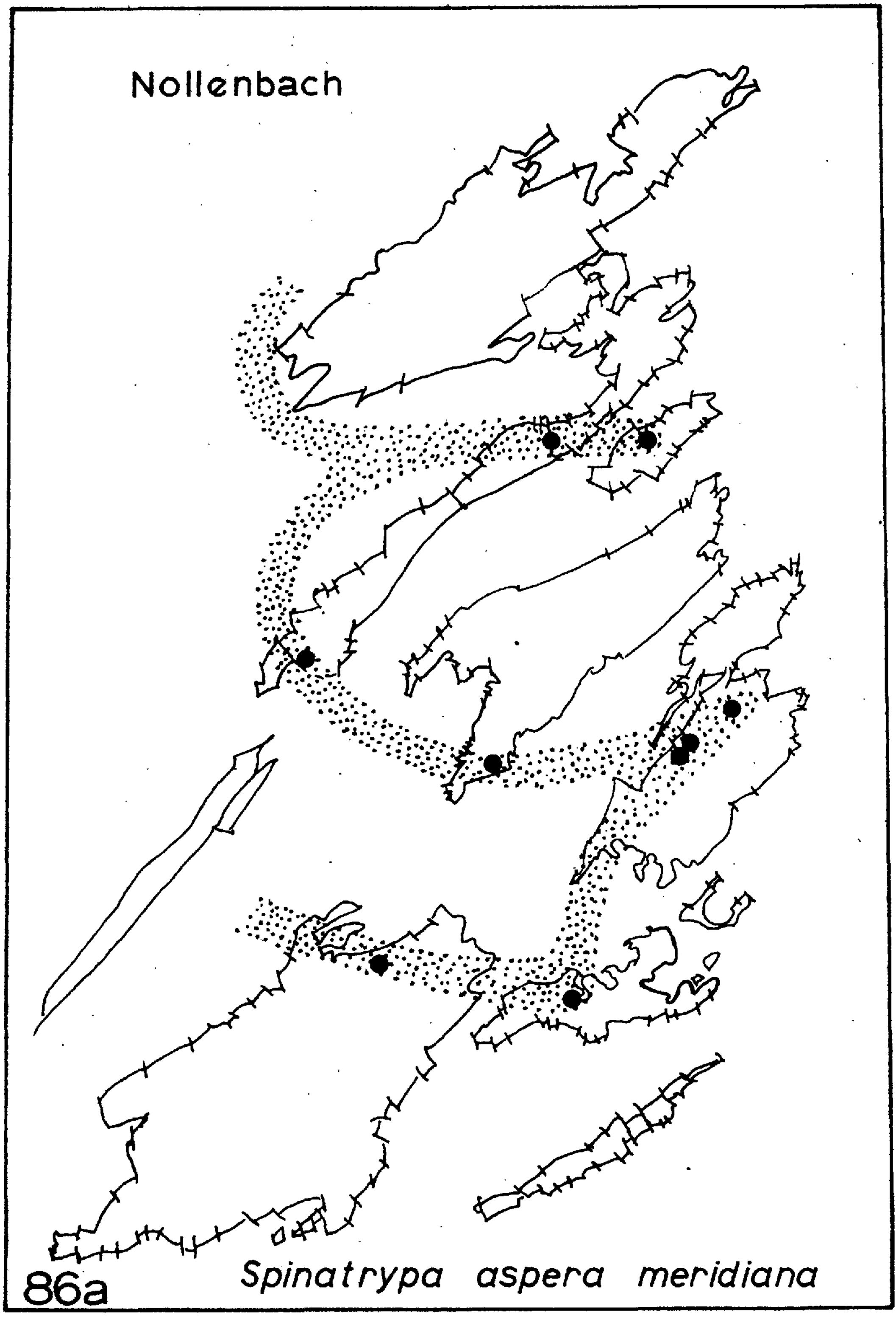
Remarks.-

This sub-species intergrades with the thicker more undulose-ribbed, more robust Spinatrypa aspera aspera. These two sub-species are partly geographically separated, but probably also of slightly different age. S. aspera meridiana can be found above S. aspera aspera at two sections, one in the Dollendorf syncline, one in the Blankenheim syncline.

The scatter diagrams and distribution curves bring out the differences in size and shape between the two sub-species : S. aspera meridiana reaches average width at 12 mm , depth at 4mm , and at average width the width/depth ratio is 2.6:1. The comparable statistics for S. aspera aspera are a width of 15 mm , depth of 7 mm , and w/d ratio of 2.0:1 (text-fig. 86).



Text-fig. 86. Scatter diagrams and frequency curves of the main dimensions of Spinatrypa aspera meridiana n.ssp. Localities St621, St621a, Nollenbach horizon, Freilingen beds.



Distribution of Spinatrypa aspera meridiana n.ssp. in the Eifel.

A striking similarity is afforded by Spinatrypa semilukiana (LJASHENKO 1951) and refigured in LJASHENKO (1959, Pl. 51, figs. 1-2), which is only slightly more convex than the Eifel atrypid, but much younger (middle Frasnian!).

Material.-

Total 286 specimens

C343(18); C345(2); C347(10); C414(67); St621a(109); St621(53); St632a(27).

### Spinatrypa fasciplicata (STRUVE 1961)

Pl. 19, figs. 5-8; Pl. 20, figs 1-2; text-figs. 87-93.

1961 Invertrypa fasciplicata STRUVE, pp. 334-335, Pl. 2, figs. 7-8.
1964 Spinatrypa fasciplicata (STRUVE), BIERNAT, pp. 315-316, Pl.6, figs. 6-11.

Range: Ahbach beds, chiefly Lahr horizon, absent in Müllert horizon. Upper Eifelian.

Remarks.-

An adequate diagnosis is given by STRUVE (op. cit.). No material has ever been sectioned. In a trench described elsewhere (text-fig. 5), portions of the Lahr horizon were exposed and yielded a small fasciplicata fauna of some 184 specimens. Many of these specimens were crushed or broken, as seems also to be typical of other localities. The original diagnosis is supplemented by statistical diagrams and serial sections.

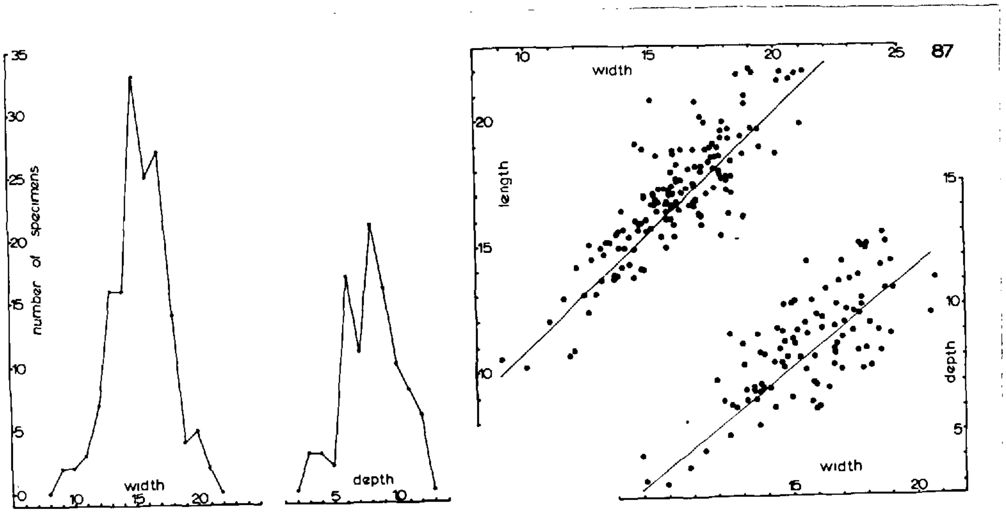
Average width is from 15-17 mm , (text-fig. 87), and average depth 8 mm (slightly greater than for S. kelusiana STRUVE). Most specimens are longer than wide. Only one specimen was sectioned (text-fig. 88), and it showed an internal morphology which compares with that of Spinatrypa aspera (SCHLOTHEIM). Teeth are short, lateral cavities absent. Crura are given off at some distance from the hinge plates and are supported by extended crural bases. Jugal processes are tipped by coarsely crystalline, spinous ends and thin jugal plates. About 6 spiralial whorls were counted.

The species is more equally convex than Spinatrypa kelusiana STRUVE, though the pedicle valve is ususlly somewhat deeper. There is not as great flattening and extinction of ribs ans the beaks are not as incurved, but more anacline like in Spinatrypa aspera (refer to text-figs. 89-93).

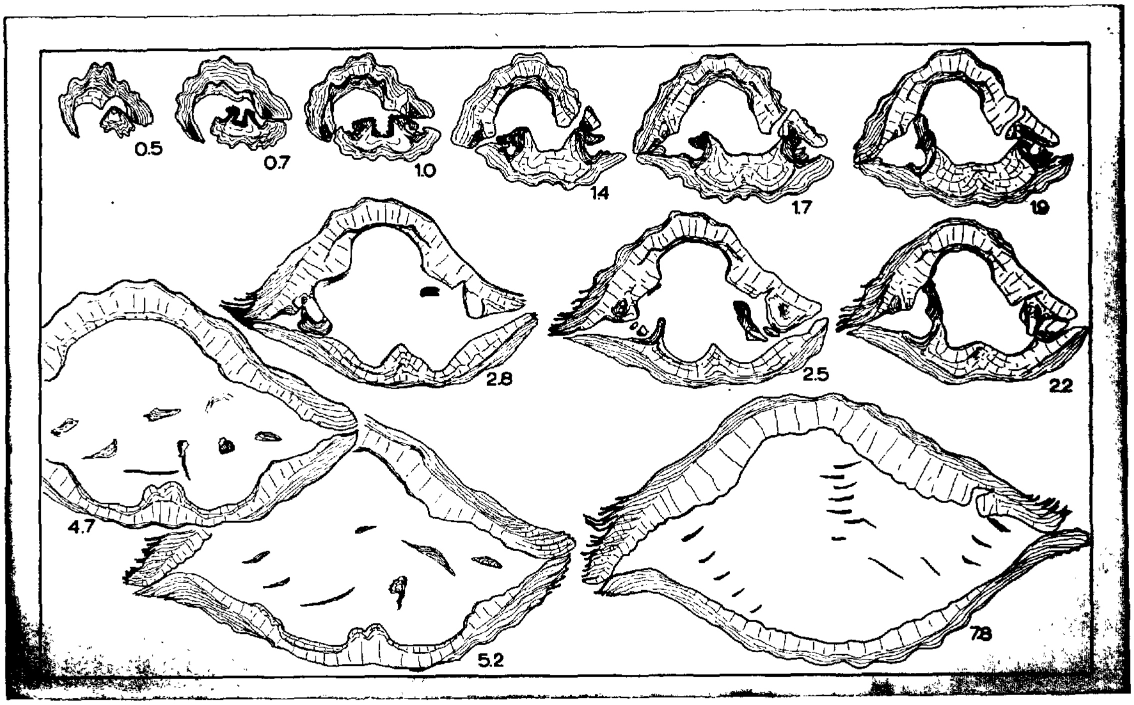
Material.-

The last two localities are uncertain. Total 191 specimens.

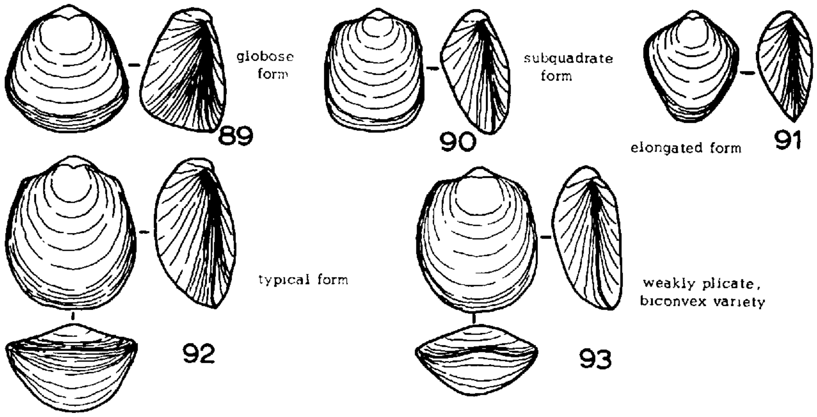
C279f(115); C279fa(69); C280(5); St117(1); St740(1).



Text-fig. 87. Scatter diagrams and frequency curves of Spinatrypa fasciplicata (STRUVE). Locality C279fa, C279fa. Lahr horizon, Ahbach beds.



Text-fig. 88. Transverse serial sections of Spinatrypa fasciplicata (STRUVE). Lahr horizon, Ahbach beds; MTB Dollendorf r55580:h77390. x4.



Text-figs. 89-93. Shell variation in Spinatrypa fasciplicata (STRUVE) from localities C279f, C279fa, Lahr horizon.

## Spinatrypa kelusiana STRUVE 1956

Pl. 20, figs. 3-9; text-figs. 94-101.

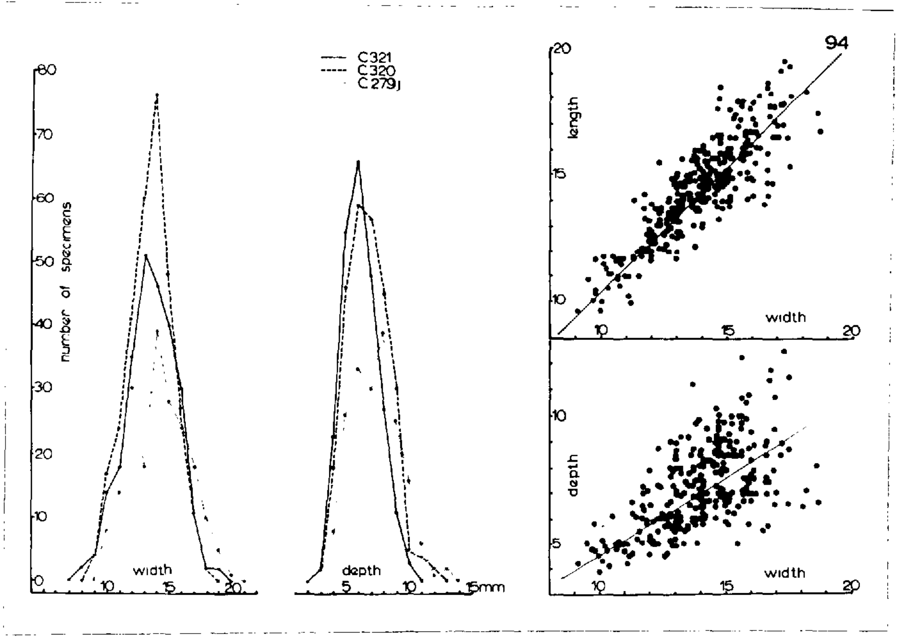
1956 Spinatrypa kelusiana STRUVE, pp. 383-409, Pls. 1-3., figs. 1, 3-24.
1961 Invertrypa kelusiana (STRUVE), STRUVE, p. 334, Pl. 2, figs. 9-11.

Range: Müllert horizon, Ahbach beds, upper Eifelian. Rare in the underlying Lahr horizon.

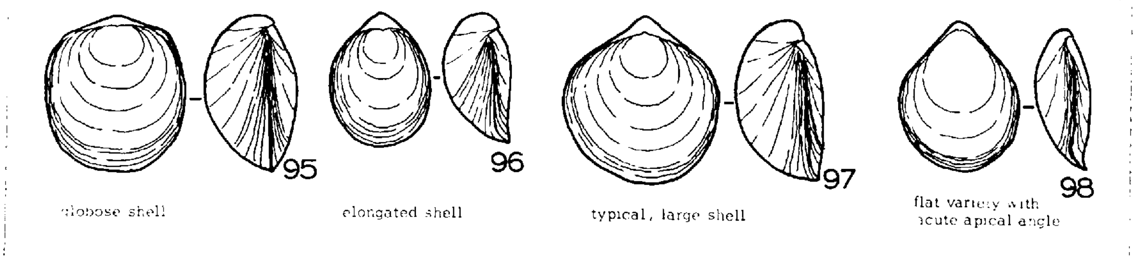
Diagnosis and external description.-
These are given in great detail in STRUVE 1956. Scatter diagrams and dimension curves corroborate STRUVE's findings about shape variation (text-figs. 94-98).

Internal structure.-
The original descriptions and a few simple transverse sections were given by STRUVE (1956, pp. 393-396, figs. 1-5). In several details there are slight deviations in the following description.

Small, minute, apparently solid deltidial plates are obscured by the ventral umbo (text-figs. 99-100). The lateral cavity is tiny, and elongated parallel to the shell wall. Teeth are short, blunt, tapering and flanked by a small lateral lobe. A weak cardinal process, with 2

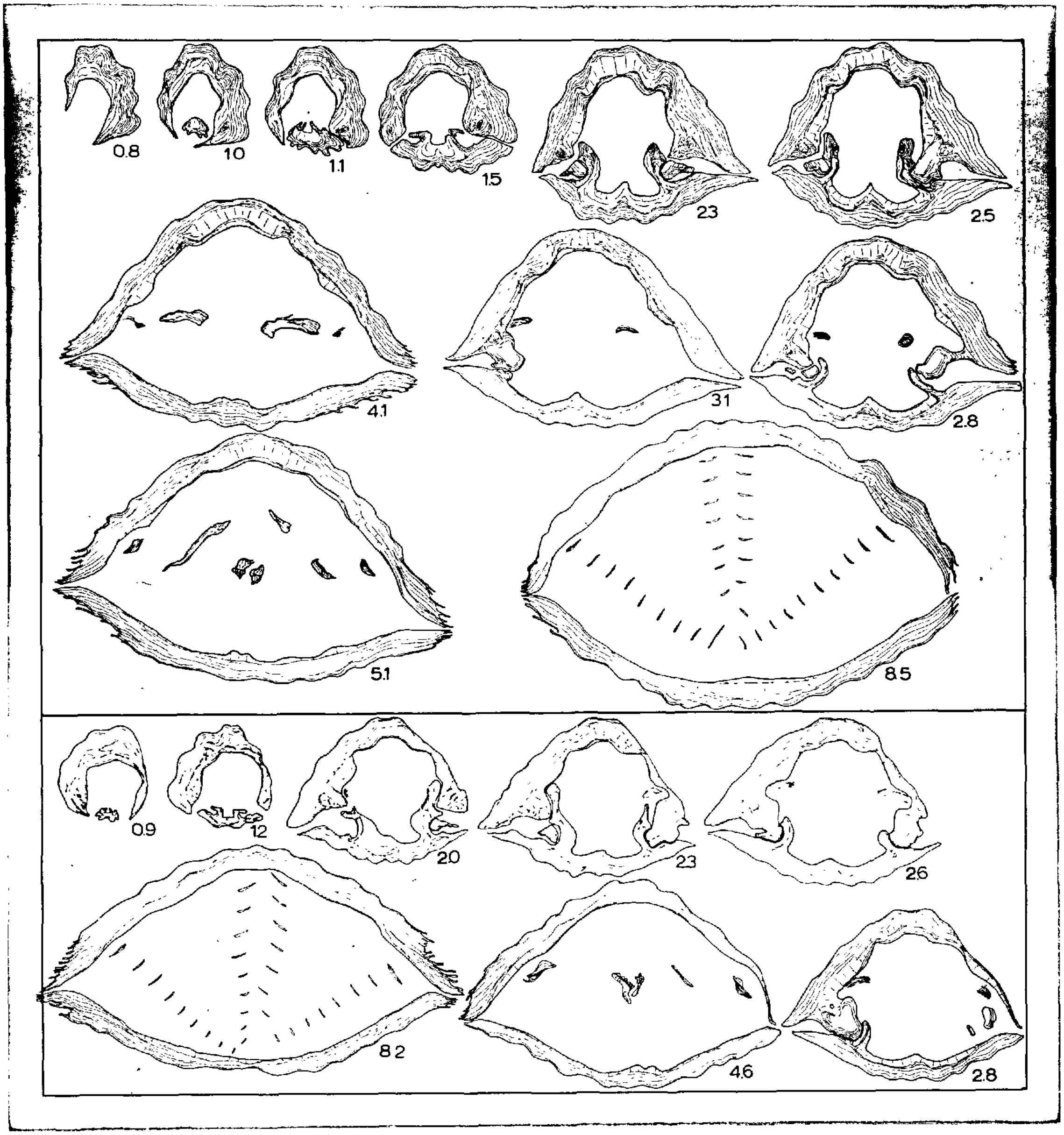


Text-fig. 94. Scatter diagrams and frequency curves of Spinatrypa kelusiana STRUVE. Scatter diagrams from locality C320. Others C320, C321, C279j.

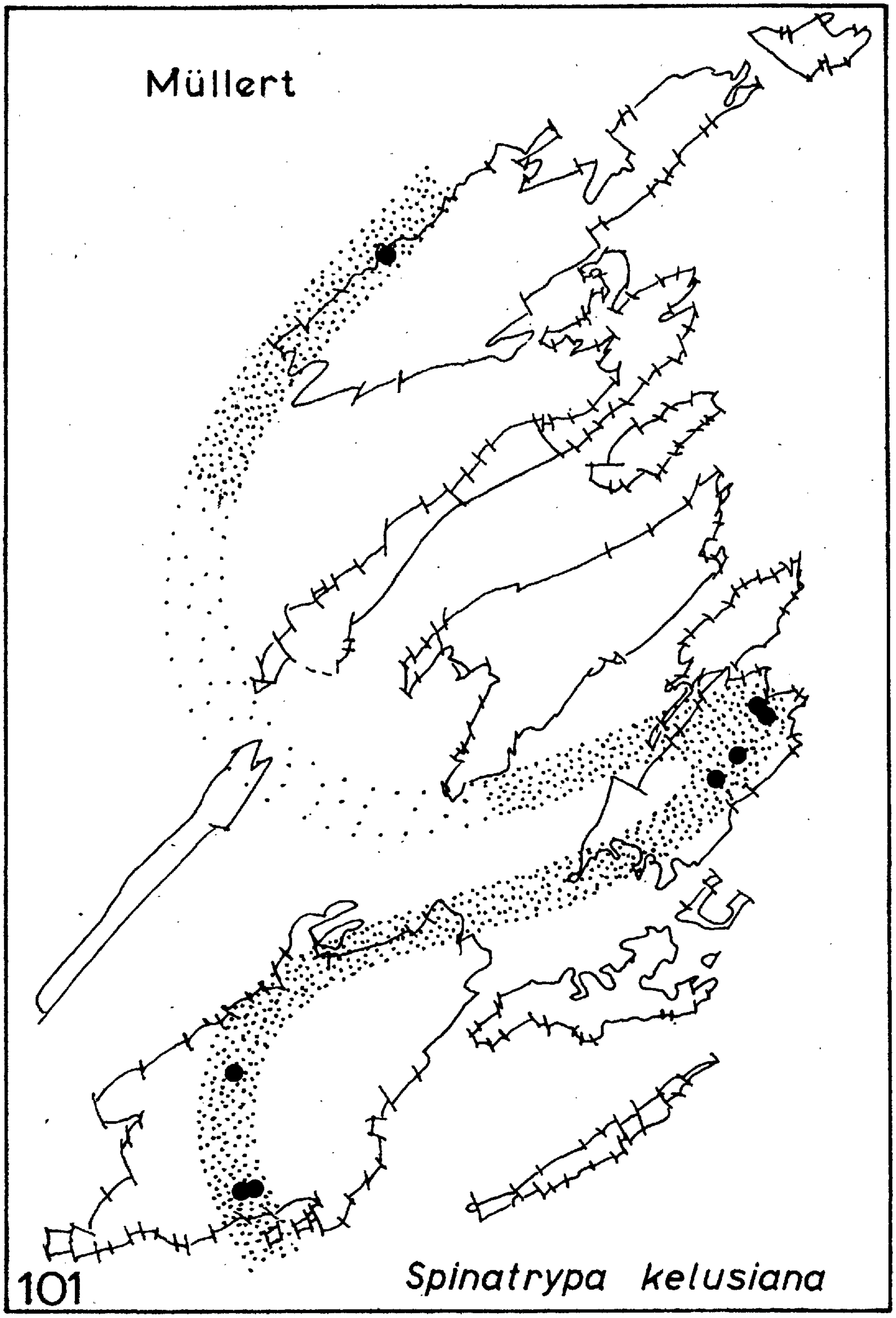


Text-figs. 95-98. Shell variation of Spinatrypa kelusiana STRUVE from random localities. Müllert horizon, Ahbach beds.

small strands in the notothyrial pit is easy to miss in section. Crural bases are elongated and crura are bent laterally only close to the ventral wall. In STRUVE (1956, p. 396) these extended crural bases are interpreted to be crura. Crura are long, thin, compact. Jugal processes, thick and short, are terminated by nodose ridges. Jugal plates are thin, subvertical and rather straight. They are not connected (as claimed by STRUVE, 1956, p. 396, Pl. 2, fig. 14a). Flatly conical spiralia bear nearly ten whorls. No spines were noticed on the whorls of the spiralia (and none were seen in prepared specimens with the shell peeled away). The acetate peels were enlarged 200 times to find such spines.



Text-figs. 99-100. Transverse serial sections of <u>Spinatrypa</u> <u>kelusiana</u> STRUVE. Müllert horizon, Ahbach beds, upper Eifelian; MTB Dollendorf r54620:h75700. x4.



Distribution of Spinatrypa kelusiana STRUVE 1956 in the Eifel

Remarks.-

The ventribiconvex shell and coarse ribs make the species easily identifiable. It is restricted to the calcareous shales of the Ahbach beds, limiting its usefulness in determining the top of the Eifelian stage. The species, as with nearly all *Spinatrypa*, is never found in coral rich horizons, though it may be associated with a few horn corals. The beginning of Givetian time in the Eifel area is marked by the inception of coral rich horizons.

Material.-

Total 1026 specimens (text-fig. 101).

C279g(14); C279h(1); C279i(7); C279j(211); C279ja(23); C279jb(15); C320(351); C321(276); C412(54); C373(2); St190(25); St528(2 ); St623(9); St639(9); St640(1); St650(2); St651(6); St740(2); St764(3); St950(11); St961(2).

## *Spinatrypa globulina* n.sp.

Pl. 20, figs. 10a-b; Pl. 21, figs. 1-4; text-figs. 102-104.

Name: Latin, *globus*, *i*, round ball, sphere; *ina*, diminutive, small. The shell is small and near-spherical.

Type locality: Road cut northeast of Blankenheim, Blankenheim syncline, MTB Blankenheim r46410:h90050.

Type stratum: Loogh beds, probably high Wotan or Rech horizon, lower Givetian.

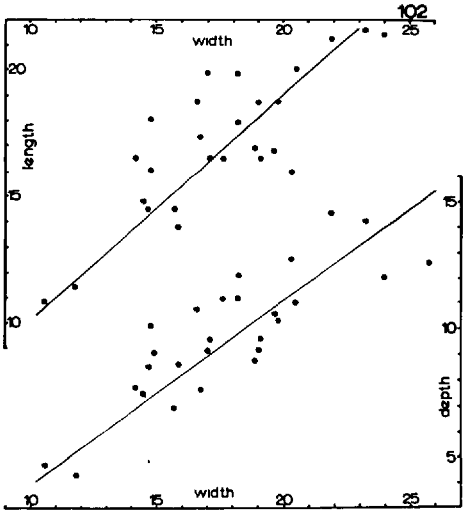
Range: Loogh beds, Wotan to lower or middle Rech horizon. Rare related, smaller specimens in Müllert horizon, Ahbach beds, upper Eifelian.

Associated fauna: Chiefly brachiopods, including *Desquamatia ajugata* COPPER, *Spinocyrtia* cf. *ascendens* (SPRIESTERSBACH), small athyrids, small horn corals (Lythophyllum?), trilobites indet. Nearly 90% *Spinatrypa* and *Desquamatia*.

Source sediment: Grayish green, pale brown weathering calcareous shales with thin interbeds of limestones. Some shells crushed, a few in lumachelle accumulations.

Diagnosis.-

Small to medium sized, rather circular and globose atrypid shells. Ribs coarse (4-5 per 10 mm ), prominent ventral mid-rib pair. Beak incurved, epicline. Strongly folded anterior commissure in late stages of growth.



Text-fig. 102. Scatter diagrams of Spinatrypa globulina n.sp. from the type locality. Loogh beds, lower Givetian.

## Description

External form.-

Mature average size falls in the 18-20 mm range of width. Rare specimens reach 25 mm. Shells are about equally wide as long. Width depth ratio comes to 1.9:1, but tapers to 1.8:1 in late maturity (text-fig. 102). Shell outline rounded, rarely elongate transversely or longitudinally. Brachial valve slightly more convex. Pedicle valve well-rounded moderately convex. Beak blunt, broad, anacline to epicline. Shoulder line straight or slightly indented. Apical angle 125-130 degrees, more acute in neanic specimens. Beak slopes round, angular median crest lacking though the ribs in the centre are thicker and elevated. Area not exposed except in small specimens. Foramen minute, not marked. Fold narrow, incised, U-shaped. Brachial valve also well - rounded. Apex covered. Side areas sloping steeply.

Ribs.-

Rounded, undulose, broad ribs cover the shell. At the margins they have a wave-length of 2.0 to 2.5 mm , but most are close to 2.5 mm. In appearance the ribs span the shape variation between Spinatrypa kelusiana (STRUVE) and S. curvirostra n.sp., i.e. some shells still have ribs which are strongly lamellose and flattened whereas others begin a more even wavy shape. This can be seen in the illustrated specimens Pl.21, figs. 1-4 Ribs are arranged in rows, elevated at each projection of growth lamellae and depressed between growth lamellae. Fragmented shells are thereby extremely nodose. Rare single spines were observed: they are thick basally (1.0 to 1.5 mm diameter), but their full length is not knowm. From the elevation of the ribs at each growth interruption, the spines would appear to have been strongly deflected, perhaps from 60 to 90 degrees on the brachial valve. Spines to not appear to have reached the abundance or length of those in Spinatrypa curvirostra n.sp.

Growth lamellae.-

Most growth lamellae are spaced widely at 3.5 to 4.5 mm. No distal crowding was noticed. Spines probably start at 1-2 mm from the shell surface.

Growth and variation.-

Smaller specimens those of about 15 mm width, are biconvex or ventribiconvex and have orthocline-anacline beaks. A small delthyrium and apical foramen are exposed. Incurvature to the epicline stage is common in mature specimens. Rare specimens retain an orthocline beak throughout life.

Variation is rife. Some small specimens are strongly reminescent of S. kelusiana in their elongate shape, their ventribiconvexity and strong mid-rib pair, but these already have more "advanced" even, undulose structure. Other specimens show strong links to the species of overlying beds, S. curvirostra in their beak incurvature, their larger size and width exceeding length. Some can be confused as immature specimens of this younger species.

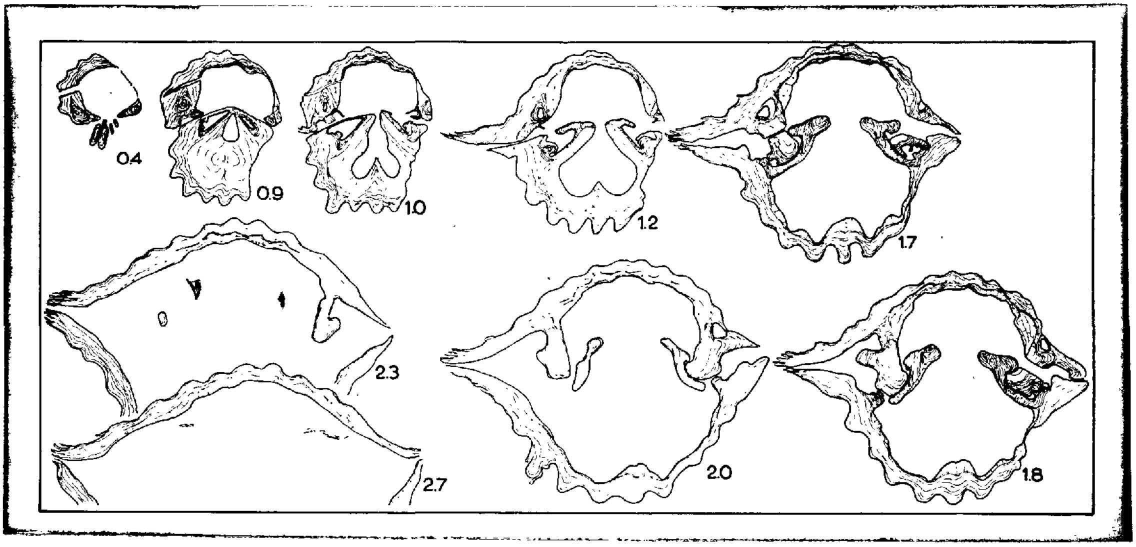
Internal structure.-

Small deltidial plates are retracted inside the delthyrial cavity : the plates are hollow. Lateral,cavities are clear-cut (lacking in S. kelusiana!). Teeth are moderately long, and flanked by small lateral lobes. A broad notothyrial pit divides thin, hinge plates. Inner socket ridges are long and thick. Crural bases and crura small, shortened. Jugal processes and spiralia were not present in the single sectioned specimen (text-fig. 103).

Remarks.-

The comparisons to the older, Eifelian Spinatrypa kelusiana STRUVE and the younger, Givetian S. curvirostra have been discussed.

The species is about twice as coarsely ribbed and much more globose and wide than Spinatrypa aspera (SCHLOTHEIM). No other comparable species in the Eifel region are known. With its robust and round shape and its evenly undulose ribs foreign species such as Spinatrypa semiorbis (BARRANDE 1847), S. semiorbis latecostata (HAVLICEK 1955), S. bifidaeformis (CHERNYSHEV 1887), are also relatively easy to distinguish.



Text-fig. 103. Transverse serial sections of *Spinatrypa globulina* n.sp. Neuenbüsch horizon, Loogh beds, lower Givetian; MTB Blankenheim r46410:h90050. x4.

In size, and also nearly in shape, the best comparison is with specimens illustrated by LJASHENKO (1959, Pl. 6, figs. 8-11) and tentatively identified by that author as *Spinatrypa* ex. gr. *bifidaeformis* (CHERNYSHEV). However, the rib structure of the Russian specimens already are more like *S. curvirostra* .sp. and this advance stage is also seen in the ventral curl of the ventral margin.

*Material*,-

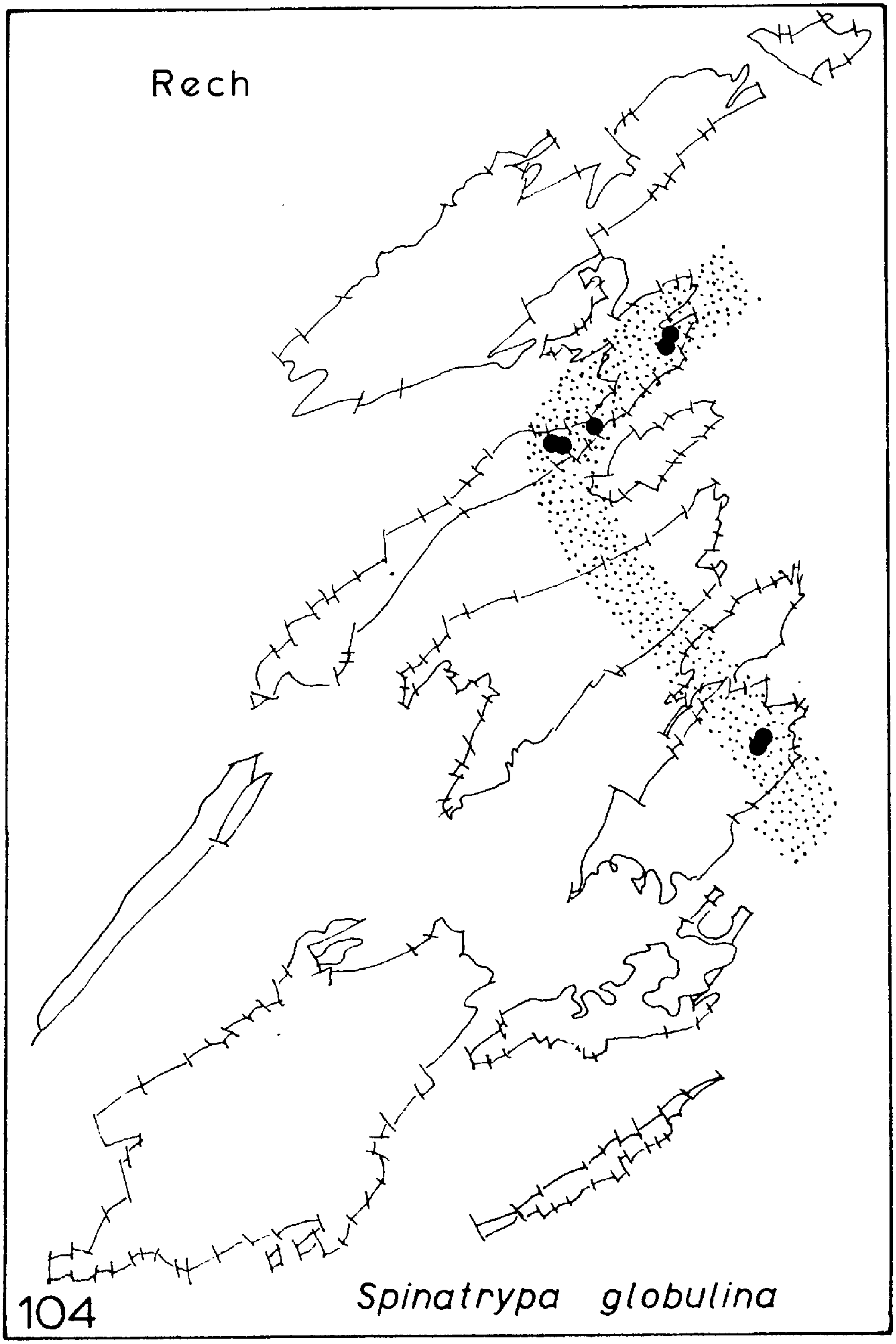
Total 104 specimens (text-fig. 104).

C499(63) locus typicus; C503(2); C504(9); St804(1); St805(6); RW143(1); RW225(1); AG232(2); AG269(3); S8t13(4); BP283(14).

In the Ahbach beds there are rare specimens which appear to be related in rib structure and convexity to *S. globulina* n.sp. These occur with the rich *S. kelusiana* beds, but are not difficult to weed out from them.

A few of these are tentatively listed here :

St128(1); St623(3); St639(2); St640(1). It is possible that the earliest related forms of *S. globulina* already appear in the late Eifelian.



Distribution of Spinatrypa globulina n.sp. in the Eifel.

## *Spinatrypa curvirostra* n.sp.

Pl. 22, figs. 1-5; Pl. 23, figs. 1-2; Pl. 24, figs. 1-3;
text-fig. 105-107.

1962 *Atrypa aspera* (SCHLOTHEIM), JUX, pp. 505-513, figs. 1a-c.

**Name:** Latin, *curvus*, *a*, *um*, curved, bent, arched; *rostra*, *orum*, beak. The strongly incurved beak is typical.
**Type locality:** North slope of the Wachtberg quarry near Sötenich, Sötenich syncline, MTB Mechernich r40160:h98850.
**Type stratum:** Scheid horizon (± Felschbach horizon), Cürten beds, lower Givetian.
**Associated fauna:** *Yunnanella* cf. *custos* SCHMIDT, *Bornhardtina* sp., *Stringocephalus* sp., rare horn corals, isolated *Hexagonaria* colonies.
**Source sediment:** Dark brown to dark gray, reddish staining calcareous shales with thin beds of limestones.
**Range:** Cürten beds, lower Givetian, possibly high Rech horizon, Loogh beds, Givetian.

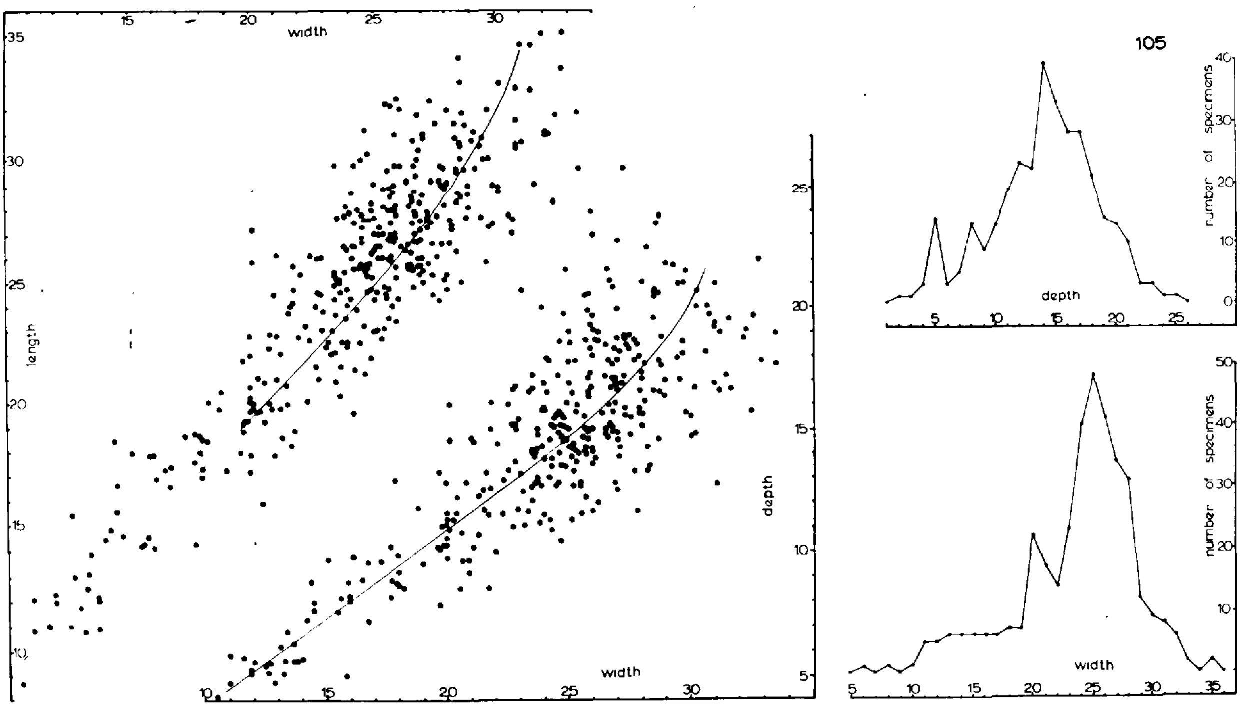
**Diagnosis.-**

Medium to large, dorsibiconvex richly spinose shells. Ribs are coarse, undulose and growth lamellae wide apart (3 to 4 mm ). Beaks pointed, epicline. Moderate anterior fold present. Internally, teeth are strongly crenulated, with elongated lateral cavities. Jugal plates thick, straight and spiralia coiled in nearly 15 whorls.

### Description

**External form.-**

Shells are longer than wide, dorsibiconvex and well-rounded in outline. Maximum width and depth occur at mid-length. Average width is 25 mm , and average depth 14 mm , maximum observed width 35 mm (text- fig 105). Hinge margins are obtusely angled; hinge corners not noticeable, rounded. The anterior fold is moderate to deep. The ventral valve is moderately convex apically and begins to flatten distally and may even be weakly concave at the margins. The shell is reasonably stable on a flat surface, though somewhat off-balance. The marginal curl is not great, and commonly less than 1 mm. or even completely absent. The beak is sharp, flat, slightly angularly crested. It is strongly incurved and pressed against the dorsal umbo. Areas are not visible; a foramen obscured or minute. The dorsal apex is covered for nearly 2 mm by the beak. The brachial valve is nearly twice as deep as the pedicle valve, roundly convex.



Text-fig. 105. Scatter diagrams and frequency curves of the main dimensions of Spinatrypa curvirostra n.sp. Locality C460b. Cürten beds, Givetian.

Ribs.-

Ribs are gently and evenly undulated and strongly interrupted along their length by heightening of the lamellae bases. Ribs are shallow and nearly ironed out just in front of each growth interruption, then gradually expand in height until they reach maximum amplitude, where a spine is given off. Some specimens have very shallow ribs throughout (Pl. 24, figs. 2a-b). Ribs are spaced at 4-5 per 10 mm and do not expand much in size after 10 mm from the apex. At 10 mm from the apex there are 6 or 7 ribs in a 10 mm arc. At the margins, more than 4 ribs per 10 mm are rare.

Growth lamellae.-

Growth lamellae are regular, spaced at 3 mm or slightly more. Distal crowding is rare. Small portions of the lamellae are free and deflected about 10 to 20 degrees between the rib crests and spines. Spines are well developed in the species, somewhat better in the specimens with more deeply troughed ribs. Spines follow the direction of the ribs, but may distally be disordered and bent. On each valve there is a variation in spine direction. On the pedicle valve, there are a few spines on the apical mid-field. Short, delicate spines about 3-5 mm. long and deflected at 40-60 degrees describe a 10 mm. band about the apical mid-field. In the trough of the anterior fold spines are best preserved and well protected. They are here also longer and thicker than elsewhere on the shell, and are sub-parallel to the commissural plane. The remaining surface, the side fields, are more sparsely spinose with 10-30 degree deflected spines. On the brachial valve, small areas about the hinge corners show short spines deflected laterally, at an angle of 30-50 degrees. The anterior side fields contain a few spines deflected at 20-40 degrees, and the remainder of the dorsal valve is nearly bare of spines. There is almost nothing on the crest of the dorsal valve and little mid-laterally. The thickest spines (those in the ventral fold trough) are 2 mm in diameter and from 10-20 mm. long. The smaller spines are located on the brachial valve.

JUX (1962) devoted a paper to spinose atrypids and dealt specifically with this species from the Sötenich syncline. In this paper, JUX (ibid., fig. 1c) reconstructed the direction of spines to run parallel to the commissural plane, and on this reconstruction based a theory that the spines served as filter-feeding mechanism. First of all, in a collection of about 800 specimens from around, and at the type locality, not a single one showed the postulated spine direction of JUX. As described above, spines take numerous directions. Secondly, the observed direction of spines seems to indicate that these were primarily of an anchoring function (pedicle valve) and protective function (brachial valve). A filter feeding function is possible, but highly unlikely.

*Growth and variation*.-

There are several gradation variations. The most common form is a longer than wide shell with fairly well defined, undulose ribs (constituting about 80%). A less common variety is wider than long, or as wide as long, and has shallow ribs of about 2.5 mm wave-length. This form has a stronger mid-rib pair and at the ventral apex two, rather than 3 ribs flank the mid-rib pair. These possibly are "remnant" *kelusiana*-like characteristics.

In young specimens, the shell is ventribiconvex, and has an orthocline beak with small 1 mm foramen and short triangular deltidial plates. The foramen divides the deltidial plates. Spines are strongly deflected (up to 60 degrees) in such small forms. The foramen does not expand with size increase but is curved under and obscured by the beak.

*Internal markings*.-

Brachial valves are scarce in a loose state. Pedicle valves common. The latter shows a large diductor scar nearly half the shell width and about 10 mm long. A weak median swelling divides the diductors. Adductor scars are small, not well impressed, 1.5 to 2 mm wide and about 3 mm long, separated by a thin ridge. Diductors are flanked by thick columnar layer, deeply perforated by ovarian markings.

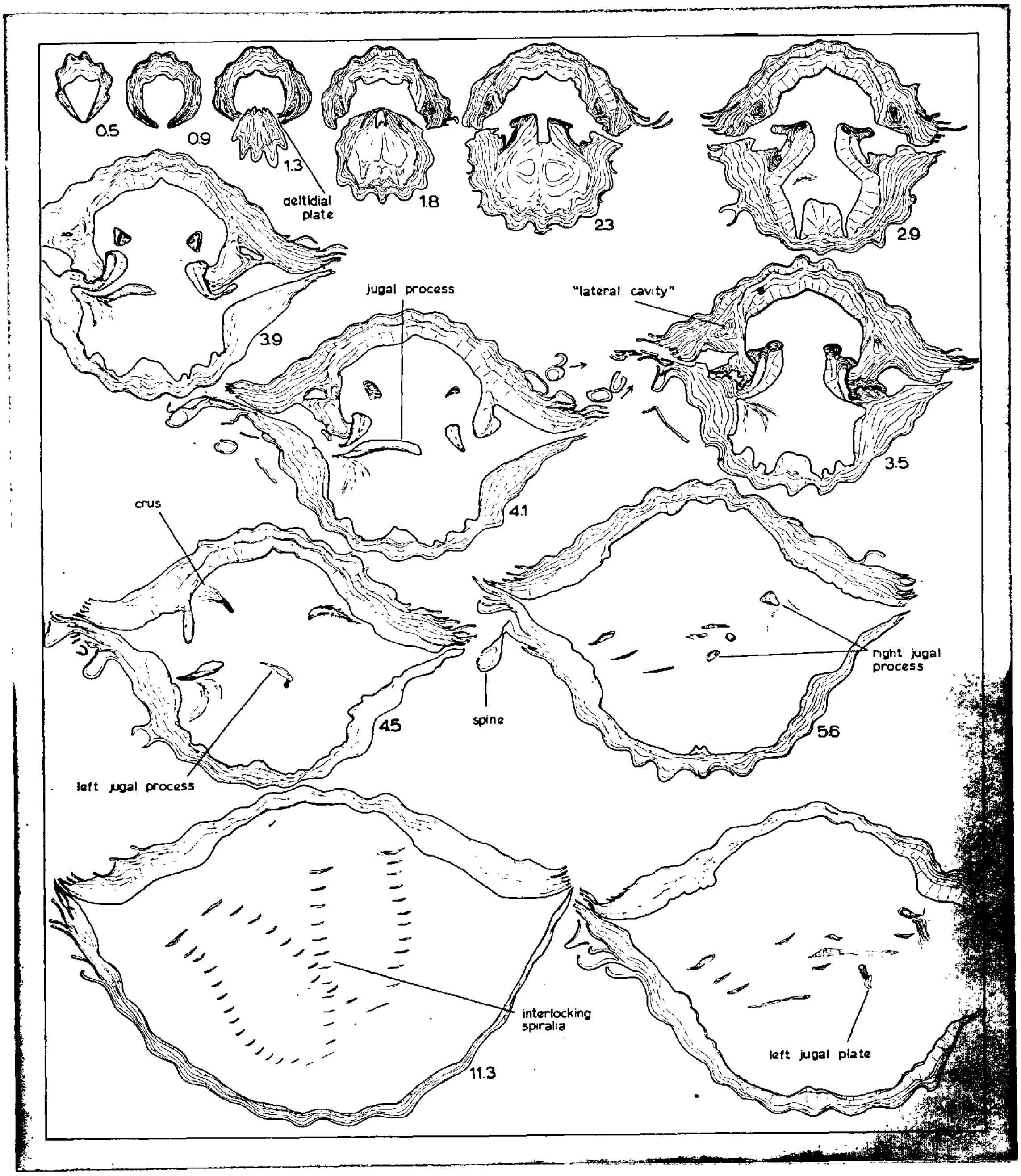
On the brachial valve, adductors are 3-4 mm wide, 6-7 mm long and divided into a deeper, coarsely striated anterior portion and weakly lined anterior portion. A thick median septum divides them. Ovarian markings are weak.

*Internal structure*.-
A pedicle collar is absent. Deltidial plates are small, retracted (less tman 1 mm wide) and do not touch (text-fig. 106). Lateral cavities are small and roundish apically, long and elongated distally. Teeth are long, the main lobes directed centrally, and the corrugated, long lateral lobes laterally. A small notothyrial pit contains a 6-8 stranded cardinal process, overlapping the hinge plates. Crura are separated from hinge plates, strongly feathered distally, Jugal process ends are not nodular; jugal plates long, straight.

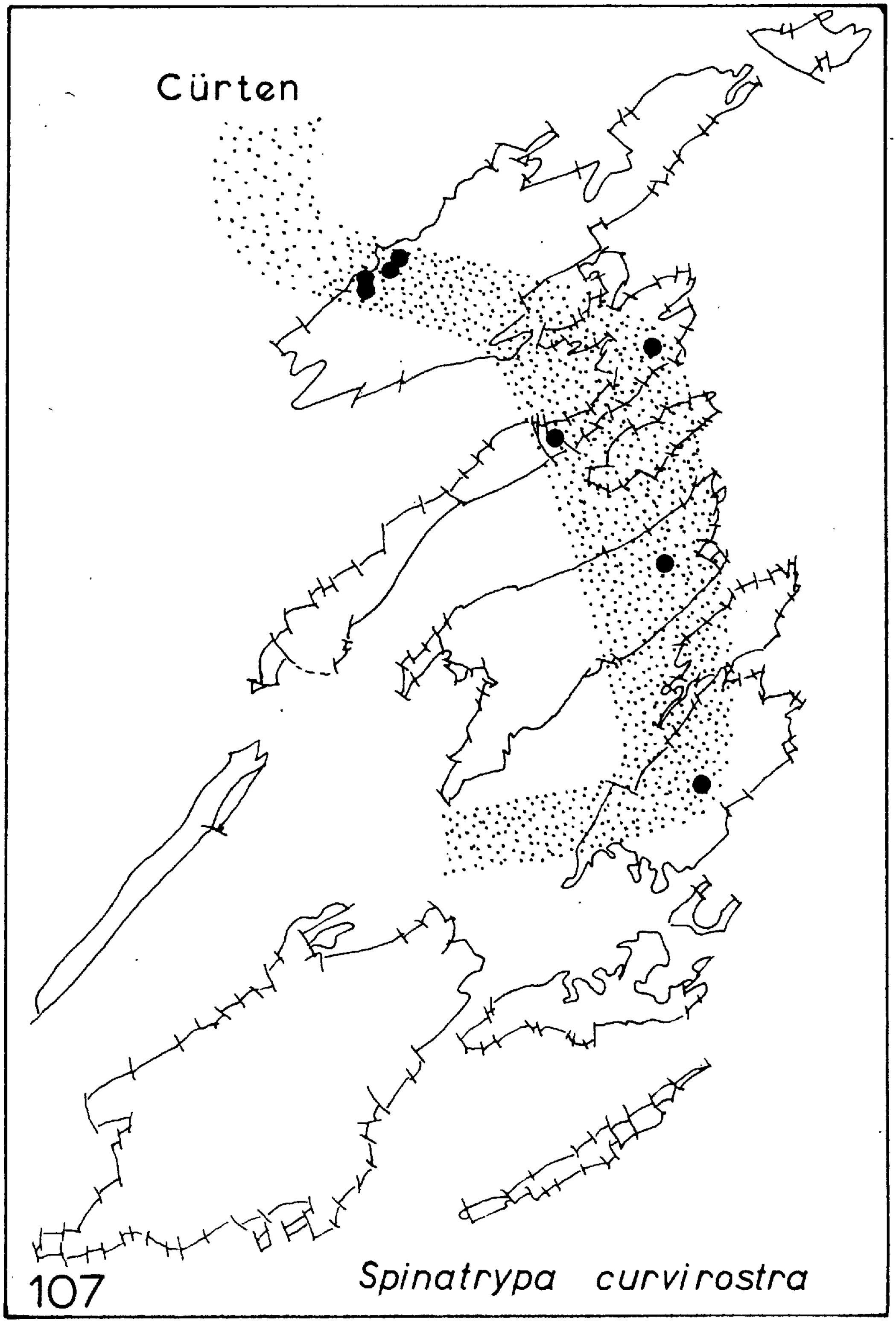
*Remarks*.-
This species has gone under the name "*Spinatrypa longispina* (QUENSTEDT)" in the recent Devonian literature of the Eifel region (e.g. PAULUS, 1961, p. 439; OCHS & WOLFART 1961; HOTZ & KRAUSEL & STRUVE 1955). But it has little to compare it with the Frasnian species, *Spinatrypa longispina* (BOUCHARD!), from the Boulonnais region in France. *S. curvirostra* n.sp. is much smaller, more globose and highly arched, more finely ribbed, more spinous and has an epicline instead of appressed beak. It was KLÄHN (1912, p. 31) who wished to designate QUENSTEDT as author of *S. longispina* although QUENSTEDT (1871, p. 215, Pl. 42, fig 104) never described the species and did not even figure a specimen (only a small portion showing spines).

*Spinatrypa mosolovica* (LJASHENKO, 1952), re-illustrated in LJASHENKO (1959, Pl. 4, figs. 1-7) is the most similar foreign species. The Eifel form only is somewhat more finely ribbed (with less prominent mid-ribs) and more spinous. It may come closer in its rib structure to specimens called *Spinatrypa* ex. gr. *bifidaeformis* (CHERNYSHEV) by LJASHENKO (1959, Pl. 6, figs. 8-11). The Eifel species seems to fall somewhere between these two in shell size, rib proportions and convexity.

*Spinatrypa coriacea* CRICKMAY 1960, from the Hume formation of northwest Canada, is larger, more flatly ribbed and with a less incurved beak. Other Canadian atrypids also differ : *S. hornensis* NORRIS 1964 is biconvex, more deeply and less undulose ribbed and lacks the epicline beak of the Eifel species.



Text-fig. 106. Transverse serial sections of *Spinatrypa curvirostra* n.sp. Cürten beds, lower Givetian; MTB Mechernich r40160:h98850. x3.



Distribution of *Spinatrypa* *curvirostra* . sp. [illegible] the Cürten.

Material.-

Total 775 specimens (text-fig. 107).

C222(53); C460a(147); C460b(390); C472(3); C473(160); R1937(50); Söt16(2); Söt25(9); Söt28(2); RW6(1); RW156(1); RW225(1); RW274(1); BP84(2); BP45(7); BP283(1); Söt7(3); St202(4); St403(1); BMB42(1); BMB44(2); BMB54(4); BMB55(2); BMB56(10 ); BMB59(38).

This is the first species from the Eifel syncline area to be abundantly represented in the Devonian east of the Rhine, Close correlations can be drawn.

## *Spinatrypa orthoclina* n.sp.

Pl. 25, figs. 1-3; Pl. 26, figs. 1-4; text-figs. 108-110.

Name: Latin adj., *ortho*, straight, normal; *clinatus*, *a*, *um*, inclined, leaning, bent. The beak is at a straight clination relative to the commissure.

Type locality: Road cut Urfey-Keldenich, Sötenich syncline, MTB Mechernich r44000:h00370.

Type stratum: Probably the *quadrigemina*-*ramosa* horizon of the Rodert beds, middle Givetian. Possibly as low as the Binz horizon, Dreimühlen beds (?).

Range: Middle Givetian, Dreimühlen-Rodert beds.

Associated fauna: Colonies of *Hexagonaria*-like corals, numerous trilobites (?*Dechenella*), *Spinocyrtia* sp. *Thamnopora* rare. Horn corals absent.

Sediment: Greenish gray calcareous shales, weathering soft.

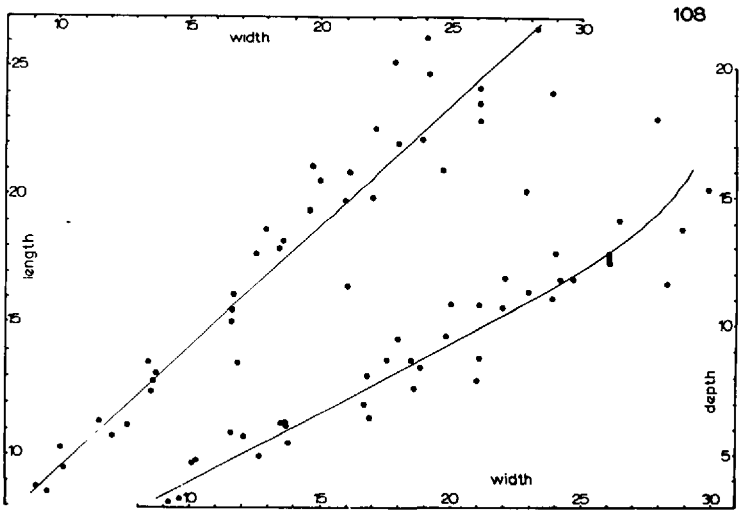
Diagnosis.-

Medium to rather large sized, coarsely ribbed *Spinatrypa* with long projecting, orthocline beak and low anterior fold. Shell relatively flat and round-outlined, biconvex-dorsibiconvex. Ribs well defined, although rare specimens show shallowing and coarsening. Internally, large lateral cavities, large socket cavities and feathery crura are typical.

### Description

External form.-

Average specimen width is from 23 to 25 mm , rarely up to 35 mm (text-fig. 108). Both valves are rather weakly convex, near-planar. Width exceeds length; the width/depth ratio is 2.1:1. On the pedicle valve, elevated mid-ribs are lacking although the mid-rib pair may be wider. Side fields are somewhat flat or gently convex. Hinge corners are round, poorly defined. The orthocline, pointed beak projects nearly 2 mm and exposes a narrow and triangular area. Deltidial plates are



Text-fig. 108. Scatter diagrams of the main dimensions of Spinatrypa orthoclina n.sp. Localities C453, C454, BP143, BP48 combined.

small, about 1.5 mm wide and as long. The foramen commonly expands through the apex, is 1 mm in diameter or a bit wider and in many specimens surrounded anteriorly by a small rim. The apical angle ranges through 130-135 degrees; shoulder lines indented. The dorsal apex is incurved and the first 1-2 mm covered by deltidial plates. The brachial valve is more convex but not globose. Mid-fields are flat and side fields gently sloping.

Ribs.-

Wave length of the ribs is moderate : at 10 mm from the apex 5-6 ribs per 10 mm and at 15 mm from the apex 4-5 ribs are most common. Apical ribs are rather sharp, with steeper and more sharply defined crests and troughs. Distal ribs tend to broaden out more in S. curvirostra n.sp. Large varieties may have a distal crowding of only 3 ribs per 10 mm , probably due to failure in rib increase. Growth interruptions are marked, with ribs tending to expand at the base of each lamella and beginning anew with smaller crests anterior to each lamellar base. At the ventral apex a single mid-rib (bifurcating after about 1 mm ) is flanked by 3 side ribs. Rarely 4 side ribs flank the main rib. On the brachial valve the weak apical trough is sided by 3 ribs.

Growth lamellae.-

The lamellae in the apical 5-8 mm are faint. Distal lamellae are even, spaced at 2.5 to 3.0 mm and strongly upturned. There is little distal crowding. Spines are rarely preserved. On the pedicle valve spines are scarcer than on the brachial valve and probably absent for much of the mid and side fields. Along the fold, spines are subhorizontal and along the sides deflected at 30 to 40 degrees. Spines appear to be much better developed on the brachial valve, covering a greater area amd more strongly turned away from the shell surface. Along the fold, spines again nearly horizontal. The longest spines observed were 6.5 mm and obviously broken. They were commonly bent or twisted but only gently.

Growth and variation.-

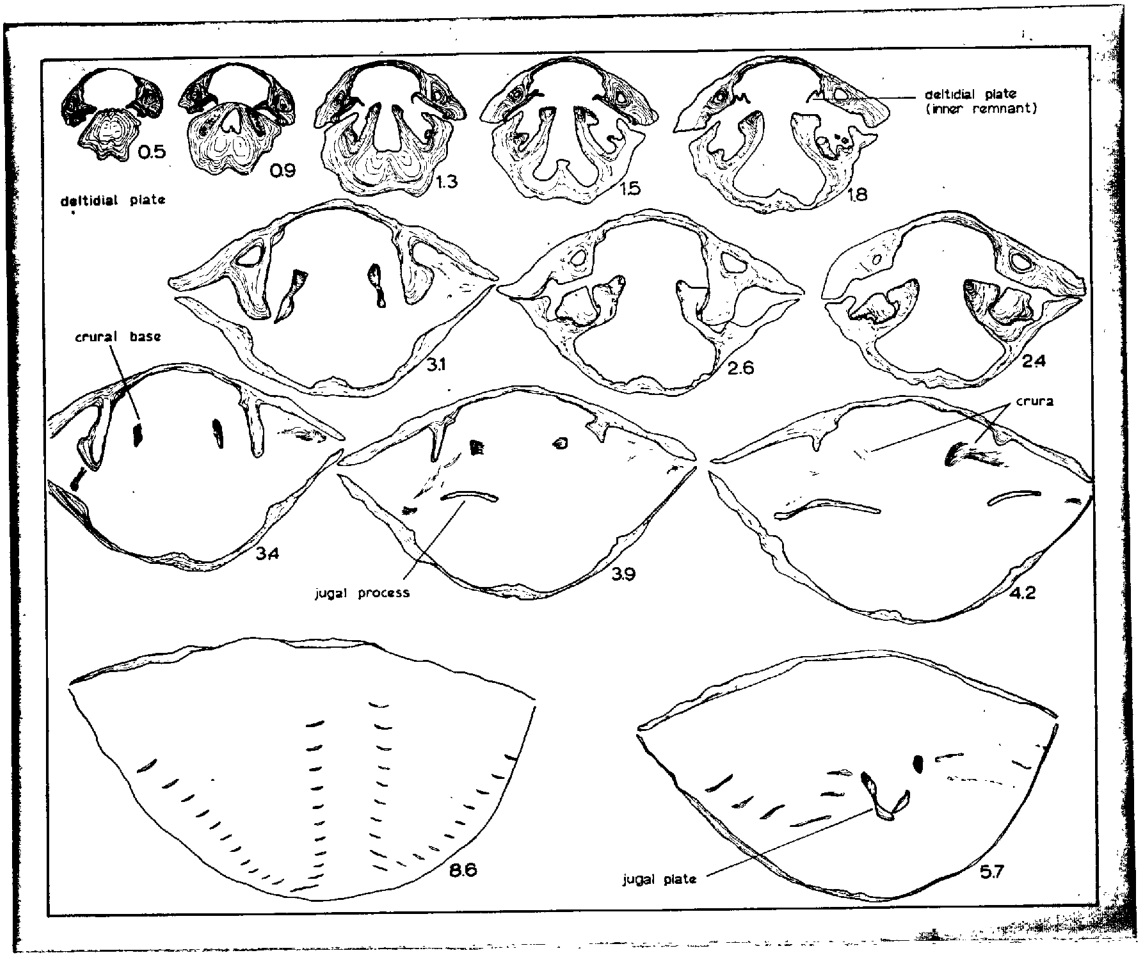
Neanic specimens have a relatively large and expansive area and a beak from weakly apsacline to orthocline. They are wider than long, weakly convex, flat, the pedicle valve slightly more convex. Spines are strongly deflected. Hinge corners are sharper, and hinge margins straighter than in older specimens. Mature and senile specimens become dorsibiconvex : ribbing may become very coarse, and flattened, occasionally reminding of Spinatrypa paffrathi (WEHRLI 1931). Beaks are commonly perforated. A flat fold develops and a rather sharply defined tongue is extended anteriorly (see Pl. 26, figs. 2a-b).

Internal markings.-

A pedicle collar was absent. Deltidial plates hollow, with the distal inner and outer portions widely apart (text-fig. 109). Inner margins crenulated. Lateral cavities are large and oval. Teeth are long, with short, thick lateral, lobes. The notothyrial pit broadens out gradually into the notothyrial cavity. Apically a small amorphous cardinal process is observed. Hinge plates are long, sub-vertical and evenly thickened from base to tip. Socket plates are thick, crural bases elevated. Crura are elaborately feathered. Jugal processes thin, weakly convex. Jugal plates are long, thick and slightly inwardly directed. Spiralia are less conical than in other species, possess 10-12 whorls.

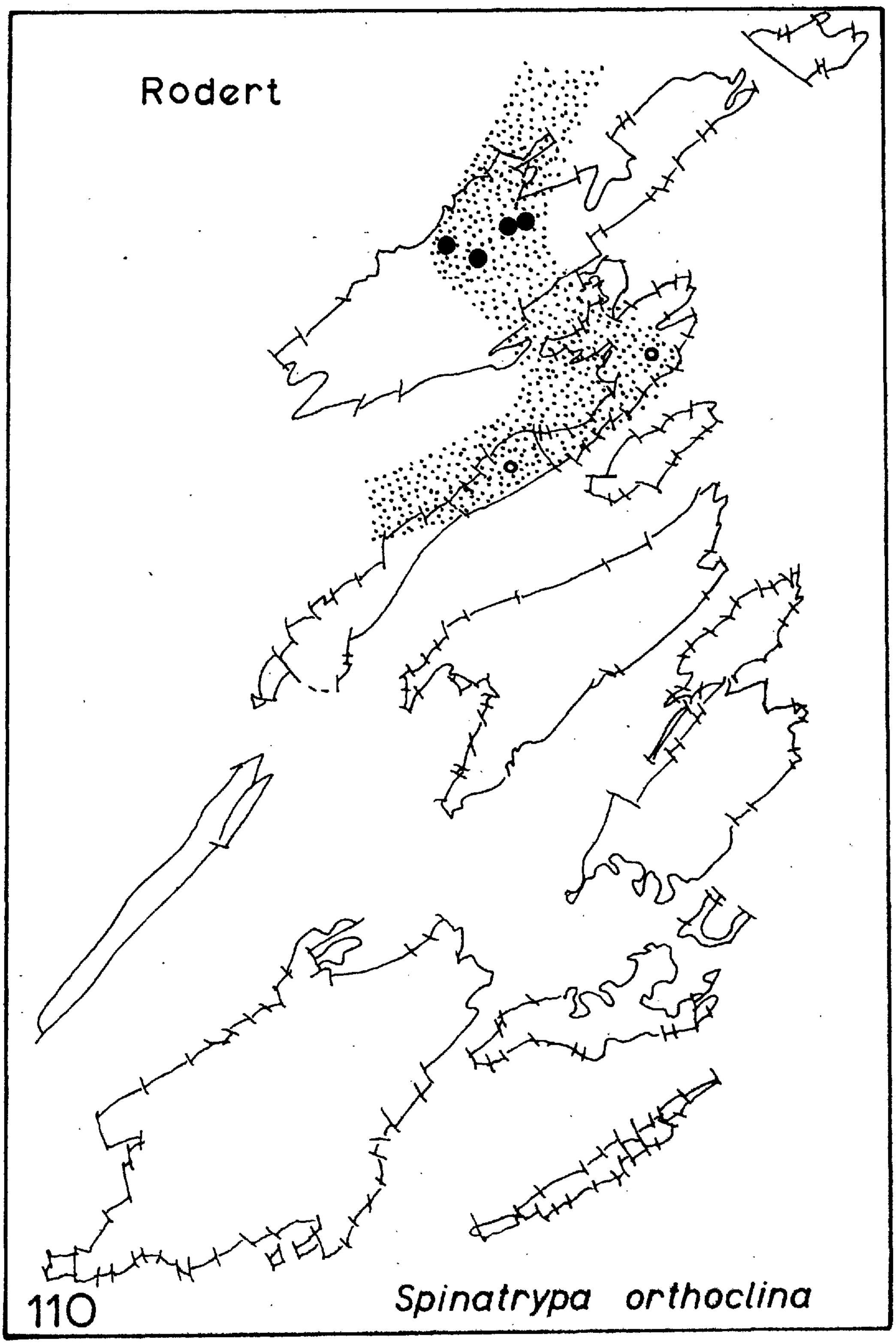
Remarks.-

Spinatrypa orthoclina n.sp. appears, surficially examined, to be identical with S. curvirostra n.sp. which is older. A detailed look reveals many differences : S. orthoclina is more planar, more sharply crested and troughed in its rib structure, lacks a prominent anterior fold, and has a pointed, projecting orthocline beak. Internally the differences are as great : S. orthoclina has large lateral cavities, long slender teeth and stumpy lateral lobes, lacks a confined notothyrial cavity and shows greater feathery structure of its crura.



Text-fig. 109. Transverse serial sections of *Spinatrypa orthoclina* n.sp. Rodert beds, middle Givetian; MTB Mechernich r44000: h00370. x3.

WEHRLI (1931) described an "*Atrypa aspera* var. *paffrathi*" from the Paffrath syncline near Köln from specimens collected by the Rev. WENDLAND. This variety bears some resemblance to *S. orthoclina* n.sp. although it is too poorly described and figured to be compared with any reliability. An attempt was made to collect topotypic material of WEHRLI's species, but this failed. Dr. JUX (University of Köln), at the request of the author, also made a fruitless attempt to find specimens at the locality mentioned by WEHRLI, and came to the conclusion (pers. commun.) that an error had been made in the source of the specimens and that these probably came from the well known locality at Hand where *Spinatrypa orthoclina* has been found very commonly. However, this seems unlikely, for several reasons. WEHRLI (1931, p. 429) mentioned that the specimens were embedded in a fine grained dolomite, whereas *S. orthoclina* at Hand is found in dark gray calcareous shales and limestones. The locality probably was correctly stated although both WEHRLI and the



Distribution of Spinatrypa orthoclina n.sp. in the Eifel

Rev. WENDLAND who collected the material, failed subsequently to find more material at the same locality. *S. orthoclina* appears to be more finely ribbed and lacks the appressed rim and broad fold of WEHRLI's form. Some of the topotypic specimens of *Spinatrypa squamosa* (SOWERBY 1840) were very similar to the variety *paffrathi* of WEHRLI in extremely coarse growth lamellae and disappearance of ribs structure.

The age of the *quadrigemina* horizon in the Paffrath syncline has previously been correlated by HOTZ & KRAUSEL & STRUVE (1955, Pl. 141) and JUX (1964, p. 164) to be similar to the Rodert beds of the Eifel synclines. This correlation is confirmed. The Urfey horizon of PAULUS (1959, p. 359), the type stratum of *S. orthoclina* n.sp., was dated as Kerpen age (i.e. upper Givetian as in COPPER 1965a), but this should be changed to Rodert age. In the Eifel synclines, *S. orthoclina* is confined to the northern Sötenich syncline. Similar material has been found elsewhere.

Material.-

The species is more widespread east of the Rhine than *S. curvirostra* n.sp. but less abundant (text-fig. 110). Total specimens 253.

C228(38); C435(6); C453(10); C454(43) locus typicus; BP29(4); BP48(4); BP143(2); RW33(2); RW46(2); RW265(1); St590(2); BMB43(29); BMB45(2); BMB46(5); BMB47(19); BMB48(5); BMB49(13); BMB50(3); BMB51(6); BMB52(6); BMB53(7); BMB57(5); BMB58(4); BMB60(2); BMB61(1); BMB62(3); BMB64(1); BMB65(10); BMB66(7); BMB67(12).

Probably the best known locality is the Torringer beds exposure near Hand, Paffrath syncline (C228).

### *Spinatrypa* cf. *trigonella* (DAVIDSON 1884)

Pl. 29, figs. 2-4.

1884 *Atrypa? trigonella* DAVIDSON, p. 40, Pl. 1, figs. 19,19a-b.
1893 *Atrypa trigonella* DAVIDSON, WHIDBORNE, p. 118, Pl. 13, figs. 11-12.

Remarks.-

In the WHIDBORNE collection (Sedgwick Museum, Cambridge) there are a number of small *Spinatrypa trigonella*. DAVIDSON (1884. p. 40) recalled that WHIDBORNE had collected the specimens on which he based his description. Their description was later revised by WHIDBORNE himself in 1893, and the specimens re-illustrated. DAVIDSON's illustrations were poor and from them the specimens could not even be identified definitely as atrypids. In a collection presented to the British Museum by G.F. ELLIOTT (as material for a paper by ELLIOTT 1961) several specimens were found which were identical to WHIDBORNE's *Spinatrypa* trigonella material. ELLIOTT's collection came from the well known Lummaton shell bed (upper Givetian) and this bed also seems to have furnished the atrypid specimens which WHIDBORNE found.

The small quarries which have supplied the classical Uncites gryphus specimens also contain small spinatrypids which are similar in size to Spinatrypa trigonella (DAVIDSON). But these specimens, from Büchel near Herrenstrunden (Paffrath syncline near Köln), are about equally wide as long, more convex and more strongly ribbed than the specimens from Devon, England.

A detailed description must be left until more material is examined.

Material.-

About 100 specimens.

BMB71(78); C528(more than 20).

## Spinatrypa cf. legayi (RIGAUX 1908)

Pl. 27, figs. 1-5; text-figs. 111-119.

1908 Atrypa legayi RIGAUX, p. 22, Pl. 2, fig. 10.

Type locality: RIGAUX (ibid.) stated that the material"Se trouve a Couderousse", in the Boulonnais, France.

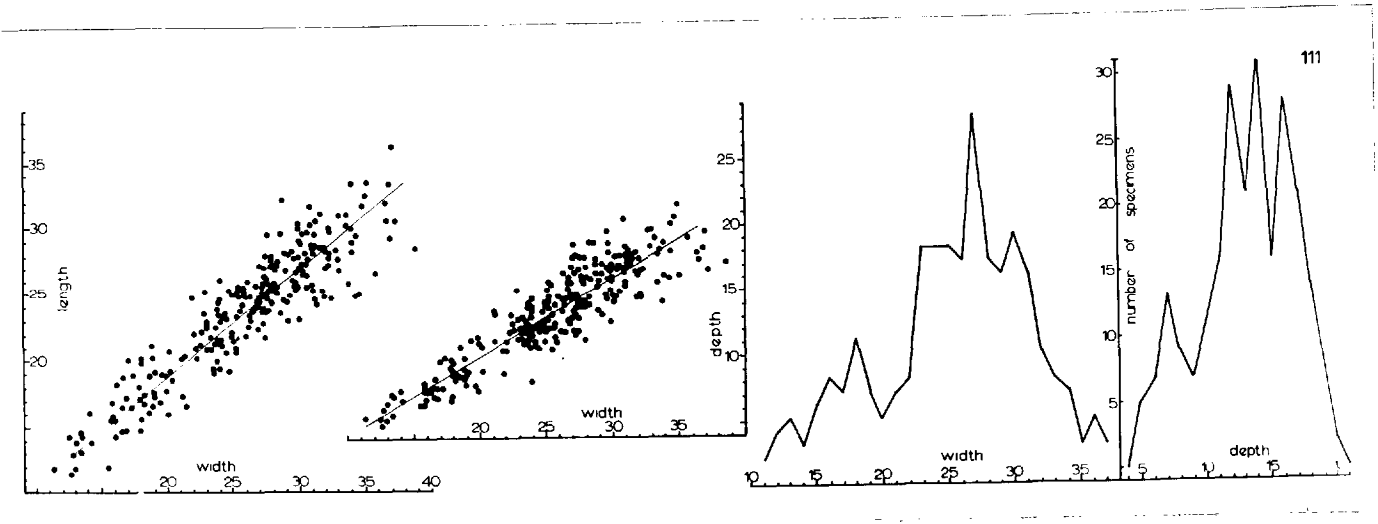
Type stratum: RIGAUX (ibid.) specified that the horizons of Sp. (Spirifer) belliloci and Pent. (Pentamerus) brevirostris contained the species.

Range: Frasnian (F2-F3), probably in upper parts of the F2 levels or at F3.

NOTE: The atrypid fauna of the Boulonnais area in France is in need of thorough revision. It is hoped to carry our this revision in the near future. The following description is based on specimens from the Frasnian rocks southeast of Aachen and may not apply to topotypic Boulonnais specimens, though these also were examined, albeit cursorily.

Diagnosis (Aachen material).-

Large, moderately coarse ribbed (5 ribs to 10 mm ), dorsibiconvex shells marked by an epicline beak and broad anterior fold. Spines are short. Ribs do not show flattening. Internally, round lateral cavities, thin small crura, and spiralia with up to 16 whorls, are typical.



Text-fig. 111. Scatter diagrams and frequency curves of Spinatrypa cf. legayi (RIGAUX). Frasnian; locality BMB2, Breinigerberg.

## Description

### External form.-

Most shells fall within a width range of 23 to 30 mm , and average at 27 mm (text-fig. 111). Maximum width occurs posteriorly, close to the hinge line. Width length ratios stand at 1.2:1 in maturity, width/ depth ratios at 1.86:1. Therefore width normally exceeds length. Outlines are shield-shaped to near-circular. Blunted hinge corners define weakly indented shoulder lines. The anterior fold is rather narrowly arched and may be sharply U-shaped in some specimens. The brachial valve is slightly deeper.

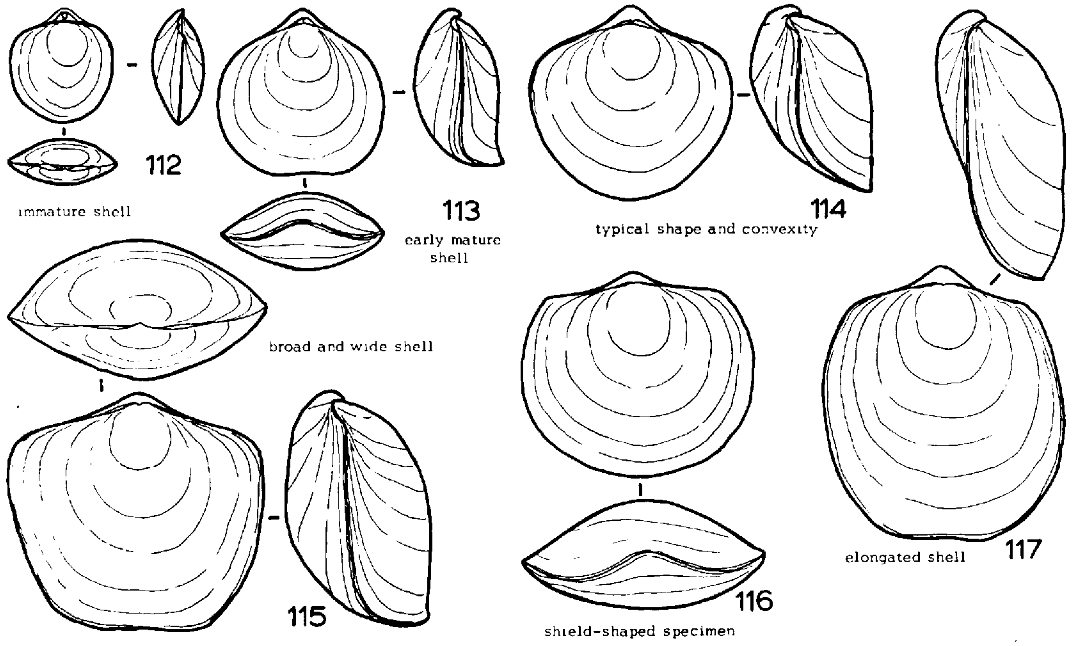
An epicline beak is inflated and swollen, projecting posterior to the hinge axis. The aeral edge is sharp, but areas themselves are obscured by the incurved beak. Apical angles are 125-130 degrees but up to 150 degrees in specimens with extended hinge lines. The ventral valve is roundly but quite deeply convex and apically expanded. The brachial apex is covered, and the valve rounded, broadly and shallowly convex, rarely highly arched. Hinge corners may be curled.

### Ribs.-

Ribs are disturbed by strong concentric raising and deepening of lamellar bases. In the centre of each row of ribs there is a trough-like depression. Wave length is fairly consistent at 2 mm (5 per 10 mm ) even on the margins. Maximum ribs observed were 7 per 10 mm. Apical ribs are finer, with the first bifurcations at 8-10 mm from the beak. Bifurcation and intercalation are difficult to follow because of growth interruption, but usually appear to occur directly after growth of a spine. Average specimens have a maximum of 26-29 ribs. On the pedicle valve three side ribs flank an apical mid-rib. Two or three side ribs flank the central rib of the dorsal apex.

Growth lamellae.-

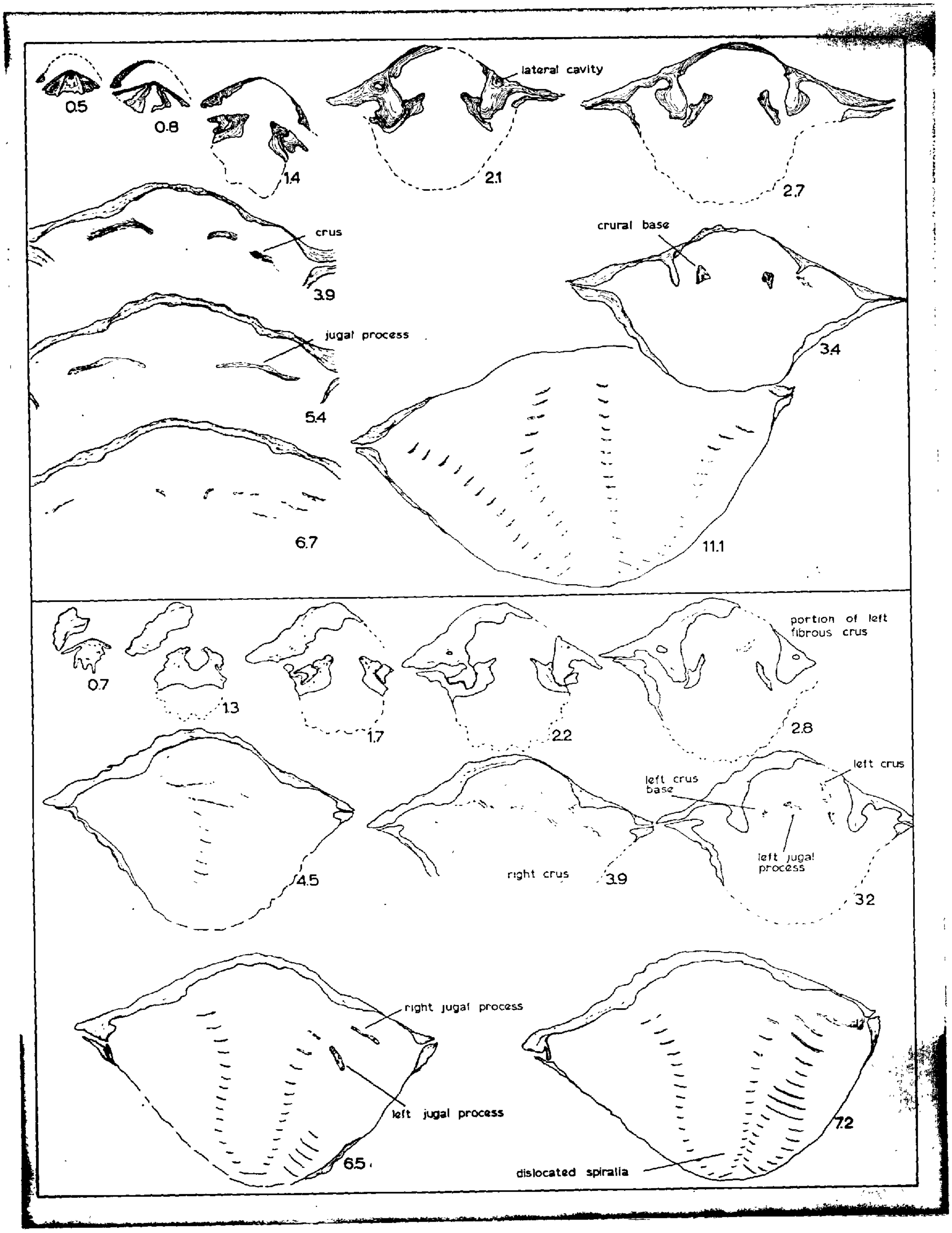
Growth lamellae are regularly spaced at about 3 mm., rarely more. Distal crowding is rare. Growth lines are limited to 4 or 5 per millimeter and appear to alternate on the rib crests and rib troughs. Spines are short and appear to be best developed postero-marginally, where they are sharply deflected (30-45 degrees) and also bent. The full length of spines is not known but from the portions preserved they appear to be not more than 10 mm long.



Text-figs. 112-117. Shell variation of Spinatrypa cf. legayi (RIGAUX). Locality BMB2. x1.

Growth and variation.-

There is a complete gradation between specimens which have obtuse hinge angles and well marked hinge corners and those which are more circular in outline (text-figs. 112-117). Young specimens are oval or nearly circular in outline. Hinge corners are not marked. Beaks are orthocline, foramina 1-2 mm in diameter (relatively large). Commissures rectimarginate. The pedicle valve equally or slightly more convex than the brachial valve.



Text-figs. 118-119. Transverse serial sections of *Spinatrypa* cf. *legayi* (RIGAUX). Frasnian (F2-F3); Breinigerberg, BMB2, x2.

Internal structure.-

No pedicle collars or deltidial plates were observed in sections of mature specimens (text-figs. 118-119). A small, round lateral cavity is located at the base of short, stubby teeth. Teeth axes are nearly vertical, at 10-20 degrees from the plane of symmetry. Hinge plates are thin, long. A cardinal process of 4-5 strands sits in the notothyrial pit. Crural bases long, elongated; crura given off at a wide distance from the hinge plates. Crural fibres are strongly feathered and curled (into complete circles in some specimens). Thin jugal processes terminate in large, nearly straight jugal plates. The greatest number of whorls in a spiralium was 16.

Remarks.-

KLÄHN (1912, p. 30-31) described these specimens from the Aachen area as Spinatrypa longispina (QUENSTEDT). Topotypic material of S. longispina from France was collected and found to be very different : specimens were much larger, more coarsely ribbed, flatter and rounder and also lacked the highly incurved beak of the Aachen atrypids. However, RIGAUX also described a species, Spinatrypa legayi (RIGAUX 1908) from the Boulonnais Devonian, which although similar in rib and incurvature of the beak, is somewhat more biconvex with deep brachial valves. RIGAUX's species must be revised before identification is positive. What is thought to be topotypic material of S. legayi was collected near Ferques in the Boulonnais at a point stratigraphically below S. longispina (BOUCHARD). S. legayi is not difficult to distinguish from S. longispina because it is smaller, has a more planate pedicle valve, and is in outline more subquadrate rather than circular.

Material.-

All 262 specimens came from a collection labelled "Breinigerberg", Aachen, MTB Stolberg (Coll. BMB2).

## Spinatrypa longispina (BOUCHARD in RIGAUX 1873)

Pl. 28, figs, 2a-d.

1873 Spirigerina longispina BOUCHARD, RIGAUX, pp. 47-48, figs. 1a-b.

Type locality: RIGAUX lists only one locality, Blacourt (RIGAUX, 1873, p. 48).

Type stratum: RIGAUX (ibid.) "Se trouve dans un tuf sableux qui forme la partie supérieure du Calcaire de Ferques". This locality and stratum were visited. Specimens were not uncommon, although not abundant.

Remarks.-

A detailed description is left until more type material can be examined. Figures of a typical large specimen of the species from the Boulonnais are given (Pl. 28, figs. 2a-d), so that they can be compared with specimens previously under that name from the Aachen area in Germany.

## Genus *Spinatrypina* RZHONSNITSKAYA 1964

Type species: *Spinatrypina margaritoides* RZHONSNITSKAYA 1964, pp. 101-103, Pl. 1, figs. 1-8.
Range: Lower Devoinan to Upper Devonian (Gedinnian-Frasnian).
Distribution: World-wide.

Diagnosis.-

Small to medium sized, biconvex-dorsibiconvex atrypids with near-orthocline beaks, small areas with disjunct deltidial plates in a small delthyrium. Ribs are tubular-imbricate, deep-troughed and embryonically spinescent. Frills are lacking. Internally, pedicle layers are thin. Teeth have small lateral cavities. Jugal processes disjunct, tipped by short, stumpy jugal plates.

Remarks.-

The relationship of *Spinatrypina* to *Spinatrypa* can be compared to that of *Desquamatia* with respect to *Atrypa*. The two genera *Desquamatia* and Spinatrypina show parallel development of deeper, more tubular ribs and expansion of a well-defined interarea and deltidial plates. Internally both show an enlargement of dental nuclei into lateral cavities.

*Spinatrypina* has deep-troughed , as compared to *Spinatrypa*'s undulose ribs and its ribs never reach the wave length of the latter. Spines also are rarely developed whereas on *Spinatrypa* spines are prominent surface features.

The two genera occupy different biotopes. *Spinatrypina* is abundant only in a coral biotope, *Spinatrypa* in a calcareous shale, non-coral enviroment. Rare occurrences of *Spinatrypa* in a coral enviroment are recorded (but not vice versa), and in such instances *Spinatrypa* "takes on" the surface morphology of *Spinatrypina*. A good example is *Spinatrypa aspera meridiana* n.sp. which shows expansion of area and deepening of ribs but can still be differentiated by the coarseness of its ribs, much fewer growth lamellae, and, internally its lack of lateral cavities.

The genus reached its acme in the Eifel region and east of the Rhine, during the Givetian, although its abundance is carried through the Frasnian. In Germany, Spinatrypina becomes scarce or nearly absent after F2c times and has not been found in late F2 or F3 sediments.

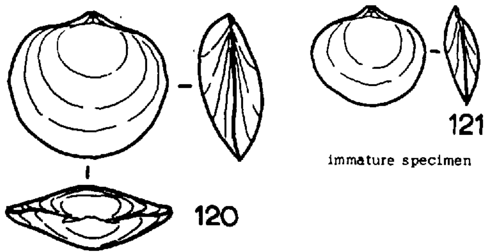
### Spinatrypina demissa n.sp.

Pl. 30, figs. 1-4; text-figs. 120-123.

Name: Latin, demissus, a, um, low-lying, low-down. This species is the oldest member of the genus in the Eifel synclines.
Type locality: Quarry along the east side of Urft creek, south of Nettersheim, Sötenich syncline, MTB Blankenheim r44690:h94770. See PAULUS (1959, Pl. 1, fig. 2) for a photograph of this locality.
Type stratum: Upper 4 m. of the Urft horizon rich in thamnoporid corals, Nohn beds, lower Eifelian. Described in PAULUS (1959, p. 354).
Associated fauna: See PAULUS (ibid.). The new species is probably referred to as Atrypa reticularis by PAULUS. The type locality is also marked by the presence of Gruenewaldtia prooemia n.sp. and abundant thamnoporid corals.
Source sediment: Brownish green, chippy, bioclastic calcareous shales rich in broken crinoid and coral debris.

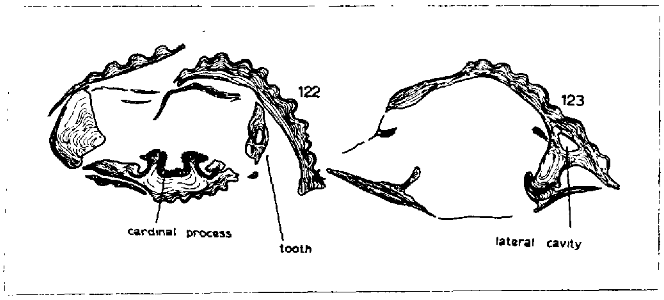
Diagnosis.-

Small (rarely medium sized), flat, biconvex shells with fine ribs (16-18 ribs per 10 mm ), interrupted by 2 mm or less-spaced growth lamellae. Margins are pressed together. A weak fold flexes the commisure (text-figs.120-121). The beak is small, pointed or angular, and heads a narrow, triangular area. Shoulders are round-edged, shoulder lines indented. Hinge corners are rounded. The pedicle valve is slightly more convex than the rather planar brachial valve.



Text-figs. 120-121. Shell variation of Spinatrypina demissa n.sp. Random localities, Schleit horizon. x1.

Internally (text-figs. 122-123), thin teeth are built about large lateral cavities. The cardinal process is thick and bushy. The columnar shell layer is thin.



Text-figs. 122-123. Transverse sections of two specimens of Spinatrypina demissa n.sp. Schleit horizon, Nohn beds; MTB Blankenheim r44690:h94770.

Remarks.-

This species is not abundant in the Eifel synclines and is only sporadically a rich constituent (as at the type locality). This is probably because of the general absence of thamnoporid thicket reefs at this time. It can be distinguished from younger species of the Eifel by its fine ribs, rather planar shell and pointed, protruding beak.

BIERNAT described a somewhat comparable species Desquamatia varistriata (BIERNAT, 1964, p. 317, figs. 1-6) a type of rib structure is shown which is certainly not typical of the genus Desquamatia. It is difficult to determine the affinities of the Polish atrypid in relation to Spinatrypina demissa n.sp. There are older Devonian species of Desquamatia which do not show the trigeneric convergence (Atrypa, Desquamatia and Spinatrypa) claimed by BIERNAT (1964, p. 318). An example is Desquamatia ovata COPPER 1965.

In its rib structure Spinatrypina demissa n.sp. is also reminescent of the genus Kerpina but internally it shows none of the morphological peculiarities of deltidial plates, collars and solid teeth of that genus. No spines were observed on any specimens, although they are just as rare on all species of Spinatrypina.

Material.-

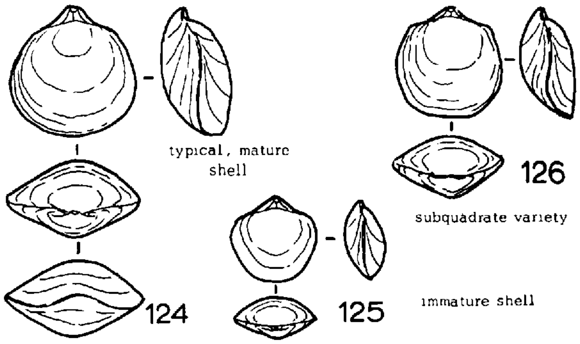
Total 162 specimens

C284c(1); C398)1 ); C451(51) locus typicus; C452(17); H1(5); H33(1); H78(1); H99(8); H107(4); H255(2); BP80(1); BP183(9); St13(3); St19(18); St302(1); St304(7); St428(2); St633(1); St711(9); St712(2); St713(1); St714(1); St715(5); Fp1262(4); Fp1264(4); RW128(1).

## Spinatrypina fabaca n.sp.

Pl. 30, figs. 5-6; Pl. 31, figs. 1-2; text-figs. 124-127.

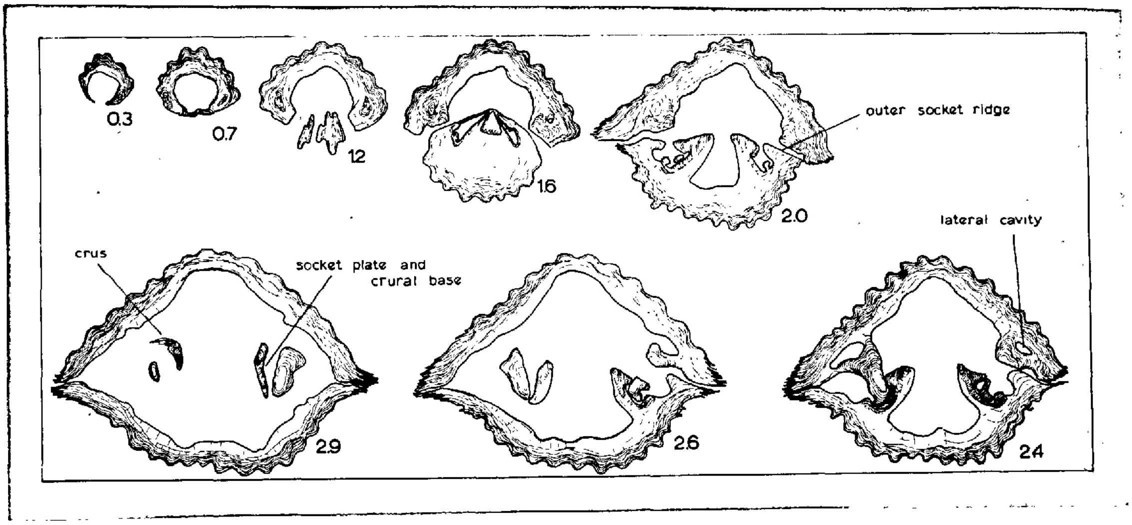
Name: Latin, faba, ae, bean; acus, a, um, pertaining to. These small atrypids look like large beans.
Type locality: Exposure on the north flank of Leukersberg on the outskirts of Rohr, Rohr syncline, MTB Aremberg r52360:h91090.
Stratum typicum: Rechert horizon (directly above the Rohr Hexagonaria horizon in Rohr), Junkerberg beds, middle Eifelian.
Range: Upper parts of the Junkerberg beds (Hönselberg-Nims) and possibly scattered in low parts of the Freilingen beds, Eifelian.
Associated fauna: At the type locality found in crevices in the coral colonies and with many thamnoporoids. Locally other brachiopods are scarce.
Source sediment: Light brown or yellowish calcareous shales rich in corals corals.



Text-figs. 124-126. Shell variation of Spinatrypina fabaca n.sp. at the type locality. x1.

Diagnosis.-

Small (less than 20 mm. wide), biconvex spinatrypinids which favour globosity but have only a weak anterior fold (text-figs. 124-126). Beaks pointed, jutting out about 2 mm , orthocline. Foramen commonly expanded, with small anterior rim. Interareal edges rounded. Shell outline round-elongated. Pedicle valve swollen, often somewhat more convex than a rather flattened brachial valve. Ribs spaced at about 10 per 10 mm , constant. Growth lamellae at 1 to 1.5 mm., crowded anteriorly. Internally (text-fig. 127), the lateral cavity is elongated parallel to the shell wall. Teeth long, sub-vertical flanked by a minor lateral lobe. Crura thick.



Text-fig. 127. Transverse serial sections of Spinatrypina fabaca n.sp. Rechert horizon, Junkerberg beds; MTB Aremberg r52360:h91090. x4.

Remarks.-

This dictinctive species can be distinguished by its shape and rib size from the more finely ribbed and planar Spinatrypina demissa n.sp. and the coarsely ribbed, larger and rounder S. wotanica (STRUVE).

The species which is most closely tied morphologically is Spinatrypina sinensis (KAYSER 1883) from Ta-kwan, China. KAYSER's collection of this species, which is stored in Berlin, was examined. The Chinese atrypid is somewhat larger, more distinctly ventribiconvex, almost planoconvex, which is rare in the Eifel atrypid. In size and shape they are similar but the Chinese form is narrower, more elongated and more pointed apically.

There are comparisons with Spinatrypina bodini (MANSUY 1912), but the latter, which comes from Indochina (North Vietnam), is still larger and more coarsely ribbed.

Material.-

Total 404 specimens

C293(22); C295(3); C300(1); C336(4); C340(173); C341(1); C351(1); C371(1); C394(29); C460(1); C463(3); C508(1); C511(1); C513(8); AG7(5); AG32(3); Ag33(4); AG43(8); AG45(1); AG52(4); AG82(1); AG82a(5); AG85a(4); AG170(5); AG177(2); AG239(7); AG239a(10); AG256(2); AG276(2); AG283(1); AG289(1): AG298(1); At21(1); St67(2); St68(3); St71(2); St79(12); St100(1); At110(1); St118(2); St119(2); St212(2); St362(1); St450(1); St525(1); St630(2); St633(12); St637(12); St63891); St736(26); St737(23); St738(9); St741(12); St742(15); St743(27); St745(1); St751(2); St821(3); St822(5); St824(4); St827(1).

## *Spinatrypina wotanica* (STRUVE 1964)

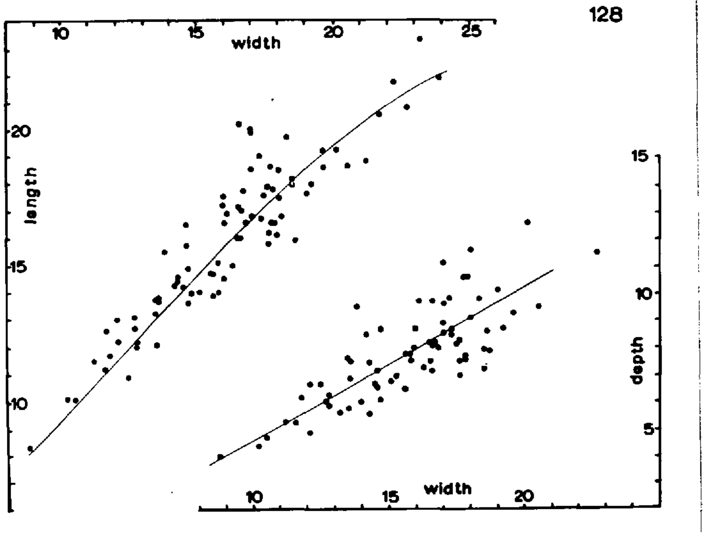
Pl. 31, figs. 3-6; text-fig. 128.

1964 *Spinatryra aspera wotanica* STRUVE, p. 529-530, figs. 2a-c.

*Diagnosis* (emended).-

A basic diagnosis is given in STRUVE (ibid.). The structure and form of the ribs differs sharply from *Spinatrypa aspera aspera* (SCHLOTHEIM), and is not similar as suggested by STRUVE. The confusion stems from the presence of *Spinatrypa aspera meridiana* which shows special adaptions (see *Ecology*) to the Freilingen environment and which cause a resemblance to species of the genus *Spinatrypina*. *Spinatrypina wotanica* has deep-troughed, imbricate-tubular ribs as distinct from shallow, undulating *Spinatrypa*-like ribs. There are more frequent growth lamellae and the growth lamellae are turned up where they leave the shell. There is a lack of spines.

A summary of dimensions is given in text-fig. 128.



Text-fig. 128, Scatter diagrams of main shell dimensions in *Spinatrypina wotanica* (STRUVE). Locality St739.

*Remarks*.-

STRUVE (1956, 1961, 1964) has placed great emphasis on the faunal change between the Eifelian and Givetian of the Eifel region, and attributed this faunal change to major phylogenetic trends and the appearance and disappearance of two critical atrypid fossil groups. This is evident in the establishment of the genus *Invertrypa* STRUVE 1961.

Here the genus *Invertrypa* is treated as modification of specific value. A complete gradation from *Spinatrypa aspera aspera* through to *Spinatrypa globulina* n.sp., through the medium of "*Invertrypa*" is almost certain. The major phylogenetic change which STRUVE believes occurs from the Ahbach to the Loogh beds can simply be explained as an ecological change, from a dark calcareous shale to a limestone coral rich environment. Therefore it was to be expected that in the lower Loogh beds *Spinatrypa* should be found which are completely gradational with *Invertrypa*. And indeed such a fauna was subsequently found near Blankenheim!

*Spinatrypina wotanica* (STRUVE), in summary, is not related to *Spinatrypa aspera* and even less to the genus *Spinatrypa*. This is confirmed not only by rib and interareal structure but also by internal morphology. One of the main internal distinctions is that *Spinatrypina wotanica* has lateral cavities, *Spinatrypa* of that age does not.

Material.-

A slab containing current-washed shells of this species is figured in Pl. B. The species is rare east of the Rhine where Loogh beds are not generally fossiliferous. Total 442 specimens.

C275(49); C279m(15); C279n(27); C279o(14); C281(76); St127(48); St128(7); St223(1); St227(2); St228(13); St235(11); St261(1); St563(1); St739 111); St804(6); St805(43); AG237(2); Os51(9); Os19(2); RW143(2); RW218(1); BMB85(2).

## *Spinatrypina soetenica* (STRUVE 1964)

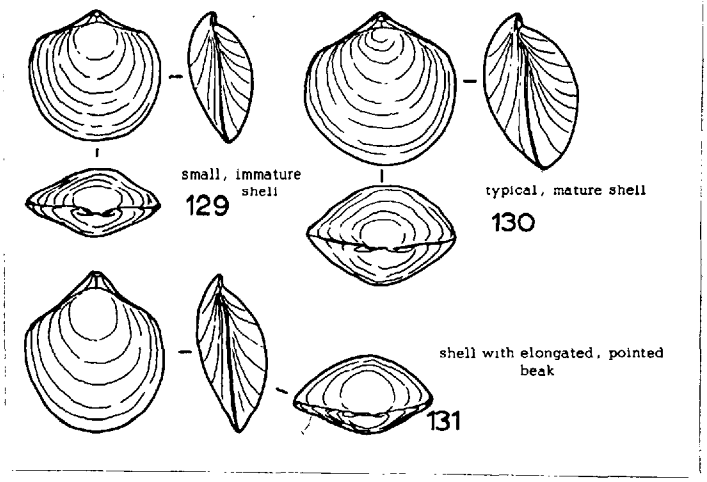
Pl. 32, figs. 1-2; Pl. 33, figs. 1-2; text-figs. 129-134.

1964 *Spinatrypa aspera soetenica* **STRUVE**, pp. 530-531, fig. 3.

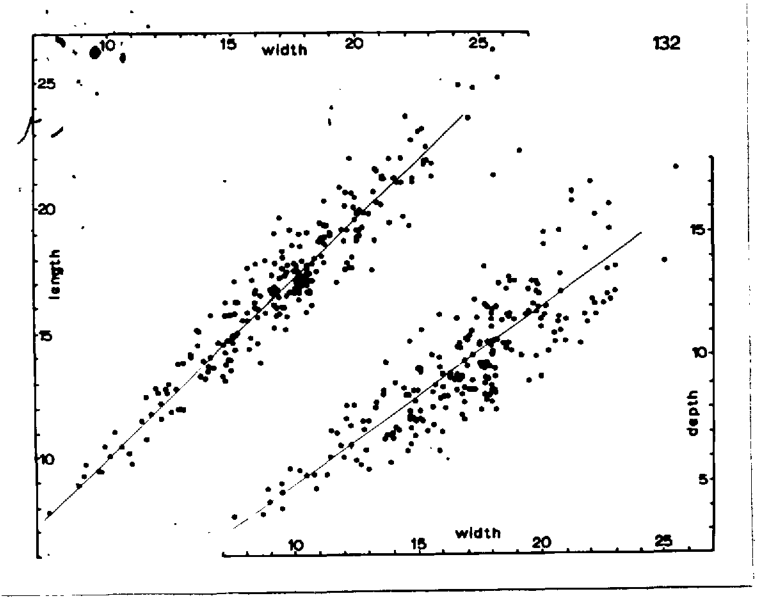
Remarks.-

As with *Spinatrypina wotanica*, this species has only a distant superficial resemblance to the group of *Spinatrypa aspera* (SCHLOTHEIM). The species can be crudely separated into two groups, perhaps deserving subspecific status, a more coarsely ribbed globose group and a finely ribbed flatter group, the latter of which conforms more closely to the holotype figured by STRUVE (1964, fig. 3). These two "variations" are illustrated in Pls. 32-33. The more coarsely ribbed form may be a remnant of the older species *wotanica*, or, alternatively, lead up to the younger but different *Spinatrypina girzenensis* n.sp. Shape variation is shown in text-figs. 129-131.

A diagnosis, type locality and stratum is given by STRUVE (1964). The range of the species is Cürten beds, lower Givetian. Scatter diagrams are shown in text-fig. 132.

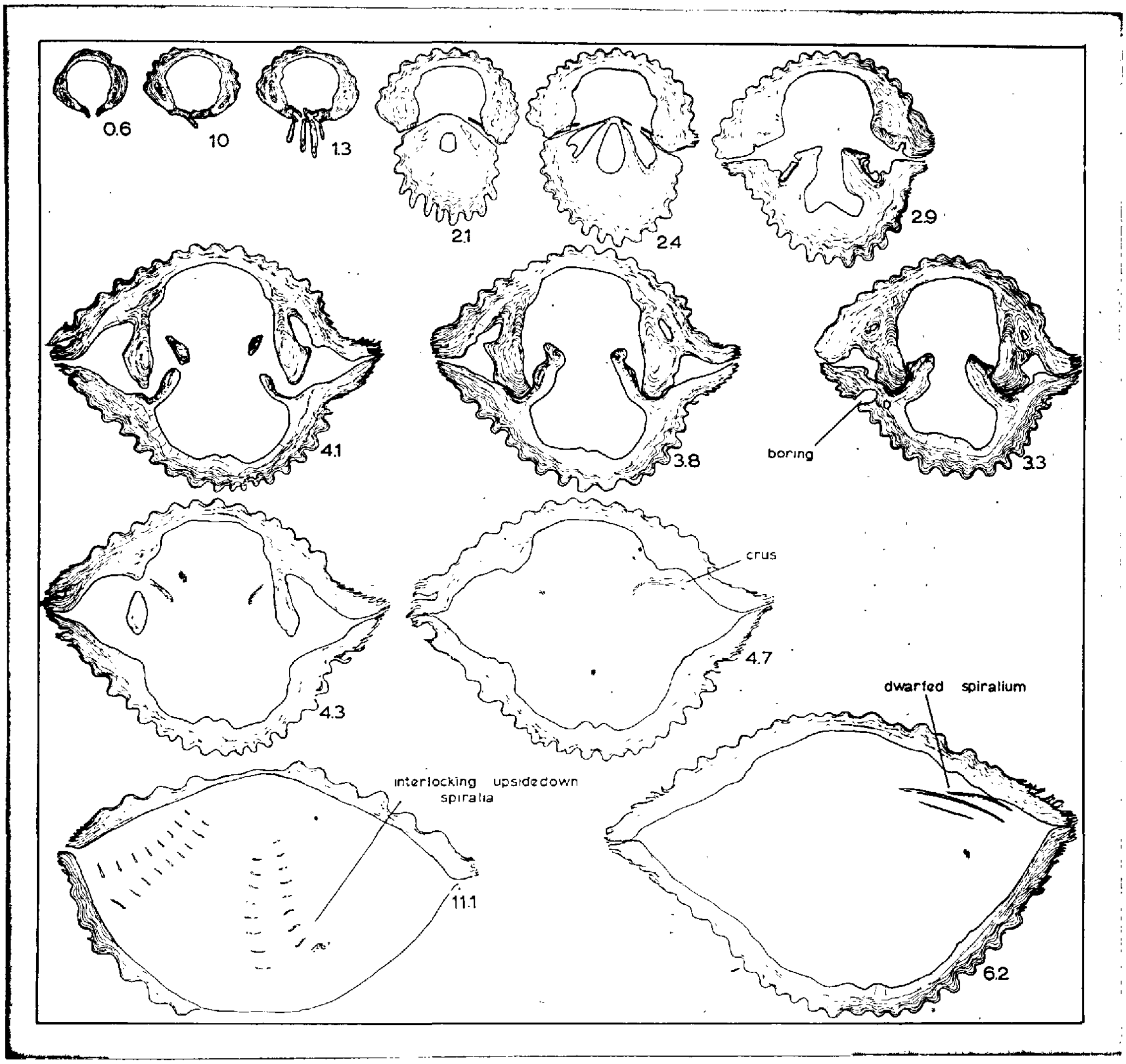


Text-figs. 129-131. Shell variation in Spinatrypina soetenica (STRUVE). Locality C460a. x1.



Text-fig. 132. Scatter diagrams of Spinatrypina soetenica (STRUVE). Locality C460a. Curten beds, lower Givetian.

Internally, a pedicle collar is lacking, deltidial plates are small, hollow. Teeth are long, with elongated lateral cavities. Crura are small, distally slightly feathered. Jugal processes were not observed. One dwarf spiralium was noticed (text-fig. 133, section 6.2 mm ). In another specimen, spiralia were broken and probably washed into an upside-down, interlocking position (text-fig. 134). About twenty specimens were ground anteriorly to determine their suitability for sectioning. None appeared to have properly oriented or normal spiralia.



Text-figs. 133-134. Transverse serial sections of <u>Spinatrypina</u> <u>soetenica</u> (STRUVE). Cürten beds, lower Givetian; MTB Mechernich r40160:h98860. Two specimens, one completely sectioned with dwarfed spiralium (3 whorls!), another (section 11.1 mm ) with interlocked spiralia. x3.

Material.-

This species is more generously distributed east of the Rhine than the older S. wotanica. It can be used to give a more precise date to the Odenthal quarry near Paffrath (MTB Burscheid r78430:h55350) which places them as older, rather than equivalent to the Hexagonaria beds at Hand near Paffrath (refer to JUX, 1964, p. 164). Total 1059 specimnns.

C333(16); C432(386); C460a(358); C460b(61); C472(9); C473(2); C474(17); C476(5); C502(2); C522(13); C527(148); BP45(1); BP124(6); BP283(9); R1937(2); Söt6(5); Söt13(3); Söt28(1); St185(1); St939(7); St941(7).

## Spinatrypina girzenensis n.sp.

Pl. 33, figs. 3-4; Pl 34, figs. 1-2.

Name: After Girzenberg, a small hill about 100 m southwest of the type locality.

Type locality: Road cut about 1 km south of Keldenich and 100 m northwest of Girzenberg, Sötenich syncline, MTB Mechernich r41660:h99230.

Type stratum: Shaly interbeds between Hexagonaria-rich horizons and overlain by coarse grained dolomites or dolomitic limestones. Age probably equivalent to Dreimühlen beds (Binz horizon?).

Range: Dreimühlen to Rodert, middle Givetian.

Associated fauna: Small athryids, spiriferids, numerous Thamnopora-like corals, abundant Aulocystis or small Roemeria-like colonial tabulates, Hexagonaria.

Source sediment: Yellowish brown calcareous shales with lumachelle heaps of brachiopods and bands of corals.

Diagnosis.-

Small to medium sized spinatrypinids with rather coarse ribs spaced at 7-9 per 10 mm. Round outlines and globose shapes are typical. Rare forms already show strong hints of flattish S. explanata-like shapes and rib form. Growth lamellae hug the shell, are barely deflected. Ribs more continuous and tubular than other Eifel forms. Orthocline beaks jut over a broad, blunt-edged area. Anterior folds are weak.

Remarks.-

No specimens have yet been sectioned. Externally they clearly belong to the Spinatrypina species group. They can be sorted out from the older S. soetenica by their coarser ribs with more shell-hugging, barely deflected, less imbricate growth lamellae. Their mature size slso is much larger and areas broader, beaks more rounded, blunt. The finely ribbed specimens of S. soetenica are completely absent, even as minor percentages in populations.

The species can be identified from the rocks east of the Rhine and is known from outcrops at Schwelm, Elberfeld and Jesinghausen, all in the Ruhr area. It is rare in the Paffrath syncline. Spinatrypina tubaecostata (PAECKELMANN) is much flatter, with coarser, more divergent and even ribs and a sharp edged area, and also is not found in the Givetian rocks. However, rare specimens (e.g. Pl. 34, figs 1a-c) show Frasnian trends in having flatter and broader, less-rounded shells.

Materials.-

Total 1047 specimens.

C307(3); C322(16); C435(47); C454(10); C459b(646); C479(41); St185(1); BP51(7); BP85(2); BP85a(2); RW22(1); RW229(1); S8t10(14); S8t12(6); BM BMB68(18); BMB76(5); BMB79(2); BMB82(1); BMB83(4); BMB87(10).

### Spinatrypina tubaecostata (PAECKELMANN 1913)

Pl. 34, figs. 305; text-figs. 135-138.

1913 Atrypa tubaecostata PAECKELMANN, pp. 281-283, Pl. 6, figs. 6, 6a-d, 7.

Type locality: In PAECKELMANN (1913, p. 281) listed as "Hauptbruch von Knappertsbusch.....Schliepershäuschen". The restricted type locality is selected as the first of these. Neither locality is accessible to-day.

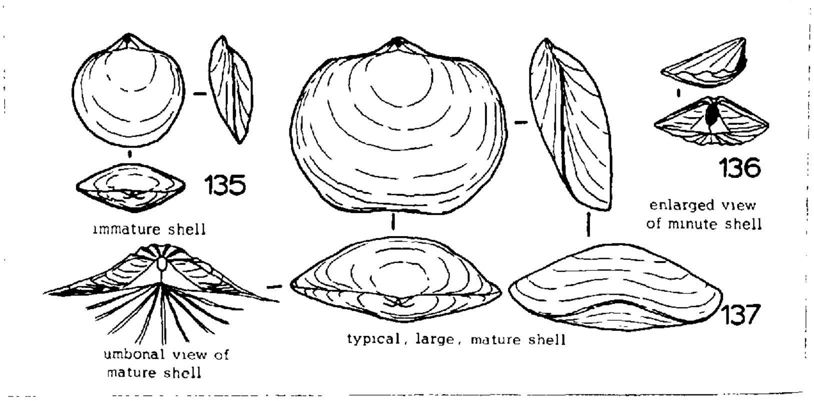
Type stratum: "Dorperkalk" (op. cit.). Frasnian F1, possibly low F2.

Diagnosis.-

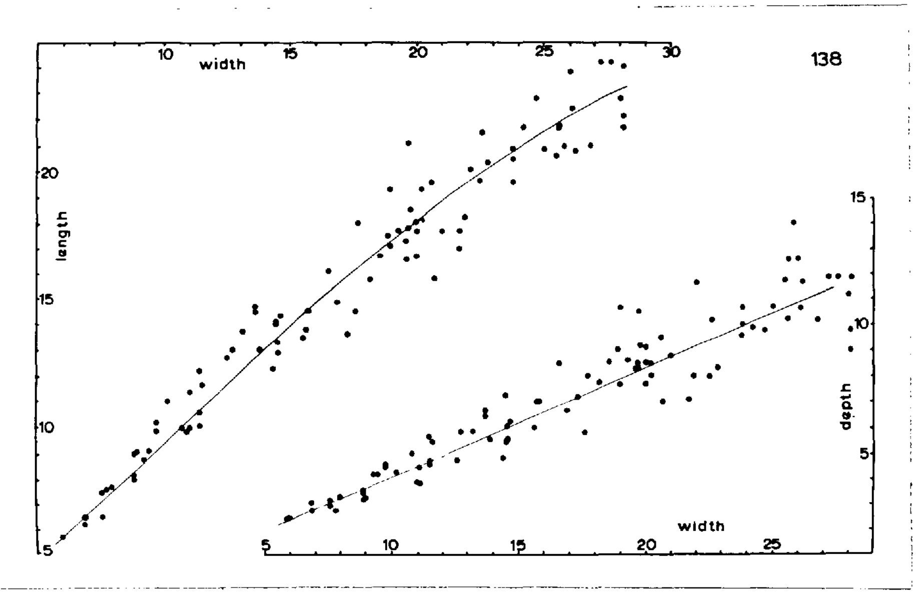
Large, flattish, coarsely ribbed spinatrypinids with triangular areas and a broad median fold. Ribs are crowded at 7-8 per 10 mm , or slightly less, growth lamellae undeflected. Rib crests narrower than rib troughs (sketches text-figs. 135-137).

Remarks.-

The PAECKELMANN collection (Berlin Museum) and the holotype and paratype (Geologisches Museum der Universität, Marburg) were examined. As PAECKELMANN (1913, p. 282) remarked, the number of ribs on specimens varies considerably. However, it appears feasible to eliminate the finely ribbed specimens and relegate them to Spinatrypina quenstedti. The remaining specimens are all coarsely ribbed. The holotype and paratype are not refigured. There exists some confusion as to the size and rib structure of the "average" specimen, and others have been selected from the PAECKELMANN collection to clarify the confusion. The species reaches a much larger mature size than in the holotype which appears to be a small, immature specimen. Size variation is shown in text-figs. 135-137 and also plotted in scatter diagrams (text-fig. 138).



Text-figs. 135-137. Shell variation of Spinatrypina tubaecostata (PAECKELMANN). Locality BMB69. Frasnian. x1.



Text-fig. 138. Scatter diagrams of the main shell dimensions of Spinatrypina tubaecostata (PAECKELMANN). Data combined from localities BMB69, BMB70.

The species can easily be identified by its rib coarseness, the triangular nature of the area and the rounding of the hinge corners from similar specimens of Spinatrypina explanata (SCHLOTHEIM). PAECKELMANN discarded SCHLOTHEIM's species as a "catch-all" name and did not compare it to the SCHLOTHEIM figures.

The most striking comparison is with *Spinatrypina bodini* (MANSUY 1912). From MANSUY's figures (ibid., Pl. 13, figs. 10a-e, Pl. 14, figs. 1a-b) even rib size and shape are very much the same. However, PAECKELMANN's species cannot be rejected as a junior synonym until comparative Asian material is re-examined.

LJASHENKO (1959, Pl. 25, figs. 6-7; Pl. 38, figs. 8-9; Pl 15, figs. 3-4; Pl. 61, figs. 6-7; Pl. 66, figs. 1-7) refers many illustrated Russian specimens to "*Spinatrypa* ex. gr. *tubaecostata* Paeck." but these are all much too finely ribbed and small (nearly ½ the rib size, and ½ shell width) to belong to PAECKELMANN's species. This error can be attributed to the immature holotype selected by PAECKELMANN.

Material.-

Total 91 specimens.

BMB69(40) Paeckelmann coll.; BMB70(51) Waldschmidt coll.

### *Spinatrypina quenstedti* n.sp.

Pl. 36, figs. 4-5.

Name: After QUENSTEDT, in honour of his contribution to the knowledge of European brachiopod faunas.
Type locality: See under *Spinatrypina explanata*,
Type stratum: Steinbreche horizon, Refrath beds (Frasnian F2a-b), Upper Devonian.

Diagnosis.-

Small, 15-20 mm wide, thick and robust shells which are biconvex to ventribiconvex with ribs spaced at 9-11 per 10 mm at the commissure. Small triangular round-edged areas and minute deltidial plates flank a foramen which commonly penetrates the ventral umbo. A weak anterior fold is present.

Remarks.-

There are two distinct forms of *Spinatrypina* at the well known Refrath locality, one is *S. explanata* (SCHLOTHEIM) and the other this small globular form. The former has a short range, but the latter probably extends into the Givetian and is even difficult to tell apart from Eifelian *S. fabaca* n.sp. The association of these two forms, which have been designated as separate species, is, at present, the only ocassion in which two species of the same genus have been found at one locality in Germany.

*Spinatrypina quenstedti* n.sp. could, alternatively, have been assigned subspecific status as *Spinatrypina exlpanata quenstedti*. There are few gradations in shape or size between the two and even rib structure is different. *S. quenstedti* has more sharply defined areas, is slightly more planar, and has more angular hinge corners than *S. fabaca* n.sp. Ribs are nearly the same.

*Material*.-

Total 238 specimens.

C201a(178); C526(12); C529(8); C530(28); C531(12).

## *Spinatrypina explanata* (SCHLOTHEIM 1820)

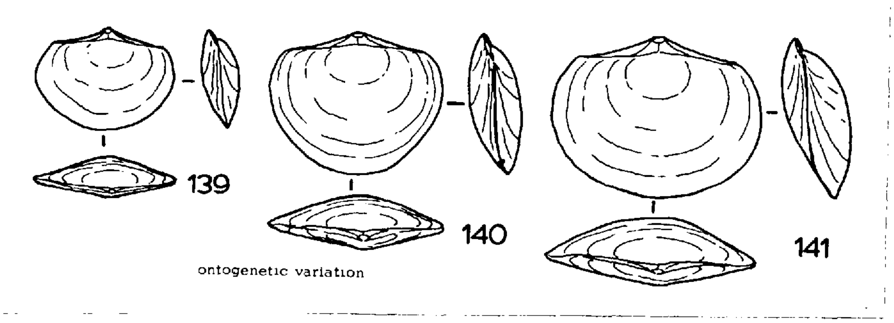
Pl. 37, figs. 1-4; text-figs. 139-143

1820 *Terebratulites explanatus* SCHLOTHEIM, p.263.
1822 *Terebratulites explanatus* SCHLOTHEIM, Pl. 18, figs. 2a-b.
1871 *Terebratula prisca explanata* SCHLOTHEIM, QUENSTEDT, p. 213, Pl. 42, figs. 98, 98a.
1885 *Atrypa reticularis* var. *explanata* (and *Atrypa explanata* in plate explanations) SCHLOTHEIM, MAURER, p. 181, Pl. 7, figs. 31,31a.

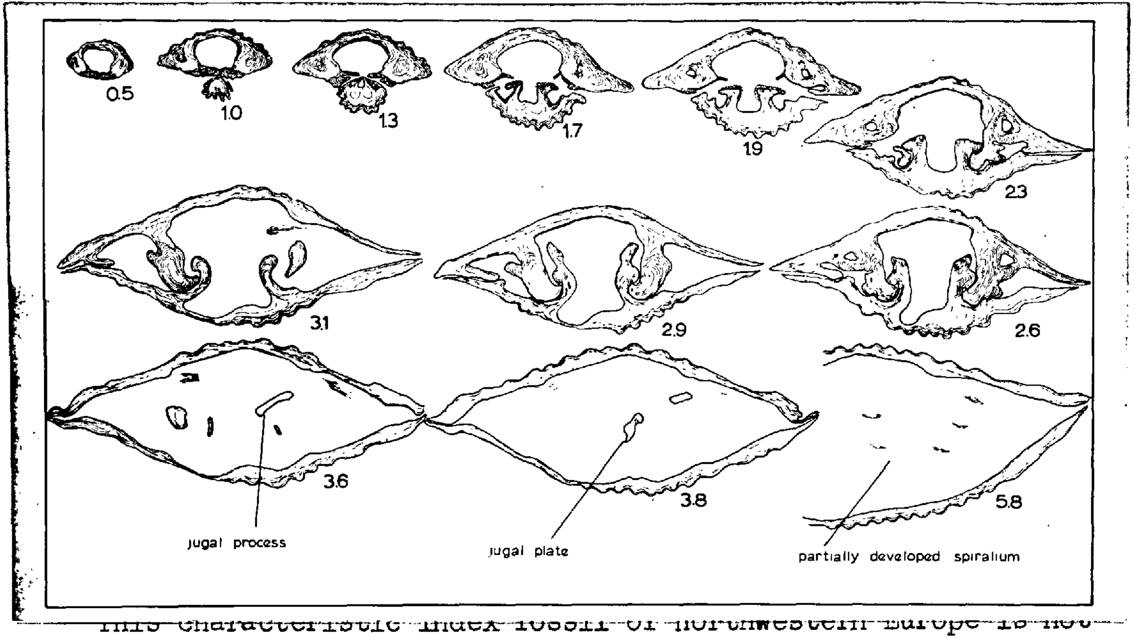
*Type locality*: In SCHLOTHEIM (1822, p. 19) "in derselben Gebirgsart aus der Eifel", the species is alleged to come from the Eifel region, where it is very rare and has only recently been found (STRUVE, 1964, p. 232). It seems likely, and is almost certain, that SCHLOTHEIM's specimens did not come from the Eifel but from Refrath. A glance at the other fauna illustrated by SCHLOTHEIM verifies this conclusion. The restricted type locality is selected to be the coral rich exposures along the sport field of Refrath, MTB Mülheim am Rhein r7814-200:h74550-80.
*Type stratum*: Steinbreche horizon, Refrath beds (Frasnian F2a-b), Upper Devonian.
*Source sediment*: Fossiliferous pale brown calcareous shales rich in corals.
*Associated fauna*: *Cyrtospirifer aperturatus* (SCHLOTHEIM), *Atrypa* (*Devonatrypa*) *europaea* (STRUVE), *Dicamara scalprum* (ROEMER), *Alveolites*, *Hexagonaria*, *Disphyllum*. Corals dominate.

*Diagnosis*.-

Flat, wider than long, near-oval spinatrypinids (text-figs. 139-141) with broad and wide, sharp-edged interareas, narrow delthyrium with apical foramen. Beak orthocline to weakly apsacline. Ribs spaced at 10-11 per 10 mm. Growth zones not well marked, lamellae undeflected non imbricate. Average spacing of lamellae at 2-3 mm. A broad, shallow fold anteriorly. Internally (text-fig. 142), short deltidial plates separate laterally into two distinct horizons. Lateral cavities wide, teeth bilobed, short, sub-vertical. Crura thick, feathery. Jugal plates short, blunt.



Text-figs. 139-141. Shell **variations** of Spinatrypina explanata (SCHLOTHEIM) from the type locality. x1.



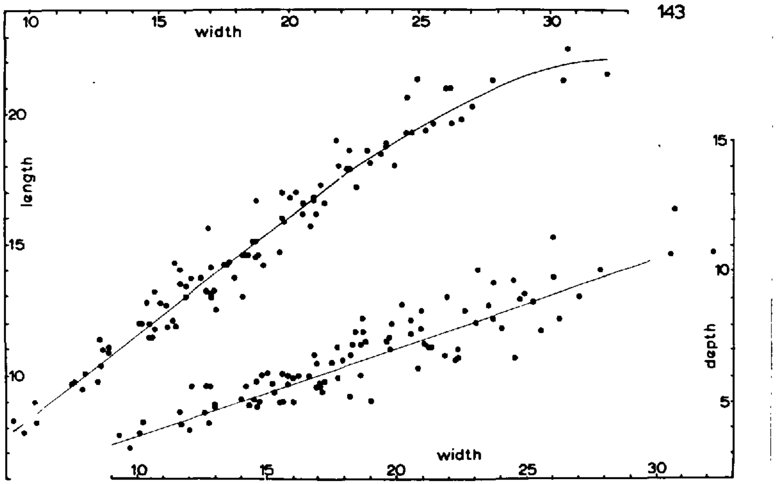
This characteristic index fossil of northwestern Europe is not abundant. At Refrath (the type locality) it is overshadowed by the longer-ranging Spinatrypina quenstedti. However, S. explanata appears to reach a much wider distribution : it is present in the Gruiten beds near Elberfeld and Düsseldorf, has been found in the Prüm syncline of the Eifel, and is probably present in the Beaulieu shales in the Boulonnais region of France.

The original SCHLOTHEIM collection (Berlin Museum) was examined. Of two specimens, a more finely ribbed one was selected as lectotype (Pl. 37, figs. 2a-d).

When he first described the species in 1820, SCHLOTHEIM specified the extraordinary flatness and width of the shell and there is no doubt that this referred to the specimens common to Refrath. Wide, planate forms are not common elsewhere except possibly if Spinatrypina tubaecostata (PAECKELMANN) is included. The latter is quite distinct because it has much wider, and broader ribs, a sharper, more pointed beak and a broader, more expanded fold. It is not known why SCHLOTHEIM (1820, 1822) consistently marked the "Eiffel" (Eifel) as source of his explanata material, except possibly through confusion of localities.

SCHRÖTER (177, Pl. 4, figs. 19-20, p. 387) described and figured two specimens as Terebratulae cancellatae, which possibly were S. explanata. These specimens were said to come from Bensberg, and probably were collected at Refrath.

In comparing the scatter diagrams of S. explanata and the S. tubaecostata ,the explanata comes out as being much wider than long and wider than deep (text-fig. 143).



Text-fig. 143. Scatter diagrams of Spinatrypina explanata (SCHLOTHEIM) from the type locality.

Material.-

Total 142 specimens

C301a(85); C526(4); C529(5); C530(8); C531(3); BMB40(1); BMB41(16); BMB92(1); BMB93(12).

One specimen (Pl. 35, figs. 4a-c) which may be reffered to this species was present in the collection of robusta n.sp. from Hofermühle (see below).

## Spinatrypina robusta n.sp.

Pl. 35, figs. 1-4; Pl. 36, figs. 1-3; text-figs. 144-151.

Name: Latin, robustus, a, um, strong, robust. The shell of this species is thick and round and large.

Type locality: Quarry south of Anger Bach nerr Hofermühle, about 1 km. south of Heiligenhaus, MTB Kettwig. The type locality was revisited. It is to-day nearly wholly overgrown and the quarry unused. Near the north-east end of the quarry a small collection in black shales yielded specimens which were similar, though not identical, to those described. Its location was MTB Kettwig r66600:h86090.

Type stratum: Frasnian, ?Dorper Kalk. This sequence correlates closely with the Refrath beds at Refrath and the Gruiten beds near Düsseldorf. It can probably be dated as early F2, perhaps F2b-c, and probably slightly younger than the beds carrying an explanata fauna. From the position on the map this may be the upper part of the Dorper Kalk.

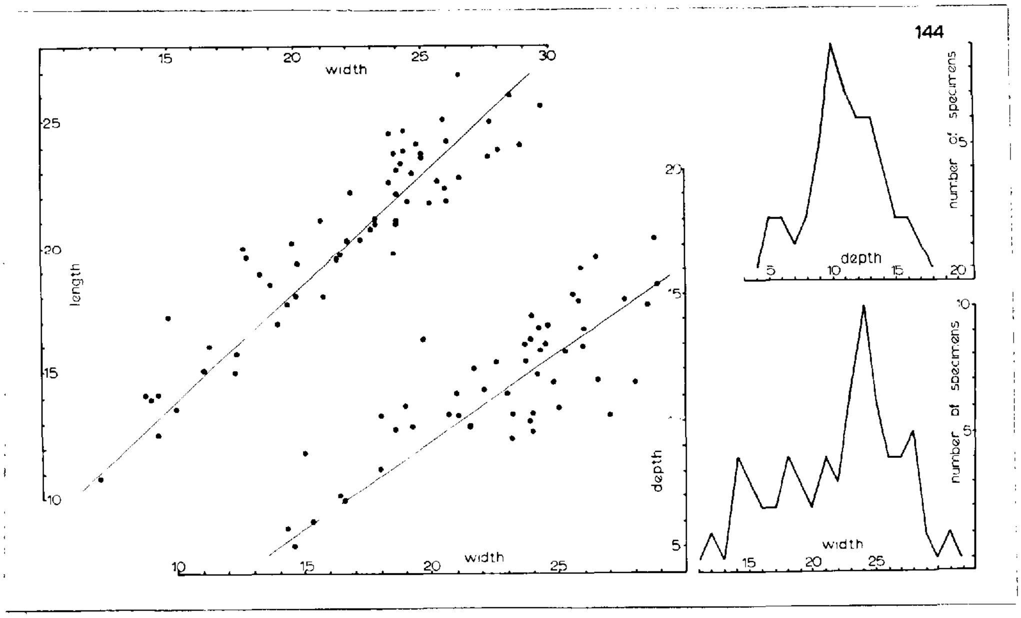
Associated fauna: Mainly thamnoporid corals. A few platy alveolitids and laminar stromatoporoids.

Source sediment: Dark gray to black shales, rather firm and hard weathering, calcareous.

Diagnosis.-

Maximum recorded width was 32 mm , average between 24 and 28 mm , and comes at nearly mid-length. Specimens are wider than long (in maturity the w/l ratio is 1.09 to 1.10) and nearly twice as wide as thick (maturity w/d ratio 1.95, text-fig. 144). The shell is rounded, hinge corners only weakly defined, The pedicle valve is slightly less convex than the brachial valve, but both are well rounded.

The ventral valve is round, moderately convex and lacks an angular crest. A blunt beak projects about 2 mm in an orthocline position. The broad, sharp-edged area is divided by a narrow triangular delthyrium filled with minute deltidial plates. The pedicle opening splits the deltidial plates and is commonly expanded into the ventral umbo. Shoulder lines are near-straight, hinge corners undefined, rounded. Hinge angle 135-140 degrees. A moderately, somewhat more convex brachial valve flattens out distally. Apices are not covered by the ventral umbo.



Text-fig. 144. Scatter diagrams and frequency curves of Spinatrypina robusta n.sp. Frasnian (F2b-c?); Hofermühle, MTB Kettwig.

Ribs.-

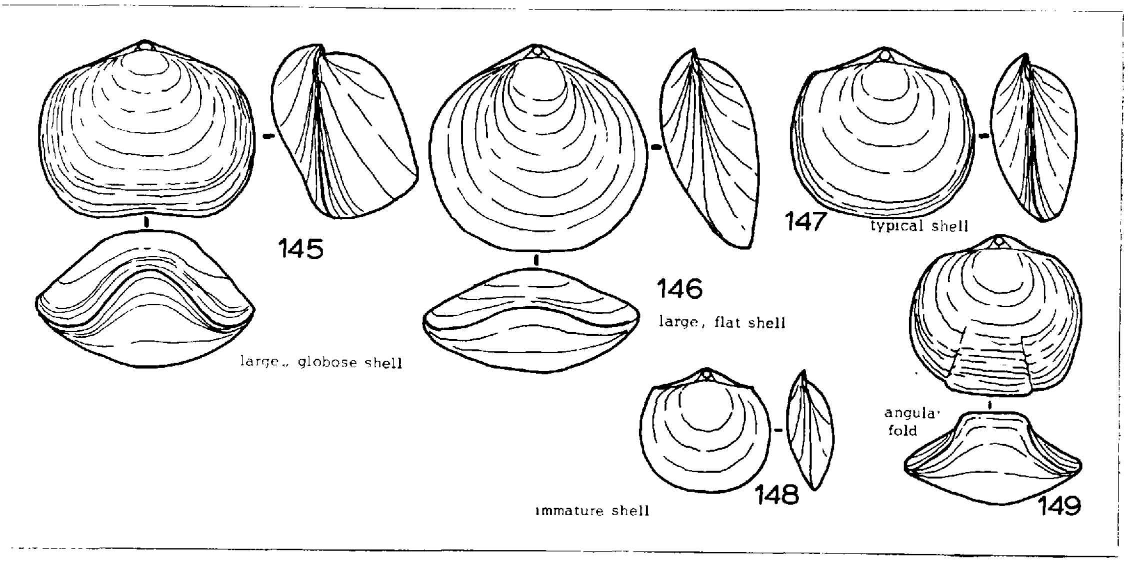
Ribs are fine, averaging at 9 per 10 mm. of arc with a minimum of 8 and a maximum of 12. Round-crested, round troughed ribs are not as straight and continuous as those in S. explanata. There is only slight distal widening of the ribs. Occasionally a group of 4 or 5 ribs may be enlarged excessively in comparison to others. Three ribs (a weak outside fourth) flank two apical mid-ribs on the ventral valve. Bifurcations are in sets, commonly at about 10 mm and 20 mm from the apex. On the brachial valve, four, nearly equi-sized ribs meet apically outside a weaker central rib.

Growth lamellae.-

Growth lamellae are regularly spaced at about 2 mm. Anteriorly there is slight crowding. Lamellae are slightly upturned. The rib troughs preserve fine concentric lines, about 4-6 per millimeter. The single spine located postero-laterally on one specimen, was short (length 1-2 mm ) and curved. It tapered rapidly to a point, and was directed at about 30 degrees to the shell surface.

Growth and variation.-

Small forms are equally convex, rather flat (text-figs. 145-149), with a proportionally large foramen. Hinge corners are more distinct in young forms. Globose specimens have a strong fold. Rare flattish specimens like those of Spinatrypina explanata were found.



Text-figs. 145-149. Shell variation of Spinatrypina robusta n.sp. Hofermühle. x1.

Internal markings.-

A loose brachial valve was available for study (Pl. 35, figs. 3a-b). It gives an indication of the muscle pattern. This valve had a small, elevated notothyrial pit. A strong, thick, rounded median septum divides the adductors. The adductors are bilobed, with 4 by 3 mm posterior lobes and 3 by 3 mm anterior lobes which are more closely set. Small ovarian markings flank the muscle scars.

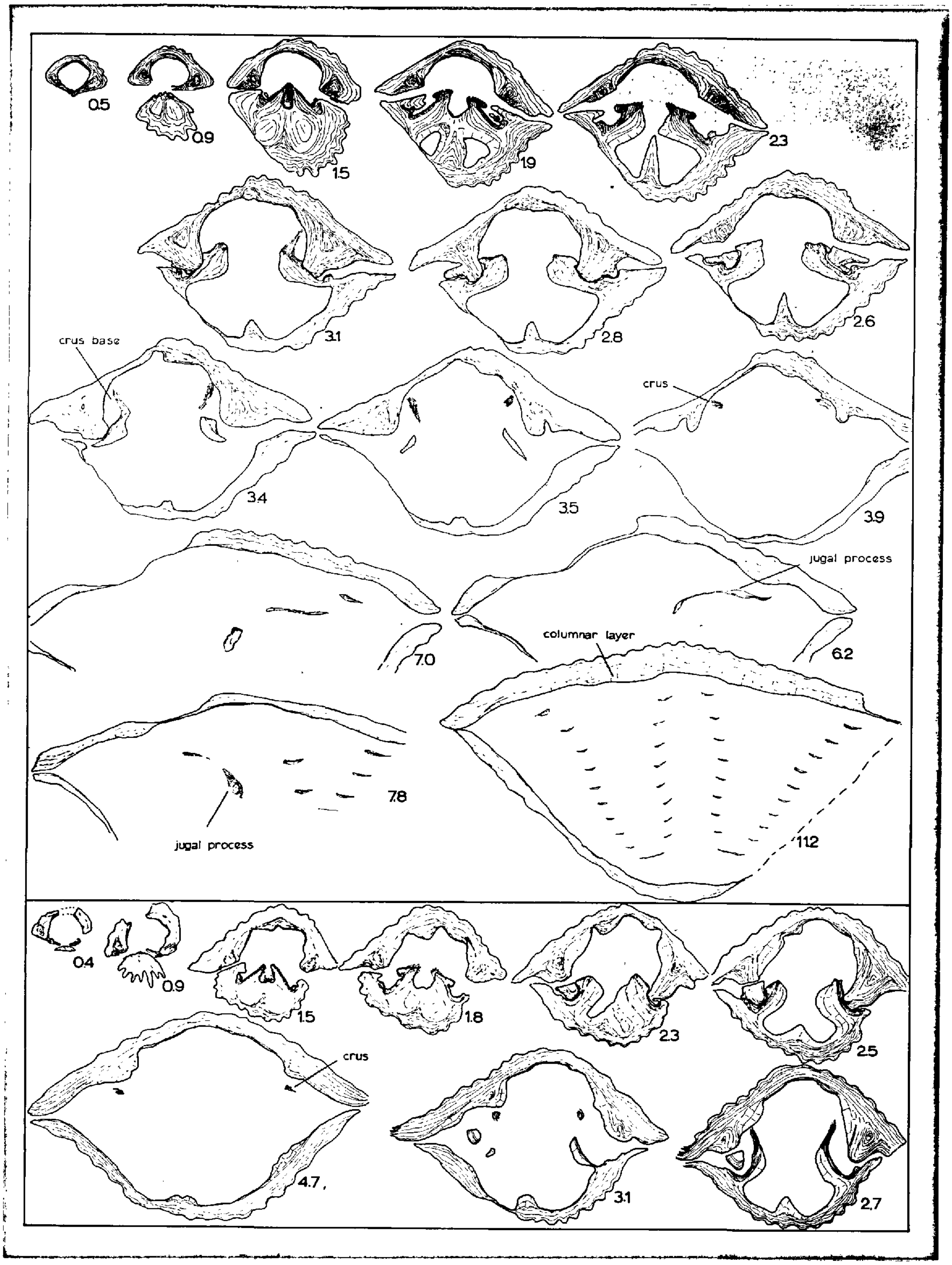
Internal structure.-

No pedicle collar was observed but moderately thick columnar layers support both the teeth and hinge plates. Short, simple, only partially hollow deltidial plates surround the foramen. Lateral cavities are minute, central nuclei large. Teeth short, blunt; lateral lobes weak anteriorly, short posteriorly (text-figs. 150-151).

A small, U-shaped notothyrial pit carries an amorphous cardinal process which nearly fills it. Crura are elevated by long projection of the inner socket ridge, and are given off at a distal stage, rather than close to the hinge plates. Jugal processes thin; jugal plates solid, stumpy and remaining sub-horizontal. Spiralia with some 10 or less whorls.

Remarks.-

Atrypa douvillei MANSUY (1912, Pl. 13, figs. 9a-h) from the Upper Devonian of Yunnan, China, is smaller and has a more prominent beak than Spinatrypina robusta n.sp. but it compares closely in roundness, globosity and rib size.



Text-figs. 150-151. Transverse serial sections of Spinatrypina robusta n.sp. Frasnian (F2b-c?); Hofermühle, type locality. x3.

*Spinatrypina tubaecostata* (PAECKELMANN) has larger ribs, is wider and flatter and has a broader area.

The species range of *Spinatrypina robusta* n.sp. is uncertain. It is very likely younger than *S. tubaecostata* and also the same age or younger than *S. explanata*. There were no typical *S. tubaecostata* in the Hofermühle collection but a few *S. explanata* were present.

Material.-

Total 93 specimens.

C220(4); BMB16(89) locus typicus.

### Genus *Kerpina* STRUVE 1961

Type species: *Kerpina vineta* STRUVE 1961, p. 353, Pl. 1, figs. 3-4.
Range: Upper Eifelian.
Distribution: Presently only known from the Eifel region, Germany.

Diagnosis.-

Small concavoconvex to ventribiconvex shell with a proportionately very large, flat area and delthyrium with procline-orthocline beaks. Ribs are straight, imbricate-tubular, somewhat *Spinatrypina*-like and lack delicate concentric sculpture. Internally, an advanced type of pedicle collar has been found in all specimens : this collar covers the walls of thick, hollowed deltidial plates. Lateral cavities are absent, teeth short. Jugal processes thick, with a layer of coarse nodules and tipped by straight, tapering-pointed jugal plates. Spiralia with 6 or 7 whorls.

Remarks.-

This genus appears to be similar in some features to only two genera, *Spinatrypina* and *Anatrypa* (partim). From *Spinatrypina*, to which it is similar in rib structure, it differs by its elaborate beak morphology and internally its deltidial plates, pedicle collar and complete lack of lateral cavities. *Spinatrypina* also does not adopt the reversed convexity relationships of *Kerpina*. From *Anatrypa*, which compares in convexity and structure of pedicle collar, it differs in its rib structure which is tubular-imbricate rather than simply imbricate, its large area and delthyrium and internally its deltidial plates.

The affinities of *Kerpina* are vague. It may have shared a common origin with *Spinatrypina* and have eventually produced an *Anatrypa* offshoot, but *Anatrypa* (sensu *Anatrypa kadzielniae* (CÜRICH)) appears to have branched off from Atrypa. BOUCOT & STATON & JOHNSON (1964, fig. 2) placed *Kerpina* in the sub-family *Carinatininae*, but it is wholly unrelated to *Carinatina* though they are common at the same fossil localities.

The peculiar beak morphology which appears to have resulted in drastic intraspecific differences in shell shape is discussed under Ecology.

Member species.-

At present only two species are known, Kerpina vineta STRUVE and K. atrypoides STRUVE, two forms which intergrade morphologically. SOWERBY (1840, Pl. 57, fig. 11) illustrated a specimen which he called Spirifera affinis SOWERBY 1823 and which, from the illustration, might have been a Kerpina specimen. The specimen from the SOWERBY collection was examined. Its preservation is not good, nevertheless it can be grouped under Spinatrypina, possibly S. soetenica (STRUVE 1964), instead of Kerpina.

### Kerpina vineta STRUVE 1961

Pl. 38, figs. 1-6; Pl. 39, figs. 1-5; text-figs. 152-164.

1961 Kerpina vineta STRUVE, p. 333, Pl.1, figs. 3-4. The type locality and type stratum are given in the same work.

Source sediment: Pale greenish-gray calcareous shales and interbeds of argillaceous limestones with abundant debris from shells, crinoids, etc. Limestones have a "pelletoidal" texture. The crinoidal debris which is abundant, consists of fragmented columnals and ossicles with rare whole calices. Crinoids become more abundant upwards.

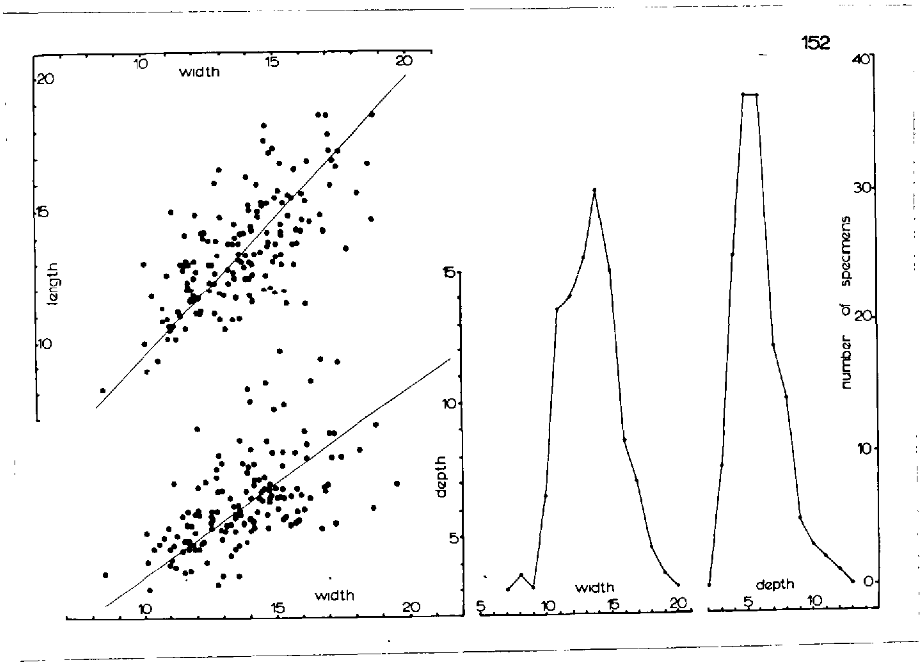
Associated fauna: Rich in brachiopods, rare in horn corals and colonial rugosans. Small, platy tabulate corals (Alveolites) are common, but thamnoporids are absent. Bryozoa are numerous. Ostracods commonly fill the insides of brachiopods. Atrypids are not large, although more argillaceous layers contain large frilly forms. Carinatina rare. Small spiriferids and athyrids common; Davidsonia locally, particularly on tabulate corals, are abundant. Rhynchonellids are not scarce. The fauna as a whole is small-sized.

Diagnosis.-

See STRUVE 1961, p. 333.

External form.-

The peculiar mode of life inferred from shell morphology, preservation and epifauna has resulted in wide divergence of shape and strong deformity of growth, mostly in later stages. Typically, shells are small in size (optimum width 14 mm, depth 5-6 mm; text-fig. 152) and may be either narrow, somewhat globose and elongated (subspecies goniorhynchia STRUVE) or wide and flattish (subspecies vineta STRUVE). There is full gradation between these shape variations and young specimens are indistinguishable. Maximum width occurs near mid-length and maximum depth anteriorly. Most shells show geniculation of the more strongly



Text-fig. 152. Scatter diagrams and frequency curves of Kerpina vineta. Localities C359, C512.

convex pedicle valve. The brachial valve is flat or weakly convex and is commonly also slightly concave at the margins.

The pedicle valve is moderately round-convex. A flattened, blunt-tipped beak projects (as much as 5 mm ) away from the dorsal apex and is flanked by a high and wide, flattish, strongly striated interarea. Deltidial plates are large, accommodated in equally large delthyrium. The unrimmed, usually twisted and mis-shapen foramen is submesothyrid to mesothyrid, and has migrated into the ventral umbo. The procline to orthocline beak, also strongly deformed, makes many specimens asymmetrical.

The planar, weakly convex to weakly concave brachial valve has an exposed uncurved apex.

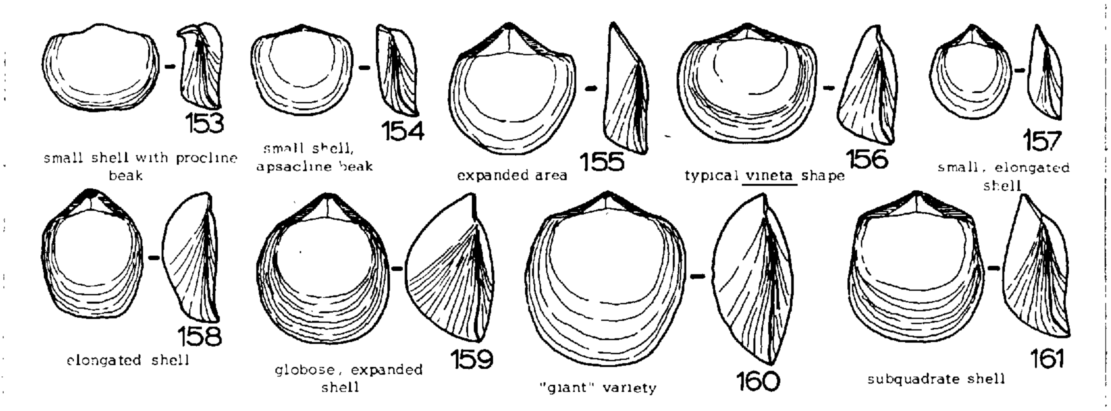
Ribs.-

Well-defined, incised ribs resemble those of Spinatrypina, but bear traces of rib structure as those of Atrypa. Spacing is 12-16 per 10 mm. of arc, with equal ribs and troughs, and no dilation or expansion from growth interruptions. There is no distal wave length increase, with rib reproduction keeping pace with size. Anteriorly, near the geniculated portion of the pedicle valve, ribs tend to flatten their crests and shallow troughs, or become "lost" in the crowding of the growth lamellae.

An apical rib pattern is difficult to establish because most apices are deformed, worn smooth or so twisted that ribs are unrecognizable. On the pedicle valve, the apex shows a thick mid-rib bifurcating at 2 mm and again very quickly in the next 0.5 to 1,0 mm. Two large ribs flank the slightly more prominent mid-rib, and near the posterior commissure are two weak, short-lived lateral ribs. On the brachial valve, the mid-rib appears late (at 1-2 mm from the apex) and is flanked by strongly divergent lateral ribs, two of which are present apically and one more towards the sides.

Growth lamellae.-

For the apical 8-10 mm. growth interruptions are spaced at 2 mm. or less, quite regularly, hug the shell surface, but are, three-dimensionally, arranged in descending step-like patterns. Distal portions of the shell are marked by strongly overlapping, overcrowded lamellae up to 20 in number. Frills are not developed, but distal margins of the lamellae are free for nearly 2 mm , particularly on the pedicle valve, but are not curved dorsally.



Text-figs. 153-161. Shell variation of *Kerpina vineta* STRUVE. Upper row *K. vineta vineta* and lower row *K. vineta goniorhynchia*. x1.

Growth and variation.-

Variation in this species is rife (text-figs. 153-161), and placing morphological end-variants side by side (as for the types of subspecies *vineta* and *goniorhynchia*) may give a misleading impression of dichotomy. The evidence suggests that two distinct modes of life position contributed to such dichotomy. The first, a *vineta vineta* shape (flat and wide) shows a beak position ranging from procline to apsacline and rarely orthocline. Numerous specimens of this subspecies have strong beak deformation and twisting of the position of the foramen : five specimens were found actually fixed (three are shown in Pl. 38, fig. 5; Pl. 39, figs. 1,3) to grooved or warped surfaces of small platy tabulate corals such as Alveolites, in a position and shape conforming to the warped shape of the coral. There is no doubt that they were attached in this position, and not that the coral subsequently grew around the shell, since it is the brachiopod which has altered its shape. In addition, loose specimens have epifauna exclusively attached to the brachial valve. These three separate lines of evidence suggest that the pedicle valve was oriented downwards, with the beak twisted and held by a short pedicle (and possibly also by fibrous muscle (?) tissue attached to the interarea). Secondly, a vineta goniorhynchia shape (narrow, globose, with weakly concave brachial valve) is marked by a weakly apsacline to orthocline beak, although over-all shape deformation is still marked. Epifauna is restricted to the pedicle valve. A life position with brachial valve downwards would be current-stable, and can most easily explain its morphological differences. Statistically the subspecies are inseparable.

Growth patterns are simple : nearly all young forms of both subspecies are identical, the variation is obviously late ontogenetic. Small forms all have weakly apsacline beaks, flattish or weakly convex brachial valves and stouter pedicle valves. The foramen is apical, deltidial plates not very large. Commissures are rectimarginate.

Internal markings.-

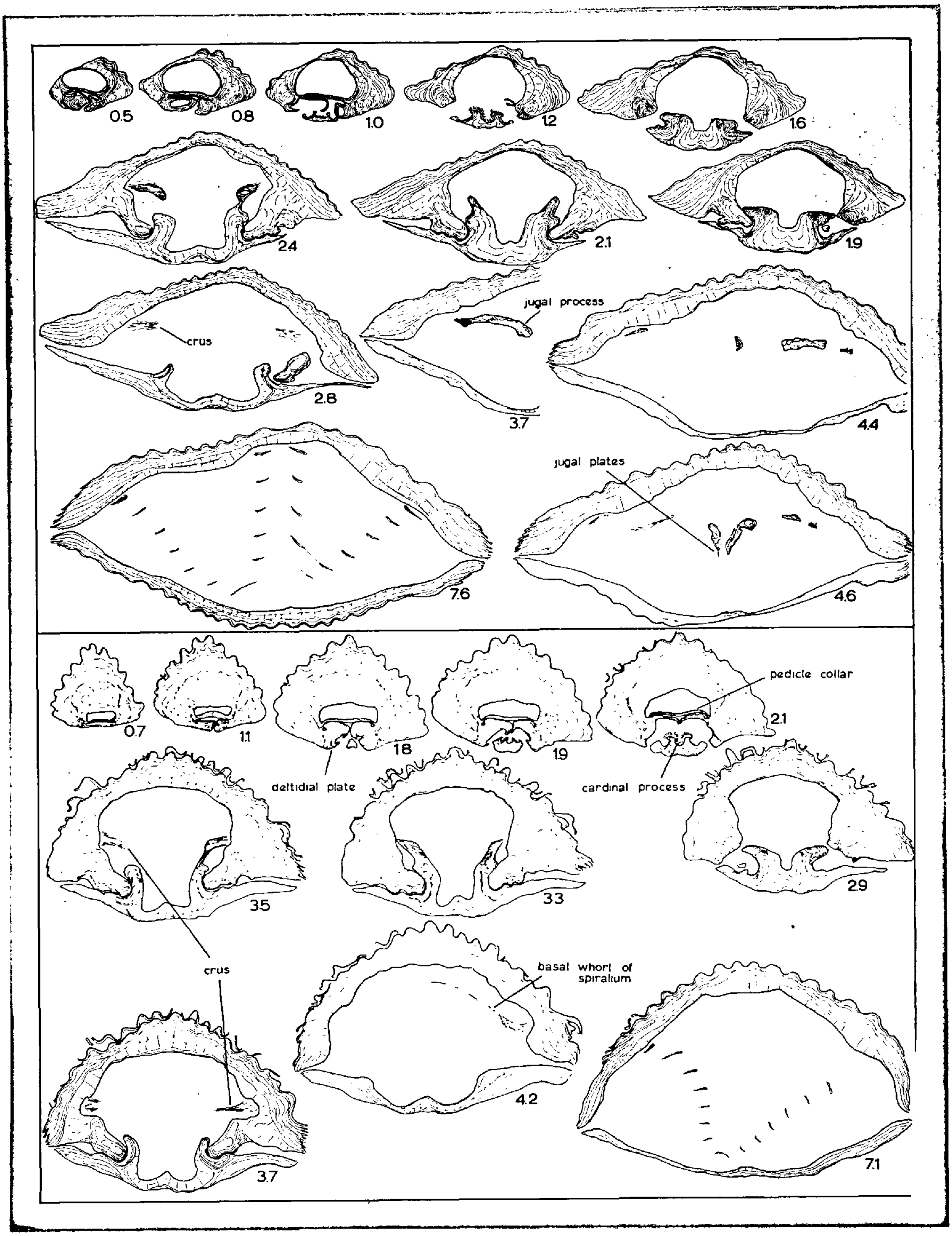
Not investigated. The shells apparently do not come very easily apart (probably because of strongly inwardly directed dentition) and no loose valves were available for study.

Internal structure.-

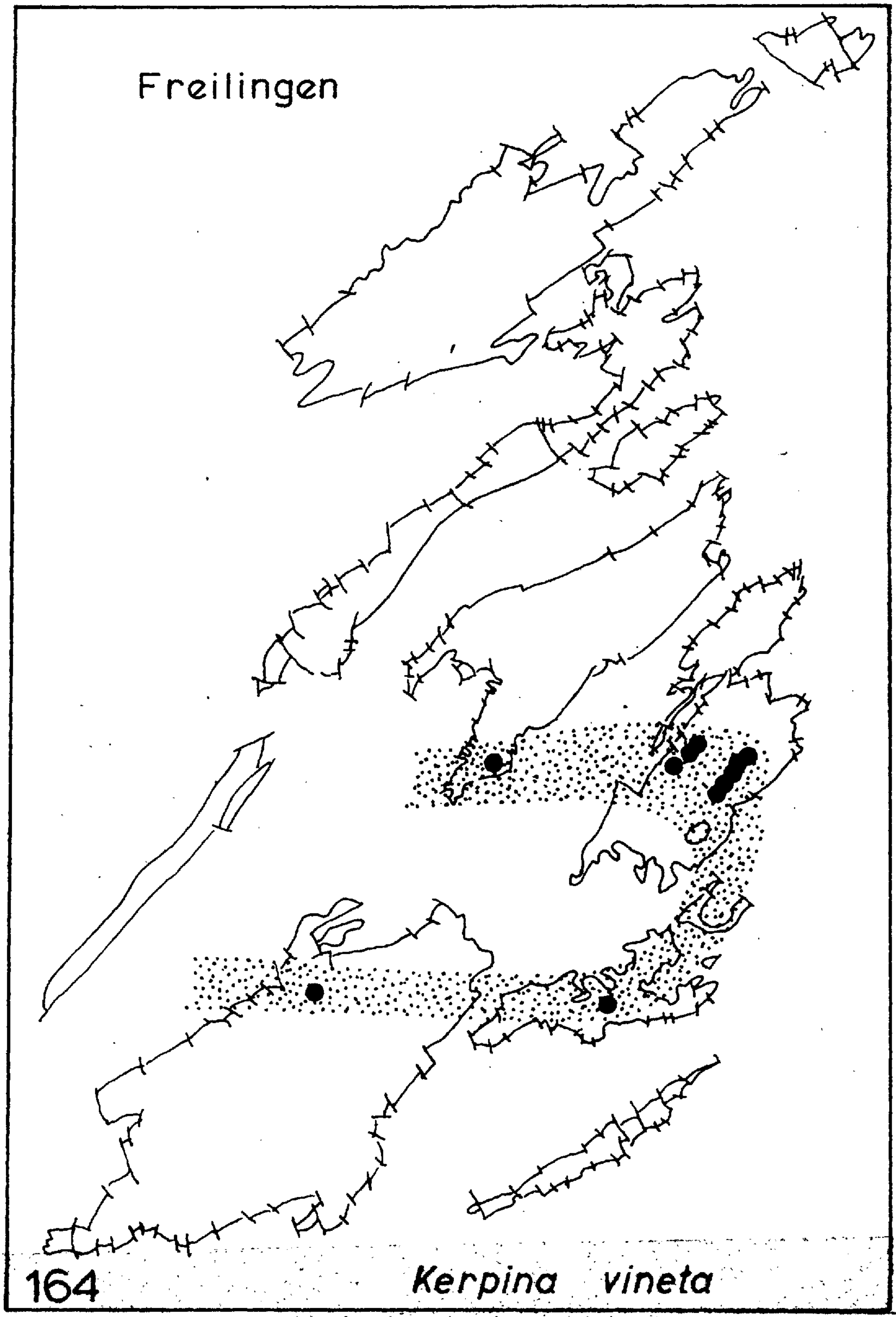
The columnar shell layer is thicker in the subspecies goniorhynchia (text-figs. 162-163).

Thick, short deltidial plates, hollow distally, are present. These touch apically and are interlocked. Inwards of the plates is a pedicle collar, completely lining the delthyrial cavity and acting as support for the deltidial plates (which they may touch, but remain distinct). Stout, stubby dental plates are inward-directed, almost horizontal in position. No dental ridges or lateral cavities are present. Teeth are blunt, and show three main crenulations, consistent in all specimens, rather than a division into main and lateral lobes.

A weak, gradually expanding cardinal pit holds a thick, narrow cardinal process with 5-8 strands, and weaker strands overlapping the hinge plates. Some strands bifurcate or dilate away from their roots. Socket plates are thick, but not well-defined and overlapped by growth lines from the cardinal block. Inner socket ridges are stout, others weak. A knobby crural base supports thick, horizontally directed crura



Text-figs. 162-163. Transverse serial sections of *Kerpina vineta* STRUVE. Eilenberg horizon, Freilingen beds, Eifelian; MTB Dollendorf r53850:h74680. 162 (top), *K. vineta vineta*, 163 (bottom), *K. vineta goniorhynchia*. x4.



Distribution of Kerpina vineta STRUVE 1961 in the Eifel.

which feather. Jugal processes are horizontal, **weakly arched**, terminating in sub-vertical jugal plates. Spiralia have about 8 whorls. One of the specimens sectioned lacked the left spiralium as well as jugal processes (text-fig. 163), the remaining spiralium filling the shell cavity and the basal whorl attached to the right crus. This special mode of attachment, highly unusual, shows a complete reversal of the coiling of the spiralium, that is, coiling clockwise.

*Remarks*.-

There is little difference between *Kerpina vineta* STRUVE and *K. atrypoides* STRUVE. The latter is generally larger, rather planar with more widely separated growth lamellae and lacking the strong apical deformations. *Kerpina vineta goniorhynchia* appears to be restricted to older parts of the Frelingen beds, but the range of *K. vineta vineta* and *K. atrypoides* is the same.

The marked, expansive interareas, twisted or large beaks, and convexi-plane shells readily allow the separation from other synchronous atrypid genera.

*Material*.-

Some 267 specimens are assigned to *Kerpina vineta*, and no attempt is here made to separate the subspecies *K. vineta goniorhynchia* and *vineta vineta*. *K. atrypoides*, which was not sectioned, is also tentatively grouped here. *K. vineta* ***goniorhynchia*** is restricted to the Eilenberg horizon, *K. vineta vineta* to the Eilenberg and Bohnert subhorizons and *K. atrypoides* to the Nollenbach horizon. (text-fig. 164).

Localities with ssp. *goniorhnchia*; C299(29); C301(8); C359(87); C360(11); C512(96); St70(9); St591(3).

Localities with *K. vineta vineta*: C298(1); C316(1); C317(4); C318(1); C343(14); C344(2); C345(4); C346(2); C353(2); C354(2); C355(1); C361(1); C362(2); C363(1); C364(11); C514(1); St8(1); St43(1); St44(1); St67(3); St68(1); St69(1); St71(2); St252(1); St594(3); St621a(2); St632a(4); St655(1); St672(3); St673(1); St707(1); St726(1); St728(1); St731(2); St732(3); St744(2); St810(2); St811(1).

## Genus *Desquamatia* ALEKSEEVA 1960

*Type species*: *Atrypa* (*Desquamatia*) *khavae* ALEKSEEVA 1960, pp. 423-424, fig. 3.
*Range*: Middle to Upper Devonian, possible high Lower Devonian. Not present in Famennian (Upper Devonian).
*Distribution*: World-wide.

*Diagnosis*.-

See COPPER 1965c.

## Subgenus Desquamatia (Variatrypa) COPPER 1965

Type species: Desquamatia ajugata COPPER 1965b.
Range: Eifelian-Givetian, Middle Devonian.

Diagnosis.-
See COPPER 1965d.

### Desquamatia (Variatrypa) iunctura n.sp.

Pl. 40, figs. 1-2; Pl. 41, figs. 1a-c; text-figs. 165-166.

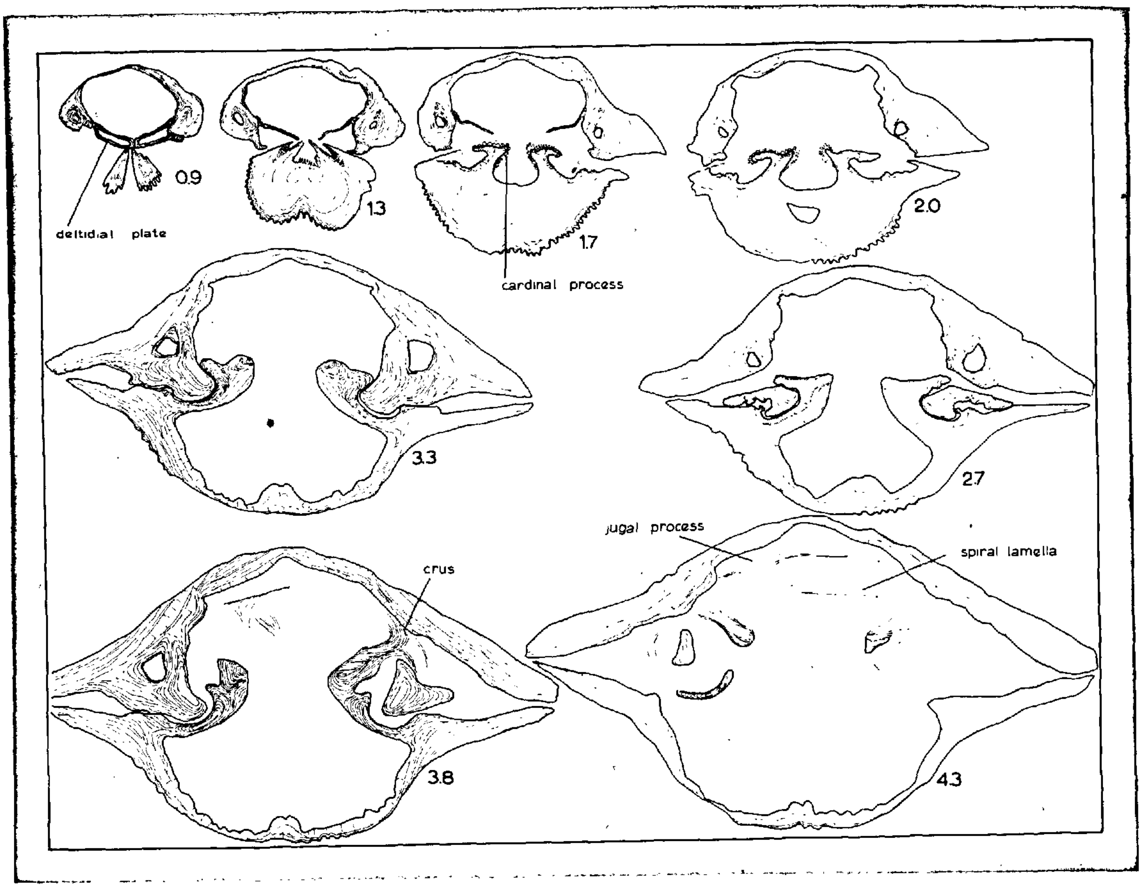
Name: Latin, iunctura, ae, a joining, joint, relationship. In the Eifel region this appears to be a species forming a link between Eifelian and Givetian members of the subgenus.
Locus typicus: Eastern slope of Hönselberg, south of Niederehe, Hillesheim syncline, Eifel. MTB Dollendorf r53870:h74680.
Type stratum: Eilenberg horizon, Freilingen beds, upper Eifelian.
Range: Rechert horizon-Nollenbach horizon. Possibly in the Ahbach beds as rare, isolated specimens.
Sediment and associated fauna: Refer to Kerpina vineta STRUVE.

Diagnosis.-
Medium to very large sized dorsibiconvex shells, with broad, wide areas, orthocline beaks, large foramen (expanded into umbones in gerontic specimens) and strong anterior fold. Ribs are straight, tubular, round-crested, deep-troughed, spaced at 10-12 per 10 mm. Growth lamellae very scarce for first 15 mm, then spaced at about 1 mm. Frills never found. Internally (text-fig. 165), a pedicle collar is lacking, deltidial plates are thin and hollow, delicate, lateral cavities large. A cardinal process is prominent. Crura feathery.

Remarks.-
The species can be confused extremely with the finely ribbed Mimatrypa insquamosa (SCHNUR) but internally marked differences exist. This homoeomorphy with an unrelated palaferellid atrypid is striking.

Desquamatia iunctura n.sp. has little in common with D. zonata (SCHNUR) : in shape, size, and surface sculpture they are easily separated. It is possible that SCHNUR (1853) included specimens of this species in his Terebratula insquamosa (SCHNUR, 1853, Pl. 44, fig. 2?).

The new species may be a good index fossil of the upper Eifelian in Germany. East of the Rhine it is found in beds of the same age at Iserlohn and Attendorn. In the northern Eifel synclines the species has not yet been found in Freilingen beds, but is common in the higher Junkerberg horizons, although in a smaller form.

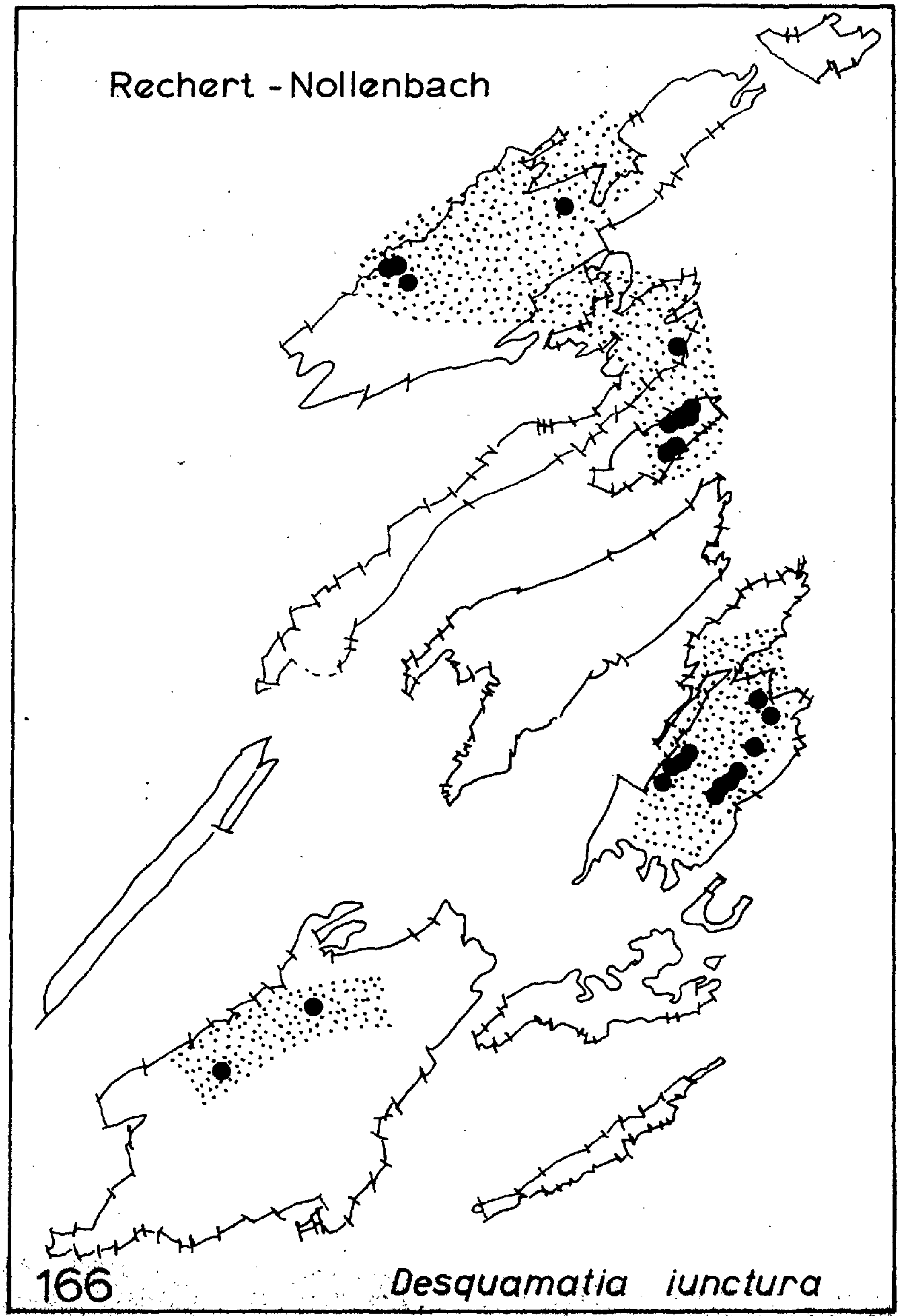


Text-fig. 165. Transverse serial sections of Desquamatia (Variatrypa) iunctura n.sp. Freilingen beds, upper Eifelian; MTB Dollendorf r51420:h75880. x2.

Material.-

The species is not abundant and specimens are spread through a biotope in which Desquamatia (Variatrypa) is a scarce faunal element. Only 96 specimens were collected (text-fig. 166).

C298)4); C301(1); C330(3); C332(1); C340(17); C343(2); C345(2); C354(1); C359(4); C361(3); C394(1); C405(1); C463(2); C465(2); C512(13); AG1(1); AG41(1); AG52(1); AG85a(2); AG239(2); BP26(1); RW23(1); St43(1); St80(1); St118(4); St122(6); St212(1); St252(1); St362(1); St252(1); St591(1); St618(1); St619(2); St672(1); St732(1); St810(1); St868(1).



Distribution of Desquamatia iunctura n. sp. in the Eifel.

## Desquamatia (Variatrypa) cf. magna (GRABAU 1931)

Pl. 41, figs. 2-3; Pl. 42, figs. 1a-c.

1931 Atrypa desquamata mutation magna GRABAU, pp. 174-176, Pl. 26, figs. 1-5.

Remarks.-

At two localities in Germnny, in black calcareous upper Givetian shales at Walheim, and in upper Givetian "Plattenkalke" near Paffrath, a large, coarsely ribbed Desquamatia occurs which bears a likeness to the species originally described by GRABAU (1931) from China. This large Desquamatia is found in the uppermost Givetian in the Kutznetsk basin of Russia, in the upper Givetian of Szechuan, China and in the same rocks in Germany. It is possibly an index fossil of the upper Givetian. It is never found with Mimatrypa desquamata (SOWERBY) which inhabited only a strict biohermal environment in rocks of that age. The two are allopatric. Desquamatia occurs in argillaceous limestones and calcareous shales, Mimatrypa in white, or light coloured, non-argillaceous, biohermal limestones.

Material.-

BMB (3) "Ob. Mitteldevon Plattenkalk, Berg-gladbach"; C239(46) Walheim. Some specimens reach a width of more than 50 mm.

## Desquamatia (Desquamatia?) schroeteri n.sp.

Pl. 42, figs. 2-3; Pl. 43, figs. 3a-d.

Name: In honour of J.S. SCHRÖTER who published the first known illustrations of Devonian atrypid brachiopods in 1777.

Type locality: Beds exposed along the sport-field and shooting stand in Refrath, Paffrath syncline, MTB Mülheim am Rhein r78120-200:h47550-80.

Type stratum: Steinbreche horizon, Refrath beds, Frasnian (F2a).

Associated fauna: Spinatrypina explanata (SCHLOTHEIM), Atrypa (Devonatrypa) europaea STRUVE, numerous tabulate corals (Alveolites!), disphyllid corals. Also Schizophoria sp., Cyrtospirifer apertutarus (SCHLOTHEIM), Guerichella sp.

Source sediment: Yellowish brown, crumbly, calcareous shales rich in coral debris.

Range: Possibly down to the Oberer Plattenkalk, sensu JUX (1964, p. 168). Absent in the Saalermühl horizon above.

Diagnosis.-

Small to medium sized, dorsibiconvex-biconvex, finely ribbed Desquamatia (about 20 ribs per 10 mm.). The ribs are straight, retaining the same wave length back to front. Globosity is rare. The interarea is relatively large, well-exposed, with an orthocline beak and deltidial plates and foramen. Growth lamellae non-deflecting, poorly defined.

Remarks.-

This species sets itself apart readily from the younger Desquamatia (Seratrypa) pectinata SCHRÖTER. It has ribs which are about half the size, which retain a constant distal sie, an orthocline beak, marked area and deltidial plates and is not as large. It has more in common with some of the Middle Devonian Desquamatia (Synatrypa) of the Eifel region.

The Langenaubach atrypid fauna, from the Frasnian reworked sediments of the Dill syncline some 100 km. to the southeast, is still undescribed. It has been mentioned by several authors, FRECH (1887, p. 16), DREVERMANN (1901, p.116) and more recently an age estimation was given by KREBS (1963, p. 72). These atrypids are more roundish, and biconvex and lack the well devolped area and orthocline beak of Desquamatia schroeteri n.sp.

LJASHENKO (1959) figured many Atrypa whose affinities to Desquamatia are uncertain and which resemble Desquamatia schroeteri n.sp. No internal structure was determined by LJASHENKO. These Russian atrypids are listed : Atrypa sokolovae LJ., A. dementjevae LJ., A. grossheimi LJ., A. martynovae LJ., A. mayselae LJ. and A. tanaica NALIVKIN (LJ. is LJASHENKO). Comparison must be left until these are redescribed, and until they can be distinguished from each other. It is not yet known if these Russian atrypids listed are, in fact, Desquamatia.

Material.-

Total 198 specimens

C201a(91); C256(107).

## Desquamatia (Seratrypa) n.subg.

Name: Latin, serus, a, um, late, lasting a long time. This subgenus appears to be one of the last survivors of the Desquamatia group of atrypids. Shortly after the group became extinct.
Type species; Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777).
Range: Frasnian, probably restricted to F1 and F2.
Distribution: Europe, North America.

Diagnosis.-

Medium to large, biconvex to dorsibiconvex Desquamatia with tendency for ribs structure to revert to an Atrypa-like state, i.e. to lose their linearity and tubular form and to become more undulating. Also with a loss of the Desquamatia (Variatrypa) type of rib micromorphology. The outlines of the shells are most commonly well-rounded, and convexity is moderate to strong on both valves. A small area and delthyrium with foramen and minute deltidial plates is exposed. Folds on the anterior margin are weak to strong.

Internally, deltidial plates are reduced mainly to an outer portion and are greatly shortened. Small lateral cavities are present. Teeth have long lateral lobes and are inwardly directed. Hinge plates and crura are thin. Spiralia so not seem to have many whorls (up to 10?). Jugal plates are Desquamatia-like.

Remarks.-

The structure of the teeth and jugal plates seem to strengthen the links of this species group to the genus Desquamatia, although a return to an Atrypa-like rib morphology and shell shape is evident. It proaably was derived from a Desquamatia (Variatrypa) ancestor, the last distinct species of which appears to be the late Givetian D. magna (GRABAU).

Member species.-

Terebratulas pectinatas SCHRÖTER, Atrypa rustica STAINBROOK, Atrypa devoniana var. bentoensis STAINBROOK, Atrypa rotunda STAINBROOK, Atrypa reticularis alta FENTON?, Atrypa oneidensis BEUS.

## Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)

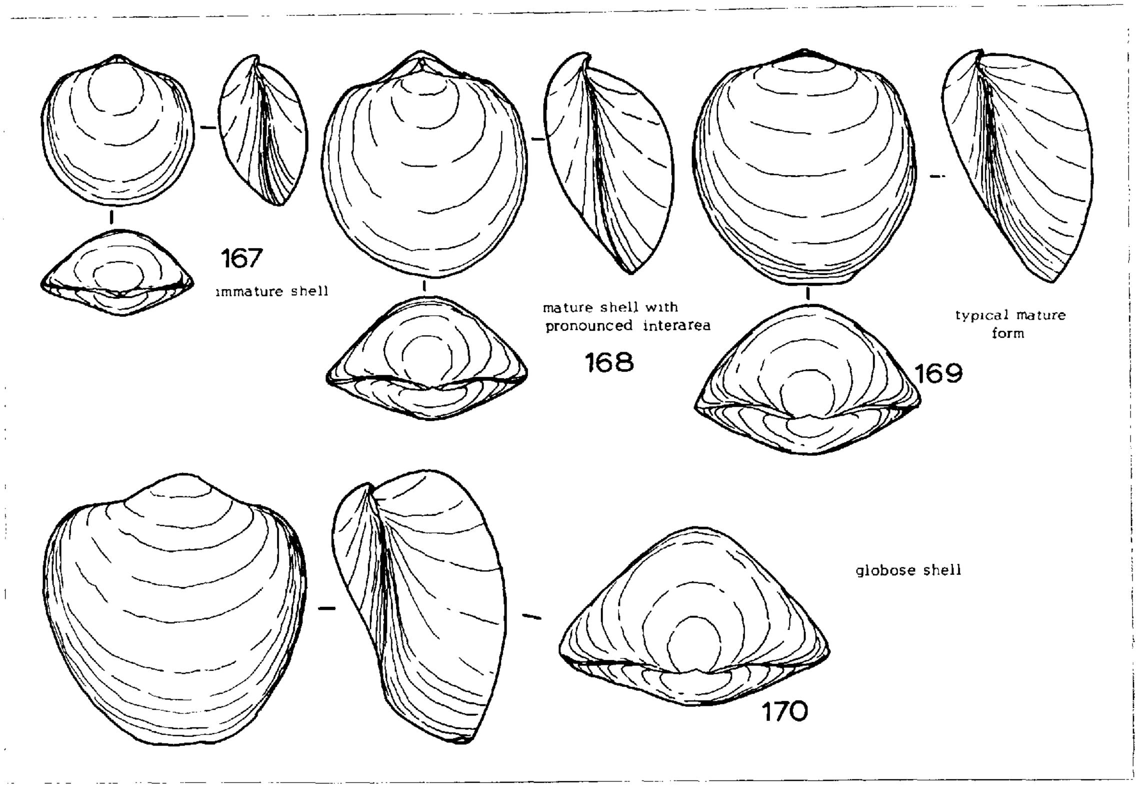
Pl. 43, figs. 1-2; Pl 44, figs. 1-2; Pl 45, figs. 1-3; Pl. 46, figs. 1-4; text-figs. 167-172.

1777 Terebratulas pectinatas SCHRÖTER, pp. 372-373, Pl. 3, figs. 10, 11, ?14.

Locus typicus: "Bensberg" (SCHRÖTER 1777, p. 373).
Restricted type locality: Small section along Saaler-Mühl Bach in the town of Refrath near Köln. MTB Mülheim am Rhein r78140:h47540.
Type stratum: Soft, platy to blocky, pale brown limestones about 5 m thick at the type locality.
Associated fauna: The fauna is almost monotypic, and consists of about 90% atrypid specimens. Cyrtospirifer aperturatus (SCHLOTHEIM) is rare. Also a few rare and isolated slender, cylindrical corals.
Range: Probably mainly F2b-c, Frasnian, Upper Devonian.

Diagnosis.-

Large sized, ovoid, longer than wide, dorsibiconvex shells with anacline-epicline beaks, a small area and triangular delthyrium with minute foramen. Ribs coarsen distally, from 12-14 ribs per 10 mm at 15 mm from the apex and 10 or less at 20 mm from the apex. Widely spaced, weakly deflected lamellae (at 3-4 mm spacing) and more strongly deflected antero-ventral shell portions. The fold is moderate to steep (text-figs. 167-170).



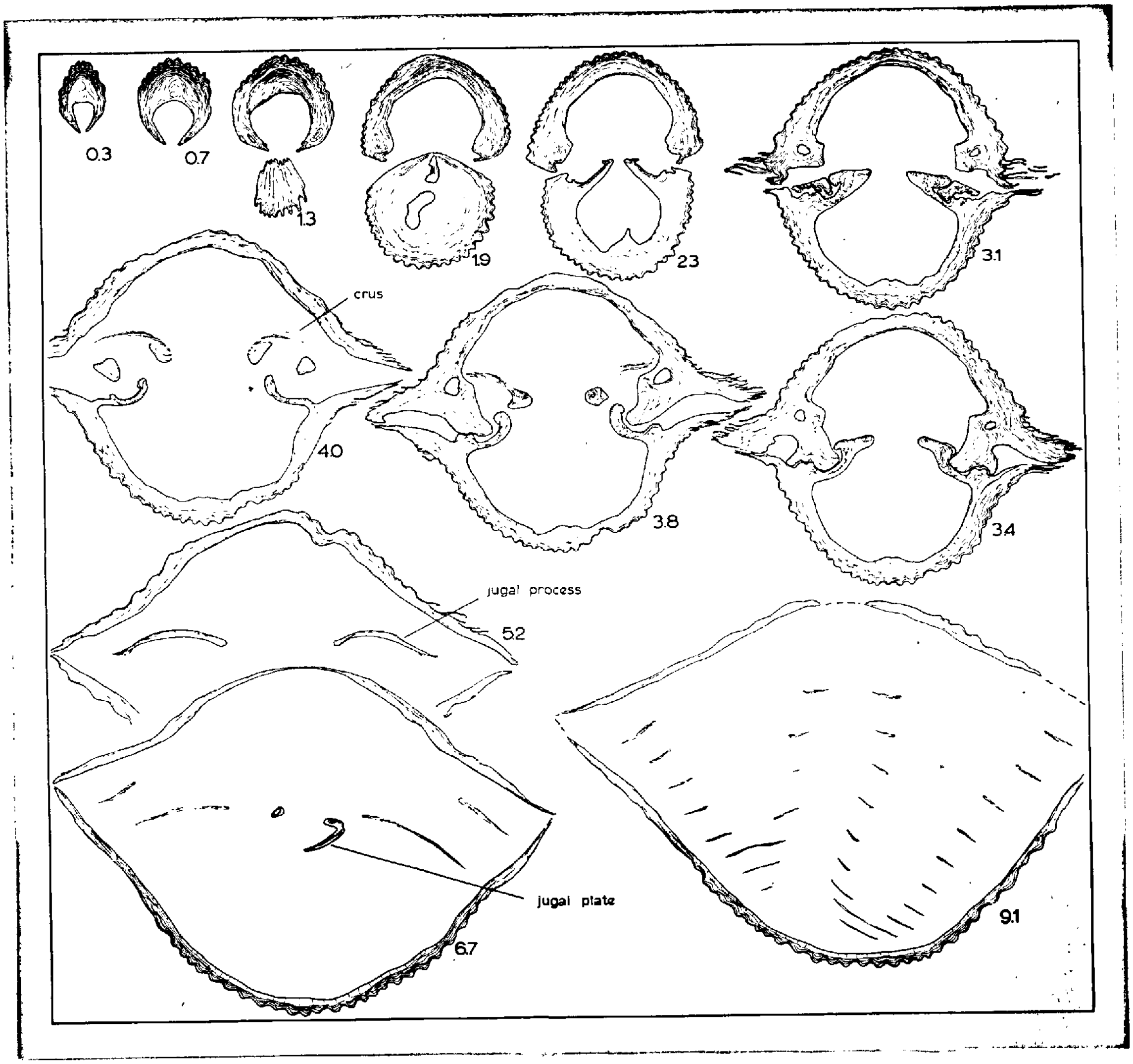
Text-figs. 167-170. Shell variation of Desquamatia (Seratrypa) pectinata (SCHRÖTER). Type locality. x1.

Internally, the shell is thin, muscle scars weakly impressed. A pedicle collar is absent. Teeth partially disjointed at the base (text-fig. 171), and have relatively large lateral cavities distally. The cardinal process is small, hinge plates thin, crura long and delicate, not feathered. Jugal plates hook-like as in normal Desquamatia (Pl. L, fig. 2). Spiralia are sparsely whorled, only 8 whorls were counted in a large specimen.

Remarks,-

This species has been represented in numerous fossil collections because of the fame of the type locality. The locality, at Refrath near Köln, has been known for about 200 years and collections from it have been labelled Paffrath, Bensberg or even Eifel(which is about 150 km. to the southwest).

Desquamatia pectinata can be distinguished from another Refrath species Atrypa (Devonatrypa) europaea STRUVE in its much finer apical ribbing, in its rib structure, in its lamellar structure, in its shape and size



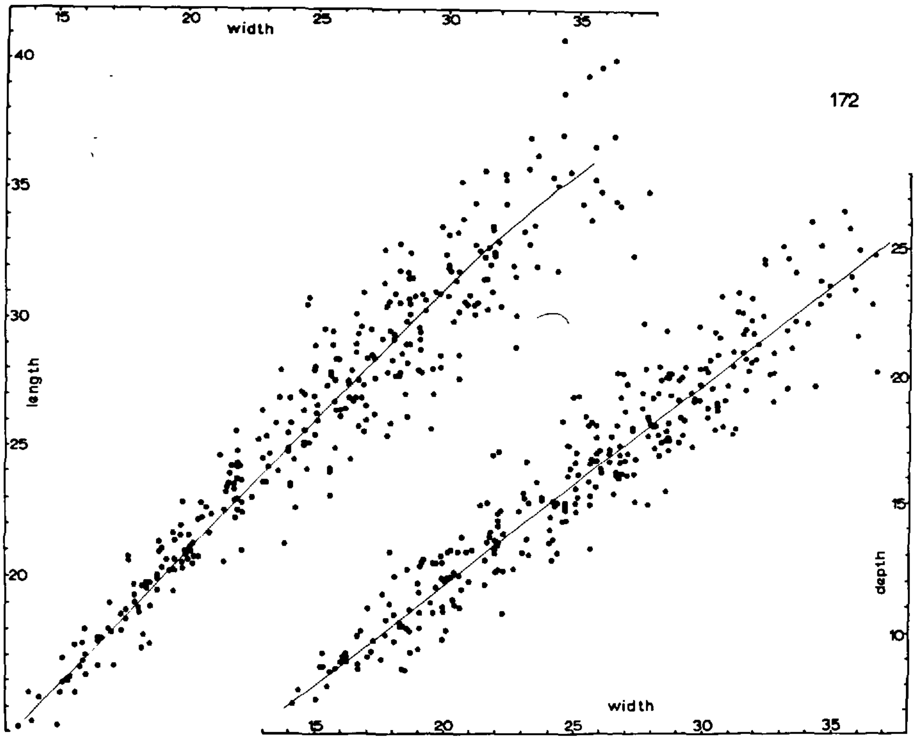
Text-fig. 171. Transverse serial sections of <u>Desquamatia</u> (<u>Seratrypa</u>) <u>pectinata</u> (SCHRÖTER 1777) Saalermühl horizon, Refrath beds, Frasnian; MTB Mülheim am Rhein r78140:h47540. x3.

and its small area and delthyrium externally. Internally it has lateral cavities, a thin shell, and thin hinge plates. A summary of size relationship is shown in text-fig. 172.

Long frills are very common on the shell margins (Pl 43, fig.2).

<u>Material</u>.-

C201b(521 specimens) MTB Mülheim am Rhein r78140:h47540.



Text-fig. 172. Scatter diagrams of Desquamatia (Seratrypa) pectinata (SCHRÖTER) from the type locality.

## Genus Gruenewaldtia CHERNYSHEV 1885

Type species: Terebratula latilinguis SCHNUR 1851, p. 7.
Range: Eifelian, Givetian?, Middle Devonian.
Distribution: Europe, Novaya Zemlya island, Urals, Kutznetsk basin, Russia. Possibly arctic Canada.

Diagnosis.-

Planoconvex to biconvex shells with long, uninterrupted ribs and lacking growth lamellae. Fine concentric microsculpture. Orthocline to anacline beaks project over a distinct, partly round-edged area, large delthyrium with disjunct deltidial plates and apical foramen. Frills not known. Weak fold on the anterior commissure.

Internally the muscles are elevated on septally raised muscle bases. Dental nuclei or lateral cavities are prominent. Jugal processes tipped with spines, disjointed.

Remarks.-

CHERNYSHEV, in establishing the genus (1885, pp. 46-47, 89) designated as type the species which SCHNUR described from the Eifel in 1851. The Eifel species appeared to CHERNYSHEV to be conspecific with Russian specimens from Kadinsk in the Ural mountains. GRUENEWALDT (1860) had previously described the Kadinsk atrypids as Spirigerina latilinguis (SCHNUR). Both CHERNYSHEV and GRUENEWALDT based their comparisons on external morphology.

In 1960 RZHONSNITSKAYA sectioned specimens of the Russian atrypids which had been compared to Terebratula latilinguis SCHNUR, and found (using STRUVE's revision in 1955 of Gruenewaldtia latilinguis as a guide) that the Russian atrypids lacked the muscle platforms which characterise the type species of Gruenewaldtia. RZHONSNITSKAYA (1960, p. 50) therefore redescribed the Russian atrypids under a new name Pseudogruenewaldtia and defined a new species P. tschernyschewi to include them. Unfortunately, by 1964 RZHONSNITSKAYA has still left Pseudogruenewaldtia in the family Palaferellidae where it does not belong. The genus Pseudogruenewaldtia does not occur in the Eifel or east of the Rhine, but it may include Frasnian atrypids as Atrypa zonata (in DAMES 1868, p. 497) and as Atrypa reticularis (in KAYSER, 1883, p. 103), respectively from southeastern Poland and China.

The North American atrypids attributed to Gruenewaldtia, e.g. "Gruenewaldtia" gregeri (ROWLEY) in GREGER 1932, anf "Gruenewaldtia" americana STAINBROOK 1945 also cannot be attributed to that genus. The first may belong to Pseudogruenewaldtia and the second possibly to Anatrypa (pendant on a revision of the latter).

The youngest known Gruenewaldtia is G. sibirica IVANOVA 1962. This is alleged to come from Givetian beds of the Kutznetsk basin in Russia. In the Eifel region of Germany the genus has never been found in Givetian. IVANOVA (1962, p. 73) also states that the genus has been found in Lower Devonian rocks, but she does not describe a species of that age. The oldest species in the Eifel region is G. prooemia n.sp. from the Weilersbach horizon in the Nohn beds (low Eifelian).

The known geographic occurrences are few because so little work has been done on internal structures of many atrypid species. In Europe, the genus is knowm from Devon (COPPER 1965), the Ardennes in Belgium (personal collection), the Eifel, Bergisches Land in Germany and eastwards as far as Poland (BIERNAT 1964). There are no reported occurrences in France, Spain, Morocco, Italy. The genus is now known from Novaya Zemlya island (Morley collection British Museum of Natural History : personally sectioned) from the Tisenhausen peninsula (refer to

MILORADOVICH, 1947, pp. 42-48). The genus is not presently known in China, Burma, Australia or New Zealand. There are still no verified occurrences in North America (except those discussed above). It is possible that an atrypid described and figured as Vagrahia sp. (BOUCOT et al, 1964, Pl. 128, figs. 10-12) from Bathurst Island in Arctic Canada, is a Gruenewaldtia.

Comparison.-

Gruenewaldtia can be separated from the Russian atrypid genera which have similar external morphology((e.g. Anatrypa NALIVKIN, ?Pseudogruenewaldtia RZHONSNITSKAYA) by their rib structure, which is straight, tubular, and lacks growth interruptions, and their microornament of numerous microscopic growth lines. Internally, they are, of course, unmistakable in their septally-elevated muscle platforms.

Unfortunately, at a critical stage in the development of Gruenewaldtia in the Eifel, during the Freilingen time, the genus is lightly confused with two other synchronous atrypids, Desquamatia and Mimatrypa, and, other than by means of sectioning each specimen, these three are virtually impossible to tell apart. Mimatrypa, which is believed to evolve from Gruenewaldtia at this stage (Freilingen beds), tends to have a flatter pedicle valve and has slightly coarser ribs, identical features present in late Eifelian Gruenewaldtia. Even laterally, Gruenewaldtia grades into Mimatrypa, the late stages of platform cementation of one grading into early stages of the other. Desquamatia is merely homeomorphic; externally it shows a strong loss of growth lamellae, but internally it is distinct in its lateral cavities and lack of muscle platforms.

### Gruenewaldtia prooemia n.sp.

Pl. 47, figs. 1-3; text-figs. 173-175.

Locus typicus: Road cutting nearly 1 km west of Lissingen on the road to Büdesheim, MTB Gerolstein r44890:h64630.
Stratum typicum: Weilersbach horizon, Nohn beds, lower Eifelian.
Range: Weilersbach-Schleit horizons, Nohn beds, lower Eifelian.
Source sediment: Dark greenish gray calcareous shales or thin bedded argillaceous limestones with abundant, small-sized bioclastic debris, poorly sorted.
Associated fauna: Primarily brachiopods, most of which are rather small, but a number of small platy tabulate corals and even a few simple corals are present. Stromatoporoids, not massive, are present near the top. Desquamatia is still rare, Atrypa common, a few Spinatrypa; rare Gypidula, a few stropheodontids and trilobite remains.

Diagnosis.-

Small, nearly biconvex atrypids with well-rounded, globose umbones and apsacline to orthocline beaks, well defined, quite large delthyria and rounded interareal edge. Commissures are weakly folded. Internally, numerous minor septa support the platforms in addition to the two major ones. There may, as well, be other major septa. Lateral cavities are large and expanded.

External form.-

Most specimens are small; maximum observed width about 22 mm , average 16-18 mm , maximum depth nearly 12 mm. Shell shape is oval, but slightly pointed at ine end. Maximum width at half-length. The commissure is weakly folded.

The ventral beak is well-rounded and globose, expanded, but blunt-tipped. Umbonal slopes are round and steep. The edge of the area is round and poorly defined. The shoulder line is weakly indented. Hinge corners are round and not defined. Delthyrium and foramen are relatively large, the foramen is commonly expanded into the umbo.

The dorsal valve is moderately convex, almost equal to that of the opposing valve. The umbo is exposed. There is little shell flattening distally. Maximum convexity is at mid-length.

Ribs.-

No rib plan was formulated due to lack of well preserved material. There appears to be little expression of the mid-rib pair which may be flanked by three or more septa. Rib concentration is about 16-18 per 10 mm of arc. Ribs are well-incised, somewhat coarse with rather deeper troughs. Crests are rounded and thicker than troughs.

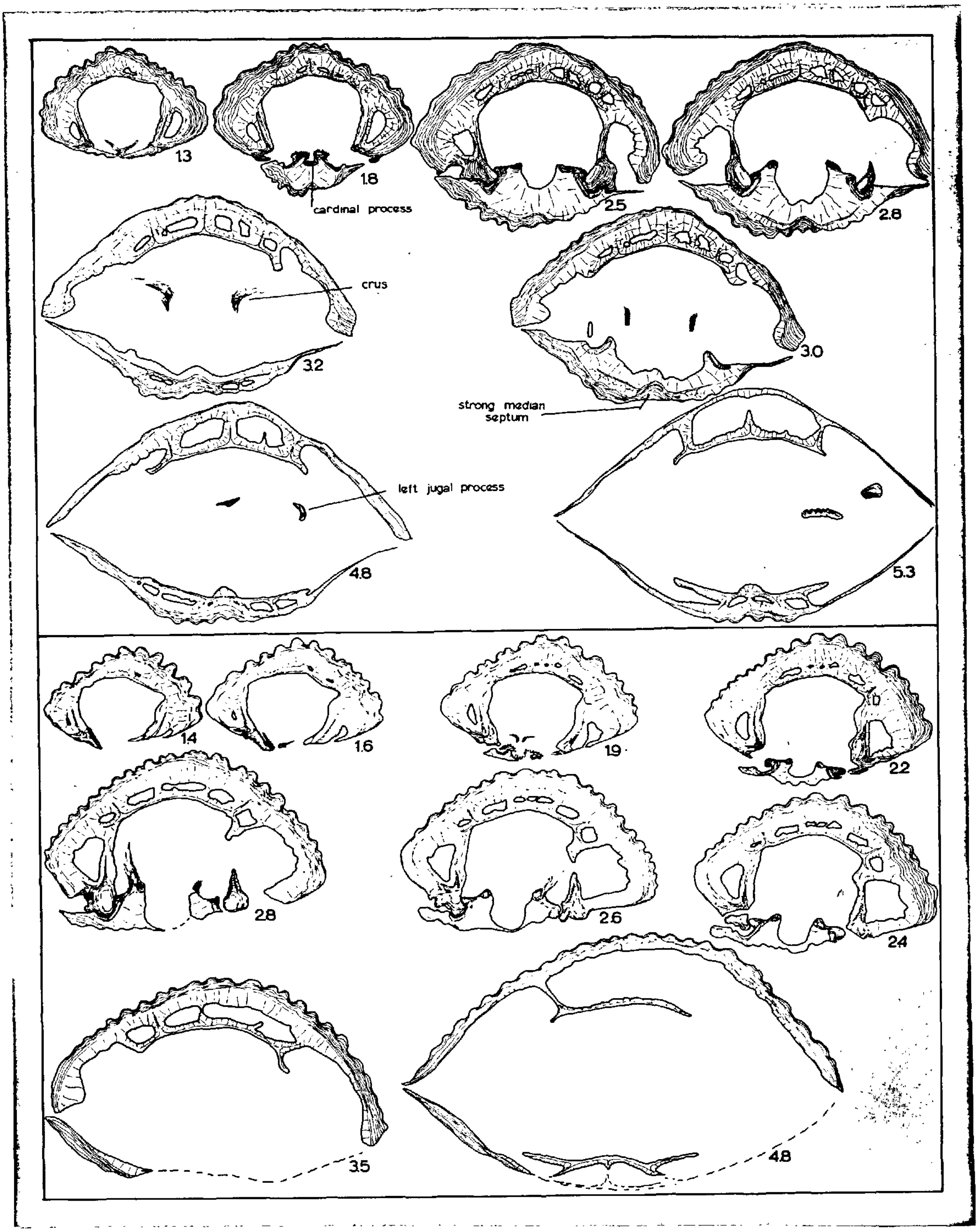
Growth lamellae.-

External identification as the genus Gruenewaldtia is rather difficult. Growth interruptions are relatively well defined and abrupt and they are more distinct and numerous than on other members of Gruenewaldtia. No frills were observed. Poorly preserved specimens showed little trace of microscopic growth lines.

Growth and variation.-

Insufficient material was available to study growth and variation. Specimens are, as a rule, small and show little beak incurvature. Initially beaks are apsacline and the interarea and foramen proportionally very large. The commissure remains nearly rectimarginate.

The variation is not great, to judge by available material. Some specimens show affinities to Gruenewaldtia matutina STRUVE, in that they are flattened and finer ribbed, and particularly in the asymmetry and irregularity of platform support.



Text-figs. 173-174. Transverse serial sections of <u>Gruenewaldtia</u> <u>prooemia</u> n.sp. Weilersbach-Schleit horizons, Nohn beds; 173 (top), MTB Gerolstein r44890:h64630, 174 (bottom), MTB Dollendorf r57000:h78230. x4.

Internal markings.-
These are still unknown.

Internal structure.-
A pedicle collar is absent (text-figs. 173-174). The deltidial plates show no definite signs of being hollow. On their inner margin, the characteristic incipient collar is preserved. Teeth are short and show extremely large lateral cavities. The main lobe is thin, the lateral lobe is insignificant. The muscle plate, particularly at the margins, is not well defined. Two major septa flank two strong minor septa, in between which are, in turn, two additional small septa. Alternatively, one major septa may replace the first two minor septa mentioned above, or numerous other minor septa may be inserted (see text-fig., 173-174).

The brachial valve shows a thick, bushy cardinal process. The cardinal block is strongly developed, but cocket plates are small. Inner socket ridges are short and stubby. Inwards, inside the socket plates, are the ventrally directed crural supports. Crura are feathery distally. Jugal processes are typically three-layered with an intermediate columnar layer. Complete spiralia have not been observed. The muscle platform, in addition to having two major lateral septa, shows a strong median septum mainly due to thickening and bulging of the shell floor. There may also be a complex of minor septa and an addtiional pair of major septa, one on each side of the central major septa.

In general, the further down the stratigraphic column, the more complex and confusing the septal arrangement. Specimens with only two major septa in each valve may already be present in the Schleit horizon, but none of these have been seen in the lower Weilersbach horizon.

Remarks.-
The species can be distinguished from Gruenewaldtia matutina STRUVE by its coarser ribs, smaller overall size and greater globosity, only weakly incurved beak and more bulbous ventral umbo. Internally these two species appear at present to be quite similar in the asymmetry and irregularity of septal distribution. Type material of G. matutina has not been sectioned in detail and the inked drawings in STRUVE (1955, figs. 8b-i) do not reveal the difference between major and minor septa and the thickness and development of the muscle plate.

Although there is a possibility that G. prooemia n.sp. is merely a subspecies or variety of G. matutina, this does not appear to be likely. The latter has strong affinities with G. latilinguis, and appears to be younger in age (upper Schleit, even as high as Ahrdorf). It is not unfeasible that G. matutina is synonymous with G. rhenana, although a distinction is made by STRUVE (1955).

*G. prooemia* n.sp. is of Weilersbach-low Schleit age and has the widest distribution of any *Gruenewaldtia* in the Eifel in spite of its rarity. It is found in the upper 4 m of the Urft horizon in the Sötenich syncline (as in PAULUS 1959, p. 354), which makes a close correlation between these horizons possible. It is thought that the specimens assigned by SPRIESTERSBACH (1942) to *G. rhenana*, the material of Hobräcker age, may be assigned to this species.

Material.-

C274a(1);Doll r5434:h7904; C398(10) Gerol r4489:h6463; C452(1) Blank r5417:h9508; BP80(1) r4464:h9486; St19(4) Doll r5477:h7459; St304(3) r5489:h7838; St830(1) r53525:h78330; H252(1) r5700:h7823; C451(1) Blank r4469:h9477.

Only 24 specimens have been found. The species and genus is decidedly rare so low in the Eifelian but its geographic distribution follows the distinctive Nohn facies patterns (text-fig. 175).

## *Gruenewaldtia rhenana* (SPRIESTERSBACH 1942)

Pl. 47, figs. 4a-d; text-figs. 176-177.

1942 *Palaferella rhenana* SPRIESTERSBACH, pp. 187-189, Pl. 7, figs. 1a-b.

Remarks.-

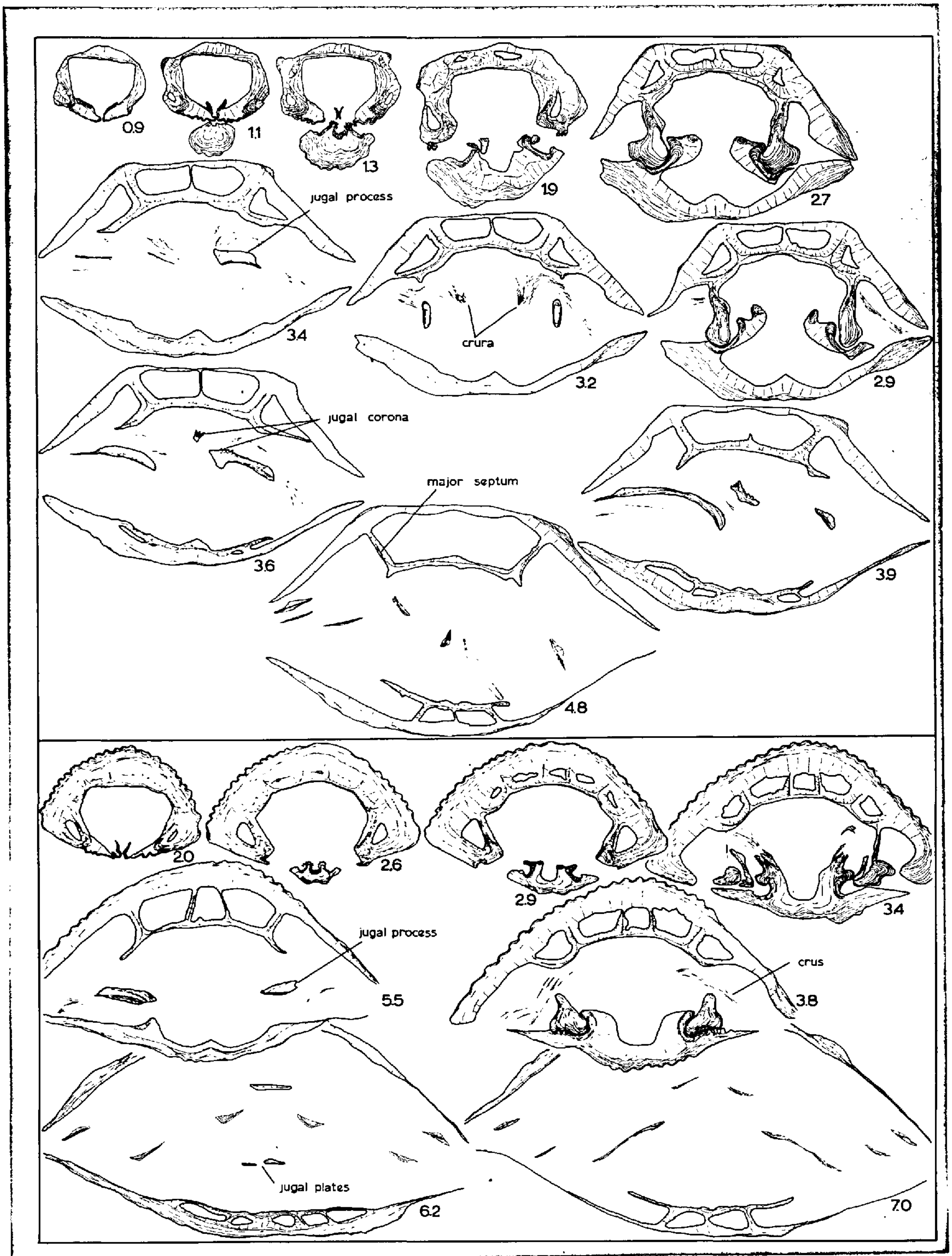
No revision of this species was undertaken. In spite of the investigation by STRUVE (1955, 1964) the true nature of *Gruenewaldtia rhenana* remains thoroughly confused until type material of SPRIESTERSBACH, or topotypic material from the Hobräcker beds east of the Rhine is serially sectioned. This doubt about the identity of SPRIESTERSBACH's species rests largely on the confusion in the designation of the type material. In his description SPRIESTERSBACH identified a specimen from the Eifel region as holotype ( in spite of the fact that he was not dealing with Eifel material), and in the explanation to the plate, he selected a specimen from the Hobräcker beds, east of the Rhine, as holotype. Two different holotypes of the same species therefore existed. When STRUVE (1955) revised the genus *Palaferella* (=*Gruenewaldtia*), very unfortunately, the Eifel specimen, for which no locality or horizon was available, was irrevocably selected as type. Later, STRUVE (1964, p.435) believed that he had accurately located the source beds of SPRIESTERSBACH's Eifel specimen, and pinpointed these beds as the Ahrdorf beds. The question then remained if the remaining SPRIESTERSBACH material, that from Hobräcker beds, was also of Ahrdorf age and therefore probably synonymous with the lectotype of *Gruenewaldtia rhenana*. Apparently STRUVE believes this correlation of Hobräcker beds with Ahrdorf beds to hold. WEDEKIND (1924, p. 91) similarly correlated the Hobräcker beds with the fauna of the Heiligenstein beds (i.e. Ahrdorf beds in the Gerolstein syncline).

The correlation between Hobräcker and Ahrdorf beds is doubtful. SPRIESTERSBACH gives the Hobräcker beds a stratigraphic position considerably below the Ohler beds which are known certainly to be of Ahrdorf age. Furthermore, despite the gradual and overlapping changes between different species of Gruenewaldtia, there is evidence from SPRIESTERSBACH's illustrations and descriptions that two species may actually be submerged by the name G. rhenana. One of these is the Eifel species of Ahrdorf age selected by STRUVE (1955) as lectotype, and the other is a species probably of Nohn age, which represents material from the Hobräcker beds.

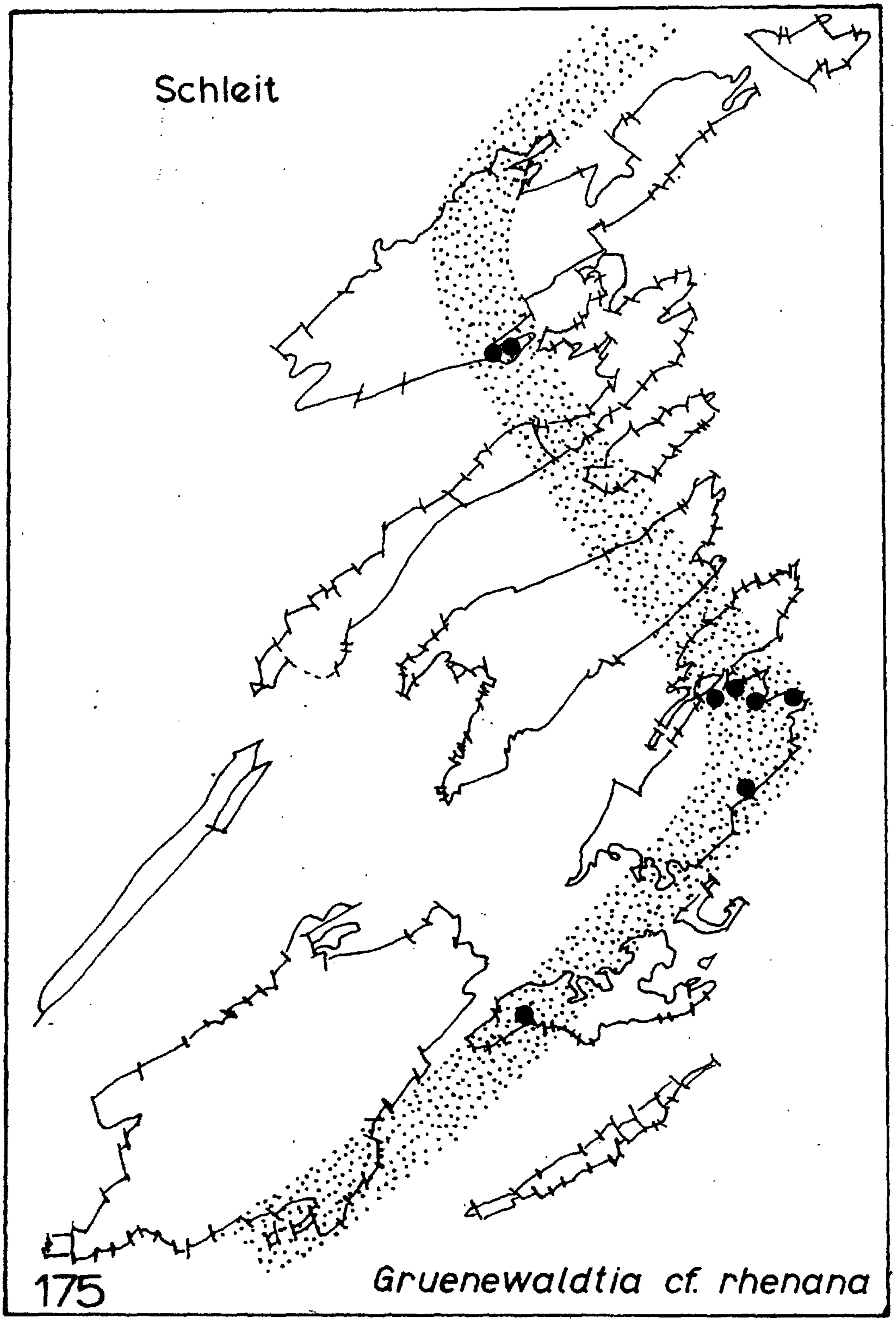
SPRIESTERSBACH (1942, pp. 187-188) deduced from prepared material from the Hobräcker beds, that the ventral muscle platform was supported by five radial septa and that the dorsal platform was supported by three septa (ibid., Pl. 7, fig.2g), 3-5 septa (ibid., p. 187) or 5 septa (ibid., p. 188). It is clear that he is not describing Gruenewaldtia latilinguis (SCHNUR), with which he never makes a comparison, though surprisingly listing it in the same faunal list as G. rhenana. The two outermost of the five ventral septa which SPRIESTERSBACH listed probably are simply down-curved portions of the muscle platform. This means that three ventral septa probably were observed. Similarly, the variation from 3-5 dorsal septa may be explained that the outer portions of the muscle platforms were counted as septa.

Two specimens of Gruenewaldtia were sectioned for comparison. The precise stratigraphic position of these specimens is not known, but they are estimated. By means of serial sectioning, a distinction can be made between major and minor septa which appears to assist in determination of stratigraphic position. This method may be applied when topotypic G. rhenana specimens are to be sectioned. A major septum is defined as one having a spine or core of calcite continuous with the single crystal which forms the muscle plate; a minor septum as one which has no spine. From the sectioned material, it seems likely that by Ahrdorf time, all major septa, other than the two main or dominant septa, had disappeared. The number of minor septa is variable, though minor septa also had disappeared by Junkerberg time, except in a remnant form (see sections of G. latilinguis (SCHNUR)). It is possible, therefore, to distinguish between G. matutina STRUVE of Nohn age (text-fig. 177) and G. rhenana (SPRIESTERSBACH) of Ahrdorf age ( in the revised sense of STRUVE 1955), as seen in text-fig. 176.

Material.-
4 specimens (to be revised)!



Text-figs. 176-177. Transverse serial sections of: *176*, *Gruenewaldtia* cf. *rhenana* (SPRIESTERSBACH), Ahrdorf beds?; "Strassenboschung zu Lennhausen, Finnentrop" (W.E. SCHMIDT coll., Berlin), *177*, *G.* cf. *matutina* STRUVE, Nohn beds?; Hillesheim syncline (HERTA SCHMIDT coll., Frankfurt). x4.



Distribution of Gruenewaldtia prooemia n.sp. in the Eifel synclines.

**Errata:** Disregard G. rhenana.

## *Gruenewaldtia latilinguis* (SCHNUR 1851)

Pl. 48, figs. 1-4; Pl. 49, figs. 1-4;
Pl. 50, figs. 3a-c; text-figs. 178-185.

1851 *Terebratula latilinguis* SCHNUR, p. 7.
1853 *Terebratula latilinguis* SCHNUR, SCHNUR, p. 183, Pl. 25, figs. 1a-f.
1871 *Atrypa reticularis* var. *latilinguis* (LINNE), KAYSER, p. 545.
1882-4 *Atrypa latilinguis* (SCHNUR), DAVIDSON, p. 41, Pl. 2, figs. 9, 9a.
1894 *Gruenewaldtia latilinguis* (SCHNUR), HALL, P. 52, figs. 34-6.
1955 *Gruenewaldtia latilinguis* (SCHNUR), STRUVE, pp. 211-1, 228-9, Pl. 1, figs. 1-2; Pl. 2, fig. 3; Pl. 3, figs. 17a-c; Pl. 4, figs. 18a-c.

*Locus typicus*: SCHNUR lists only Gerolstein as a locality for his species, but it is more abundant in other parts of the Eifel, particularly in the Hillesheim syncline and on the north flank of the Prüm syncline. The type locality is herewith designated as the SW end of Hönselberg, Hillesheim syncline, MTB Hillesheim r52960:h73640 (type locality Hönselberg horizon).

*Stratum typicum*: Honselberg horizon, Junkerberg beds, middle Eifelian. A fauna possibly already Rechert age (C394) contains abundant *Gruenewaldtia* which show advanced features such as strong thickening and coagulation of the muscle platforms, crural bases widely separated from socket plates and monostructural deltidial plates and pedicle collars.

*Source sediment*: Moderate brown calcareous shales with rarer thin interbeds of argillaceous fine grained limestone commonly showing "pelletoidal" microtexture. Little bioclastic debris is present. Specimens are well-preserved.

*Associated fauna*: A rich brachiopod horizon in which atrypids, particularly *Gruenewaldtia* and *Desquamatia* (*D. subditiva* COPPER) play a major role. There are other small species of *Atrypa* and *Spinatrypa* (rare). Other common brachiopods are *Uncinulus*, *Hypothyridina*, *Pugnax*, *Pentamerus*, *Dicamara* and *Athyris*. Corals are not very abundant.

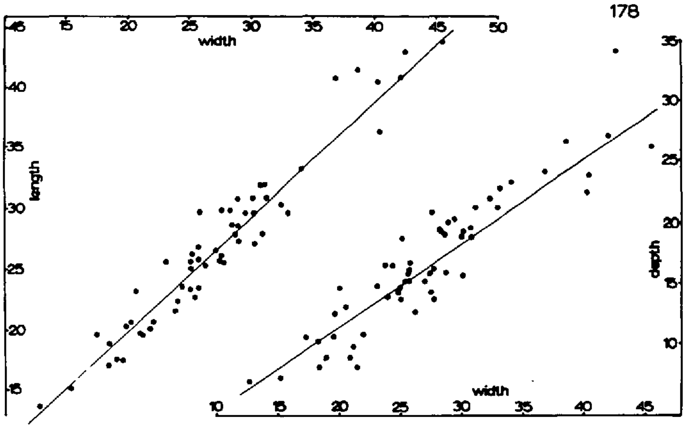
*Diagnosis*.-

Large finely ribbed *Gruenewaldtia* with two major septa supporting both muscle platforms; the ventral platform may be additionally buttressed by a small single or forked remnant septum and two weaker, lateral minor septa (between major septa), and the brachial platform may have a single weak median support. A pedicle collar may be present but is usually only poorly developed. The lateral cavity consists only of a thin slit or may be absent.

## Description

External form.-

Maximum observed width 45 mm , length 43 mm and depth 34 mm ; the majority come in 24-30 mm range of width (text-fig. 178). Outlines are round, globosity common. A weak anterior fold is not expressed in the form of a ridge and trough on either valve. Margins are often slightly appressed. The pedicle valve is more convex. Maximum width is at mid-length.



Text-fig. 178. Scatter diagrams of Gruenewaldtia latilinguis (SCHNUR). Data combined from localities C302, C357, C389, C394. Hönselberg-Rechert horizons.

The strongly convex, well-rounded, rather bulbous posterior portions of the pedicle valve are typical. Convexity decreases distally. Hinge corners are rounded, but still weakly defined. The beak protrudes well above the hinge line and is strongly incurved in maturity. The beak slopes and edge of the palintrope are also rounded. Deltidial plates are small to moderately sized and crenulated. The apical foramen is not expanded into the umbo - it is flanked by two slightly upturned deltidial plates.

The brachial valve is broadly convex and more planar than the pedicle valve. The apex is often inturned and hidden by deltidial plates and beak.

Ribs.-

The radial ornamentis fine and extremely regular, maintaining a spacing of 18-21 per 10 mm of arc from back to front. Rib plans have been described by STRUVE (1955, p. 229). On the pedicle valve an apical single mid-rib bifurcates roughly three times in the first 4 mm ; 3 to 4 ribs flank the mid-rib at the apex. The brachial apex is obscured in maturity, but a few young specimens show a small median groove with a weak rib and 4 to 5 lateral ribs at the apex. The rapid bifurcation on the ventral valve and intercalation on the dorsal valve and their variation from one specimen to the next make a detailed rib plan of little value.

Ribs themselves have wide crests which tend to overshadow or bulge over the thin, narrow troughs. As a result, the growth lines in troughs are obscured.

Growth lamellae.-

No distinct lamellae are present and they are usually so vague and indistinct as to be virtually absent. Weak swellings are observed at 15 mm from the apex and further anteriorly, but these are intermittent and discontinuous. STRUVE (1955, Pl. 4, fig. 23a) figures a short "Wachstumslinie" which cannot be interpreted as a frill.

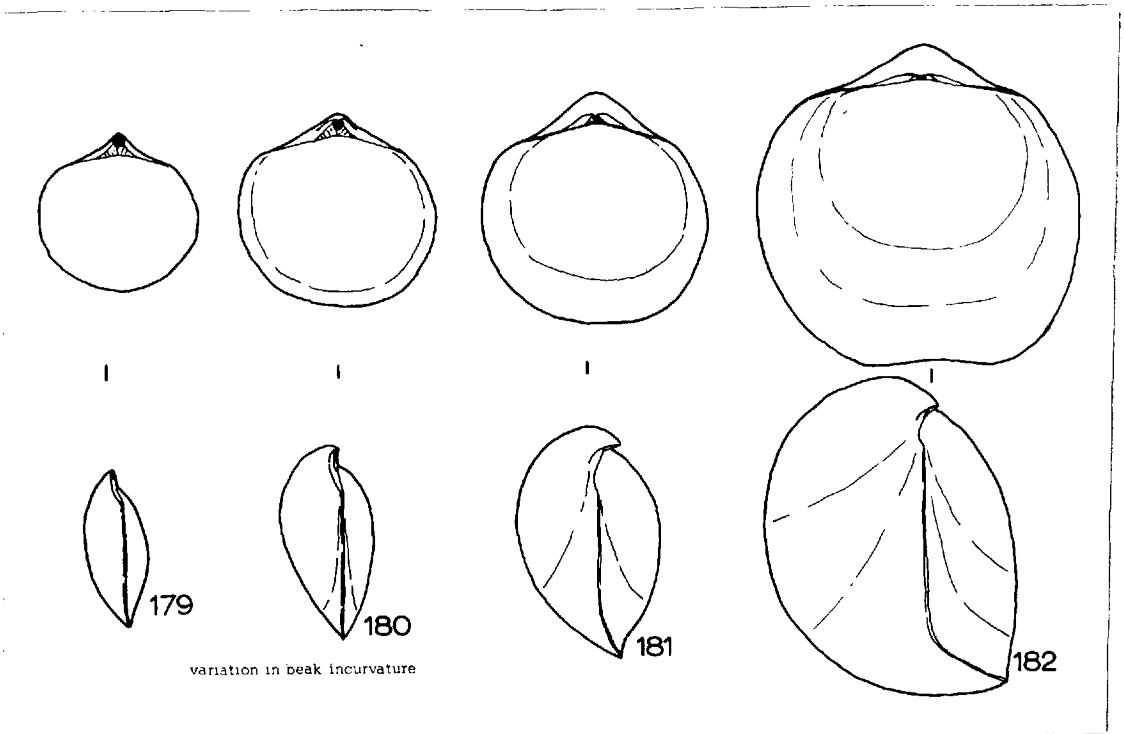
Internal markings.-

The characteristics markings are shown in STRUVE (1955, Pl. 3, figs. 17a-c). Although this species is of doubtful affinity to topotypic material of G. latilinguis and is called G.latilinguis var. P. by STRUVE (op. cit., p. 230). It is possible that this form corresponds to material collected at locality C394, of Rechert-Nims age.

Fresh information is presented in specimens from this locality and figured on Pl. 48. The pedicle clearly was attached to the wall of the delthyrial cavity, leaving a striking circular muscle scar (Pl. 48, fig. 1). A slit-like depression separates the slim, elongated, small adductor scars. From, and underneath the muscle platform extends a broad median ridge. Ovarian markings are numerous, minute and radially arranged. The brachial valve shows strong variation of muscle platforms with the size of specimen. A small specimen shows a straight-margined, angular, very smooth platform with a weak median septum which is barely visible. In a larger specimen, the angularity and thinness of the platform have largely disappeared. The median septum is thick and round, and divided anteriorly. Ovarian markings are distinguishable only at the sides of the muscle platforms.

Growth and variation.-

The two most obvious ontogenetic changes are those of globosity and beak incurvature (e.g. as in fig.. 179-182). There is no migration of the foramen through the umbo and no twisting of the beak. Concomitant with beak incurvature, the ventral muscle platform also shows curvature dorsally, up to a degree where the plane of the deltidial plates makes an acute angle with the distal portions of the platform. The platform essentially remains parallel to the plane of the lateral commissure.

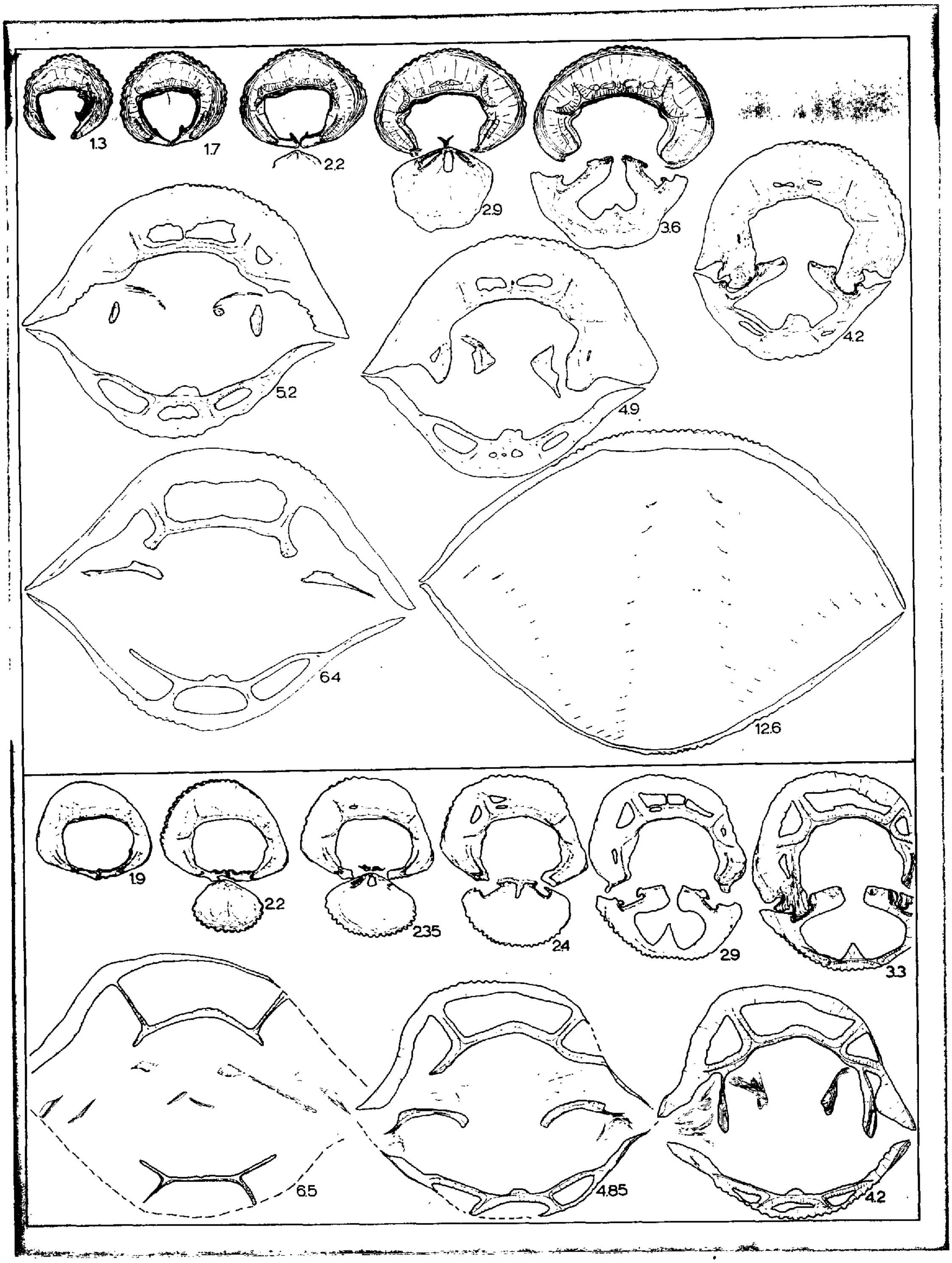


Text-figs. 179-182. Variation in beak incurvature with age. Gruenewaldtia latilinguis. Random localities. x1.

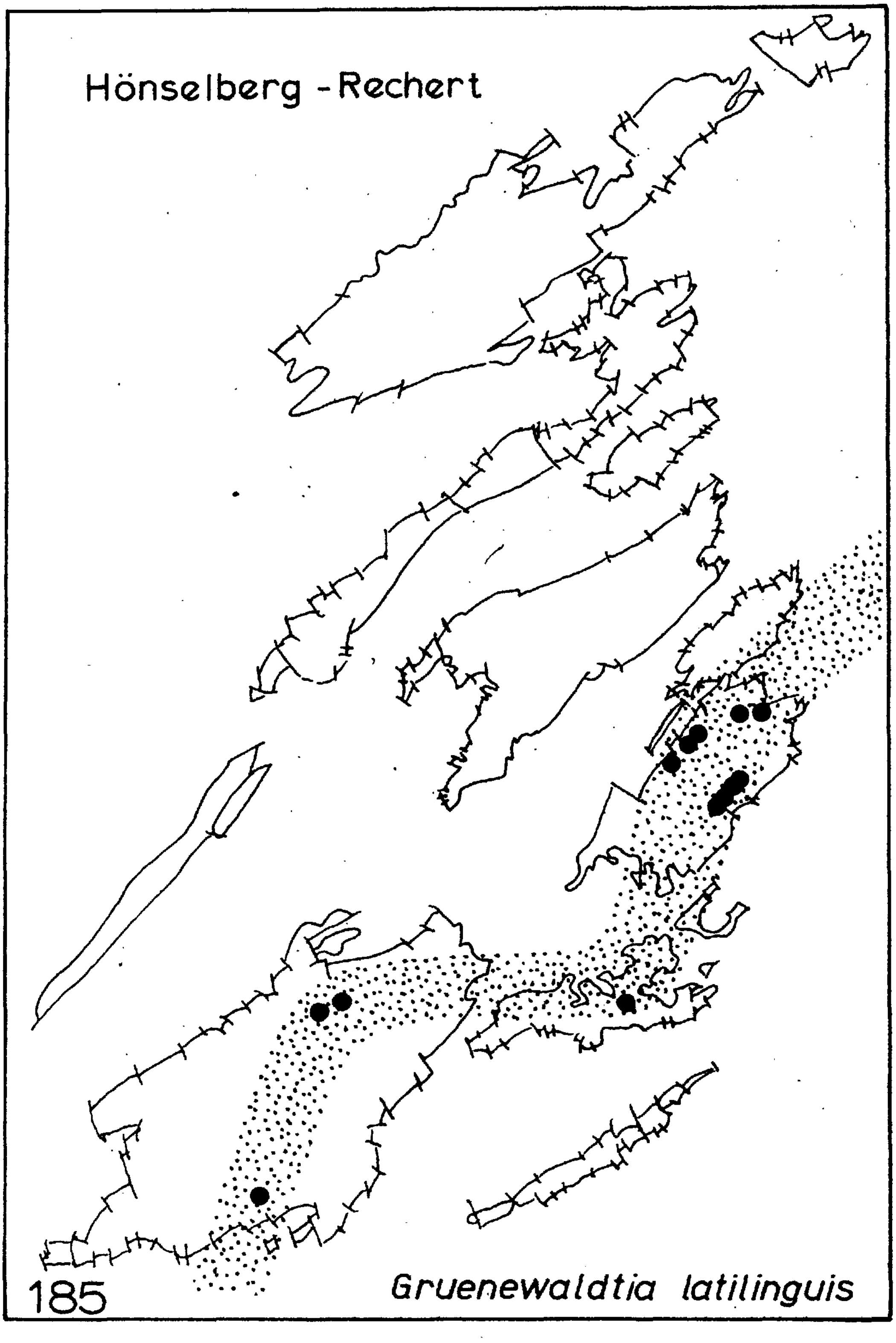
Internal structure.-

A weak pedicle collar is present : it consists of a thin, often only poorly or partially preserved free neck at the apex which, distally, is connected to the dental plates in thicker layers. The deltidial plates show a variety of structure which is difficult to interpret. The outer portions of the deltidial plates show few growth lines and consist of rather coarse calcite crystals; the inner margins are lined by the typical inward protrusions. Teeth are sub-vertical to vertical in position, straight and moderately long, with slight distal inward geniculation of the main lobe. Lateral lobes are very weak. Lateral cavities are slit-like or virtually absent. Septal support for the muscle platform is discussed in the diagnosis.

The narrow, deep notothyrial pit and moderately thick hinge plate show a well-developed cardinal process. Socket plates are thin. Crura are horizontal and slightly curved and may be strongly feathered distally. A curved stack of fibres (Pl. K, fig. 3) supports the jugal processes. which show stout, ventrally directed bulbous ends with short spines. A small jugal plate is attached at right angles. The basal spiralial whorl has a thick supporting columnar layer posteriorly. Spiralia with up to 15 whorls were examined.



Text-figs. 183-184. Transverse serial sections of *Gruenewaldtia latilinguis* (SCHNUR). **Hönselberg** horizon, Junkerberg beds, middle Eifelian; 183 (top) MTB Dollendorf r54290:h75310, x2½, 184 (bottom), MTB Gerolstein r36850:h65960. x3.



Distribution of <u>Gruenewaldtia</u> <u>latilinguis</u> (SCHNUR 1851) in the Eifel.

Remarks.-

In his description, SCHNUR (1853, p. 183) appropriately and correctly remarked that the species was "selten" or rare. It is more abundant than other species of the genus in the Eifel region, but, compared to the abundance of other atrypids, its occurrence is isolated. In the Eifel region, it has not yet been found north of Ahütte in the Hillesheim syncline. Outside the Eifel it has now been found in the Chercombe Bridge shales of Devon, England (BIERNAT 1964). It is an index fossil of the middle Eifelian.

G. latilinguis can be distinguished from other Gruenewaldtia in its large size, the fineness of its ribs, the later ontogenetic beak incurvature and internally by its highly elevated muscle platforms with only a few irregular minor remnant septa in addition to the major septa of each valve. It may have a partially developed pedicle collar, but never a whole fused deltidial plate-pedicle collar structure as In G. apsaklina or related forms of Freilingen age.

Material.-

Total 138 specimens

C295(1); C300(5); C302(18); C303(2); C304(1); C326(2); C352(4); C353(3); C356(2); C357(12); C383(1); C390(1); C389(14); C393(1); C394(33); C413(1); C513(11); St8(1); St68(1); St73(1); St449(1); St491(1); St500(1); St624(2); St633(9); St639(2); St736(6); St741(1).

## Gruenewaldtia cf. apsaklina STRUVE 1961

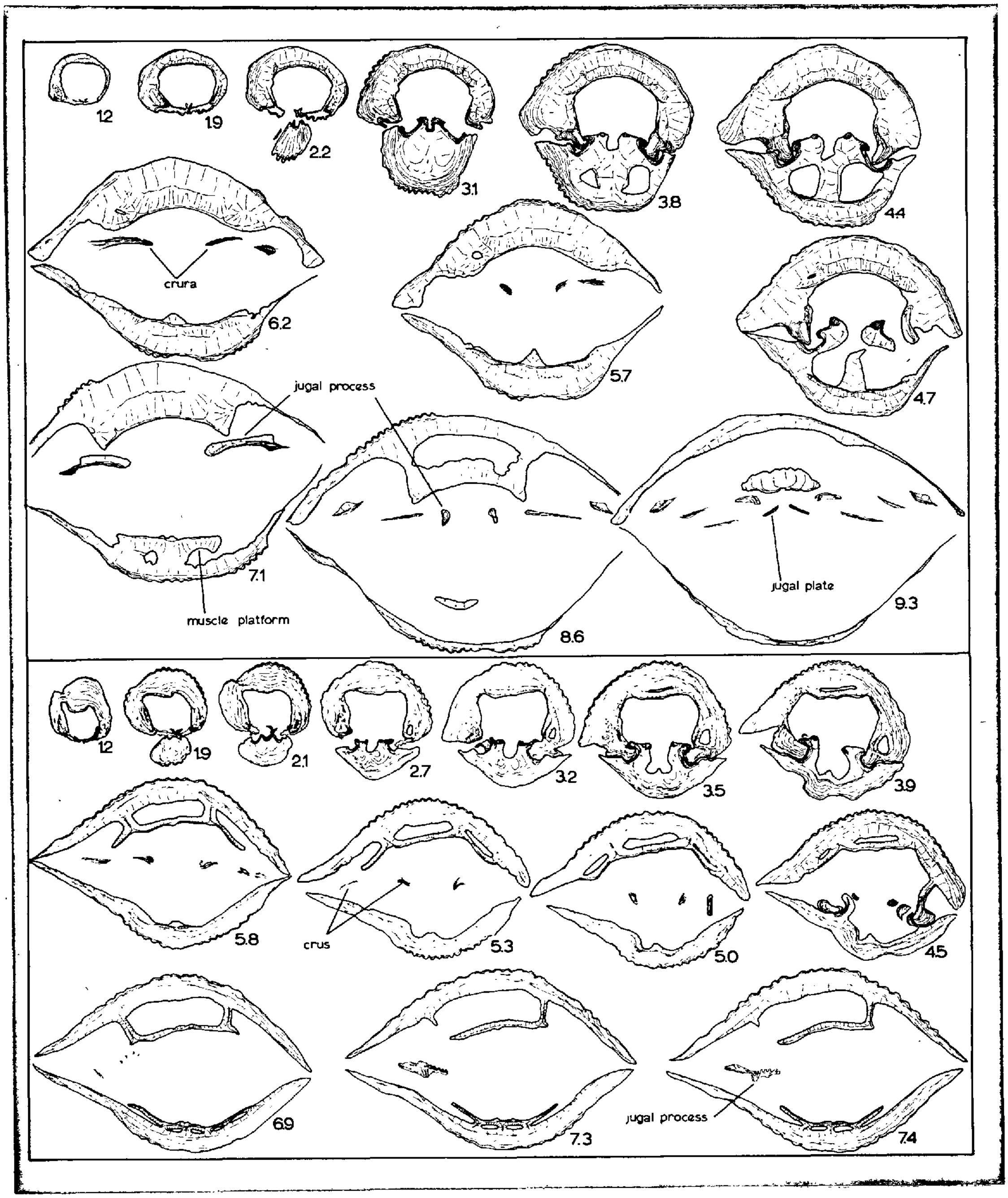
Pl. 49, figs. 4a-b; Pl. 50, figs. 1-2; text-figs. 186-188.

1961 Gruenewaldtia apsaklina STRUVE, pp. 335-336, P. 3, figs. 14-16.

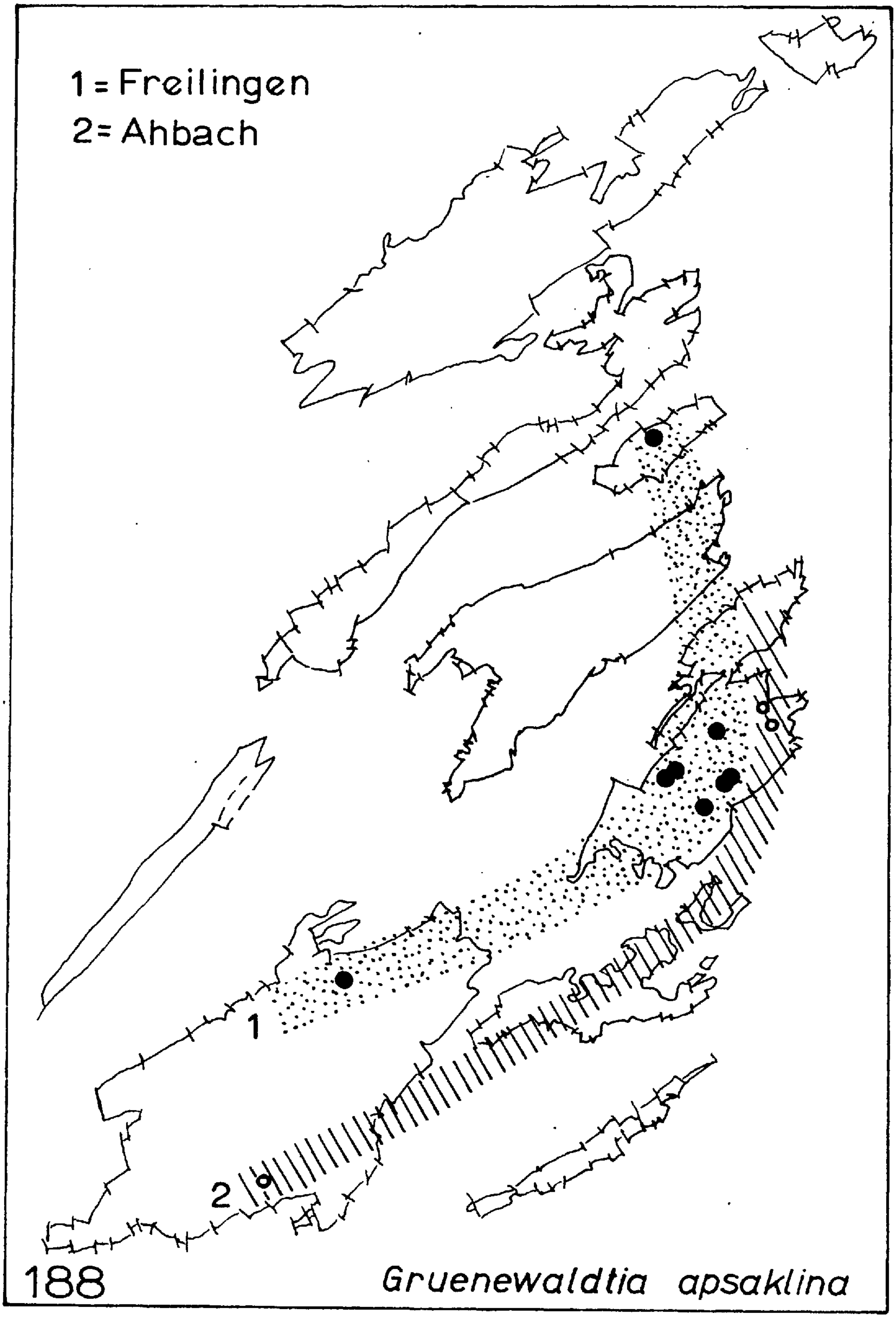
Remarks.-

A diagnosis, type locality and type stratum were cited in STRUVE (ibid.). In the collection of additional material from the stratitypic Freilingen beds, no other specimens with the apsacline beak and the angular features of the type specimen of G. apsaklina were found. Instead numerous, highly variable specimens, of different sizes, shapes and rib coarseness turned up in the Freilingen beds. This is not unexpected. The Freilingen beds appear to mark the period of transition from genus Gruenewaldtia to Mimatrypa, and it was commonly observed among the atrypids that variation was most rife before species or genera became very abundant, and relatively stable or settled in their morphology.

Some specimens reached a large size (up to a width of 55 mm ). Most specimens had deeply incised, rather coarse ribs, and rounded outlines, in which they differed from older, finely ribbed Gruenewaldtia latilinguis (SCHNUR).



**Text-figs.** 186-187. Transverse serial sections of *Gruenewaldtia* cf. *apsaklina* STRUVE. 186, Bohnert subhorizon, Freilingen beds; MTB Dollendorf r53030:h77310, 187, Eilenberg horizon, Freilingen beds; MTB Dollendorf r53850:h74680. x2.



Distribution of Gruenewaldtia apsaklina (STRUVE 1961) in the Eifel.

The most significant structures are internal. Pedicle collars absent. Teeth short, stubby, inwardly directed. Lateral cavities are usually completely suppressed. The muscle platforms are thickly reinforced by columnar calcite, and are low. Two short major septa support each platform and a thick median septum is common to the brachial platform, Minor septa for the ventral platform are absent, a rare remnant septum is present in some specimens. Socket plates are thin, crura short, slightly feathered. Jugal processes are stout, with spinous extremities and small inwardly deflected jugal plates. More than 11 spiral whorls were not observed.

*Material*.-

Total 32 specimens. Specimens from the Ahbach beds are also listed. Distribution is text-fig. 188.

C279d(1); C279e(1); C301(1); C343(2); C359(6); C362(1); C382(1); C512(1); AG6(1); St626(1); St591(1); St632a(2); St621a(1); Ahbach beds: C279fb(2); C372(2); C450(1); St190(3); St649(2).

## Genus *Mimatrypa* STRUVE 1964

*Type species*: *Terebratula prisca* var. *flabellata* C.F. ROEMER, 1844, p. 66, Pl. 5, figs. 4a-b.
*Range*: Upper Eifelian-upper Givetian, Middle Devonian.
*Distribution*: Europe, Russia, possibly northwestern Canada.

*Diagnosis*.-

STRUVE (1964) defined the genus three weeks prior to the diagnosis of the genus *Desatrypa* COPPER (1964), which became a junior synonym of *Mimatrypa*. The first to realize a link between *Atrypa flabellata* ROEMER and the genus *Gruenewaldtia* CHERNYSHEV was SPRIESTERSBACH (1942, p. 189) and not STRUVE, as STRUVE claimed in 1964 (p. 433). SPRIESTERSBACH (op. cit.) stated that a specimen of *Atrypa flabellata* from the Flinzkalk at Iserlohn (as figured in TORLEY, 1908, Pl. 4, fig. 11) belonged to the genus *Palaferella* SPRIESTERSBACH. Although SPRIESTERSBACH's identifications were not correct (e.g. he did not realize the link between *Gruenewaldtia* and *Falaferella*) he must be credited for relating the *flabellata*-group to the *Atrypa*-group of brachiopods. The fact that SPRIESTERSBACH (1942) arraigned his description between the pentamerids and rhynchonellids is as irrelevant as the fact that the productids were spaced between the strophomenids and pentamerids.

## *Mimatrypa insquamosa* (SCHNUR 1853)

Pl. 51, figs. 1-6; Pl. 53, figs. 5-6;
Pl. 56, figs. 3a-b; text-figs. 189-191.

1853 *Terebratula insquamosa* SCHNUR, p. 182, Pl. 24, figs. 5a,b (?Pl. 44, fig. 2).
1964 *Mimatrypa insquamosa* (SCHNUR), STRUVE, p. 437, fig. 4.
1964 *Desatrypa insquamosa* (SCHNUR), COPPER, fig. 2(1a-b).
1965 *Mimatrypa insquamosa* (SCHNUR), COPPER, text-fig. 3, 4a, 5a.

*Type locality*: SCHNUR (1853, p. 234) quotes Schönecken and Gerolstein as localities, but it does not seem to be present at the former. The well known "Mühlwäldchen Mergel" locality (MTB Gerolstein r46370-420: h65180) has provided specimens for most of the collections and may also have been known to SCHNUR. This is selected as the *locus typicus restrictus*.
*Type stratum*: Lower Givetian, "Mühlwäldchen Mergel". SCHNUR (1853, p. 182) states "Im Kalk; nicht so häafig" (transl., "in limestone, not so abundant").

*Diagnosis*.-
Medium sized, equally and moderately convex shells of subcircular outline, a broad, wide flattish area, orthocline beak, relatively large deltidial plates and apical foramen. Ribs are spaced at about 10 per 10 mm., tubular and only marred marginally by a few rare growth lamellae which are not deflected.

Internally it possesses striking pedicle collars, a prominent cardinal process.

*Remarks*.-
The main features which distinguish *M. insquamosa* from *M. flabellata* are the biconvex shell, the bifurcatiig equally sized ribs and internally the presence of a collar. SCHNUR (1853, p. 182) disregarded ROEMER's previously described *Terebratula prisca* var. *flabellata* and delegated it as a variety of his own *T. insquamosa*. In some remarks at the end of his classical work on Eifel brachiopods, SCHNUR (1853, p. 233) also correlated his *T. insquamosa* with SOWERBY's *Atrypa desquamata*, though on p. 231 (ibid.) he said *Atrypa desquamata* "ist *Ter. squamifera* m.". It is difficult to see what was meant by these synonymies.

The stratigraphic distribution of *flabellata-insquamosa* group is not clear, and the precise age of these two species is uncertain. The earliest *Mimatrypa insquamosa* straddle the Eifelian-Givetian boundary. As it is presently used, *M. insquamosa* may still include two, or more different species : one, similar to the lectotype (COPPER, 1964, figs. 2(1a-b)), is finer ribbed and shows mimicry of late Eifelian *Gruenewaldtia* from which it is believed to have been derived, and two, a more coarsely ribbed from which is probably restricted to the Givetian, and is illustrated on Pl. 51, figs. 6a-e. The latter is more commonly found with M. flabellata.

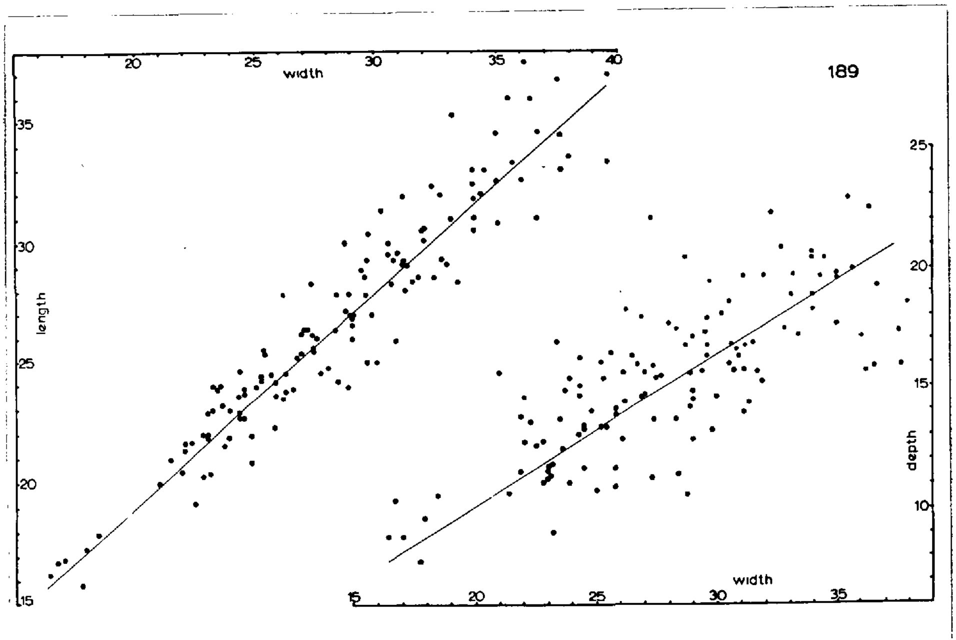
The transverse serial sections of M. insquamosa which were figured in COPPER (1965a, figs. 3, 4, 5) are from material whose source is unknown but probably the Mühlwäldchen locality rather than Baarley as stated. More sections are shown in text-figs. 190-191. A personal collection was made at Baarley (MTB Hillesheim r49330:h66050) and this collection included many specimens of M. insquamosa but very few M. flabellata. This locality has not been mentioned in the literature but swells to three the number of localities which have yielded rich Mimatrypa faunas (the other ones are Dachsberg, between Pelm and Gerolstein and "Mühlwäldchen"). A fourth locality contained specimens which resemble M. insquamosa but which have not yet been sectioned (refer to C391).

Material.-

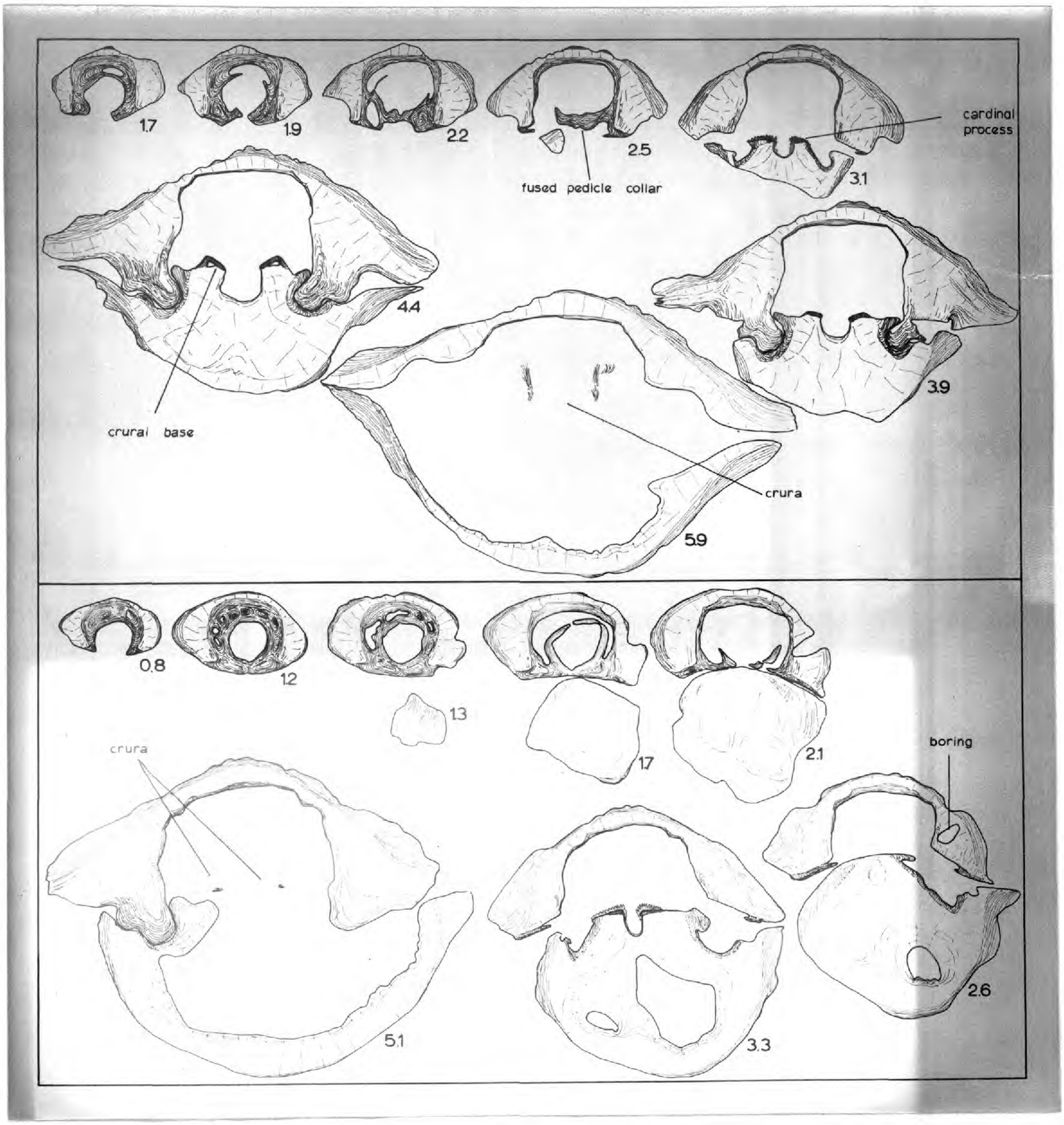
95 specimens are listed. The Paläontologisches Museum in Berlin houses a large collection of this species (125 specimens) and this collection has been plotted in scatter diagrams (text-fig. 189).

C133(18); C279j(2); C362(1); C391(17); C401(54); St804(1); St805(2).

The range is late Ahbach (Eifelian) probably to late Loogh (Givetian).



Text-fig. 189. Scatter diagrams of the main dimensions of Mimatrypa insquamosa (SCHNUR). Collections: Bahnhof Erweit (DOHM 1913) and Grabung Mühlenberg (DIENST & GROSS 19340. Berlin Museum.



Text-figs. 190-191. Transverse serial sections of Mimatrypa insquamosa (SCHNUR). Loogh beds, lower Givetian; precise locality unknown, "Mühlwäldchen", probably MTB Gerolstein r46370-420:h65180. x3.

## *Mimatrypa flabellata* (C.F. ROEMER 1844)

Pl. 52, figs. 1-4; Pl. 53, figs. 1-4; text-figs. 192-194.

1844 *Terebratula prisca* var. *flabellata* C.F. ROEMER, Pl. 5, figs. 4a-b.
1853 *Terebratula insquamosa* SCHNUR var. *flabellata* ROEMER, SCHNUR, Pl. 24, figs. 5c-e.
1871 *Terebratula flabellata* ROEMER, QUENSTEDT, Pl. 43, figs. 2-5.
1928 *Atrypa flabellata* F. ROEMER, LEIDHOLD, Pl. 6, figs. 6a-b, Pl. 7, fig. 1a-c.
1964 *Mimatrypa flabellata* (C.F. ROEMER), STRUVE, figs. 1-3, 5.
1964 *Desatrypa flabellata* (C.F. ROEMER), COPPER, fig. 2(3a-c).

Type locality: ROEMER (1844, p. 66) states the locality to be limestones near Gerolstein. The restricted type locality is designated as "Mühlwäldchen", MTB Gerolstein r6370-420:h65810.
Type stratum: This is settled as being the Mühlwäldchen Mergel which are dated by STRUVE (1964, p. 438) as Loogh age, lower Givetian.
Range: Loogh-?Gürten beds, Givetian. STRUVE (1964, p. 439) extends the species down to the lower parts of the Lahr horizon, Ahbach beds (Eifelian) and marks *M. flabellata* as the *Mimatrypa* ancestral species This interpretation is questioned. It appears more likely that the ancestral form was closer to *M. insquamosa* (SCHNUR).

Diagnosis.-

Convexoplane, highly dorsally arched shells with small, round-edged area, short deltidial plates and a foramen commonly expanded into the ventral umbo. Apical ribs are very fine and delicate, distal ribs extremely coarse because ribs only rarely increase. Growth lamellae absent except distally. No commissural fold.

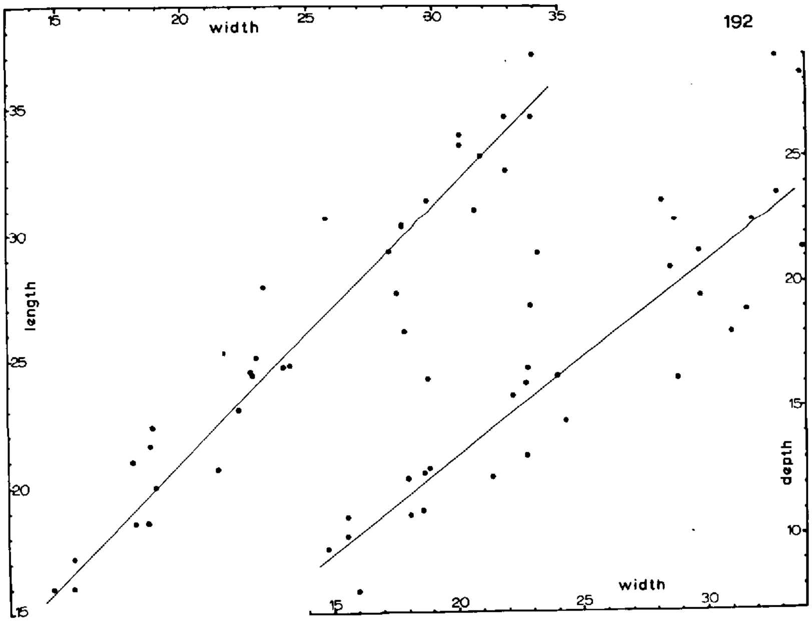
Internally a thick pedicle valve, thin deltidial lining and minute crura are typical. Spiralia have never been found.

### Description

External form.-

In outline the shells are sub-oval. Maximum width and depth come at mid-length. The pedicle valve is nearly plane or slightly convex. The brachial valve is well-rounded and can be gibbous in late growth stages so that the apical mid-field protrudes beyond the ventral apex. A summary of the size variation is shown in text-fig. 192.

A blunt, orthocline-apsacline beak protrudes over a round-edged area. Deltidial plates are small and meet but do not fuse on the outer surface. A round, apical foramen may penetrate the umbo. Hinge corners are round, poorly defined only slightly projecting. The dorsal apex is obscured by the foramen and deltidial plates and is strongly curved



Text-fig. 192. Scatter diagrams of the main dimensions of Mimatrypa flabellata (C.F. ROEMER). Data combined from all "Mühlwäldchen" collections.

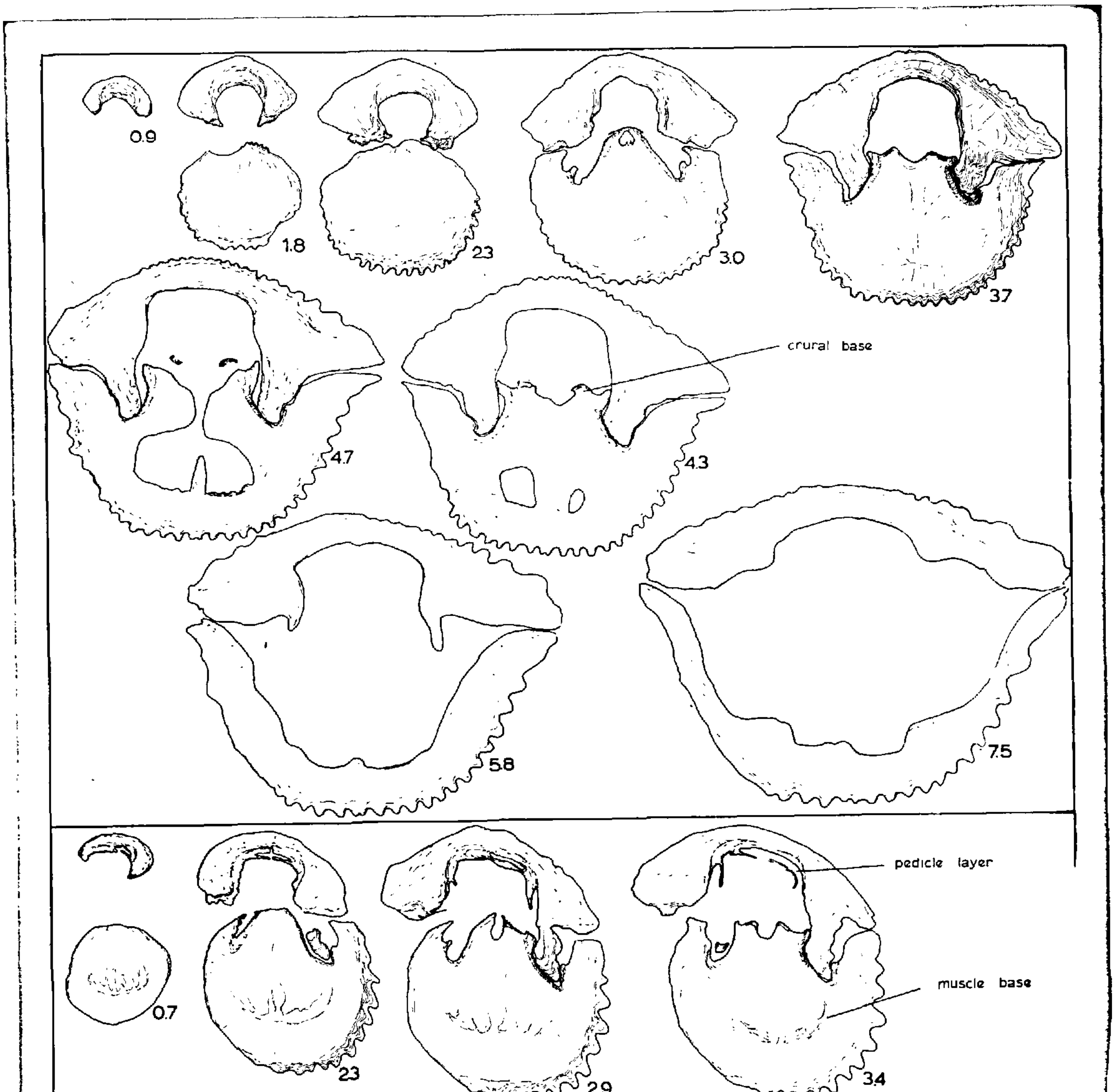
over the hinge axis. The dorsal mid-field flattens in maturity but the sides drop steeply. The deep brachial valve is not accentuated by an anterior fold.

Ribs.-

The most striking feature about the rib pattern, that there is no bifurcation and intercalation of ribs, was mentioned by ROEMER (1844, p. 66). Apically the ribs are very fine and crowded at almost 20 per 10 mm , but distally they expand enormously to less than 5 per 10 mm Such expansion is not known in other atrypids but is quite common in the rhychonellid group brachiopods. Ribs are rather angularly crested at the margins and the troughs appear to have grown faster than the crests. Ribs towards the sides of the brachial valve have a steep inner slope and gentle outer slope and lose their symmetry.

Growth lamellae.-

The ribs are virtually uninterrupted by growth lamellae except distally in mature specimens. Frills are absent. Small growth lines are not vertical but oriented at an angle of 60 to 70 degrees dipping anteriorly and laterally.



Text-figs. 193-194. Transverse serial sections of *Mimatrypa flabellata* (C.F. ROEMER). Loogh beds, Givetian; about MTB Gerolstein r46310:h65180. *193*, x3; *194*, x2.

Internal markings.-

LEIDHOLD (1928, Pl. 7, fig. 1a, Pl. 6, fig. 6b) and STRUVE (1964, figs. 1-3, 5) have illustrated the morphology of muscle scars and ovarian markings. Additional photographs are given on Pl. 51, figs. 1-5. Fig. 3 of STRUVE (1964, ibid.) is probably enlarged greater than the x2 stated.

Internal structure.-

The columnar layer is thick and dominant, (text-figs. 193-194), the fibrous layer thin and the outer layer is up to 1 mm. thick towards the sides of the shell (latter unusual).

A thin pedicle layer, solid or partially hollow anteriorly, lines the delthyrial cavity. Deltidial plates are short, solid, thick and in the specimens sectioned, not united. In late growth stages there is little deltidial plate growth and the centre is occupied largely by the foramen. Teeth are massive, long and vertical, with weak lateral lobes (or none at all) and no dental ridges or dental nuclei. The notothyrial pit is minute, lined by 3-4 small cardinal process strands. Sockets are deep and thin socket plates steeply inclined. Inner socket ridges absent or faint. Crura are minute. Jugal processes and spiralia are unknown. The lack of spiralia was noticed by QUENSTEDT (1885, p. 702; 1852, p. 46). STRUVE (1964, p. 435) when diagnosing the subfamily Palaferellinae observed that the spiralia were basically as in the Atrypinae. STRUVE (1964) does not give sections or photographs of such spiralia.

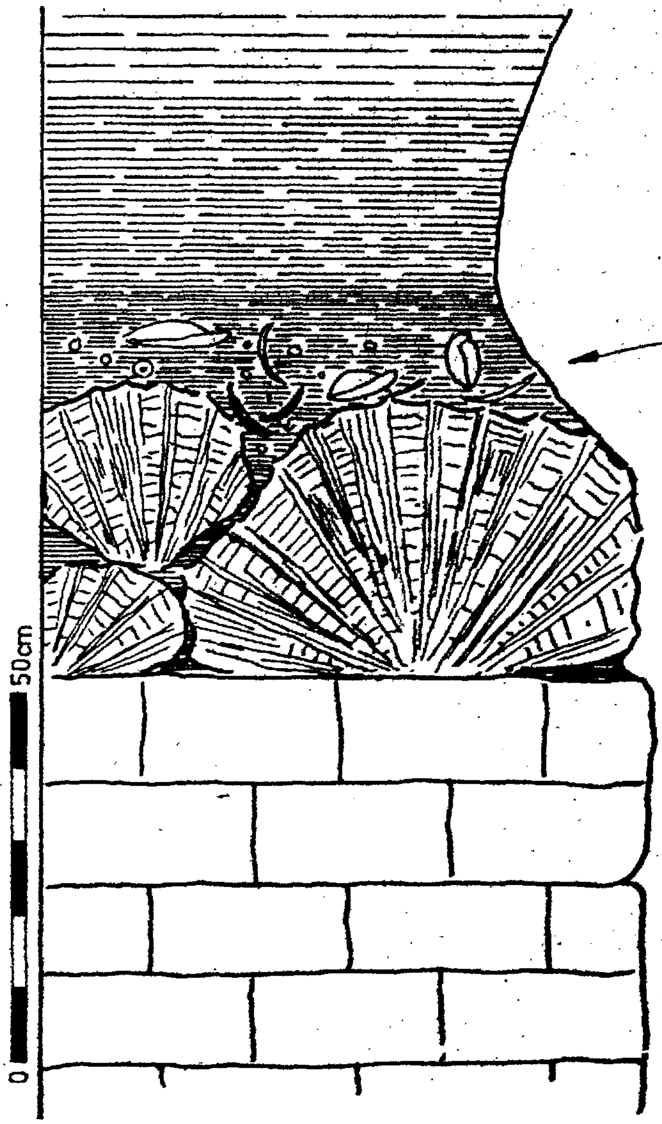
Remarks.-

The diagnostic features of this species are absent in other Mimatrypa and the species is easily set apart from others. A few gradational specimens showing insquamosa-like features have been found. These specimens retain the basic convexoplane shape of M.flabellata but are finer ribbed and show bifurcating-intercalating ribs. One of these is figured in Pl. 53, figs. 1a-d.

The species may be a good index fossil of the lower Givetian, for very similar atrypids have been found in the Urals in strata of nearly the same age. I.A. BREIVEL probably was the first palaeontologist to figure the internal structure of a specimen of the flabellata group of atrypids (BREIVEL in KHODALEVICH et al, 1959, p. 55, fig. 22). EICHWALD (1859, Pl. 35, figs. 22a-c) may have known specimens of this species more than 100 years ago when he figured "Orthis oriens" from the Ural mountains, Russia.

Material.-

Most of the material labelled "Gerolstein" is likely to have come from the "Mühlwäldchen" locality near Gerolstein. Some collections are more richly represented by Mimatrypa flabellata than others, which leads



greenish blue shales, abundant thamnoporid corals at the base, crinoidal debris at the top.

*Mimatrypa insquamosa* (Schnur), rare *M. flabellata* (C.F. Roemer)

large and small colonial rugosans (up to 1m. diam.): *Hexagonaria*, *Spongophyllum*

pale green, pure limestones, thick bedded, unfossiliferous

Occurrence of *Mimatrypa* at Baarley, Gerolstein (locality C400) one to believe that the species may be localized in a thin stratum. The DIENST & GROSS collection (Berlin Museum) which is labelled "Grabung am Mühlenberg" yielded many more specimens than the DOHM collection (Berlin Museum) in which only a single specimen was found. Furthermore, there are slight differences in adhering sediment and preservation of these two collections. The DOHM collection was marked "Bahnof Erweit".

At Dachsberg only the finely ribbed *Mimatrypa insquamosa* apparently has been found. Similarly at "Auf Baarley" which lies opposite Dachsberg, a personal collection yielded only one specimen of *M. flabellata*.

C401(1) MTB Hilllsheim r49330:h66050 (see text-fig.
St770(?1) MTB Dollendoff r5134-5:h7575-80.

## *Mimatrypa fretterensis* n.sp.

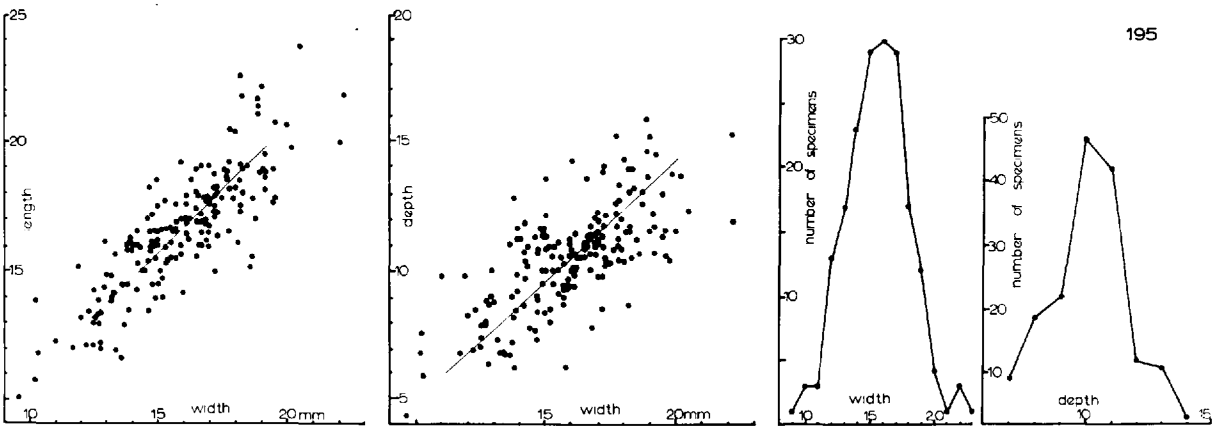
Pl. 54, figs. 1-3; Pl. 55, figs. 1-11; text-figs. 195-203.

1895 *Atrypa flabellata* (GOLDFUSS) ROEMER, HOLZAPFEL, pp. 261-262
?1865 *Atrypa* cf. *arimaspus* (EICHWALD) DE VERNEUIL, HOLZAPFEL, Pl. 16, figs. 13, 13a.
1908 *Atrypa flabellata* ROEMER, TORLEY, p. 24, Pl. 4, fig. 11.
1934 *Atrypa* sp. (=*flabellata* bei HOLZAPFEL), TORLEY, p. 124, Pl. 9, figs. 76, 77.

*Name*: After Fretter, the name of the river which flows through Frettertal, the type locality.
*Type locality*: Frettertal, near Finnentrop, Bergisches Land, Germany. MTB Altenhundem.
*Type stratum*: "Massenkalk" at Frettertal. The exact horizon is unknown because a visit to the locality proved fruitless and the fossiliferous nests and beds could not be found. HOLZAPFEL (1908, p. 114) placed the age as upper Givetian but not as high as the Massenkalk fauna of Bilveringsen.
*Range*: Estimated as middle to upper Givetian.
*Associated fauna*: See HOLZAPFEL, (1895, 1908).
*Source sediment*: Light gray to white, massive, unbedded limestone.

*Diagnosis*.-

Small, slightly longer than wide, biconvex-dorsibiconvex shells furrowed by moderately coarse ribs which bifurcate. Beak orthocline to weakly apsacline. Internally no open pedicle collar; small spiralia present.



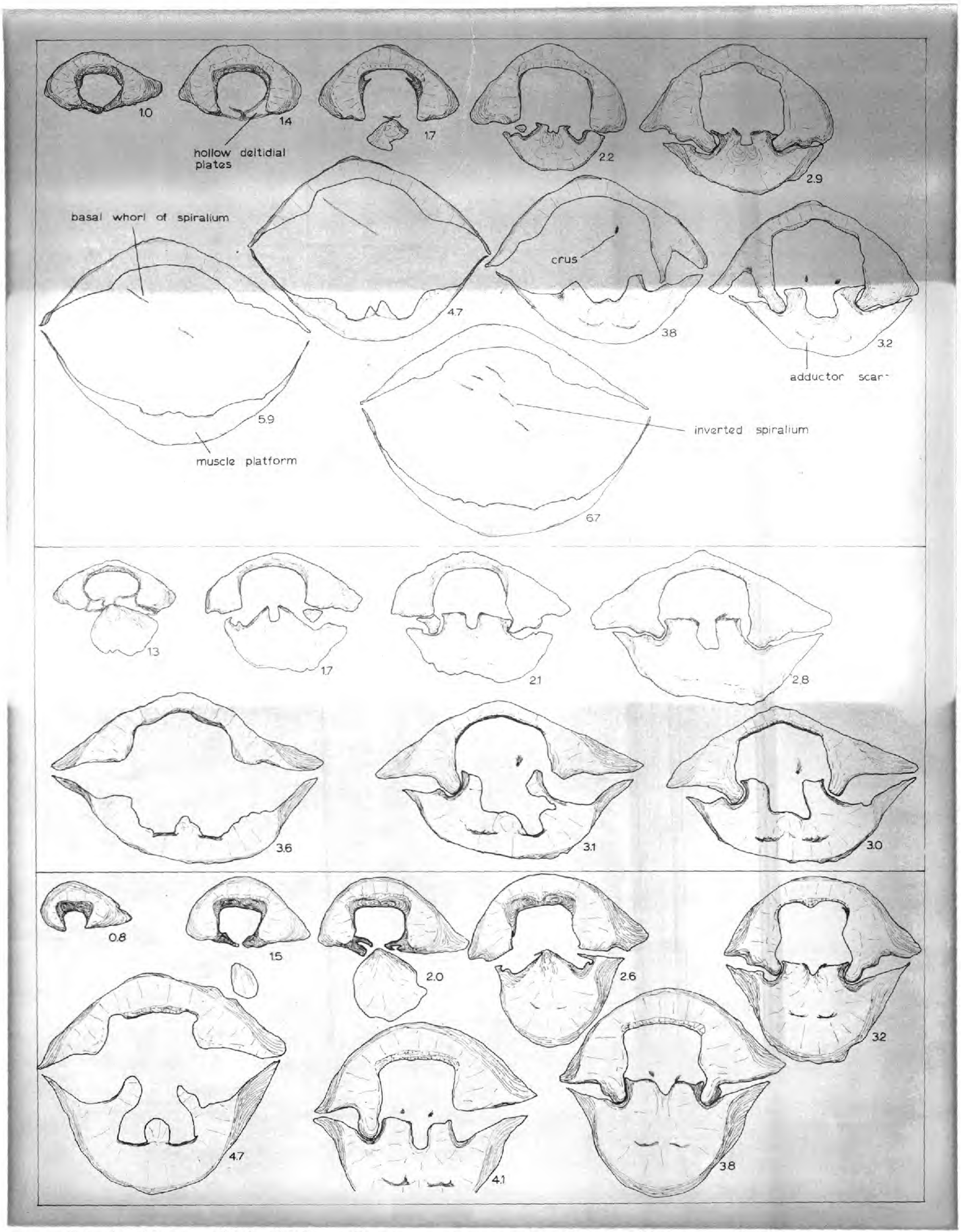
Text-fig. 195. Scatter diagrams and frequency curves of <u>Mimatrypa fretterensis</u> n.sp. Combined collections from Frettertal.

## Description

### External form.-

The average mature size is between 15 and 17 mm wide and 10 to 11 mm thick (text-fig. 195). Longer than wide shells reach maximum width at mid-length, maximum depth towards the umbones. The brachial valves tend to globosity while the pedicle valves remain weakly convex or planar in comparison. The anterior commissure is rectimarginate or weakly sulcate.

The ventral apex juts out about 2 mm , rather much for its small size. The orthocline-apsacline, usually blunt (rarely pointed) beaks project over small, 1 mm wide foramina and deltidial plates which are seen to be crenulated in better preserved specimens. The interarea is sharp-edged, well defined, encompassed by a shoulder angle of 110-120 degrees. Shoulder lines are straight or weakly concave. Hinge corners rounded, although better defined than in <u>M. flabellata</u>. The brachial valve is rounded, sometimes, but not usually steeply and has a somewhat flat mid-field.



Text-figs. 201-203. Transverse serial sections of <u>Mimatrypa</u> <u>fretterensis</u> n.sp. Middle to upper Givetian; "Frettertal", MTB Altenhundem. x3.

Ribs.-

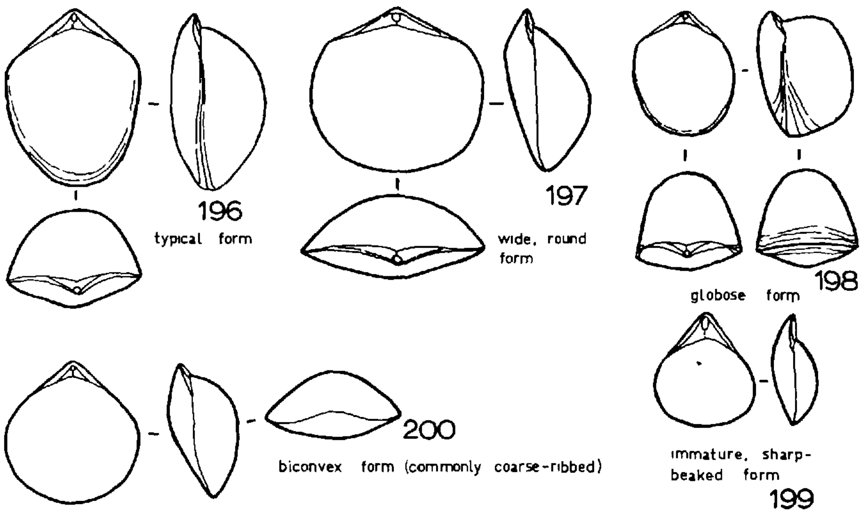
Approximately 9-10 ribs per 10 mm mark the shell margins. Ribs are round-crested and round-troughed but appear to show some variability in coarseness and roundness. Bifurcations (on the pedicle valve) and intercalations (on the brachial valve) are frequently in pairs or threes. The ventral apex sees 8 ribs but no defined mid-rib or ribs.

Growth lamellae.-

On or two majot growth interruptions break the monotony of the ribs of many specimens but some also show lamellae only at the margins. Some of the more lightly coloured specimens have bands of light and dark gray which are not reflected in growth interruptions. These concentric bands do not represent colour bands.

Growth and variation.-

The mature variation is very great, with only the beak and commissure remaining permanent (text-figs. 196-200). The shape of the beak may vary from more pointed to blunt, the outline from oval to circular, and shape globose to flattish. Flattish specimens tend to be more finely ribbed (12 ribs per 10 mm) and the more convex specimens coarsely ribbed (about 9 ribs per 10 mm). A separation of such varieties does not seem feasible.



Text-figs. 196-200. Shell variation in Mimatrypa fretterensis n.sp. Random localities from Frettertal. x1. (fig. 199, x2).

Internal structure

Deltidial plates are solid apically, (text-figs. 201-203) hollow distally and lack the inner protrusions of other Mimatrypa. The pedicle layer is thin. Teeth straight, near-vertical and lack lateral lobes. A small, amorphous cardinal process partly fills a tapering notothyrial cavity. Hinge plates massive. Socket plates are thin, crura short and bushy. Broken and disjointed spiralia were noticed in some specimens. TORLEY (1934, p. 124), remarked that spiralia were located rather far from the hinge margin and that spiralia had 10 whorls. The wide separation from hinge plates can be confirmed and it seems that spiralia are not connected to crura in some specimens. A jugal process was not observed. It may be missing.

Remarks.-

In convexity and shell outline mature specimens of Mimatrypa fretterensis n.sp. can be compared to immature M. flabellata, but the numerous bifurcations of the ribs in the former destroy the similarity. M. flabellata is about three times the size of the Fretter species. Internally there are also differences : spiralia are not known in flabellata, and the shape of the hinge plates, the deltidial plates and the teeth also differ.

Several specimens from limestones at Villmar (Berlin coll.) were examined (refer to Pl. 54). The affinity of these is in doubt. They are not very similar to M. fretterensis. More detailed work is required.

Material.-

All the specimens come from east of the Rhine, and are deposited in the Berlin Museum. Total 236 specimens.

Denckmann Coll. (53); Jordan Coll. (133); Spriestersbach Coll. (5); Krüger Coll. (21); Loretz Coll. (4); Henke Coll. (9); Torley Coll. (11).

## Genus Carinatina NALIVKIN 1930

Type species: Orthis arimaspus EICHWALD 1840, p. 108.

Range: Lower to Middle Devonian. The exact distribution of this genus is still not known. In some classifications the first Carinatina are said to derive from Spirigerina in upper Silurian time (e.g. RZHONSNITSKAYA, 1964, p. 95). BOUCOT et al (1964) mark the inception of the genus in Emsian time (upper Lower Devonian), but ALEKSEEVA (1962, p. 181) stretches it down to the Gedinnian. The extent of the genus appears to depend on which early species are assigned to it.

Distribution: World-wide. The most westerly occurrence in Europe is from Devon (COPPER 1965a), the most southerly in Italy (GORTANI 1911, 1915). It is also present in Brittany, France (BARROIS 1895, LEMAITRE 1934) and the Ardennes, Belgium (MAILLEUX 1941).

Diagnosis.-

Flat, biconvex or convexoplane shells with large orthocline-apsacline beak, and large delthyrium with apical foramen. The ventral valve is usually marked by a median ridge or carina and the dorsal valve with a corresponding depression. Ribs are tubular, with fine concentric microsculpture. Growth lamellae un-deflected, wide apart (often not visible except distally) and distally a very thin marginal flange with numerous fine ribs surrounds the shell.

Only the internal structure of one species, Carinatina plana (KAYSER) is known. In it, deltidial plates are hollow, a thin pedicle layer is present, teeth lack dental nuclei or lateral cavities. A marked cardinal process consisting of a brush-like covering of the cardinal block, and heavily supported, thick crura are typical. The jugal processes are weighted by a bulbous plate (Pl. K, fig. 2). Jugal plates are small, short, and thick.

Remarks.-

The genus is so distinct that it is difficult to confuse in its remarkable morphology with other atrypids. It is possible that it has been mistaken for some chonetids or stropheodontids, and the literature shows that the early workers assigned it either to Orthis or Orthisina. This species group was raised to full generic rank by NALIVKIN in 1947. The honour of first separating this group of atrypids must fall to HOLZAPFEL (1895, p. 267) who suggested more than 70 years ago "dass die Atr. signifera einer besonderen Gruppe, vielleicht Gattung angehört" (transl., that A. signifera belonged to a special group, perhaps a genus).

Two North American species, Atrypa dysmorphostrota CRICKMAY and Atrypa sinuata CLELAND, are dissimilar in being much more convex and in having undulating rather than tubular ribs, and perhaps they can be assigned to a new subgenus of Carinatina or even a distinct genus.

The relationship of the Plectatrypa-Spirigerina groups of atrypids to Carinatina is still vague and must remain a dilemma until they are internally examined. Similarly Vagrania cannot yet be explained in the present classification.

Member species.-

Carinatina plana (KAYSER), C. signifera (SCHNUR), C. italica (GORTANI), C. carnica (GORTANI), C. arimaspus (EICHWALD), C. praearimaspa NIKIFOROVA, C. subplana KHODALEVICH, C. eudokia RZHONSNITSKAYA, C. salairica (PEETZ)?, C. brevita KULKOV, C. localis KHODALEVICH, C. paradoxa (SCUPIN), C. insolita (SCUPIN), C. comata (BARRANDE)?.

## Carinatina plana (KAYSER 1871)

Pl. 57, figs. 1-3; Pl. 58, fig. 3; text-figs. 204-209.

1871 Atrypa reticularis var. plana KAYSER, pp. 546-6, Pl. 10, figs. 3a-d.
1962 Carinatina plana (KAYSER); SIEHL, Pl. 24, fig. 4.
1964 Carinatina plana (KAYSER); BIERNAT, pp. 329-330, Pl. 13, figs. 10-12.

Type locality: Herewith restricted to the western slope of the north extension of Hönselberg, Hillesheim syncline, MTB Dollendorf r53850: h74680. KAYSER, other than mentioning the Eifel, made no note of specific collecting localities.

Type stratum: According to KAYSER (1871, p. 546), the species "scheint ganz auf die Crinoiden-Schicht beschränkt zu sein". Since most actual references to the Crinoiden Schichten imply the Freiligen beds, this designation is correct. Type strata are the Freilingen beds, most material coming from Eilenberg and Bohnert horizons. Rare specimens are present in the younger Ahbach beds. The species cannot definitely be identified from older rocks.

Associated fauna: Rich in brachiopods including Kerpina vineta, Desquamatia iunctura, Gruenewaldtia cf. apsaklina, Atrypa sp., and numerous other brachiopod groups. Rhynchonellids are common, as are athyrids, small spiriferids and chonetids. Crinoid ossicles are extremely abundant.

Source sediment: Greenish-gray richly calcareous shales and numerous bands of fine grained limestones with rather coarse detritus of crinoids.

### Diagnosis.-

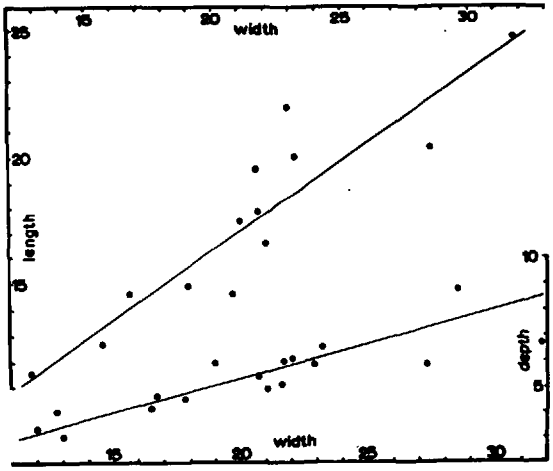
Small to medium sized, flat Carinatina with thin and weakly developed carina, coarse high ribs. Pedicle valve planar to concave, brachial valve shallow convex. Internally, a thin pedicle layer, large hollow deltidial plates, a wide, brush-like cardinal process are typical. The jugal plates are thick and knob-like.

## Description

### External form.-

Most specimens are between 20 and 24 mm wide : width is about 1.2 times length and about 3.7 times depth for this size. Maximum known width 38 mm (paratype KAYSER), maximum depth 8.5 mm (text-fig. 204). The "curled-up" commissure (seam), present only in late maturity, gives the shell a semi-circular outline. Otherwise most specimens are square or sub-quadrate. The interarea is wide and prominent and posterior commissure markedly straight, somewhat reminiscent of stropheodontids or chonetids. The anterior commissure is rectimarginate or broadly plicated. The central carina and corresponding trough are not always prominent, sometimes strongly suppressed.

204



Text-fig. 204. Scatter diagrams of the main shell dimensions of Carinatina plana (KAYSER 1871). Localities C359, C512.

The pedicle valve is flat apically, concave laterally and distally; concavity increases and becomes marked in specimens with seams. The carina, composed of two adjacent, elevated mid-ribs is nearly 1 mm high, but tapers to nil, at the valve margin and is not sharply expressed at the apex. Hinge corners may be sharp, squared, or blunt, rounded. The beak projects 1-2 mm above the hinge line is consistently apsacline, without any late ontogenetic or ephebic curvature. It is inclined at 30-4- degrees. Large, triangular deltidial plates fill the wide, expansive delthyrium. A small (1 mm diam.) foramen occupies its apex. The interarea is wide, sharp-edged, unmarked by parallel growth lines as in Kerpina.

The brachial valve is weakly convex - the shallow marginal trough is due to the seam. The apex is slightly incurved and projects less than 0.5 mm above the hinge line. The sharp median trough weakens and disappears distally.

Ribs.-

The material shows strong, well-defined ribs of a type not yet known in other species of the genus. They are spaced at nearly 10 per 10 mm arc apically but coarsen to roughly 7 per 10 mm distally. Ribs are equally round-crested and deep troughed. Lateral ribs are broader and thicker and somewhat asymmetrical in cross-section. On the pedicle valve the lateral ribs generally bifurcate early, central ribs later. It is striking, and unusual for atrypids, that intercalation in the ventral mid-area is not uncommon. The second notable feature is the multiplicity of marginal ribs in specimens which have the seam developed, - all ribse become fine, 10-14 per 10 mm , and coarse ribs become rapidly finer and equivalent to the new marginal ribs. The marginal ribs retain their distinctness in round crests and deep troughs.

Growth lamellae.-

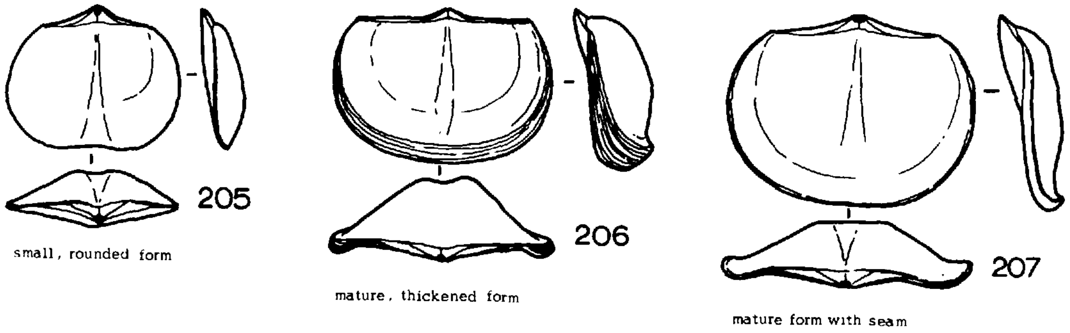
Very few specimens show growth interruptions. Where present, the single interruption occurred at 13-15 mm from the apex, with no additional marginal changes. Frills were not present in examined material.

Microscopic growth lines cover rib crests and troughs (Pl. D, fig. 1). Although only rarely preserved, these growth lines are characteristic and unmistakable. Two sets are present : one, a primary thick set spaced at 3-4 per mm and two, a secondary set 3-6 minute lines between each of the above coarse lines. The finer micro-growth lines become smaller distally and have nearly faded at the beginning of new coarse lines.

Growth and variation.-

The origin and function of the seam which is developed in large, presumably ephebic specimens, is uncertain. The seam, consisting of a round, circular, rim-like ventral flexure of the commissure (see Pl. 57, figs. 2-3), may have served in stabilization of the shell.

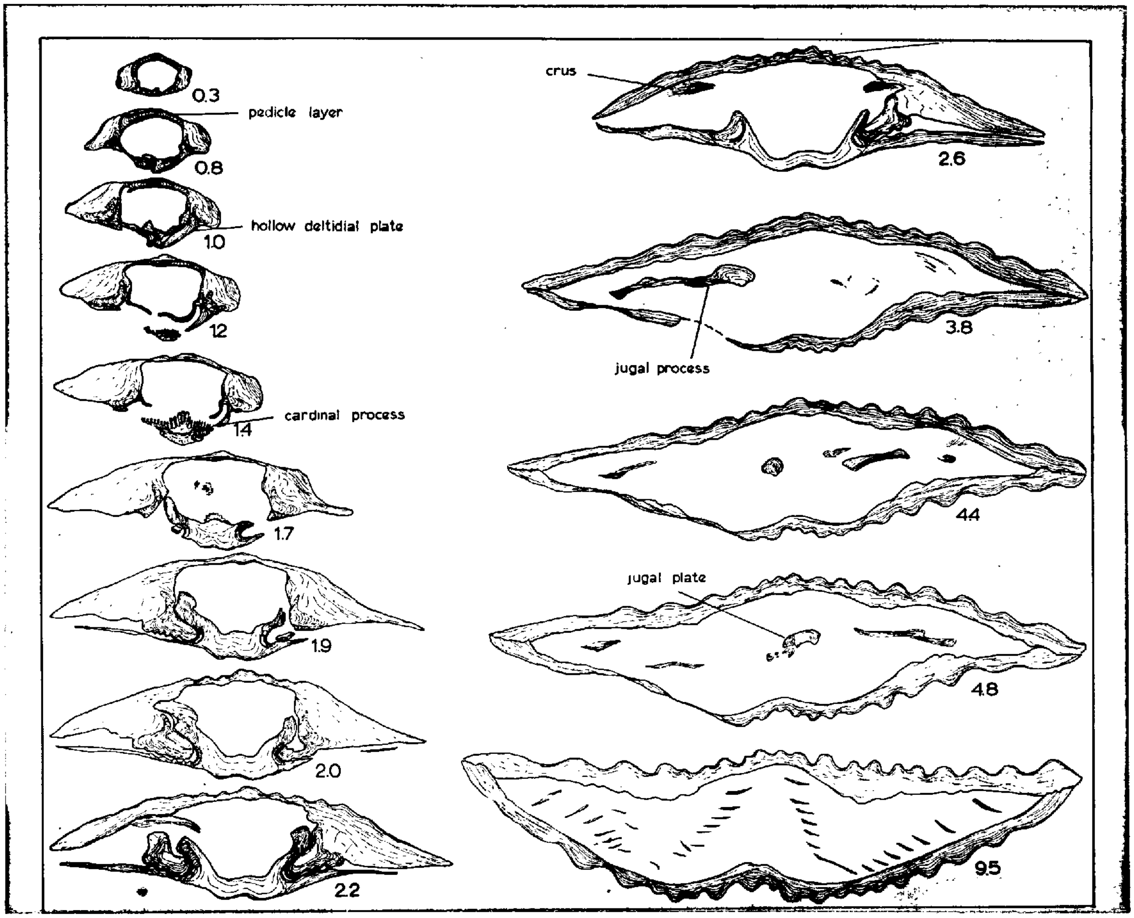
There is some variation from specimens with rounded hinge corners, and rounded outline, to those having a very sharp edged hinge corner and strongly defined interarea (text-figs. 205-207). This is obvious in early stages. There is no beak incurvature, or twisting. Shape outline varies little in early stages. Foramina remain constant in size and show no expansion. The trough and carina are not expressed early and late in ontogeny.



Text-figs. 205-207. Shell variation of Carinatina plana (KAYSER). Random localities. x1.

The changes in convexity (e.g. concavity in the pedicle valve, weak convexity rather than planation in the brachial valve), as well as the dorsal direction of the seam, make it likely that the late ontogenetic mode of life of the species was ventral valve down. The earlier mode of life, with a planated shell and carina present, possibly was a vertical position, posterior margin downwards. The direction of the foramen and inclination of the beak appear to confirm this.

Internal structure.-
The first and only internal figures of this species are by SIEHL (1962, Pl. 24, fig. 4). There are unfortunately, a number of detailed features in SIEHL's diagrams which could not be ascertained in my own material; this problem appears to be due to differences in the drawing of serial sections. SIEHL shows remarkable deltidial plates, and tooth structures (which highly detailed acetate peels have failed to reveal), but missed the obvious peculiarities of the cardinal process and jugal processes.



Text-fig. 208. Transverse serial sections of Carinatina plana (KAYSER). Eilenberg horizon, Freilingen beds, upper Eifelian; MTB Dollendorf r53850:h74680. x4.

A pedicle collar is absent. The pedicle layer is flattish, but shows typical circular growth lines (text-fig. 208, 0.3-1.2 mm ). Deltidial plates are large, hollow, interlocking medially, weakly crenulated externally. Teeth are blunt, short and completely lack lateral cavities. The main lobe is sub-horizontal and inwardly directed, crenulated on contact with the socket plates. No lateral lobes. Apically the shell floor shows a weak median ridge (?septum). No thick, calcite, layers flank the muscle depressions.

The cardinal process is wide and pads the dorsal apex, rather than resting in the notothyrial pit, which is absent. The process consists of 15-25 projections, the central ones being longest and thickest. Socket plates are thin apically, but thicker and reinforced distally; there are no true hinge plates because the intervening space is filled with a solid cardinal block. Crural bases are stoutly wrapped around the crura and socket plates. Crura are sub-horizontal and accommodated next to the teeth by a simple notch. Jugal processes are two layered, with only a thin, separating layer. Distally, a massive bulky knob, fixed to both sides of the jugal processes, carries small, finely crystalline or amorphous jugal plates; there is no fusion. Up to 9 whorls make up the flatly conical spiralia : cone apices are directed inwards.

Remarks.-

The species is strongly homeomorphic with other major brachiopod groups, particularly chonetids. An unrelated synchronous brachiopod 'Chonetes' sarcinulata (SCHLOTHEIM) is very difficult, in a poorly preserved state, to distinguish from Carinatina plana. Worn specimens are particularly troublesome and virtually identical - both species have similar ribbing, convexity and apical morphology. They can be held apart most easily by microsculpture : 'Chonetes' sarcinulata shows numerous minute projecting spines on the ribs, Carinatina plana shows concentric micro-growth lines (Pl. D, fig. 1). Internally, of course, there is no doubt of their identity.

Another associated species with which it can, but need not be, confused is Kerpina vineta STRUVE, an atrypid which BOUCOT et al (1964, p. 810) incorrectly placed in the Carinatininae. From Kerpina it is distinguishable by its microsculpture (the ornament of Kerpina is similar to that of Spinatrypina), as well as its convexity (dorsiconvex) and apical morphology (well defined interarea, lack of areal growth lines, consistent jutting foramen).

From other known Carinatina it is easily distinguishable by its coarse ribs. Atrypids nominally cited by VERNEUIL (in MURCHISON et al, 1845, Pl. 10, figs. 11a-c) as Terebratula arimaspus EICHWALD are similar in rib coarseness, but these forms show a strong distal shallowing of ribs and very finely costate frill and rim not present in Carinatina plana.

The only forms definitely known as C. plana are from the Eifel. All others must still be regarded as spurious until accurately re-examined and re-defined. SPRIESTERSBACH (1942, p. 191, Pl. 6, figs. 5a-b) figured Atrypa arimaspus EICHWALD but the longitudinal striation he figured is atypical of Carinatina and the form may not be an atrypid at all. Carinatina signifera (SCHNUR) has been considered by some authors (e.g. HOLZAPFEL, LEMAITRE) a subjective senior synonym of C. plana (KAYSER). HOLZAPFEL (1895, p. 265) claimed that in 1871 KAYSER had not realized the significance of SCHNUR's 'Leptaena' signifera, and implied that if he had known, he would have placed it in synonymy with Carinatina plana. This appears to be doubtful. It is recognized by HOLZAPFEL himself (op. cit.) : "so ist allerdings die Atrypa plana in den Schnurschen Abbildung nicht zu erkennen." KAYSER, in turn, noted that he could not find the original to Leptaena signifera in the SCHNUR collection at Bonn, and attributed SCHNUR's figure to a mysterious error (1871, p. 632). HOLZAPFEL apparently found wax impressions in the Bonn collection, of which he said, "deren offenbar das von E. Kayser vermisste Original zur Schnur's Abbildung ist". Whether HOLZAPFEL actually had "original" material is not known, nevertheless HOLZAPFEL remarked that the ribs were drawn much too fine in SCHNUR's figure. HOLZAPFEL can, in a sense, be regarded as the founder of the genus Carinatina since he was the first to suggest that a new genus for the distinctive group of Atrypa signifera and Atrypa arimaspus would be suitable.

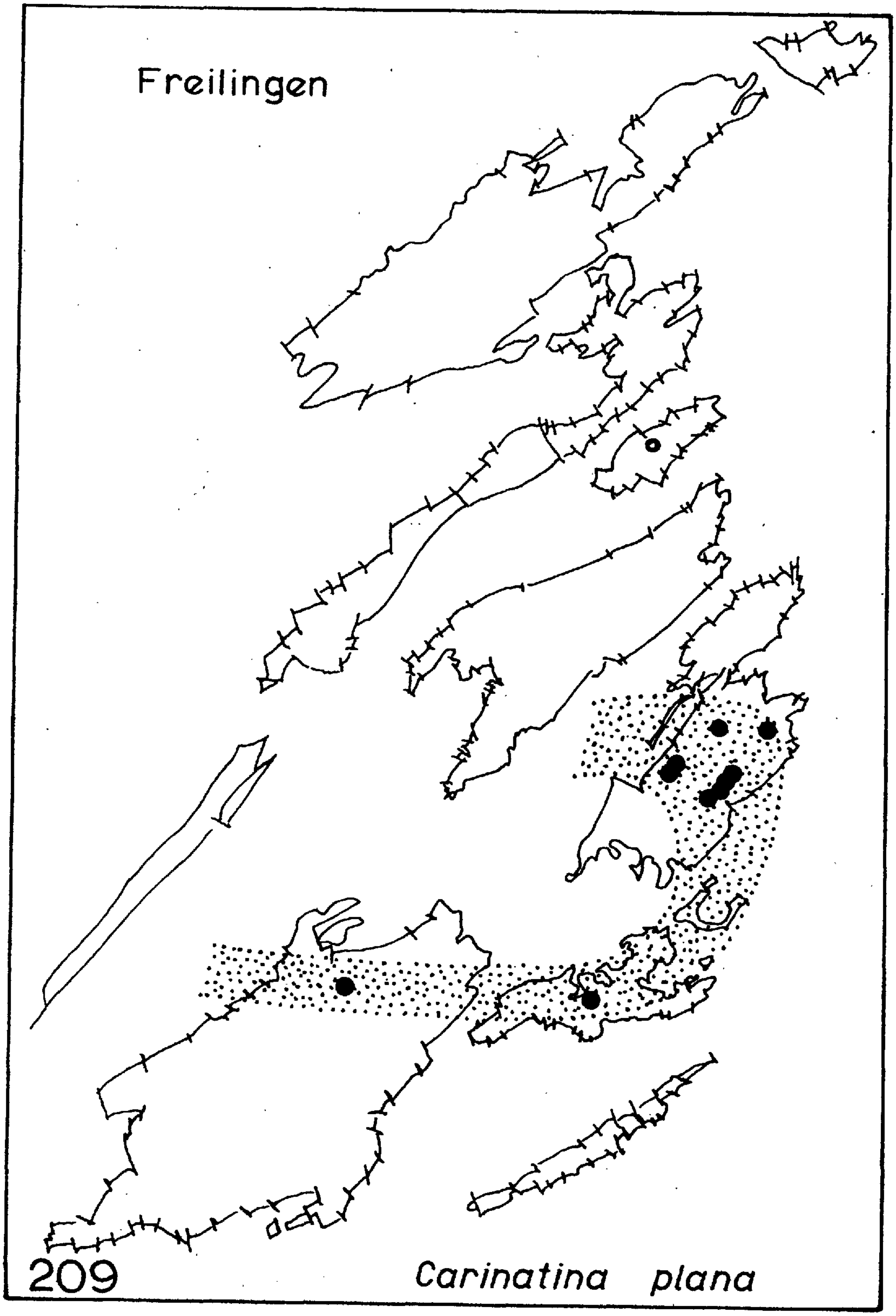
Since Carinatina is not indigenous to the Eifel, its origins are cryptogenetic for this area. Carinatina plana is the oldest species of the genus in the Eifel (which elsewhere extends through the Lower Devonian, possibly also the Silurian), and its first appearance, albeit doubtful, is in the Rechert horizon of the Junkerberg beds. Its vertex is reached in Freilingen time, but it is never abundant. The youngest Carinatina plana are of Müllert (Ahbach) age and are not distinguishable from older forms. It is noticeable that the carina is not well-marked in many specimens and sometimes even absent.

STEININGER (1853, Pl. 8, figs. 5, 5a-b) described and figured a new species "Orthis gerolsteinensis" which appears to be similar externally to the Carinatina plana described by KAYSER nearly 20 years later. But STEININGER's specimens have not been found and the material he figured (probably idealized) cannot definitely be attributed to Carinatina. In STEININGER's description a small interarea is specified and is confirmed in the illustration. This is not typical of Carinatina plana.

Material.-

Carinatina plana is rare, and forms only a minute, albeit distinctive, part of the atrypid population. A total of 41 specimens were examined.

C293(7); C301(1 ); C344(1); C353 (1); C359(10); C382(3); C512(12); St44(1); St67(1); St621a(4); St811(1); C279a(1); St193(1); St649(2); St765(1) after SIEHL 1962.



Distribution of Carinatina plana (KAYSER 1871) in the Eifel synclines.

### Carinatina cf. signifera (SCHNUR 1853)

Pl. 58, figs. 1-2, 4-5.

1853 Leptaena signifera SCHNUR, p. 242, Pl. 45, fig. 5.

Range: Givetian?, Middle Devonian.
Type locality: Gerolstein (SCHNUR 1853, p. 238, 242).
Type stratum: Unknown. SCHNUR (ibid., p. 242) states "Im Kalk zu Gerolstein". There are no well developed limestone sections in the lower or middle Eifelian of the Gerolstein syncline, and the most likely source would be an upper Eifelian or Givetian limestone or dolomite. The age of SCHNUR's specimen is possibly lower Givetian.

Remarks.-

No topotypic material from the Gerolstein syncline, or even the Eifel as a whole, was available for comparison. STRUVE (in HOTZ & KRAUSEL & STRUVE 1955, p. 102, 115) lists the occurence of this species in the Freilingen beds and the Ahbach beds, but the specimens which were available to STRUVE could not be examined.

In the Senkenberg collection there were five other specimens (some of which are figured in the plates) from the Givetian at Finnentrop in the Attendorn syncline east of the Rhine. These specimens appear to match the SCHNUR illustrations although they are more coarsely ribbed. The chief comparison lies in the long, single skirt around the anterior and lateral margins of the shell and also in the round elevated rim which marks the border of the shell cavity. On the Finnentrop material the ribs are crowded at 16-18 per 10 mm on the rim or seam but are still finer distally. This also is characteristic of Carinatina plana (KAYSER). The mid-area of the shell has 12-14 ribs per 10 mm , i.e. slightly finer than in C. plana, and the ribs are much shallower and undulating than the sharp, deep-troughed, tubular ribs of C. plana.

Before Carinatina signifera (SCHNUR) can be confirmed as a valid species, three requirements are necesaary : type material must be examined, topotype material from the Eifel must be collected, and the vertical distribution of the species ascertained.

KAYSER (1871, p. 632) examined the SCHNUR collection in Bonn and stated that he could not find the specimen in SCHNUR's figure (1853, Pl. 45, fig. 5). KAYSER therefore assumed an error had occurred. However, HOLZAPFEL (1895, p. 265) also examined the SCHNUR collection and was able to find wax impresssons of the missing specimens. HOLZAPFEL (1895, Pl. 16, figs. 12, 12a) gave excellent figures of some specimens which were similar, though finer ribbed, than the specimens from Finnentrop. HOLZAPFEL's material came from Frettertal, which is near Finnentrop. He also stated (ibid., p. 267) that the species signifera was restricted to the Stringocephalus beds, hence the Givetian.

BARROIS (1886, Pl. 4, figs. 6a-f) illustrated "Orthisina davyi n.sp." which can be referred to Carinatina. The specific identification with either Carinatina plana (KAYSER) or C. signifera (SCHNUR) remains doubtful, because the variation in rib size and shape which BARROIS shows in the figures is large. BARROIS (1886, Pl. 4, fig. 6f) appears to have been the first author to recognise the distinctive micromorphology of the ribs.

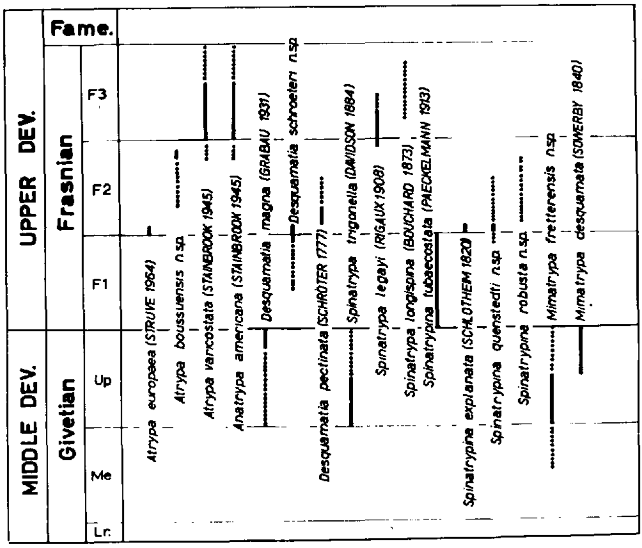
Material.-

Total 5 specimens

XVII283(5) Drevermann collection, "Ob. Mitteldevon, Finnentrop".

# VIII CONCLUSIONS

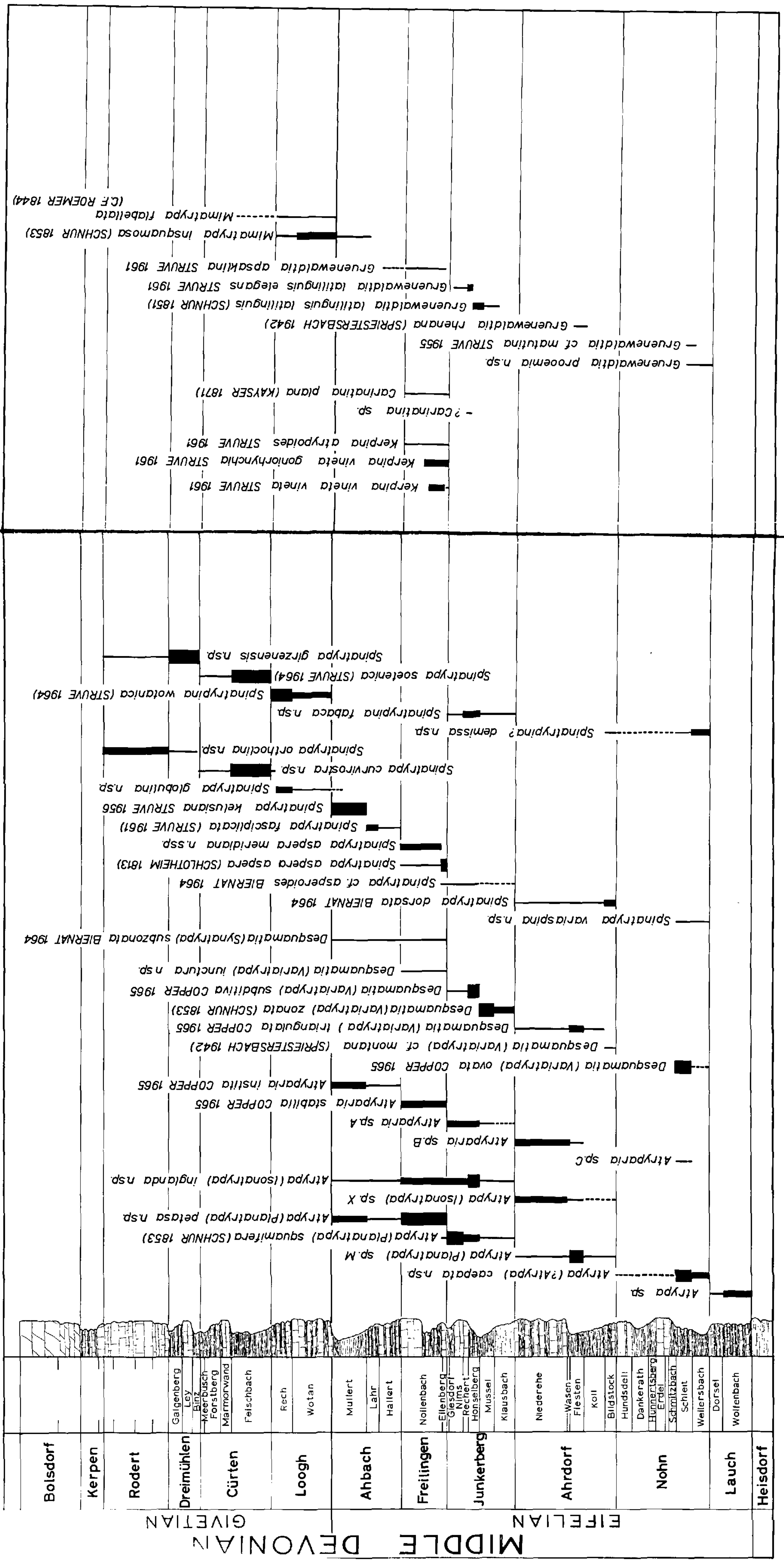
The Middle and Upper Devonian rocks of north-western Europe contain a rich atrypid brachiopod fauna. A part of this fauna is described. Text-figs. 210-211 show the vertical distribution of the atrypid species studied.



Text-fig. 210. Vertical distribution of atrypids in the Aachen area and Westfalen, Germany.

The absence of the genus *Atrypa* in the Givetian is noticeable and may be of importance to correlations. This absence may be a world-wide event. GRABAU (1932, p. 167) remarked that in Chinese Devonian the *A. reticularis* group was almost entirely replaced by the *A. desquamata* (i.e. *Desquamatia*) group, so the absence of *Atrypa* in the Givetian of Asia parallels that in Europe. Similarly, not a single true *Atrypa* has yet been described from Givetian rocks of North America, although the rocks there contain a prolific fauna. The significance of this is not clear.

The following atrypid names are nomina dubia and need further revision or elimination : *Spirifer sowerbyi* DEFRANCE, *Atrypa squamosa* SOWERBY, *A. insperata* PHILLIPS, *A. trigonella* DAVIDSON, *A. reticularis* var. *sagittata* MAURER, *Orthisina davyi* BARROIS, *Terebratula eifliensis* STEININGER, *A. aspera* var. *paffrathi* WEHRLI.



Text-fig. 211. Distribution of atrypid species in the Eifel Devonian synclines. The stratigraphic column is derived from data provided by STRUVE 1961. Errata: for Spinatrypa soetenica and S. girzenensis read Spinatrypina.

Comparisons with atrypid faunas from other parts of the world are only tentative because the techniques used in this study (particularly for internal morphology) have not been tried.

The Devonian fauna of the Lysa Gora area in Poland contains atrypids which are very similar, and in most instances conspecific, with those of the Eifel in Germany. A horizon by horizon comparison is feasible even though this area in Poland is separated from the Eifel by a distance of more than 1000 km. BIERNAT (1964) described, and brought up to date, many of the Polish species, and on the basis of a visit to the collections of the Eifel in the Senckenberg Museum in Frankfurt, drew correlations. The Skaly beds, which BIERNAT gives a lower Givetian age, contain a fauna which *is restricted* to the Eifelian of the Eifel region. Moreover, BIERNAT employed many out of date stratigraphical terms of the Eifel region (e.g. Rommerscheim beds were replaced by Junkerberg beds in STRUVE 1961), and made factual errors (e.g. confusing the lower Givetian *Fleringen* beds with the Eifelian *Freilingen* beds).

Horizons in the Eifel region can also be correlated in part with those of Devon in England. For example, the shales at Chercombe Bridge carry a *Gruenewaldtia latilinguis* (SCHNUR) fauna which is characteristic of the Hönselberg-Nims horizons in the Eifel (COPPER 1965a). These localities in Devon are a linear distance of more than 700 km from the Eifel. Thus horizon correlations on the basis of atrypids are at least successful over areas more than 1700 km apart.

The Devonian faunas of Spain and North Africa (Morocco, Algeria, Tunisia, Libya) are not well known, but it seems very likely that when they are described and figured their faunas will closely match those of the Eifel region because rich faunas from those areas have been mentioned. TERMIER & TERMIER (1950) figured some atrypids from Morocco which are identifiable as members of the genera *Desquamatia*, *Spinatrypa* and *Atrypa*, but *Carinatina*, *Mimatrypa* and *Gruenewaldtia* have never been described. COTTREAU (1940, Pl. 7, fig. 9) may have figured a palaferellid brachiopod. The *Atrypa reticularis* of TERMIER & TERMIER (1950, Pl. 101, fig. 14) possibly can be referred to *Desquamatia zonata* (SCHNUR). H. TERMIER (1936) did not describe Eifelian or Givetian atrypid genera, though establishing a new Silurian-lower Devonian genus *Dubaria* (junior synonym =*Rhynchatrypa* SIEHL 1962). A specimen from the Algerian Devonian figured by FLAMAND (1911, P. 12, figs. 2, 2a-b) shows possibilities of close relations with Eifel faunas and possibly is a member of the genus *Atryparia*

Correlations of the Eifel faunas with Middle Devonian faunas of the 'hercynian' type are difficult. The two distinct fossiliferous facies zones do not have many atrypid genera in common. In the Eifel, 'hercynian' genera such as *Karpinskia*, *Puncatrypa*, *Septatrypa* and *Dubaria* are missing and *Carinatina* is only rare, Faunal lists of BARRANDE and

HAVLICEK (Prague Devonian), SCUPIN, FRECH and GORTANI (Austrian and Italian Alps) and STEVANOVIC and ZIVANOVIC (Yugoslavian Devonian) differ markedly from a faunal list of the Eifel region.

Striking parallels exist between the Frasnian faunas of Germany, North America and the Urals and the Kutznetsk basin, and this seems to have been a period when there were good channels of communication between these areas. The likeness between the rich faunas from Bensberg in Germany and thos of Iowa has already been stressed by JUX (1964) and STRUVE (1964). It is possible that atrypids on both sides of the Atlantic may be conspecific. Detailed comparisons have not yet been made.

Comparisons of the classic European Devonian sections with those of the U.S.S.R. (Urals, Kutznetsk) have been made by the Russian palaeontologists. RZHONSNITSKAYA (1962), for example, correlated the Pesterovk limestones of the Kutznetsk basin with the Eifelian Rommersheim beds of the Eifel on the basis of Mimatrypa flabellata (ROEMER) and rhynchonellid species. Unfortunately Rommersheim beds(correct name=Junkerberg) do not contain Mimatrypa flabellata which is much younger (lower Givetian). Particularly active in the field of Devonian brachiopod correlations have been the Russian palaeontologists CHERKESOVA (Nova Zemlya), RZHONSNITSKAYA (Urals, central Asia, Salairica), KHODALEVICH (eastern Urals), MARKOVSKY (European Russia), BUBLICHENKO (Kazakhstan) and DOMRACHEV (Urals). But more accurate work in the field of internal morphology is needed before identifications can be verified.

The Givetian-Frasnian faunas of the Eifel region may have a good deal in common with Asian faunas like those described from Yunnan in China (particularly GRABAU 1931), Burma (MANSUY 1912 and REED 1908) and those of the Pamirs in Pakistan (REED 1922). REED (1908, p. 144)correlated the Burmese faunas with the 'Calceola' beds of Europe (i.e. upper Eifelian-lower Givetian), and it is possible that REED((1908, Pl. 18, figs. 11-13) described the index fossil Mimatrypa flabellata as Rhynchonella (Camarotoechia) sp. A and sp. B. This would be the most easterly occurrence yet known of Mimatrypa

The atrypid fauna from Japan is too sparse and poorly described to make adequate comparisons. OKUBO (1956, pp. 39-40) described a new species Atrypa pauciplicata from a single poor specimen and this is possibly Spinatrypa. SUGIYAMA (1942) proposed a new mutation japonica for Atrypa desquamata, but this atrypid is clearly unrelated to Mimatrypa desquamata (SOWERBY) from England.

Devonian atrypid faunas from Australia are difficult to relate to those from the Eifel area, and considerable nomenclatorial confusion exists. In 1951 COLEMAN identified several new species and subspecies from Australia. COLEMAN's Atrypa reticularis teicherti is rather similar to Atrypa caepata n.sp. from the Eifel Eifelian. A. multimoda COLEMAN can be identified as a Desquamatia but other species, Atrypa aspera prideri and A. parva appear to be confused, and figured specimens within each of these can be assigned to different genera.

Regrettably, VEEVERS (1959a, 1959b) incorrectly redefined and revised COLEMAN's species, assigning them to catch-all, meaningless species like A. desquamata. A. aspera and A. reticularis. From comparative material of two of these species sent by Dr. VEEVERS it appears that COLEMAN may have been right in his first assessment. VEEVERS (1959a Pl. 15, fig. 13) redescribed an Atrypa desquamata kimberleyensis which does not belong to Atrypa, nor to desquamata, not to the original subspecies kimberleyensis of COLEMAN! An interesting Australian species was the Spinatrypa aspera prideri in VEEVERS (1959b, Pl. 2, figs. 1-9) which does not belong to the subspecies prideri COLEMAN. This particular atrypid shows striking similarity to atrypids (still undescribed) from the Ferques limestone of the Boulonnais area, France.

Faunas of the North American Devonian are still only partially known, though excellent illustrations of the external morphology have been given by HALL, WEBSTER, FENTON & FENTON, STAINBROOK, BRANSON, WILLARD and CLELAND. A large-scale revision of the eastern North American faunas of New York, Pennsylvania, Illinois, Iowa, Kentucky, Missouri, Wisconsin and Maryland is necessary to bring nomenclature and classification, as well as internal morphology, up to date.

Many species have been described from the Devonian of Canada in such areas as Manitoba, Alberta and Mackenzie Territory. The faunas of the Canadian Arctic (Banks, Melville, Bathurst and Cornwallis islands) are poorly known and have not been described. The brachiopods collected during the expedition of the Danish vessel 'Fram', which visited Ellesmere island, were described by MEYER in 1913 and a comparison made with faunas from Gerolstein in the Eifel. The upper part of the Hume formation in Mackenzie Territory of northern Canada, contains a rich fauna probably of lower Givetian age (i.e. about Loogh-Cürten beds in the Eifel). These faunas and those from Alberta have been described by WARREN & STELCK (1944, 1956), CRICKMAY (1960, 1963), McLAREN & NORRIS (1962) and NORRIS (1964). The last mentioned work contains Atrypa nasuta n.sp. (NORRIS, 1964, Pl. 15, figs. 4-9) which may be related to Mimatrypa. If this relationship holds, it so far the only Mimatrypa recorded in North America.

It is evident that at the present stage of knowledge about atrypid faunas, comparisons run into serious doubts and difficulties. Before atrypids can be reliably used in large-scale correlations uniformity in description, especially with attention to internal morphology, is an essential requirement. A great deal of painstaking and, unfortunately, laborious systematic work is needed before the full range of variation of individual European species is known. The revision of European atrypid faunas must be completed : this means an examination of all French and Belgium atrypid material and also a re-examination of the basic'hercynian' atrypid faunas as they occur in eastern parts of Germany, in Austria and in the Carnic Alps, Italy. A taximetric study of atrypid faunas can only then be attempted when it is known which atrypid species are synchronous, i.e. when it is known which morphological characters can be attributed to geographical and which to chronological variation. No dendrograms showing the development of atrypid species in Europe have been drawn. Not enough is known at present about the stratigraphic distributions of critical 'linking' species.

The development of the two main families treated in this study, the Atrypidae and Palaferellidae, also cannot be traced at the present time. This is because very little is known about the internal structure of the important Silurian atrypid genera. The type species of Atrypa, A. reticularis (LINNE) must be revised and the revision based on topotypic material.

# PLATE 1

Figs. 1a-e Atrypa (Atrypa) reticularis (LINNE 1758)

-- Silurian; Gotland, Sweden. --

Linnaean Society Collection, London. a) ventral, b) dorsal, c) lateral, d) posterior, e) anterior. Photograph of the LECTOTYPE figured in ALEXANDER (1949, pl. 9, figs.1a-d). Compare with Gotland material illustrated in BOUCOT, JOHNSON and STATON (1964, pl. 126, figs 1-5). x2.

Figs 2-4 Atrypa sp. indet.

-- Eifelian, Dorsel horizon, Lauch beds; Gerolstein syncline, MTB Gerolstein r44760:h64810. --

2. Specimen PC11. Loose broken ventral valve. Lack of pallial sinuses noticeable. x2.

3. Specimen PC12. Ventral view of finely ribbed specimen with Atrypa (Isonatrypa) affinities. x2.

4. Specimen PC13, a) dorsal, b) ventral.view. Specimen with Atrypa (Planatrypa) affinities. x2.

1

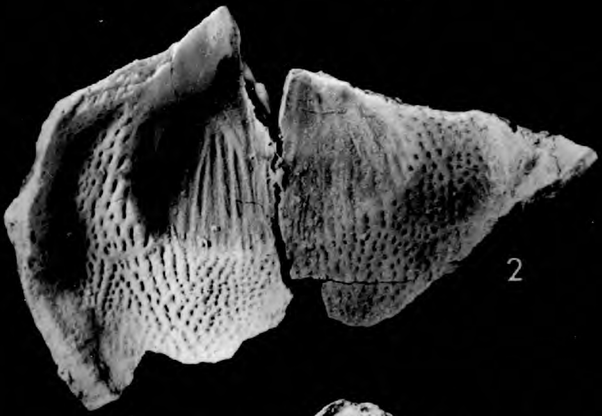

1a


1b

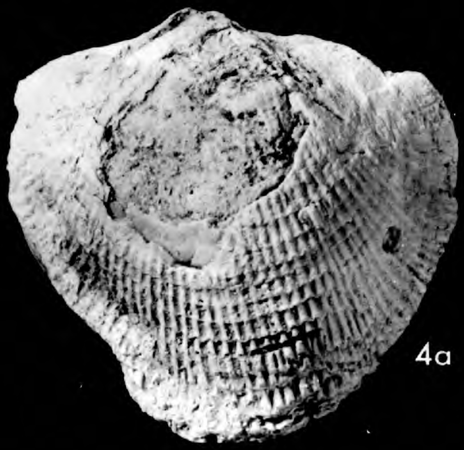

1c

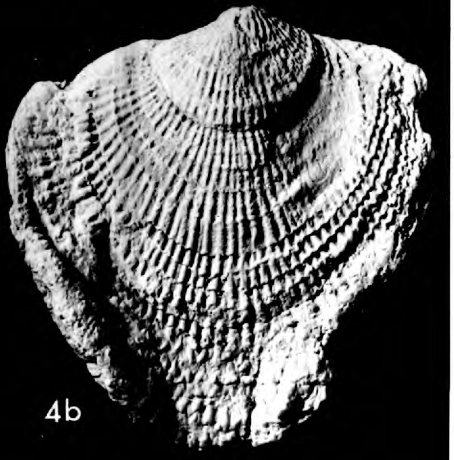

1d


1e


2


3


4a


4b

# PLATE 2

Figs. 1a-d Atrypa sp. indet.

-- Eifelian, Wolfenbach horizon, Lauch beds; Ahrdorf syncline, MTB Dollendorf r52480:h80380. --

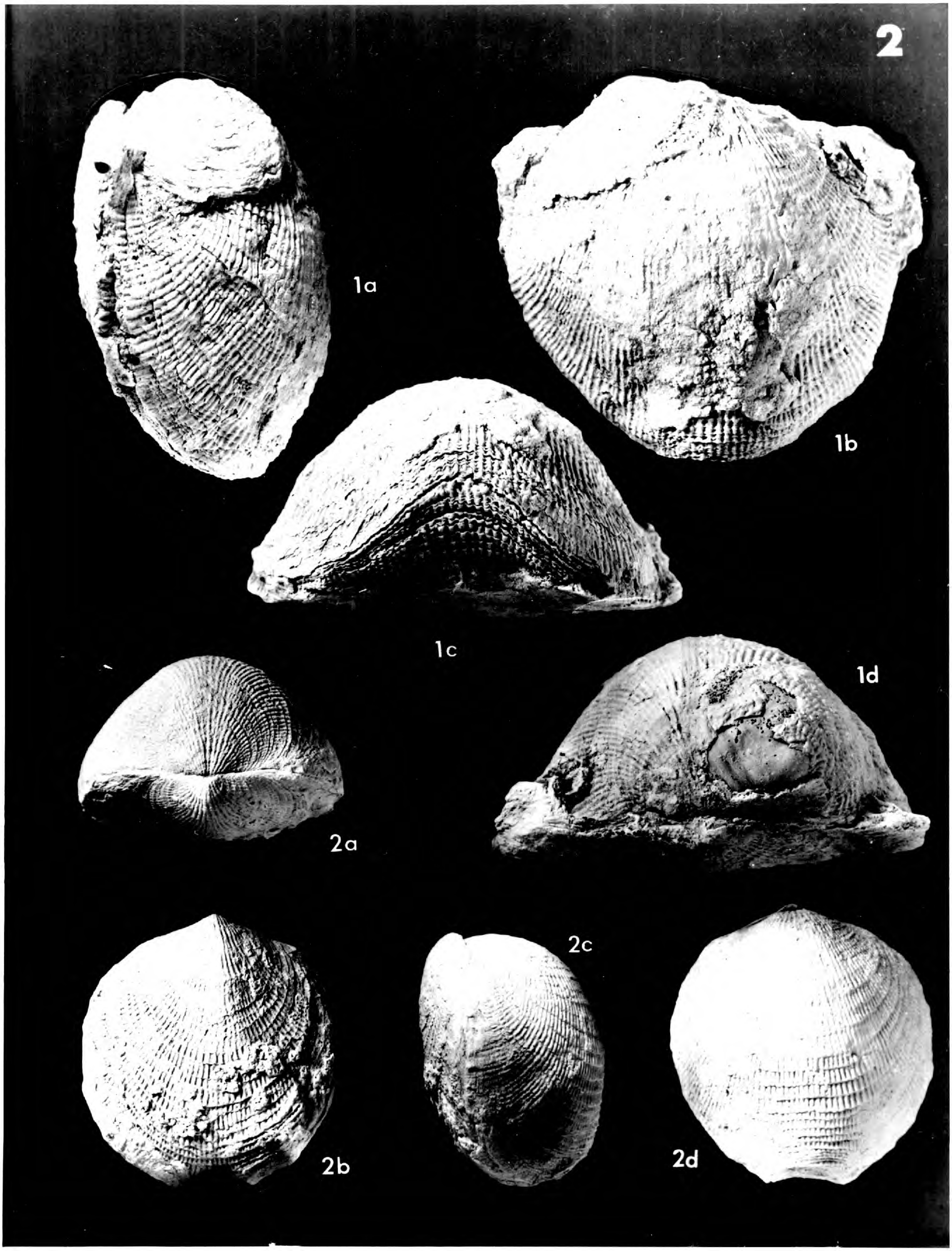
Specimen PC10, a) lateral, b) dorsal, c) anterior, d) posterior. Large convexoplane atrypid typical of the Wolfenbach horizon in the Ahrdorf syncline. An inarticulate brachiopod Crania is cemented to the dorsal valve. Note the rib mimicry. x2.

Figs. 2a-d Atrypa (Atrypa ?) caepata n.sp.

-- Lower Eifelian, Schleit horizon, Nohn beds; Hillesheim syncline, MTB Dollendorf r54340:h79040. --

HOLOTYPE PC14, a) posterior, b) ventral, c) lateral, d) dorsal. x2.

2



# PLATE 3

Figs. 1-4 *Atrypa* (*Atrypa* ?) *caepata* n.sp.

-- Lower Eifelian, *1-3*, Schleit horizon, *4*, Weilersbach horizon, Nohn beds; Hillesheim syncline, MTB Dollendorf, *1*,*3*, r54340:h79040, *4*, r56980:h78350. --

*1*. Paratype PC15, a) lateral, b) ventral, c) dorsal, d) posterior. x2. More equally convex shell with small marginal frill.

*2*. Paratype PC16, Prüm syncline, MTB Prüm r31730-750: h62900. a) ventral, b) dorsal, c) posterior. x2. Planar pedicle valve and appressed beak show early traces of *Atrypa* (*Planatrypa*) relation.

*3*. Paratype PC17, dorsal view of shell mould. x2.

*4*. Paratype PC18, a) ventral, b) dorsal view of ventral valve, c) dorsal. x2. Prepared specimens to show inner markings.


1a


1b


1c

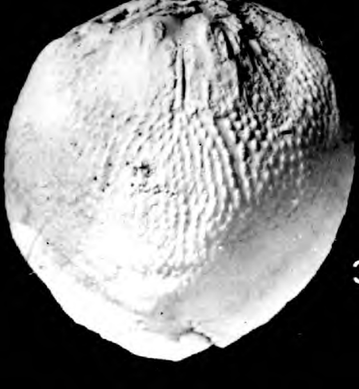

1d


2a


2b


4a


2c


3


4b


4c

# PLATE 4

Figs. 1-3 Atrypa (Planatrypa) sp. M.

-- Middle Eifelian, Flesten horizon, Ahrdorf beds; Hillesheim syncline, 1, MTB Dollendorf r52500-10:h77275-330, 2, 3, r55250:h75410. --

1. Specimen PC19, a) ventral, b) dorsal, c) lateral, d) posterior. x2.

2. Specimen PC20, a) lateral, b) dorsal, c) ventral, d) posterior. x2.

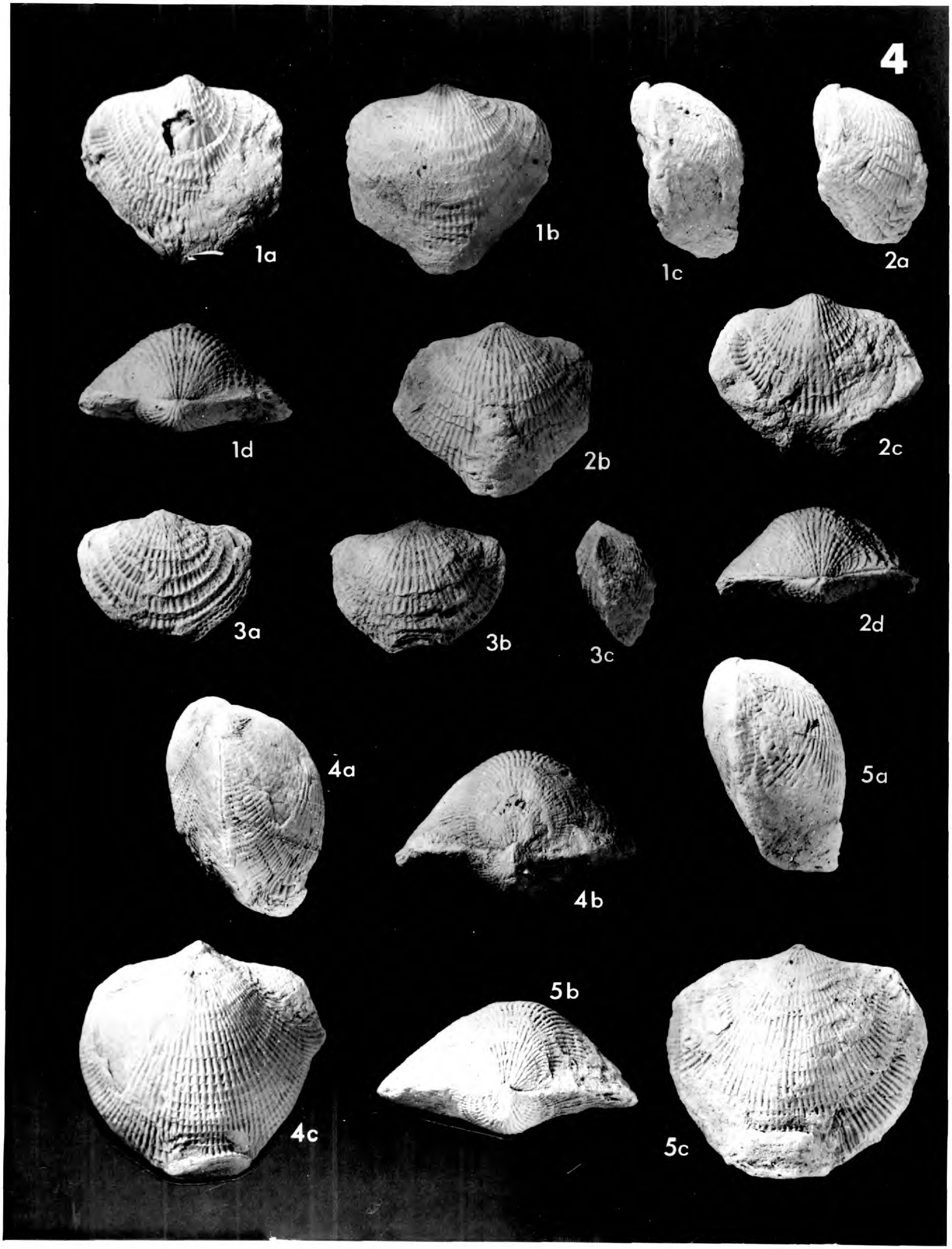
3. Specimen PC21, a) ventral, b) dorsal, c) lateral. x2.

Figs. 4-5 Atrypa (Isonatrypa) sp. X.

-- Middle Eifelian, Niederehe horizon (low), Ahrdorf beds; Hillesheim syncline, MTB Dollendorf r55790:h78000. --

4. Specimen PC22, a) lateral, b) posterior, c) dorsal. x2.

5. Specimen PC23, a) lateral, b) posterior, c) dorsal. x2.


4
1a
1b
1c
2a
1d
2b
2c
3a
3b
3c
2d
4a
5a
4b
5b
4c
5c

# PLATE 5

Figs. 1-2 Atrypa (Planatrypa) squamifera (SCHNUR 1853)

-- Middle Eifelian, Giesdorf horizon, Junkerberg beds; Prüm syncline, MTB Schonecken r32200:h60330. --

1. Hypotype PC24, a) ventral, b) dorsal, c) posterior. x2. Highly arched specimen.

2. Hypotype PC25, a) ventral, b) dorsal, c) posterior. x2. Flatter specimen with weakly extended hinge corners.

5


1a


1b


2a


2b


2c


1c

## PLATE 6

Figs. 1-3 *Atrypa* (*Planatrypa*) *squamifera* (SCHNUR 1853)

-- Middle Eifelian, Giesdorf horizon, Junkerberg beds; 1, 2, Prüm syncline, MTB Schönecken r32200:h60330, 3, Hillesheim syncline, MTB Dollendorf r54290:h75310. --

1. Hypotype PC24 (refer to Pl. 5), lateral view. x2.

2. Hypotype PC25 (refer to Pl.5), lateral view. x2.

3. Hypotype PC26, dorsal view of ventral valve. x2.

Figs. 4-12 *Atrypa* (*Planatrypa*) *petasa* n.sp.

-- Upper Eifelian, Eilenberg horizon-Bohnert subhorizon, Freilingen beds; Hillesheim syncline, 4, 5, MTB Dollendorf r54290:h75310, 6, 9, MTB Dollendorf r54310:h75390, 7, 8, 10, 11, 12, MTB Dollendorf r55640:h77390. --

4. Paratype PC27, ventral valve. x2.

5. Paratype PC28, dorsal valve. x2.

6. Paratype PC29, ventral valve. x2.

7. Paratype PC30, ventral valve. x2.

8. Paratype PC31, dorsal valve. x2.

9. Paratype PC32, ventral valve. x2.

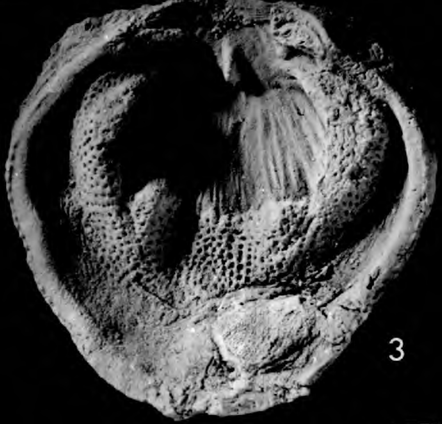
10. Paratype PC33, ventral valve. x2.

11. Paratype PC34, dorsal valve. x2.

12. Paratype PC35, dorsal valve. x2.

1

2



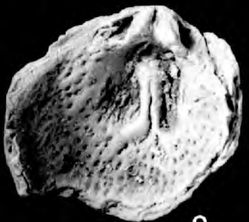
3

4

5

6

7



8

9

10

11

12

# PLATE 7

Figs. 1-3 Atrypa (Planatrypa) petasa n.sp.

-- Upper Eifelian, Freilingen beds; Hillesheim syncline, 1, 3, MTB Dollendorf r55640:h77390, 2, MTB Dollendorf r53870: 74680. --

1. HOLOTYPE PC36, a) ventral, b) dorsal, c) lateral, d) posterior, e) anterior. x2.

2. Paratype PC37, a) dorsal, b) lateral, c) posterior, d) ventral. x2.

3. Paratype PC38, a) anterior, b) dorsal, c) ventral, d) lateral, e) posterior. x2.


1a


1b


1


1d


1e


2a

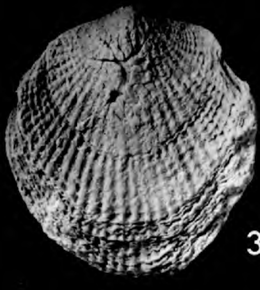

2b


2c


3a


2d


3b


3c


3d


3e

# PLATE 8

Figs. 1-2 Atrypa (Isonatrypa) inglanda n.sp.

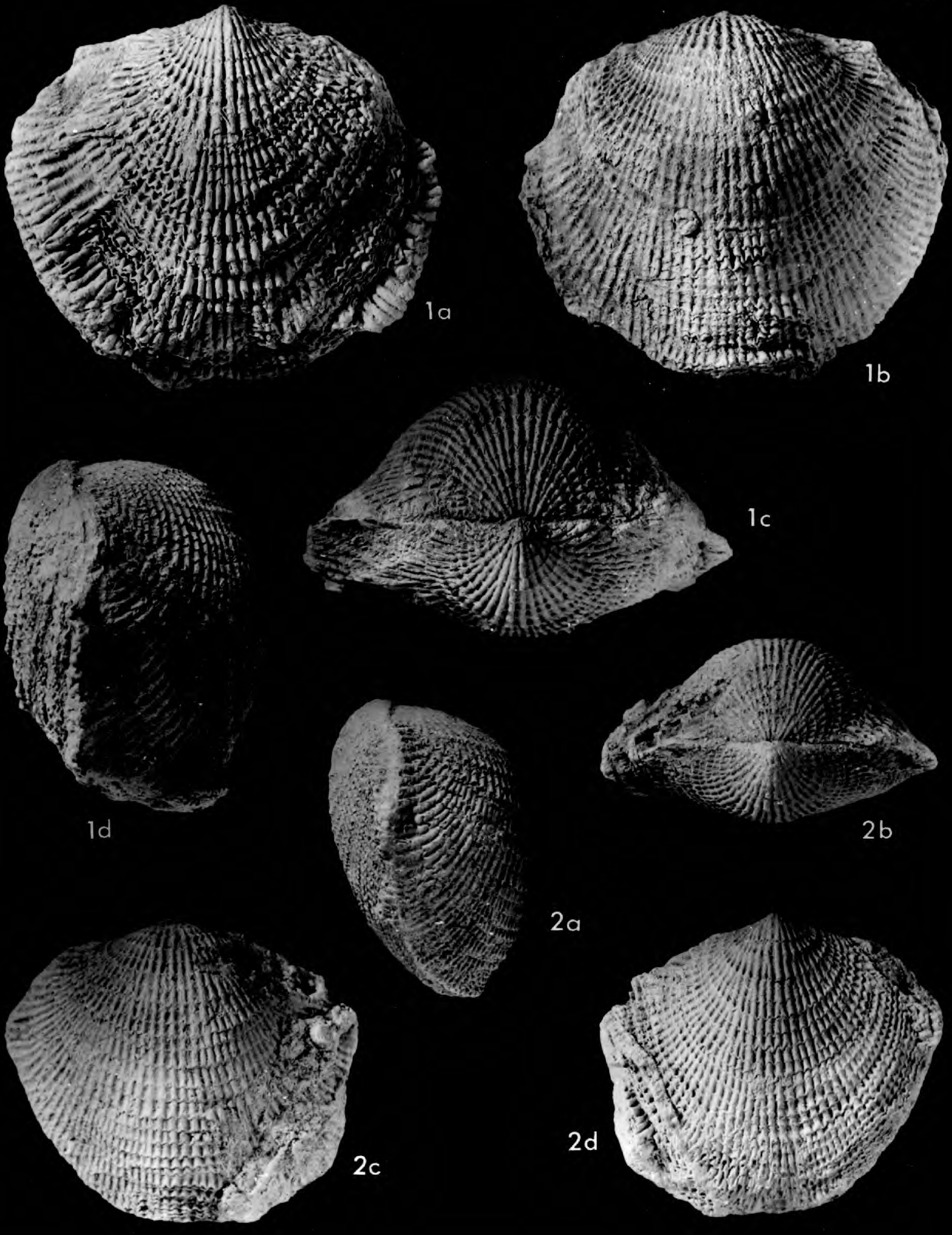
-- Upper Eifelian, Eilenberg horizon, Freilingen beds; Hillesheim syncline, 1, MTB Dollendorf r54290:h75310, 2, MTB Dollendorf r53850:h74680. --

1. HOLOTYPE PC39, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

2. Paratype PC40, a) lateral, b) posterior, c) dorsal, d) ventral. x2.

In figs. 1a-d. the holotype shows deflected growth lamellae and a tendency towards more tubular ribs. In figs. 2a-d paratype PC40, lamellae hug the shell surface and ribs are more subdued.

8



## PLATE 9

Figs. 1-5 *Atrypa* (*Isonatrypa*) *inglanda* n.sp.

-- Upper Eifelian, about Eilenberg horizon, Freilingen beds; Sötenich syncline, 1, 2, 4, 5, MTB Mechernich r38020:h96980; 3, MTB Mechernich r37910:h96450. -- All dorsal views of ventral valves. Paratypes 1. PC41, 2. PC42, 3. PC43, 4. PC44, 5. PC45. x2.

Figs. 6 *Atryparia* sp. B.

-- Middle Eifelian, high Niederehe horizon, Ahrdorf beds; Gerolstein syncline, MTB Gerolstein r46430:64960. -- HOLOTYPE PC46, a) dorsal, b) posterior, c) ventral, d) lateral. x2.


1

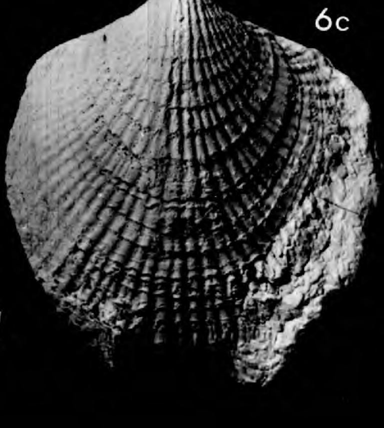

2


3


6a


4


6b


6c


5


6d

# PLATE 10

Figs. 1-3 *Atryparia* sp. A.

-- Middle Eifelian, Nims-Giesdorf horizons, Junkerberg beds; 1, 3, Rohr syncline, MTB Aremberg r50730:h90230; 2, Sötenich syncline, MTB Mechernich r46500:h01490. --

1. HOLOTYPE PC47, a) lateral, b) dorsal, c) ventral, d) posterior. c2.

2. Paratype PC48, ventral valve. x2. Note the rim of calcite tissue on the apex : this is the pedicle layer.

10


1a

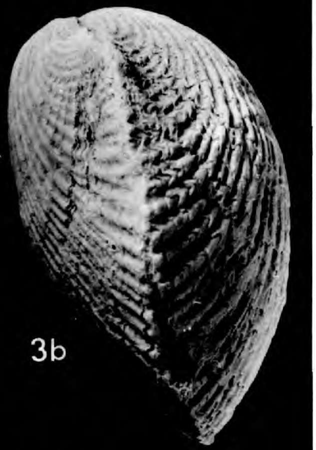

1b


1c

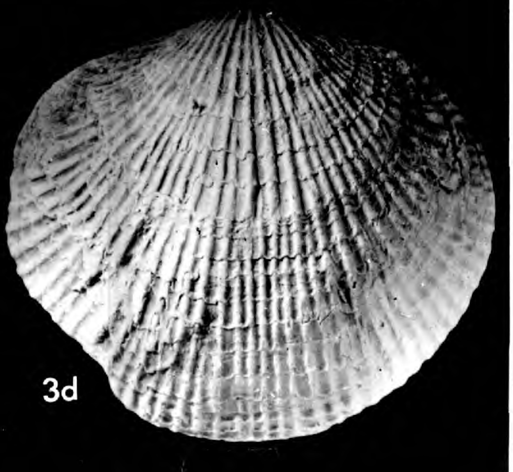

1d


2


3a


3b


3c


3d

# PLATE 11

Figs. 1-3 Atryparia stabilia COPPER 1965

-- Upper Eifelian, Eilenberg horizon to Bohnert subhorizon, Freilingen beds; Hillesheim syncline, 1, MTB Dollendorf r53850:h74680, 2, 3, MTB Dollendorf r51000:h75720. --

1. Paratype PC50, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

2. Paratype PC51 ventral view of broken dorsal valve. The thickness of the hinge plates is notable. x2.

3. Paratype PC52, a) posterior, b) ventral, c) dorsal, d) lateral. x2.

The flatter ventral valve, the coarsening, more widely crested and deeply troughed ribs are characteristic.


1a


1b


1c


2


3a


1d


3b


3c


3d

## PLATE 12

Figs. 1-2 Atryparia institta COPPER 1065

-- Upper Eifelian, Müllert horizon, Ahbach beds; Hillesheim syncline, 1, MTB Dollendorf r54550:h75730, 2, MTB Dollendorf r54900:h77960. --

1. Paratype PC53, a) ventral, b) lateral, c ) dorsal, d) posterior. x2.

2. Paratype PC54, a) dorsal, b) ventral, c) lateral, d) posterior. x2.

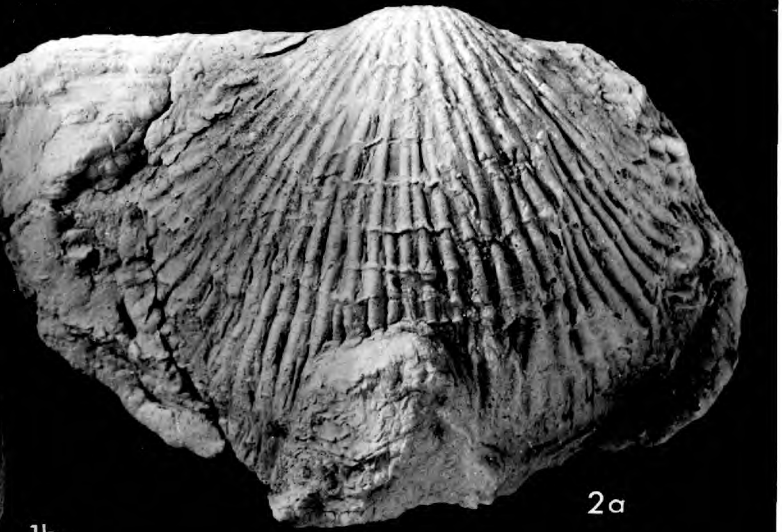
Young specimens are biconvex, elongated.

Note the thick growth of lamellae into frills.

**12**


1a


1b


2a


1c


2b


2c


1d


2d

# PLATE 13

Figs. 1-2 _Atrypa_ (_Atrypa_) _boussuensis_ n.sp.

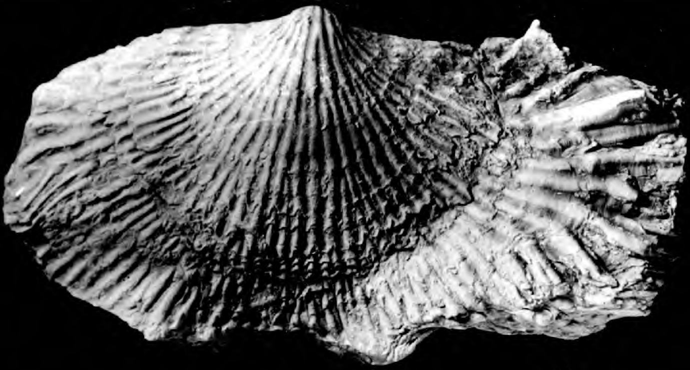
-- Frasnian, upper 5 m of F2i;Dinant basin, Belgium, quarry of the Boussu cemetery, north wall. --

_1_. HOLOTYPE PC55, a) ventral, b) posterior. x2.

_2_. Paratype PC56, a) dorsal, b) ventral, c) posterior, d) lateral. x2.

_3_. Paratype PC57, a) posterior, b) lateral, c) ventral, d) dorsal. x2.

Note the widening of rib troughs and heightening of rib crests on the extended frill of fig. 1.



1a

2a

2b

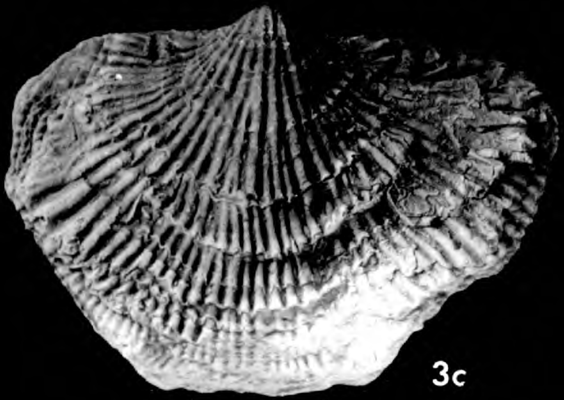
1b

2c

3a

3b

2d



3c

3d

# PLATE 14

Figs. 1-3 Atrypa (Atrypa) boussuensis n.sp.

-- Frasnian, upper 5 m of F2i; Dinant basin, Belgium, quarry of the Boussu cemetery, north wall. --

1. Paratype PC58, a) ventral, b) dorsal, c) lateral, d) anterior. x2.

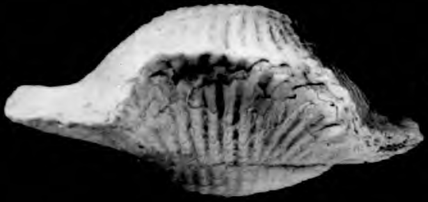
2. Paratype PC59, a) ventral, b) lateral, c) anterior. x2. A highly arched, globose specimen.

3. Paratype PC60, a) ventral, b) posterior. x2.


1a

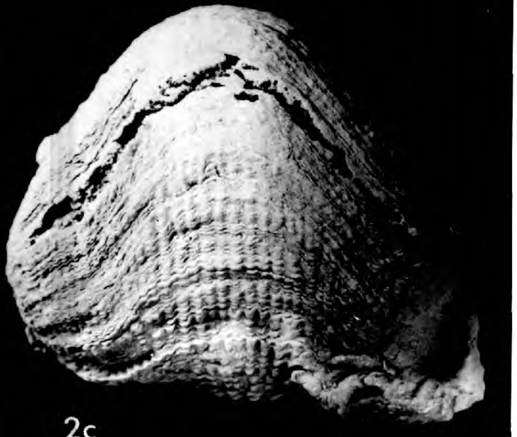

1b


1c


1d


2a


2b


2c


3a


3b

# PLATE 15

Figs. 1-4 Anatrypa cf. americana (STAINBROOK 1945)

-- Frasnian, F3; Aachen area, "Breinigerberg" MTB Stolberg r17700:h22500. --

1. Hypotype BMB13.1, a) ventral, b) dorsal, c) lateral, d) posterior, e) anterior. x2.

4. Hypotype BMB13.2, a) lateral, b) anterior, c) ventral, d) posterior, e) dorsal. x2.

3. Hypotype BMB10.1, ventral valve. x4

2. Hypotype BMB10.2, ventral valve. x4.

Figs. 5-7 Anatrypa (?) sp.

-- Frasnian limestone (?), possibly Iberg Kalk; MTB Villmar, "Bodensteiner Ley, Villmar" (Jordan coll., Berlin Museum). --

5. BMB27.1, a) lateral, b) dorsal. x2.

6. BMB27.3, a) ventral, b) dorsal. x2.

7. BMB26.1, a) ventral, b) dorsal. x2.

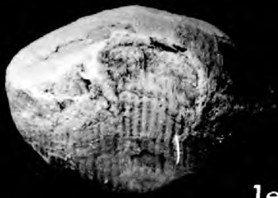

1a


1b


1c


4a


1d


1e


4b


4e


4d


4c


5a


2


3


5b


6a


6b


7a


7b

# PLATE 16

Figs. 1-3 Spinatrypa variaspina n.sp.

-- Lower Eifelian, Weilersbach-Schleit horizons, Nohn beds; Hillesheim syncline, 1, MTB Dollendorf r54890:h78380, 2, 3, MTB Dollendorf r57000:h78230. --

1. HOLOTYPE PC61, a) dorsal, b) ventral, c) posterior, d) lateral. x2.

2. Paratype PC62 , a) dorsal, b) lateral, c) ventral, d) posterior. x2.

3. Paratype PC63, a) ventral, b) posterior, c) dorsal, d) lateral. x2.

Figs. 4-6 Spinatrypa dorsata BIERNAT 1964.

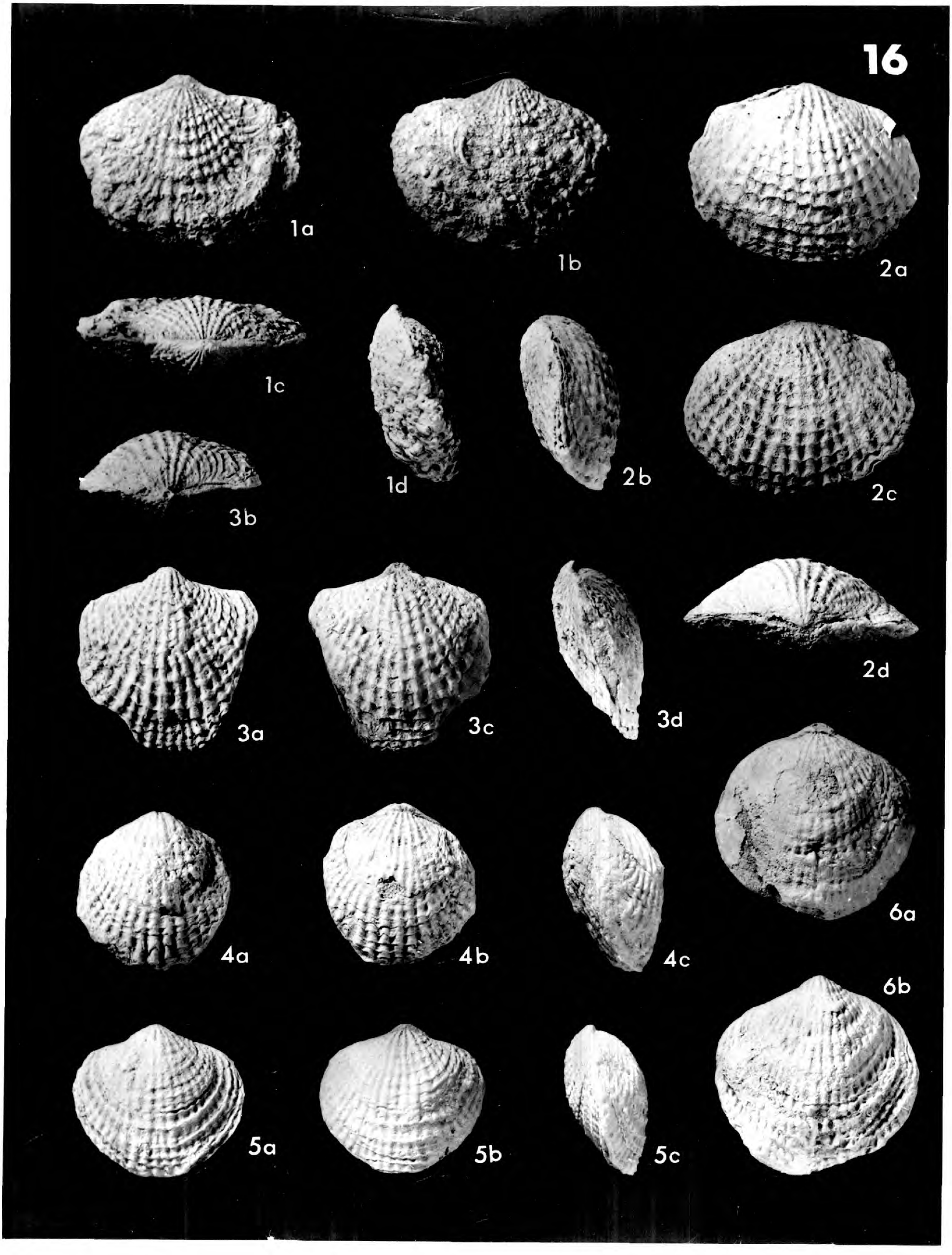
-- Middle Eifelian, Ahdorf beds; Ahrdorf syncline, 4, 5, MTB Dollendorf r56340:h83560, Bildstock horizon, 6, Hillesheim syncline, MTB Dollendorf r55790:h78000, Flesten-Niederehe horizons. --

4. Hypotype PC64, a) ventral, b) dorsal, c) lateral. x2.

5. Hypotype PC65, a) ventral, b) dorsal, c) lateral. x2.

6. Hypotype PC66, a) dorsal, b) ventral. x2.

Specimens from the higher Ahrdorf horizons are larger than those at the base (fig. 6).



16

# PLATE 17

Figs. 1-7 Spinatrypa aspera aspera (SCHLOTHEIM 1813)

-- Upper Eifelian, base of the Freilingen beds, about Eilenberg horizon; Sötenich syncline, MTB Mechernich r37910:h96450. --

1. Hypotype PC67, a) ventral, b) dorsal. x2.
2. Hypotype PC68, a) ventral, b) lateral. x2.
3. Hypotype PC69, a) ventral, b) dorsal, c) posterior. x2.
4. Hypotype PC70, a) ventral, b) dorsal. x2,
5. Hypotype PC71, a) ventral, b) dorsal. x2.
6. Hypotype PC72, a) posterior, b) ventral, c) dorsal. x2.
7. Hypotype PC73, a) dorsal, b) ventral. x2.

Figs. 1, 3, 5 are specimens which already show strong trends towards a Spinatrypa aspera meridiana n.ssp. morphology, i.e. wider, flatter shell, larger area, deeply troughed ribs.

17


1a


1b


2a


2b


3a


3b


3c


4a


5a


5b


4b


7a


6a


7b


6b


6c

# PLATE 18

Figs. 1,4 Spinatrypa aspera meridiana n.ssp.

-- Upper Eifelian, Bohnert subhorizon, Nollenbach horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf r5100:h75720. --

1. Paratype PC74, a) ventral, b) posterior, c) dorsal. x2.

4. HOLOTYPE PC75, a) dorsal, b) ventral, c) posterior. x2.

Figs. 2-3, 5-11 Spinatrypa aspera aspera (SCHLOTHEIM 1813)

-- Upper Eifelian, base of the Freilingen beds, about Eilenberg horizon; Sötenich syncline, 2, MTB Mechernich r38020:h96980, 3, 5-10, MTB Mechernich r37910:h96450, 11, MTB Mechernich r39320:h98390. --

2. Hypotype PC76, ventral. x2.

3. Hypotype PC77, ventral. x2.

5. Hypotype PC78, dorsal valve. x2.

6. Hypotype PC79, ventral valve. x2.

7. Hypotype PC80, ventral valve. Note the small curved crura protruding from the shell apex. x2.

8. Hypotype PC81, dorsal valve. x2

9. Hypotype PC82, ventral. x2.

10. Hypotype PC83, ventral valve. x2.

11. Hypotype PC84, a) ventral, b) dorsal. x2.


1a


1b


4a


1c

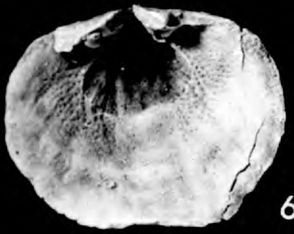

2


4b


5


3


4c


6

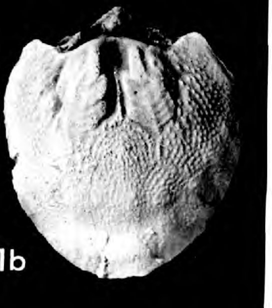

7


8


9


10

11a


11b

# PLATE 19

Figs. 1-3 Spinatrypa cf. asperoides BIERNAT 1964

-- Upper Eifelian, 1, Nollenbach horizon, 2, 3, Eilenberg horizon, Freilingen beds; Hillesheim syncline, 1, MTB Dollendorf r55640:h77390, 2, MTB Dollendorf r52815-205: h76365-400, 3, MTB Dollendorf r52225-50:h76445-60. --

1. Hypotype PC85, a) ventral, b) dorsal, c) posterior. x2.

2. Hypotype PC86, a) lateral, b) dorsal, c ) ventral. x2.

3. Hypotype PC87, a) posterior, b) dorsal, c) ventral. x2.

Figs. 5-8 Spinatrypa fasciplicata (STRUVE 1061)

-- Upper Eifelian, lower parts of the Lahr horizon, Ahbach beds; Hillesheim syncline, MTB Dollendorf r55530-7-: h77390. --

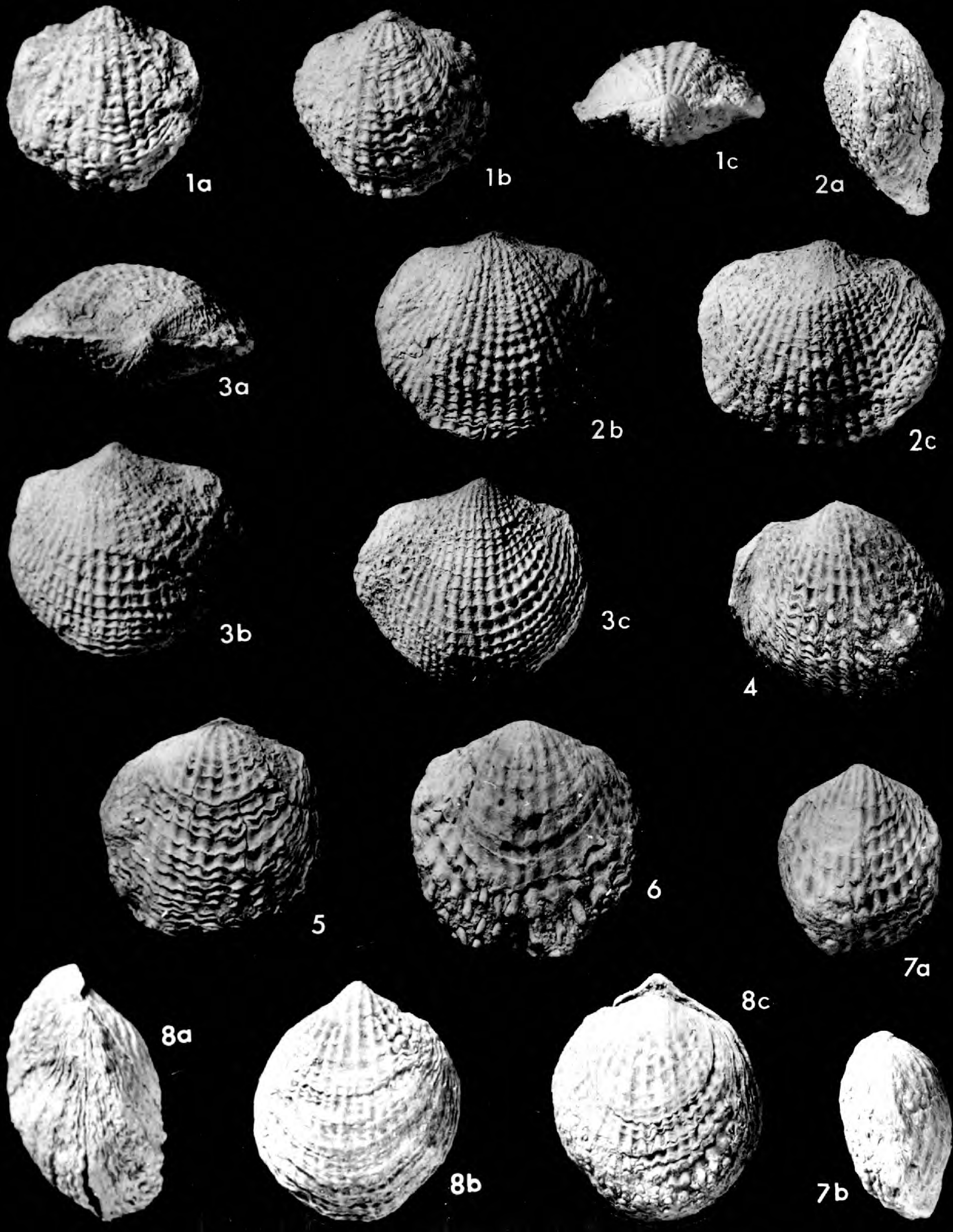
5. Hypotype PC88, dorsal. x2.

6. Hypotype PC89, ventral. x2

7. Hypotype PC91, a) ventral, b) lateral, x2.

8. Hypotype PC90, a) lateral, b) ventral, c) dorsal. x2.

19



# PLATE 20

Figs. 1-2 Spinatrypa fasciplicata (STRUVE1961)

-- Upper Eifelian, lower parts of the Lahr horizon, Ahbach beds; Hillesheim syncline, MTB Dollendorf r55530-70:h77390. --

1. Hypotype PC92, a) ventral, b) dorsal. x2.
2. Hypotype PC93, a) ventral, b) dorsal. x2.

Figs. 3-9 Spinatrypa kelusiana (STRUVE1956)

-- Upper Eifelian, Müllert horizon, Ahbach beds; 3, 5, 6, MTB Dollendorf r55460:h77380, 4, MTB Dollendorf r55480:h77390, 7-9, MTB Dollendorf r54620:h75770. --

3. Hypotype PC94, a) dorsal, b) ventral. x2.
4. Hypotype PC95, a) ventral, b) lateral. x2.
5. Hypotype PC96, a) lateral, b) ventral. x2.
6. Hypotype PC97, dorsal. x2.
7. Hypotype PC98, ventral. x2.
8. Hypotype PC99, ventral. x2.
9. Hypotype PC100, ventral. x2.

Fig. 10 Spinatrypa aff. globulina n.sp.

-- Upper Eifelian, upper part of Müllert horizon, Ahbach beds; Hillesheim syncline, MTB Dollendorf r54550:h75730. --

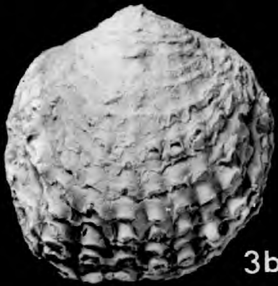

1a


1b


2a


2b


3a


3b


4a


4b


6


5a


5b


7


10a


8


9


10b

# PLATE 21

Figs. 1-4 Spinatrypa globulina n.sp.

-- Lower Givetian, Neuenbusch horizon (equivalent to low Rech or high Wotan horizon in the Hillesheim syncline), Loogh beds; Blankenheim syncline, MTB Blankenheim r46410:h90050. --

1. HOLOTYPE PC102, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

2. Paratype PC103, a ) ventral, b) dorsal, c) lateral, d) posterior. x2.

3. Paratype PC104, a) lateral, b) ventral. x2.

4. Paratype PC105, a) ventral, b) dorsal, c) lateral, d) posterior. x2.

Paratype PC103, with its elongated shell, strong midribs and smaller size shows affinities with Spinatrypa kelusiana STRUVE 1956.


1a


1b


1c


1d


3a


2a


3b


2b


4a


2c


2d


4b


4c

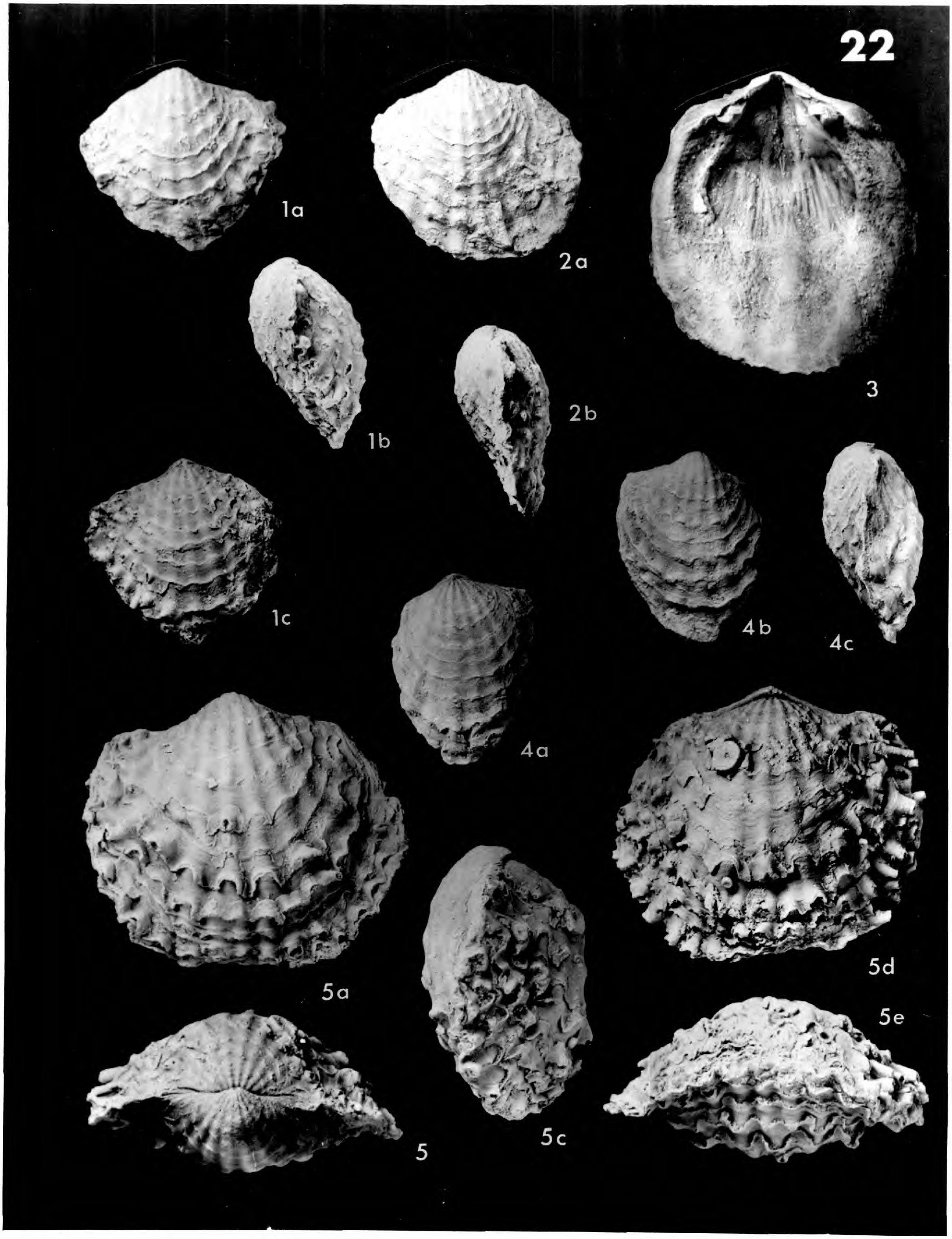

4d

# PLATE 22

Figs. 1-5 Spinatrypa curvirostra n.sp.

-- Lower Givetian, Scheid horizon (equivalent roughly to Felschbach horizon), Cürten beds; Sötenich syncline, MTB Mechernich r40160:h98850. --

1. Paratype PC106, a) ventral, b) lateral, c) dorsal. x2.
2. Paratype PC107, a) ventral, b) lateral. x2.
3. Paratype PC108, dorsal view of ventral valve. x2.
4. Paratype PC109, a) dorsal, b) ventral, c) lateral. x2.
5. Paratype PC110, a) ventral, b) posterior, c) lateral, d) dorsal, e) anterior. x2.


22
1a
2a
3
1b
2b
1c
4b
4c
4a
5a
5d
5e
5
5c

# PLATE 23

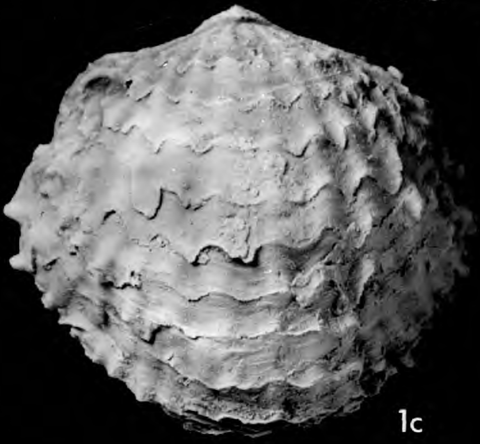
Figs. 1-2 Spinatrypa curvirostra n.sp

-- Lower Givetian, Scheid horizon (equivalent roughly to Felschbach horizon), Cürten beds; Sötenich syncline, MTB Mechernich r 40160:h98850. --

1. Paratype PC111, a) ventral, b) lateral, c) dorsal, d) posterior. x2.

2. HOLOTYPE PC112, a) dorsal, b) posterior, c) lateral, d) ventral, e) anterior. x2.

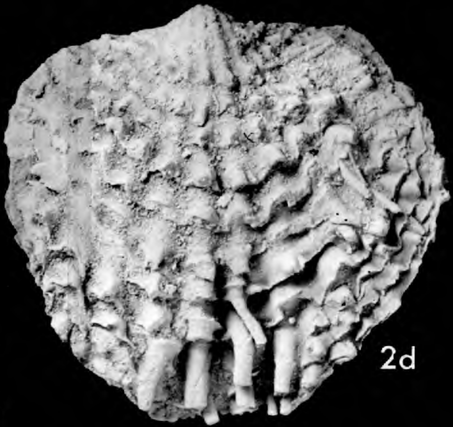

1a


1c

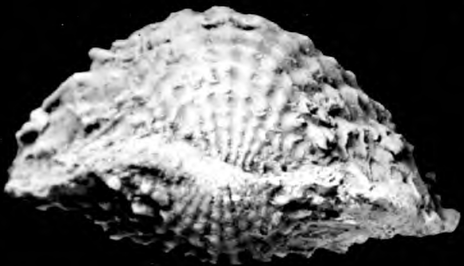

1b

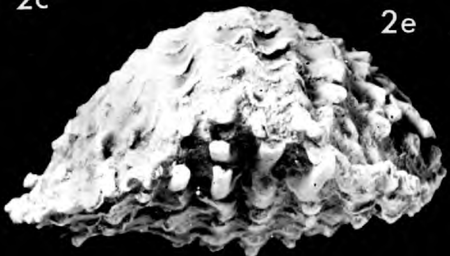

1d


2a


2d


2c


2b


2e

## PLATE 24

Figs. 1-3 *Spinatrypa* *curvirostra* n.sp.

Lower Givetian, Scheid horizon (equivalent roughly to Felschbach horizon), Cürten beds; Sötenich syncline, MTB Mechernich r40160:h98850. --

1. Paratype PC113, a) dorsal, b) lateral, c) posterior. x2.
2. Paratype PC114, a) dorsal, b) ventral. x2.
3. Paratype PC115, a) dorsal, BO ventral, c) lateral. x2.

Paratype PC114 shows rather long extension of the growth lamellae. Note the strong anterior spines of paratype PC115.


1a

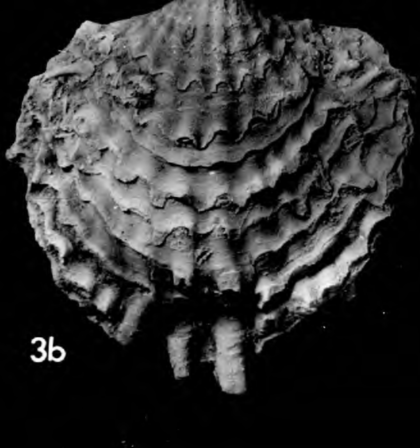

2a


1b


1c


2b

3a


3b


3c

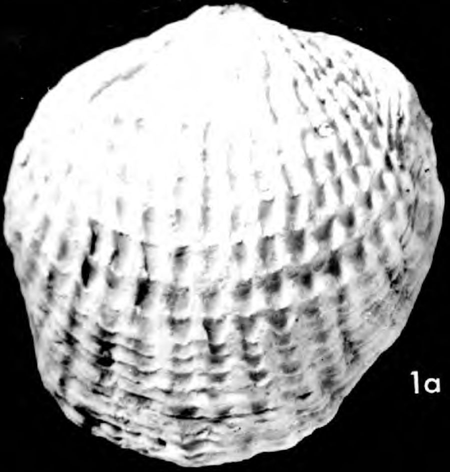
# PLATE 25

Figs. 1-3 Spinatrypa orthoclina n.sp.

-- Middle Givetian, low Rodert beds; Sötenich syncline, MTB Mechernich, 1, r42300:h99100, 2, 3, r44000:h00370. --

1. Paratype PC116, a) dorsal, b ) ventral, c) posterior. x2.
2. Paratype PC117, a) ventral, b) dorsal. x2.
3. Paratype PC118, a) ventral, b) lateral, c) dorsal. x2.

25


1a


1b


2a


2b


1c


3a


3b


1d


3c

## PLATE 26

Figs 1-4 *Spinatrypa* *orthoclina* n.sp.

Middle Givetian, Rodert beds; 1, 2, Sötenich syncline, MTB Mechernich, 1, r44000:h00370, 2, r45020:h00840; 3, 4, Paffrath syncline, MTB Mülheim am Rhein r76800:h51120. --

1. HOLOTYPE PC119, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

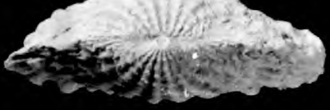
2. Paratype PC120, a) ventral, b) dorsal. x2.

3. Paratype PC121, peeled shell mould, a) dorsal, b) ventral. x2.

Paratype PC120, a large, coarsely ribbed shell, appears to be more typical of beds slightly younger than those of the holotype material. The HOLOTYPE PC119 is an immature specimen, but shows better the orthocline, projecting beak.


1a


1b


1c


1d


2a


2b


3a


3b


4

# PLATE 27

Figs. 1-5 Spinatrypa cf. legayi (RIGAUX 1908)

-- Frasnian, F2 or F3; Aachen area, MTB Stolberg about r7700:h22500. --

1. Hypotype PC123, a) dorsal, b) ventral, c) lateral, d) anterior, e) posterior. x2.

2. Hypotype PC124, a ) lateral, b) ventral. x2.

3. Hypotype PC125, a) anterior, b) ventral, c) lateral. x2.

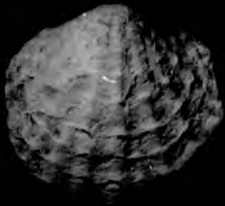
4. Hypotype PC126, ventral. x2.

5. Hypotype PC127, ventral. x2.


1a


1b


2a


2b


1d


1c

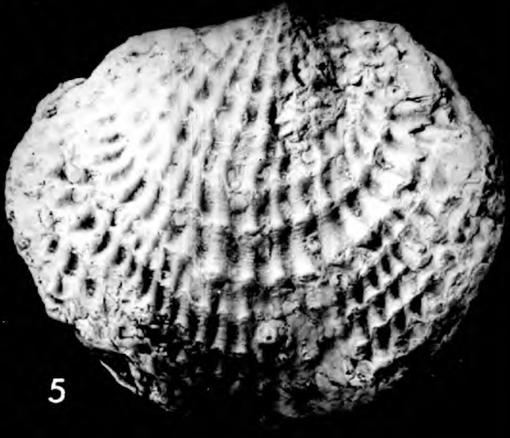

3a


1e


3b


3c


4


5

# PLATE 28

Figs 1a-d Spinatrypa legayi (RIGAUX 1908)

-- Frasnian; Boulonnais area, France, west end of quarry south of Les Communes, Ferques limestone. --

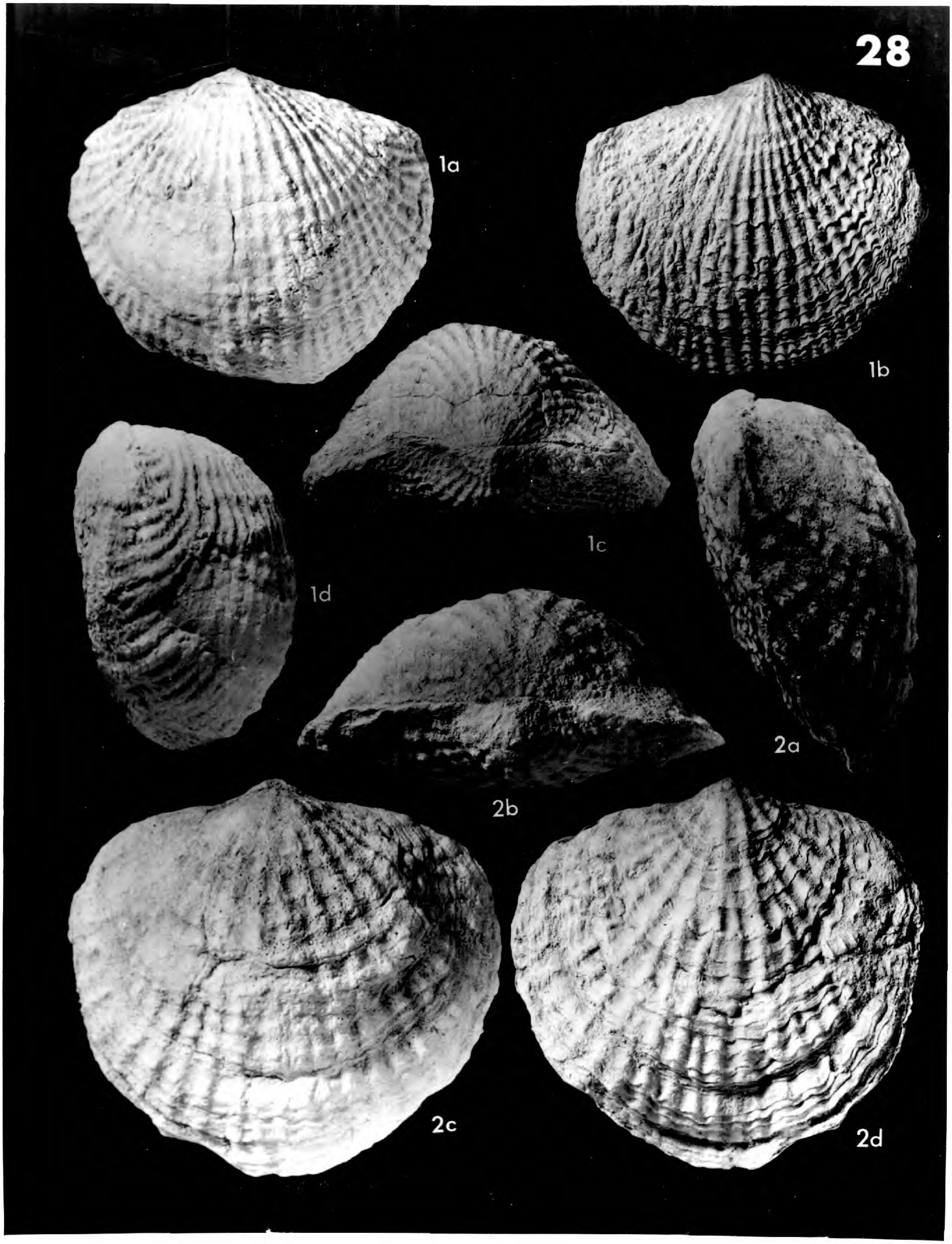
Hypotype PC128, a) dorsal, b) ventral, c) posterior, d) lateral. x2.

Figs. 2a-d Spinatrypa longispina (BOUCHARD in RIGAUX 1873)

-- Frasnian, calcareous shales above the Ferques limestone; Boulonnais area, France, southeast corner of Parisienne quarry. --

Hypotype PC129, a) lateral, b) posterior, c) dorsal, d) ventral. x2.

The distinction between these two species is clear: S. legayi is more finely ribbed, and more dorsibiconvex, as well as smaller in size.


28
1a
1b
1c
1d
2a
2b
2c
2d

# PLATE 29

Figs. 1a-d Atrypa ? (Devonatrypa) europaea (STRUVE 1964)

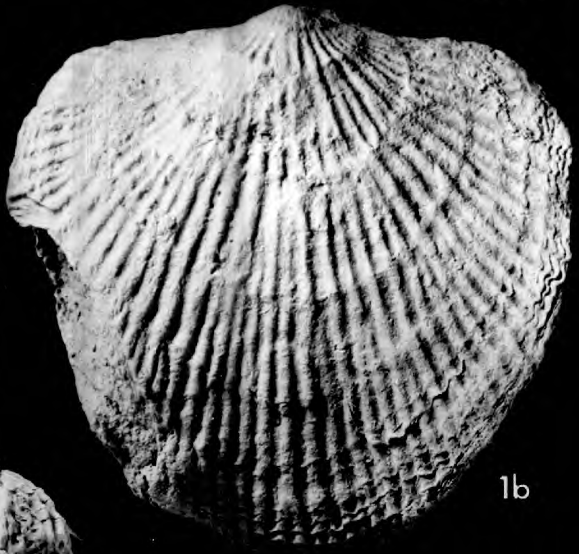
-- Frasnian, F2a, Steinbreche horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140-200:h74550-80. -- Hypotype PC130, a) dorsal, b) ventral, c) posterior, d) lateral. x2.

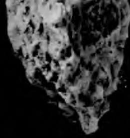
Figs. 2-4 Spinatrypa cf. trigonella (DAVIDSON 1884)

-- Upper Givetian Büchel beds (equivalent roughly to Kerpen beds); Paffrath syncline, MTB Kürten r82175:h53200. --

2. Hypotype PC131, a) dorsal, b) lateral, c) ventral. x2.
3. Hypotype PC132, a) posterior, b) ventral, c) dorsal. x2.
4. Hypotype PC133, a) ventral, b) dorsal, c) lateral. x2.


1a


1b


2b


1c


2a


2c

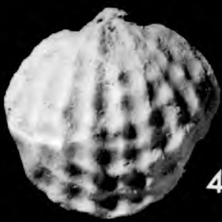

3a


1d


3b


4a


3c


4b


4c

## PLATE 30

Figs. 1-4 Spinatrypina ? demissa n.sp

-- Lower Eifelian, Nohn beds, 1, 2, Urft horizon (about Weilersbach-Schleit horizons), 3, Weilersbach horizon, 4, low Schleit horizon; 1, 2, Sötenich syncline, MTB Blankenheim r44690:h94770, 3, Hillesheim syncline, MTB Dollendorf r56950-7020:h78210-50, 4, r56900:h78130. --

1. HOLOTYPE PC134, a) dorsal, b) anterior. x2.

2. Paratype PC135, a) dorsal b) posterior. x2.

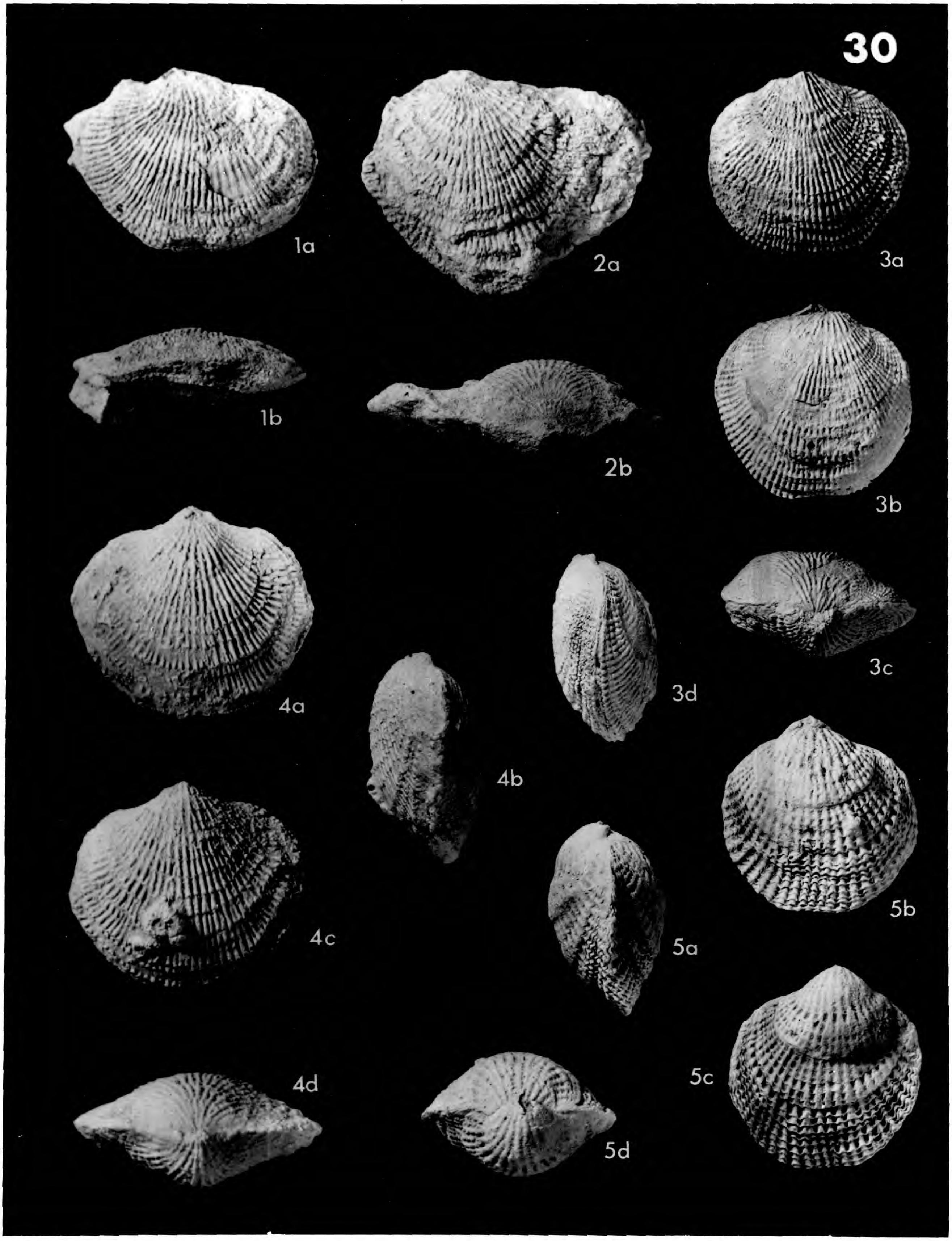
3. Paratype PC136, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

4. Paratype PC137, a) dorsal, b) lateral, c) ventral, d) posterior. x2.

Figs. 5a-d Spinatrypina fabaca n.sp.

-- Middle Eifelian, directly above Rohr horizon (i.e. about Rechert horizon), Junkerberg beds; Rohr syncline, MTB Aremberg r52360:h91390. --

Paratype PC138, a) lateral, b) dorsal, c) ventral, d) posterior. x2.


30
1a
2a
3a
1b
2b
3b
4a
3d
3c
4b
5b
4c
5a
4d
5c
5d

# PLATE 31

Figs. 1-2 Spinatrypina fabaca n.sp.

-- Middle Eifelian, directly above Rohr horizon (i.e. about Rechert horizon), Junkerberg beds; Rohr syncline, MTB Aremberg r52360:h91390. --

1. Paratype PC139, a) ventral, b) dorsal, c) lateral. x2.

2. HOLOTYPE PC140, a) ventral, b) dorsal, c) lateral, d) posterior. x2.

Figs. 3-6 Spinatrypina wotanica (STRUVE 1964)

-- Lower Givetian, Loogh beds, 3, 5, Wotan horizon, 4, 6, middle to high Rech horizon; Hillesheim syncline, MTB Dollendorf 3, 5, r52550-620:h76745-800, 4, r45815:h77240, 6, r54855-730:h77060-310. --

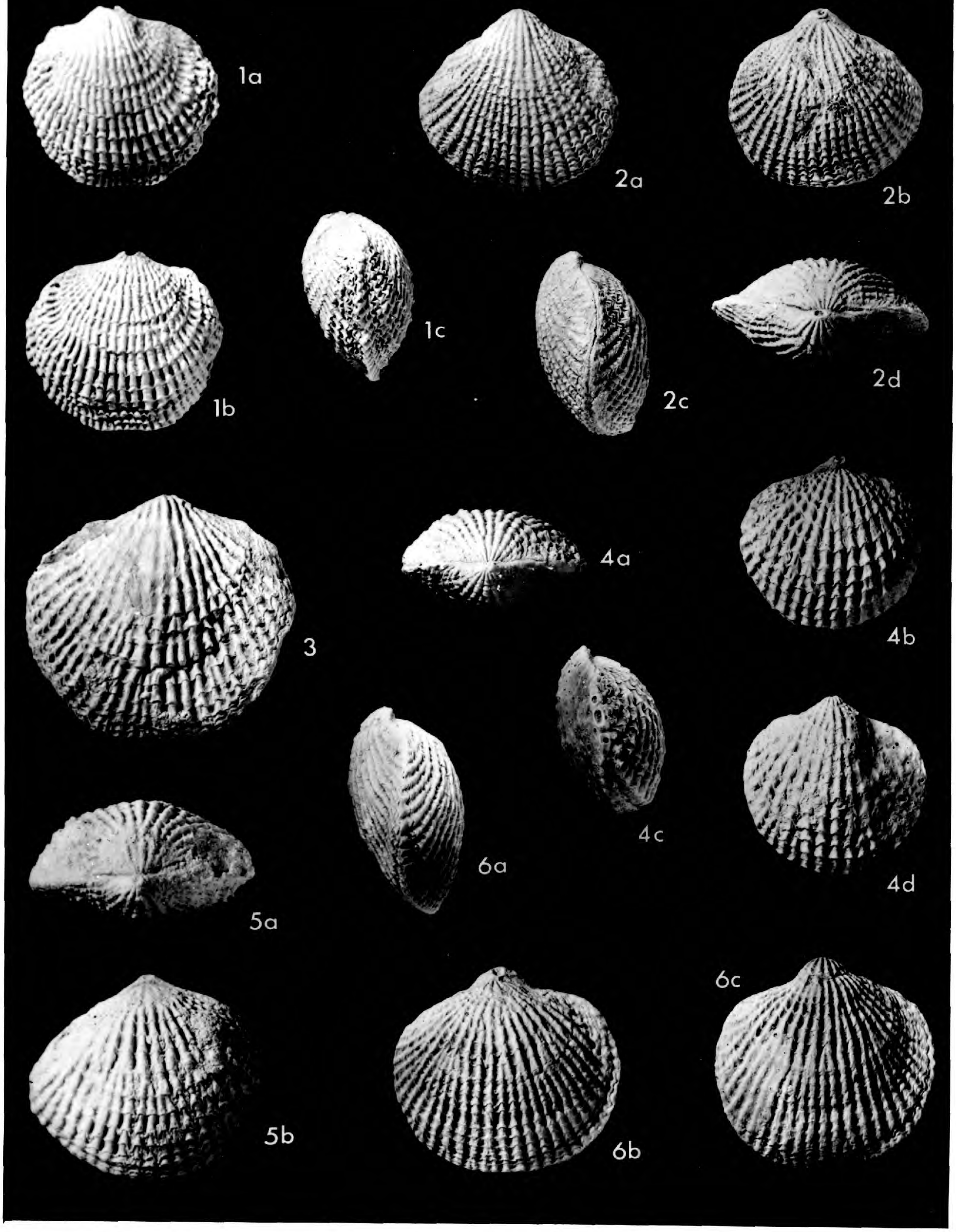
3. Hypotype PC141, ventral. x2

4. Hypotype PC142, a) posterior, b) dorsal, c) lateral, d) ventral. x2.

5. Hypotype PC143, a) posterior, b) dorsal. x2.

6. Hypotype PC144, a) lateral, b) dorsal, c) ventral. x2.

**31**



# PLATE 32

Figs. 1-2 Spinatrypina soetenica (STRUVE 1964)

-- Lower Givetian, about Felschbach horizon, Cürten beds; Sötenich syncline, MTB Mechernich r40160:h98850. --

1. Hypotype PC145, a) dorsal, b) ventral, c) posterior d) lateral. x2

2. Hypotype PC146, a) dorsal, b) ventral, c) posterior, d) lateral. x2.

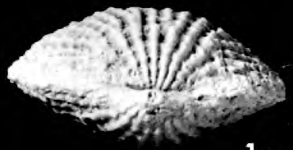
This coarse ribbed variety (possible a subspecies) is distinct from holotypic material from neanic to mature growth stages.


1a


2a

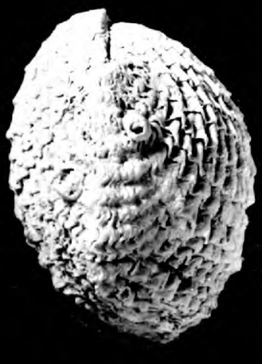

1b


2b


1c


2c


1d


2d

# PLATE 33

Figs. 1-2 Spinatrypina soetenica (STRUVE 1964)

-- Lower Givetian, about Felschbach horizon, Cürten beds; Sötenich syncline, MTB Mechernich r40160:h98850. --

1. Hypotype PC147, a) lateral, b) posterior, c) ventral, d) dorsal. x2.

2. Hypotype PC148, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

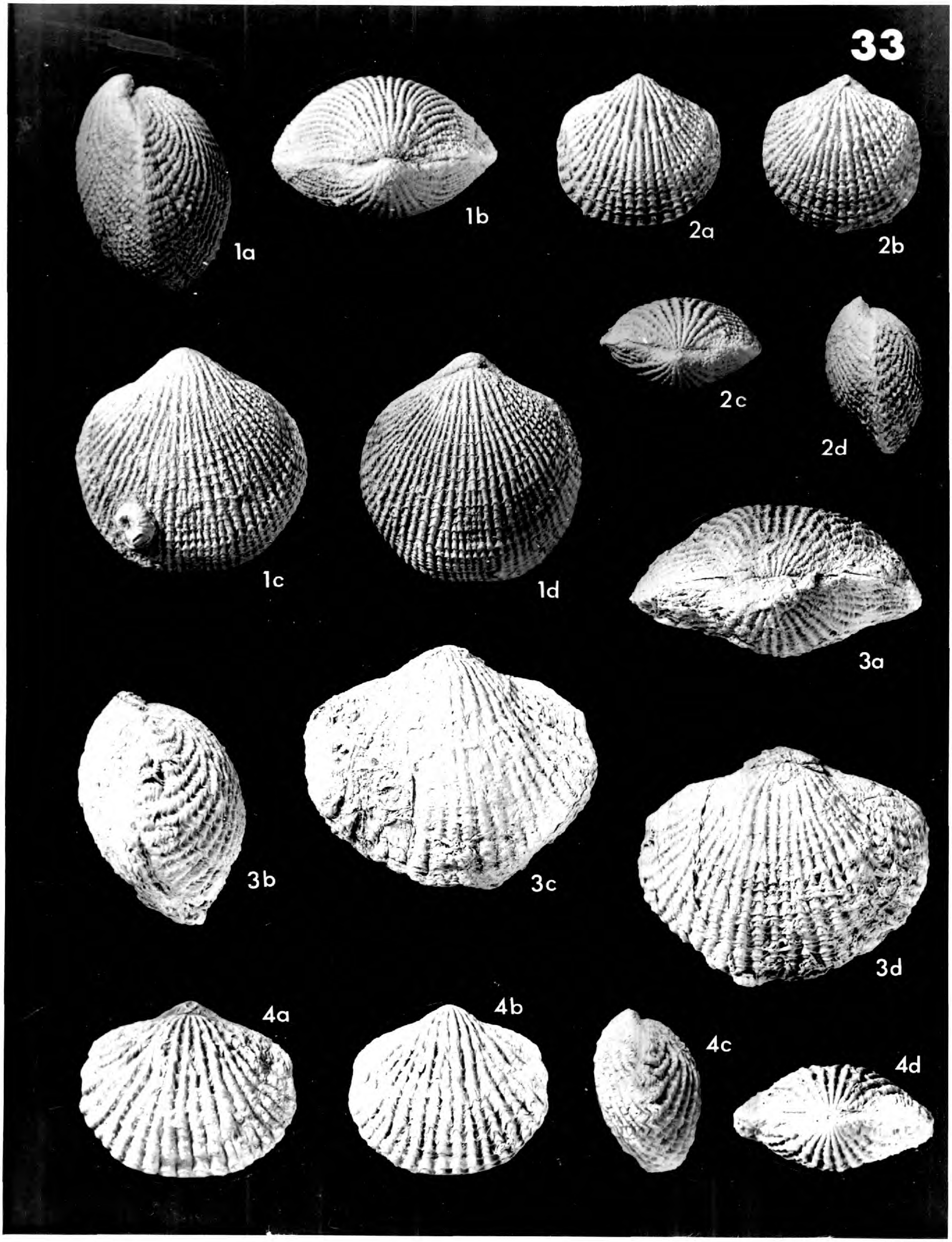
Figs. 3-4 Spinatrypina girzenensis n.sp.

-- Middle Givetian, Dreimühlen beds; Sötenich syncline, MTB Mechernich r41650:h99220. --

3. Paratype PC149, a) posterior, b) lateral, c) ventral, d) dorsal. x2.

4. HOLOTYPE PC150, a) dorsal, b) ventral, c) lateral, d) posterior. x2.

33



# PLATE 34

Figs. 1-2 Spinatrypina girzenensis n.sp.

-- Middle Givetian, Dreimühlen beds; Sotenich syncline, MTB Mechernich r41650:h99220. --

1. Paratype PC151, a) dorsal, b) ventral, c) lateral, d) posterior. x2.

2. Paratype PC152, a) posterior, b) dorsal, c) ventral, d) lateral. x2.

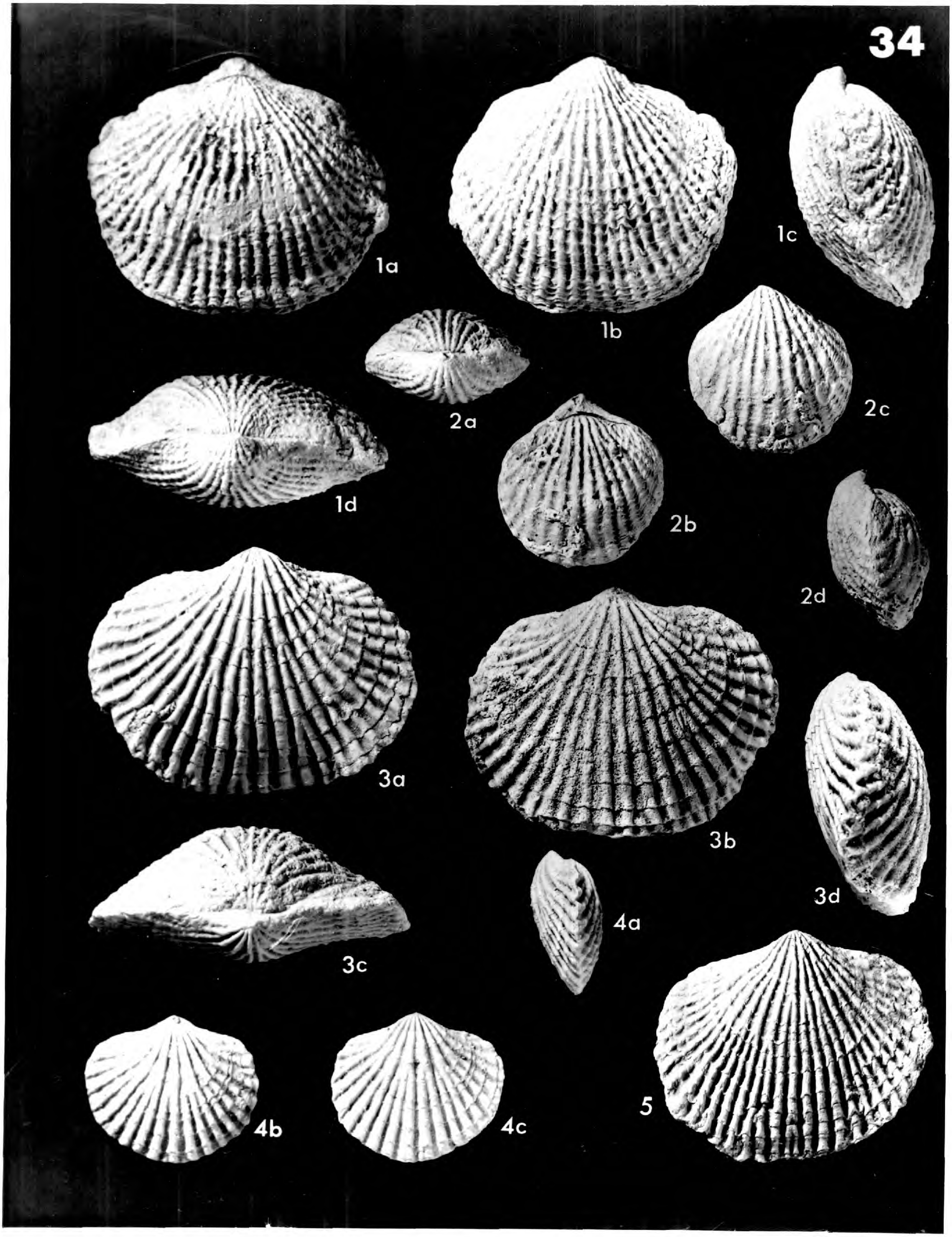
Figs. 3-5 Spinatrypina tubaecostata (PAECKELMANN 1913)

-- Frasnian, Dorper Kalk (F2c to F3?); Herzkamp syncline, MTB Elberfeld, "Knappertsbusch". --

3. Hypotype PC153, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

4. Hypotype PC154, a) lateral, b) dorsal, c) ventral. x2.

5. Hypotype PC155, ventral. x2.


1a
1b
1c
1d
2a
2b
2c
2d
3a
3b
3c
3d
4a
4b
4c
5

# PLATE 35

Figs. 1-4 Spinatrypina robusta n.sp.

-- Frasnian, F2b-c (?), probably base above Dorper Kalk and Gruiten beds; Herzkamp syncline, MTB Kettwig, Hofermühle. --

1. Paratype PC156, a) ventral, b) lateral, c) dorsal, d) posterior. x2.

2. HOLOTYPE PC157, a) ventral, b) dorsal, c) lateral. x2.

3. Paratype PC158, dorsal valve, a) oblique ventral view, b) normal ventral view. x2.

4. Paratype PC159, a) dorsal, b) ventral, c) lateral. x2. Fig 4 shows a specimen with rib structure and planar shell very similar to Spinatrypina explanata (SCHLOTHEIM 1820).


1a

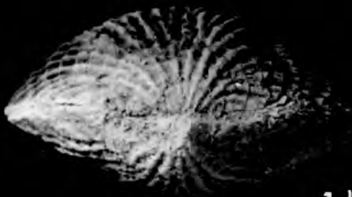

1b


2a


1c

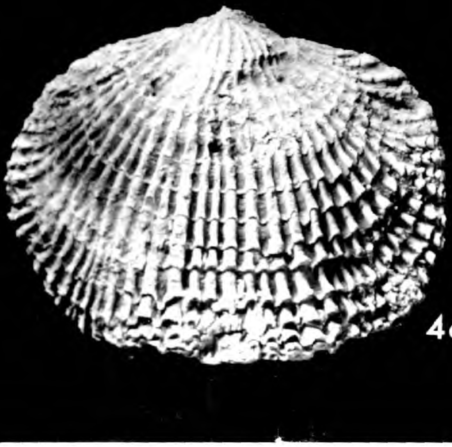

2c

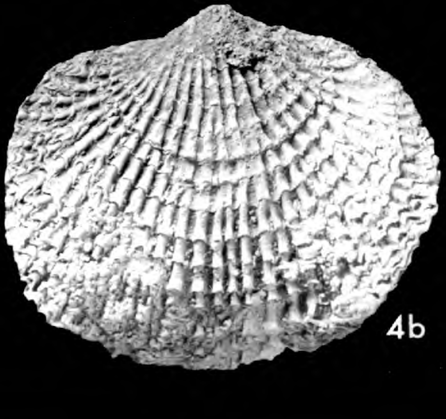

2b


1d


3a


3b


4a


4b


4c

# PLATE 36

Figs 1-3 <u>Spinatrypina</u> <u>robusta</u> n.sp.

-- Frasnian, F2b-c (?), probably base above Dorper Kalk and Gruiten beds; Herzkamp syncline, MTB Kettwig, Hofermühle. --

<u>1</u>. Paratype PC160, a) ventral, b) lateral. x2.

<u>2</u>. Paratype PC161, a) dorsal, b) ventral, c) lateral. x2.

<u>3</u>. Paratype PC162, a) dorsal, b) ventral, x2.

Figs 4-5 <u>Spinatrypina</u> <u>quenstedti</u> n.sp.

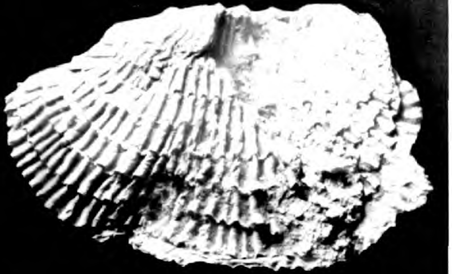
-- Frasnian, F2a, Steinbreche horizon, Refrath beds; Paffrath syncline, MTB Mulheim am Rhein r78140-20:h47550-80. --

<u>4</u>. Paratype PC162, a) ventral, b) lateral, c) posterior, d) dorsal. x2.

<u>5</u>. HOLOTYPE PC163, a) dorsal, b) ventral, c) lateral, d) posterior. x2.


1a


1b


3a


3b


2a


2c


2b


4a


4b


4c


4d

5a


5b



5c

5d


# PLATE 37

Figs 1-4 Spinatrypina explanata (SCHLOTHEIM 1820)

-- Frasnian, F2a, Steinbreche horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140-20:h47550-80. --

1. Hypotype PC164, a) ventral, b) dorsal, c) lateral, d) posterior. x2.

2. LECTOTYPE SCHLOTHEIM coll. (Berlin Museum), a) ventral b) dorsal, c) lateral, d) posterior. x2.

3. Hypotype PC165, a) posterior, b) dorsal, c) lateral, d) ventral. x2.

4. Hypotype PC166, a) posterior, b) lateral, c) dorsal, d) ventral. x2.


1a

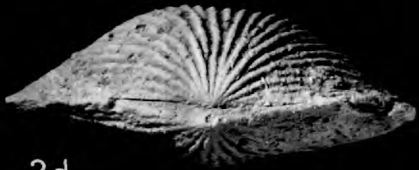

1c


2a


1b


2b


2c


2d


1d


3c


4b


4a


3a


4c


3b


3d


4d

# PLATE 38

Figs. 1-6 Kerpina vineta STRUVE1961

-- Upper Eifelian, Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf, 1, 2, 5, r53805:h74680, 3, 6, r53870:h 74680, 4, r54340:h75320. --

1. Hypotype PC167, a) dorsal, b) ventral, c) lateral. x2.
2. Hypotype PC168, a) dorsal, b) lateral, c) ventral. x2.
3. Hypotype PC169, a) dorsal, b) lateral, c) ventral. x2.
4. Hypotype PC170, a) ventral, b) lateral, x2.
5. Hypotype PC171, posterior view of specimen attached (?cemented) to a playt alveolitid coral. x2.
6. Hypotype PC172, a) dorsal, b) lateral. x2.

Figs 2 and 4 can be grouped under Kerpina vineta goniorhynchia STRUVE 1961, the remainder under K. vineta vineta STRUVE 1961.


1a


1b


1c


2a


2b


2c


3a


3b


4a


3c


4b


6a


6b


5

# PLATE 39

Figs. 1-5 Kerpina vineta STRUVE 1961

-- Upper Eifelian, Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf 1, r52185-205:h76365-400, 2, 5, r53850:h74680, 3, r53870:h74680, 4, r54340:h7536. --

1. Hypotype PV173, dorsal view of specimen attached to an alveolitid coral. x2.

2. Hypotype PC174, a) dorsal, b) ventral. x2.

3. Hypotype PC175, dorsal view of specimen attached to an alveolitid coral. x2.

4. Hypotype PC176, a) ventral, b) dorsal, c) lateral. x2.

5. (lower row of figs.) Hypotype PC177, a) lateral, b) dorsal, c) ventral. x2. Deformed specimen.

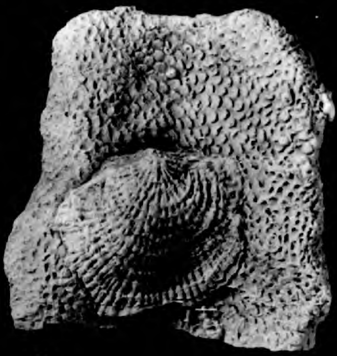
Figs. 5a-c (central, right-hand side)

Kerpina cf. vineta STRUVE 1961

Locality and horizon unknown. Specimen in a collection labelled "Gerolstein" (Berlin Museum) with Mimatrypa insquamosa (SCHNUR). Lower Givetian (?). a) posterior, b) dorsal, c) anterior. x2.


1

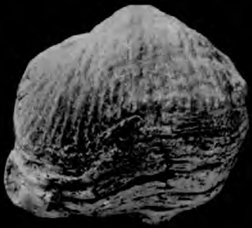

2a


3


2b


4a


5a


5b


4b


5c


4c


5c


5a


5b

# PLATE 40

Figs. 1-2 *Desquamatia* (*Variatrypa*) *iunctura* n.sp

-- Middle to Upper Eifelian, *1*, Hönselberg horizon, Junkerberg beds, *2*, Eilenberg horizon, Freilingen beds; Hillesheim syncline, *1*, MTB Hillesheim r51880:h72420, *2*, MTB Dollendorf r53870:h74680. --

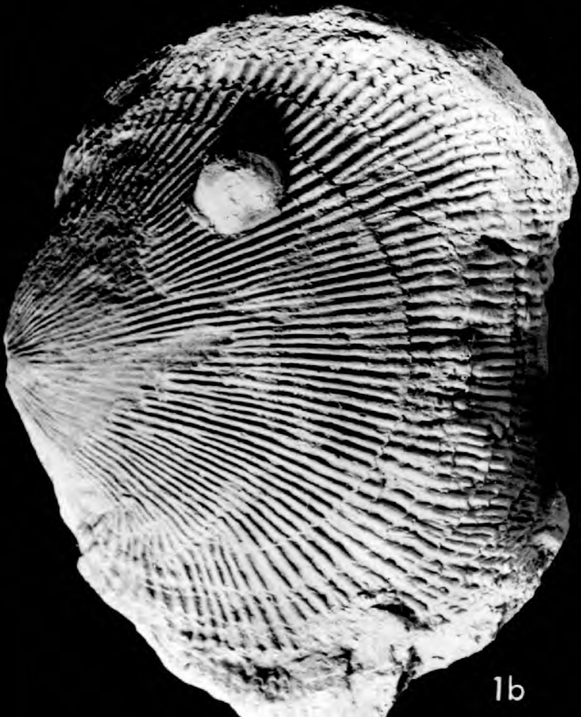
*1*. Paratype PC178, a) dorsal, b) ventral, c) posterior. x2.

*1*. HOLOTYPE PC179, a) posterior, b) anterior. x2.

1a

2a

2b



1b

1c

# PLATE 41

Figs. 1a-c *Desquamatia* (*Variatrypa*) *iunctura* n.sp.

-- Upper Eifelian, Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf r 53870:h 74680. -- HOLOTYPE PC179, a) ventral, b) dorsal, c) lateral. x2.

Figs.2-3 *Desquamatia* (*Variatrypa*) cf. *magna* (GRABAU 1931).

-- Upper Givetian, about Bolsdorf beds or higher; 2, Aachen area, MTB Roetgen r12790:h18070, 3, Paffrath syncline, MTB Mülheim possibly r78:h51. --

2. Hypotype PC180, a) ventral, b) lateral. c) posterior. x2.

3. Hypotype PC181, ventral view of peeled shell. x2.

Hypotype PC180 came in a black, calcereous shale, PC181 is preserved in a dolomite.

41

# PLATE 42

Figs. 1a-c Desquamatia (Variatrypa) cf. magna (GRABAU 1931)

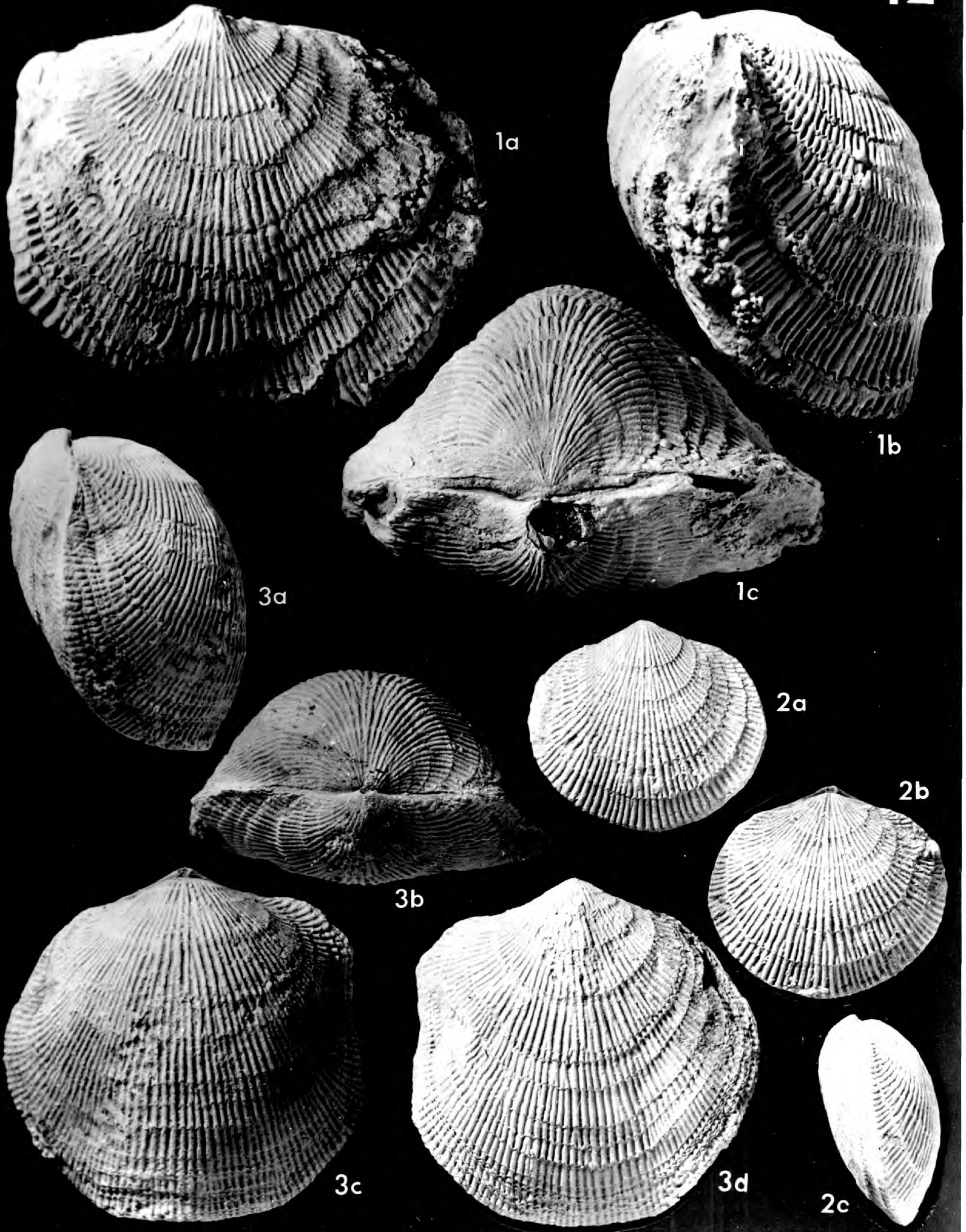
-- Upper Givetian; Aachen area, MTB Roetgen r12790:h18070. -- Hypotype PC182, a) ventral, b) lateral, c) posterior. x2.

Figs. 2-3 Desquamatia (Seratrypa) schroeteri n.sp.

-- Frasnian, F2a, Steinbreche horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140-200:h47550-80. --

2. Paratype PC183, a) ventral, b) dorsal, c) lateral. x2.

3. HOLOTYPE PC184, a) lateral, b) posterior, c ) dorsal, d) ventral. x2.


1a
1b
1c
3a
2a
2b
3b
3c
3d
2c

# PLATE 43

Figs. 1-2 Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)

-- Frasnian, F2b-c, Saalermühl horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140:h47540. --

1. Paraneotype PC185, a) ventral, b) dorsal, c) posterior. x2.

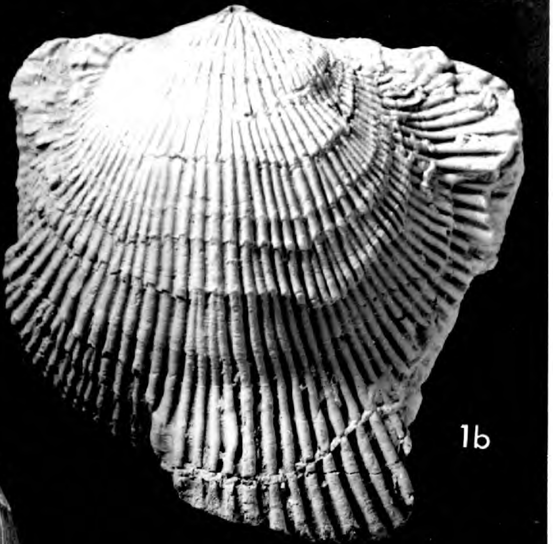
2. Paraneotype PC186, dorsal view of frilled specimen. x2.

Figs. 3a-d Desquamatia (Seratrypa) schroeteri n.sp.

-- Frasnian, F2a, Steinbreche horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140-200:h47550-80. --

Paratype PC187, a) lateral, b) ventral, c) posterior, d) dorsal, x2.


1a


1b


3a


3b


1c


3c

2


3d

# PLATE 44

Figs. 1-2 Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)

-- Fraenian, F2b-c, Saalermühl horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140:h47540. --

1. Paraneotype PC188, a) ventral, b) lateral, c) posterior, d) dorsal. x2.

2. NEOTYPE PC189, a) posterior, b) lateral, c) ventral, d) dorsal. x2.

1a

1d

1c

1b

2b

2a

2c

2d

# PLATE 45

Figs. 1-3 Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)

-- Frasnian, F2b-c, Saalermühl horizon, Refrath beds; Paffrath syncline MTB Mülheim am Rhein r78140:h47540. --

1. Paraneotype PC190, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

2. Paraneotype PC191, a) ventral, b) dorsal, c) posterior, d) lateral. x2

3. Paraneotype PC192, frilled ventral valve (uppermost dorsal view), PC193 (pedicle valve, ventral view). x2.


1a


1b


1c


2a


2b


1d


2c


3


2d

# PLATE 46

Figs. 1-4 Desquamatia (Seratrypa) pectinata (SCHRÖTER 1777)

-- Frasnian, F2b-c, Saalermühl horizon, Refrath beds; Paffrath syncline, MTB Mülheim am Rhein r78140:h47540. --

1. Paraneotype PC194, a) ventral, b) lateral, c) posterior. x2.

2. Paraneotype PC195, a) dorsal, b) lateral, c) ventral, d) posterior. x2.

3. Paraneotype PC196, ventral view of peeled specimen. Note the reflection of ribs on the inner shell surface.

4. Paraneotype PC197, a) dorsal, b) ventral views of peeled specimen. x2.

All specimens on this page, excepth PC197, are of the more finely ribbed variety.


1a


1b


2a


2c


3


2b


2d


1c


4a


4b

# PLATE 47

Figs. 1-3 *Gruenewaldtia prooemia* n.sp.

-- Lower Eifelian, Nohn beds, Weilersbach-Schleit horizons; 1, Hillesheim syncline, MTB Dollendorf r54340:h79040, 2, 3, Gerolstein syncline, MTB Gerolstein r44890:h64630. --

1. Paratype PC198, a) ventral, b) lateral, c) posterior. x2.
2. HOLOTYPE PC199, a) lateral, b) ventral, c) dorsal. x2.
3. Paratype PC200, a) ventral, b) posterior. x2.

Figs. 4a-d *Gruenewaldtia* cf. *rhenana* (SPRIESTERSBACH 1942)

-- Middle Eifelian, Flesten horizon, Ahrdorf beds; Hillesheim syncline, MTB Dollendorf r54470:h74450. --

Hypotype PC201, a) ventral, b) dorsal, c) posterior, d) lateral. x2.

47


1a


1b


2a


2b

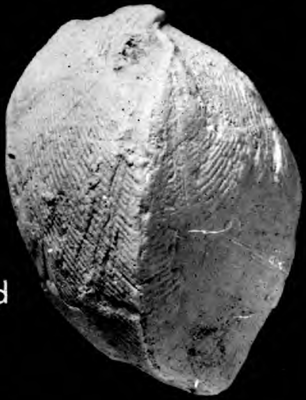

1c

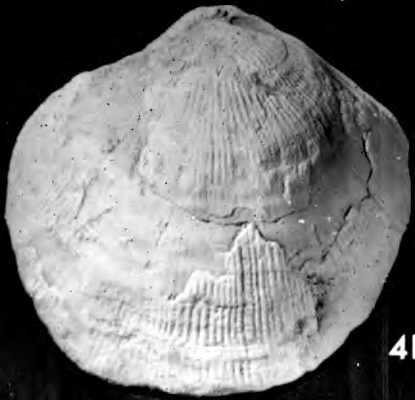

3a


2c


3b


4a


4d


4b


4c

# PLATE 48

Figs 1-4 Gruenewaldtia latilinguis (SCHNUR 1851)

-- Middle Eifelian, Rechert-Nims horizons, Junkerberg beds; Prüm syncline, 1, 2, 3, MTB Prum r35400:h65290, 4, MTB Gerolstein r38470:h66980. --

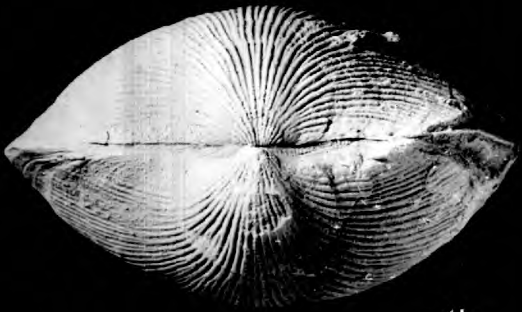
1. Hypotype PC202, dorsal view of ventral valve. x4.
2. Hypotype PC203, brachial valve. x4.
3. Hypotype PC204, brachial valve. x4.
4. Hypotype PC205, a) lateral, b) posterior, c) ventral d) dorsal. x2.

1

2

3

4a



4b

4c

4d

# PLATE 49

Figs 1a-d *Gruenewaldtia latilinguis latilinguis* (SCHNUR 1851)

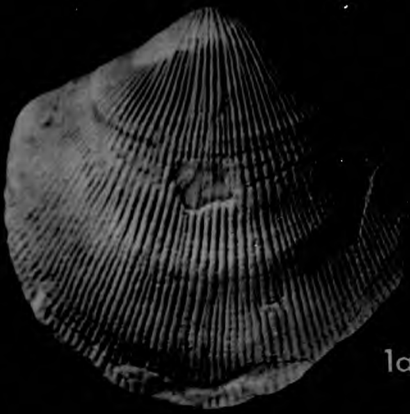
-- Middle Eifelian , Hönselberg horizon, Junkerberg beds; Hillesheim syncline, MTB Dollendorf r54340:h75320. -- Hypotype PC206, a) ventral, b) dorsal, c) lateral, d) posterior. x2.

Figs 3a-b *Gruenewaldtia latilinguis elegans* STRUVE 1961

-- Middle Eifelian, Rechert-Nims horizons, Junkerberg beds; Prüm syncline, MTB Prüm r35400:h65290. -- Hypotype PC207, a) dorsal, b) posterior (this specimen in serial section text-fig. 186.) x2.

Figs. 4a-b *Gruenewaldtia* cf. *apsaklina* STRUVE 1961

-- Upper Eifelian, Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf r53850:h74680. -- Hypotype PC208, a) posterior, b) dorsal (this specimen in serial section text-fig. 187.) x2.



1a

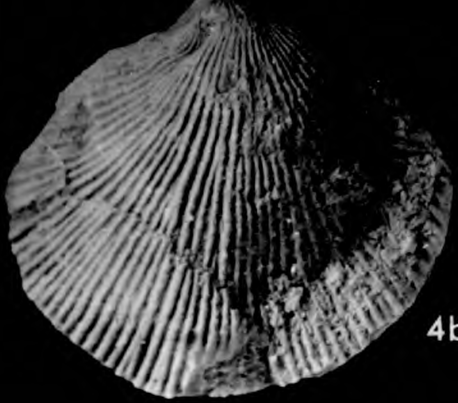
1b

1c

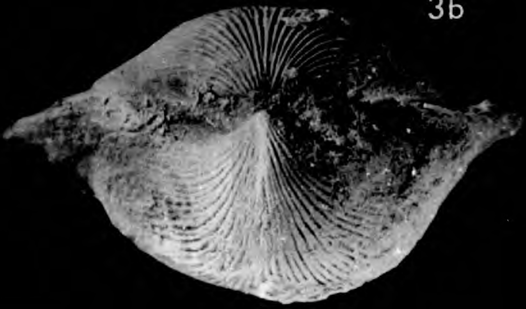
1d

3a

4a



4b



3b

# PLATE 50

Figs. 1a-b Gruenewaldtia aff. apsaklina STRUVE 1961

-- Upper Eifelian , Freilingen beds, horizon B (GLINSKI 1961); Rohr syncline, MTB Aremberg r50800:h90200. -- Hypotype PC209, a) lateral, b) ventral. x2. This specimen is easily confused externally for Mimatrypa insquamosa (SCHNUR).

Figs. 2a-b Gruenewaldtia cf. apsaklina STRUVE 1961

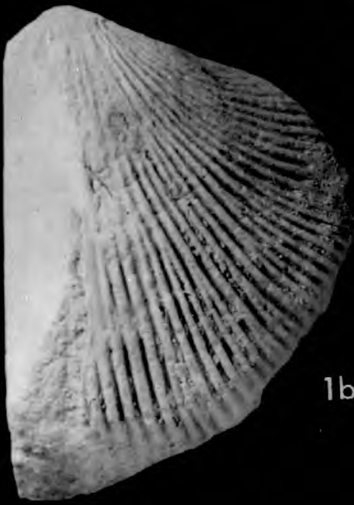
-- Upper Eifelian , Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf r53850:h74680. -- Hypotype PC210, a) dorsal, b) posterior. x2.

Figs. 3a-c Gruenewaldtia latilinguis elegans STRUVE 1961

-- Middle Eifelian ., Rechert-Nims horizons, Junkerberg beds; Prüm syncline, MTB Prum r35400:h65290. -- Hypotype PC211, a) posterior, b) ventral, c) dorsal. x2.

1a

2a



1b

2b

3a

3b

3c

## PLATE 51.

Figs. 1-5 Mimatrypa insquamosa (SCHNUR 1853)

-- Lower Givetian, probably upper Loogh beds; Gerolstein syncline, MTB Hillesheim r49330:h66050. --

1-5. ventral valves, 1) Hypotype PC212, 2) Hypotype PC213, 3) Hypotype PC214, 4) Hypotype PC215, 5) Hypotype PC216. x2.

Figs 6a-e Mimatrypa cf. insquamosa (SCHNUR 1853)

-- Lower Givetian, Wotan horizon (?), Loogh beds; Gerolstein syncline, "Mühlwäldchen" (?), MTB Gerolstein about r46420:h65180. --

Hypotype PC217, coarsely ribbed variety which seems to be most abundant at the "Mühlwäldchen" localities, a) dorsal, b) posterior, c) ventral, d) anterior, e) lateral. x2.

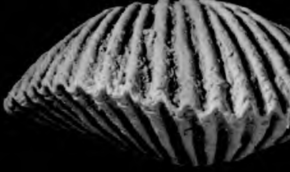

1


2


3


5


4


6d


6b


6c


6a


6e

# PLATE 52

Figs. 1-4 Mimatrypa flabellata (C.F. ROEMER 1844)

-- Lower Givetian, Wotan horizon (?), Loogh beds; Gerolstein syncline, "Mühlwäldchen" (?), MTB Gerolstein about r46420:h65180. --

Berlin Museum Coll.

1. HOLOTYPE ROEMER coll. Berlin Museum, a) ventral, b) dorsal, c) posterior, d) anterior, e) lateral. x2.

2. Hypotype Berlin coll., a) lateral, b) posterior. x2.

3. Hypotype Berlin coll., a) lateral, b) posterior. x2.

4. Hypotype Berlin coll., a) lateral, b) posterior. x2.

**52**


1a


1b


1d


1c


1e


2a


3a


4a


4b


3b


2b

# PLATE 53

Figs. 1-4 Mimatrypa flabellata (C.F. ROEMER 1844)

-- Lower Givetian, Wotan Horizon (?), Loogh beds; Gerolstein syncline, "Mühlwäldchen" (?), MTB Gerolstein about r46420:h65180. --

1. Hypotype Berlin coll., wide, flat variety, a) ventral, b) dorsal, c) posterior, d) anterior. x2.

2. Hypotype Berlin coll. (see Pl. 52, figs. 2), ventral. x2.

3. Hypotype Berlin coll. (see Pl. 52, figs. 4), ventral. x2.

Figs 5-6 Mimatrypa cf. insquamosa (SCHNUR 1853)

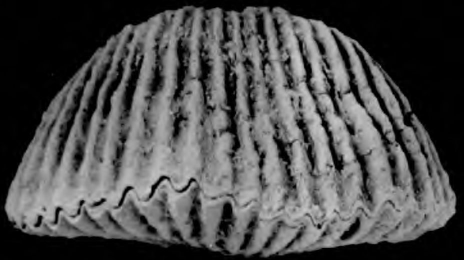
-- Lower Givetian, Wotan horizon (?), Loogh beds; Gerolstein syncline, MTB Gerolstein r46420:h65180, Mühlwäldchen". --

5. Hypotype PC218, posterior view. x2. A thick globose variety which may be characteristic of the lower parts of the "Mühlwäldchen Mergel".

6. Hypotype PC219, a) dorsal, b) posterior, c) ventral. x2. A planar, sharply ribbed, angularly beaked variety, possibly characteristic of middle to high layers of the Mühlwäldchen Mergel".


1a


1b

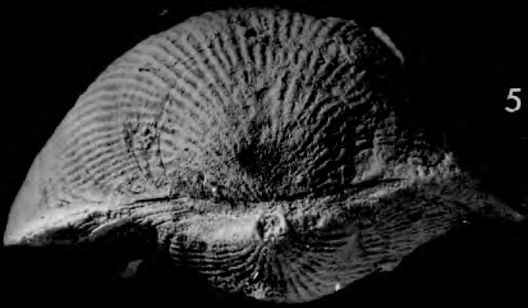

1d


1c


2


3


4


5


6a


6b


6c

## PLATE 54

Figs. 1-3 *Mimatrypa* spp.

-- Middle to upper Givetian; "Villmar", MTB Villmar. --

1. BMB22.1, a) ventral, b) dorsal, c) lateral. x2. Large, flat, asymmetrical specimen.

2. BMB22.3, a) ventral, b) dorsal, c) lateral, d) posterior. x2. Roundly ribbed, inflated specimen.

3. BMB22.2, a) lateral, b) ventral, c) dorsal. x2. Specimen similar to fig. 1.

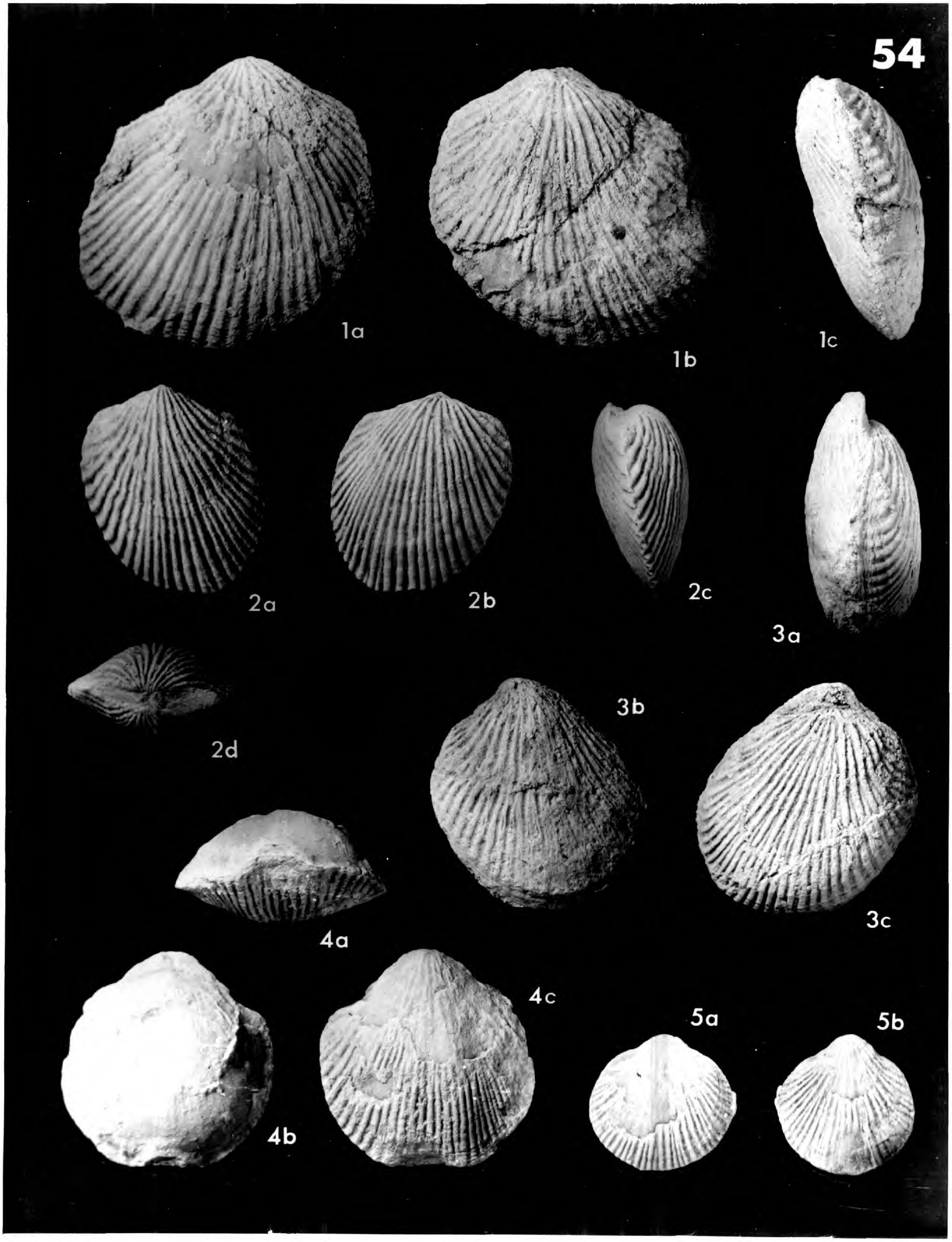
Figs. 4-5 *Mimatrypa fretterensis* n.sp.

-- Middle to Upper Givetian; "Frettertal", MTB Altenhundem. --

4. Paratype BMB6.3, a) anterior, b) dorsal, c) ventral. x2. Note the small, weakly developed fold.

5. Paratype BMB6.4, a) dorsal, b) ventral. x2.

54



# PLATE 55

Figs. 1-11 Mimatrypa fretterensis n.sp.

-- Middle to upper Givetian; "Frettertal," MTB Altenhundem. --

1. Paratype BMB7.5, a) lateral, b) ventral, c) dorsal. x2.

2. Paratype BMB4.1, lateral. x2.

3. Paratype BMB7.2, anterior. x2.

4. Paratype BMB7.7, ventral. x2.

5-6. HOLOTYPE BMB7.1, 5) dorsal, 6) ventral. x2.

7. Paratype BMB6.2, ventral. x2.

8. Paratype BMB7.6, lateral. x2.

9. Paratype BMB5.1, anterior. x2.

10. Paratype BMB7.3, a) dorsal, b) anterior. x2.

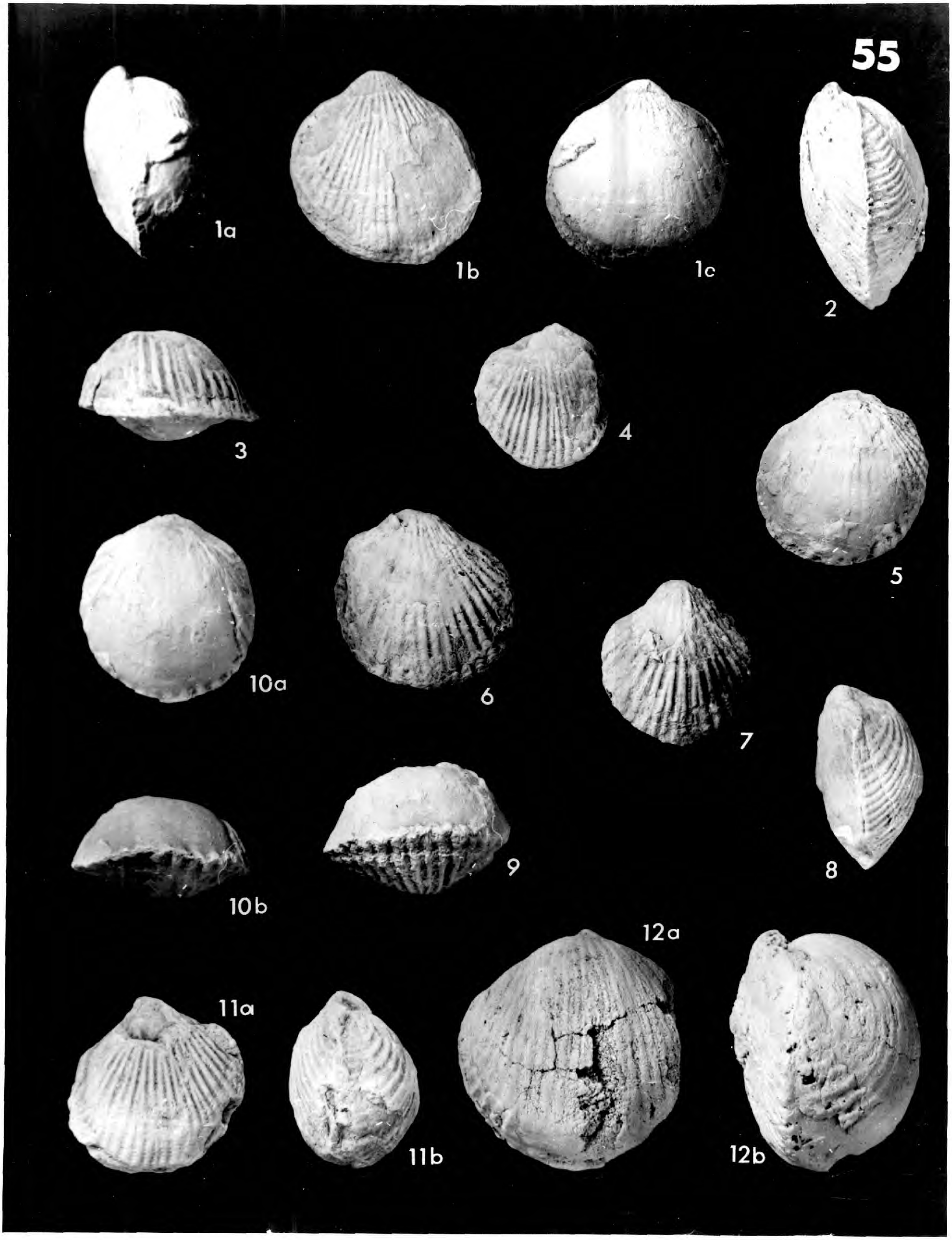
11. Paratype BMB7.4, a) ventral, b) lateral. x2.

Figs. 12a-b Mimatrypa sp.

-- Middle to Upper Givetian; "Frettertal," MTB Altenhundem. --

Specimen BMB6.1, a) dorsal, b) lateral. x2.

This specimen is strongly reminescent of Mimatrypa flabellata with which it seems to have greater affinities than Mimatrypa fretterensis n.sp.


55
1a
1b
1c
2
3
4
5
10a
6
7
8
10b
9
12a
11a
11b
12b

# PLATE 56

Figs. 1-2 Mimatrypa desquamata (SOWERBY 1840)

-- Upper Givetian, "Massenkalk"; Bilveringsen east of Iserlohn, MTB Iserlohn. --

1. Specimen figured by LEIDHOLD (1928, pl. 6, figs 4a-c) as "Atrypa globosa n.sp", Berlin Museum Coll., a) ventral b) dorsal. x1.

2. Specimen figured by LEIDHOLD (1928, pl. 7, figs. 2a-b) as "Atrypa circularis n.sp.", Berlin Museum Coll., a) ventral b) dorsal x1.

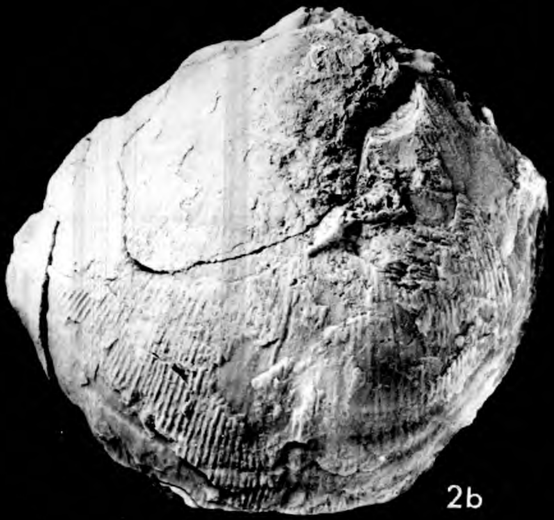
Figs 3a-b Mimatrypa cf. insquamosa (SCHNUR 1853)

-- Lower Givetian, Wotan horizon (?), Loogh beds; Gerolstein syncline, MTB Gerolstein r46420:h65180, "Mühlwäldchen." -- Hypotype PC218 (refer to Pl. 53, fig. 5), a) ventral, b) dorsal. x2.


1a


1b


2a


2b


3a


3b

# PLATE 57

Figs. 1-3 Carinatina plana (KAYSER 1871)

-- Upper Eifelian , 1-2, "Crinoidenschicht" (KAYSER 1871, p. 546) likely Freilingen beds, 3, Eilenberg horizon, Freilingen beds; 1-2, locality unknown, 3, Hillesheim syncline, MTB Dollendorf r53850:h74680. --

1. Paralectotype KAYSER collection Berlin Museum, figured in KAYSER (1871, pl. 10, fig. 3d), a) dorsal, b) posterior, c) ventral. x2.

2. LECTOTYPE KAYSER collection Berlin Museum, figured in KAYSER (1871, pl. 10, figs. 3a-c), a) ventral, b) dorsal, c) posterior, d) anterior. x2.

3. Hypotype PC220, a) ventral, b) dorsal. x2.

1a

1b

1c

2a

2b

2c

2d

3a

3b

# PLATE 58

Fig. 3 Carinatina plana (KAYSER 1871)

-- Upper Eifelian , Eilenberg horizon, Freilingen beds; Hillesheim syncline, MTB Dollendorf r53850:h74680. -- Hypotype PC220 (refer to Pl. 57, figs. 3a-b), posterior. x2.

Figs. 1-2, 4-5 Carinatina cf. signifera (SCHNUR 1853)

-- Givetian; Attendorn syncline, MTB Altenhundem, "Finnentrop". -- Drevermann collection, Natur-Museum Senckenberg, Frankfurt am Main.

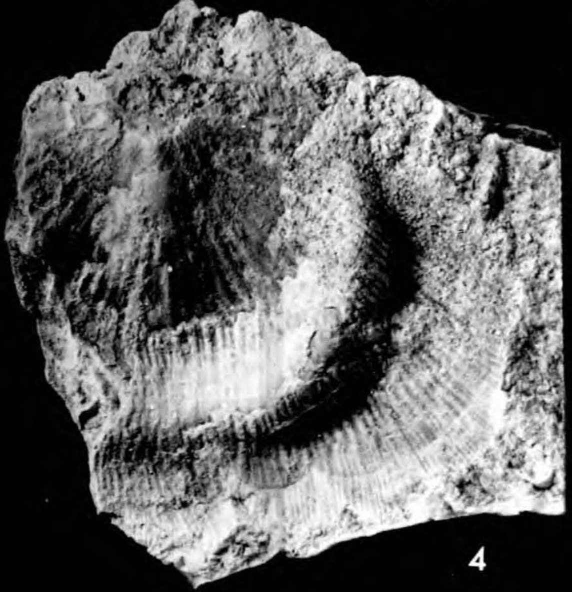
1. Hypotype PC221, dorsal. x2.
2. Hypotype PC222, dorsal. x2.
3. Hypotype PC223, ventral. x2.
5. Hypotype PC224, a) ventral, b) impression of ventral valve on the host limestone. x2.

**58**

1

2

3



4

5a

5b

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## ADDENDA

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# EUROPEAN MID-DEVONIAN CORRELATIONS

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A GROUP of brachiopods belonging to the atrypid family Palaferellidae Spriestersbach[1] shows a pattern of muscle platform development which may be of value in the correlation of Middle Devonian sediments in the western hemisphere. A brief description of important features in this rapidly evolving phylogenetic lineage is given.

The family Palaferellidae at present contains only a single genus, *Gruenewaldtia* Chernychev, which is characterized by the presence, in both valves, of muscle platforms which are elevated from the shell floor by a variable number of septa. In a continuous, overlapping and intergrading, morphological series ranging in age from the lower Eifelian to upper Givetian (Middle Devonian), it can be shown that in the Palaferellidae muscle platforms initially were supported by numerous septa and that, with time, these septa decreased in number until support of the platform was reduced, in the case of the pedicle valve, to two septa. The final stage was reached when the platforms became solidly cemented to the shell floor and had only a brief anterior overhang. The end-product of this lineage, forms with cemented platforms, no longer fit categorically into the genus *Gruenewaldtia*, and a new genus, *Desatrypa*, is arbitrarily proposed for these. To avoid subsequent confusion it is described briefly:

'Order' Atrypida. Family Palaferellidae. *Desatrypa* n.gen.

*Genotype species. Atrypa desquamata* Sowerby 1840 (ref. 2), Pl. 56, Figs. 19–22.

*Stratigraphic range.* Upper Eifelian to upper Givetian, Middle Devonian.

*Diagnosis.* Biconvex to dorsi-biconvex atrypids with a prominent, wide inter-area and continuous, deep-troughed ribs interrupted marginally by weak, incipient concentric growth lamellæ. No frills or spines developed.

Internally, raised muscle platforms are cemented to the shell floor (a suture line may or may not be visible). Teeth are strong and lack lateral cavities. Massive hinge plates and thick cardinal blocks are typical. Crura are minute, vestigial and structurally different from those in normal atrypids. Some species completely lack dorsally

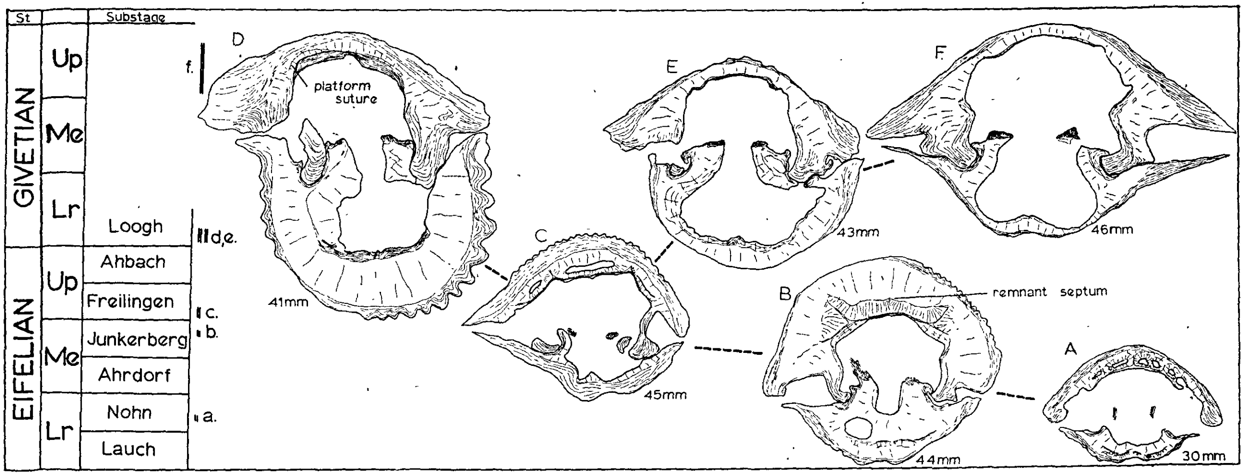

**Fig. 1.** Transverse sections of different palaferellid atrypids showing the septal development in the pedicle valve. All figures are half-size and are taken at the same stage of crural development. *A*, *Gruenewaldtia* sp. (non *G. rhenana* (Spriestersbach)) from the Schleit horizon, Nohn beds, lower Eifelian; *B*, *Gruenewaldtia latilinguis* (Schnur), upper Junkerberg beds, middle Eifelian; *C*, *Gruenewaldtia* sp. (non *G. apsaklina* Struve), Freilingen beds, upper Eifelian; *D*, *Desatrypta flabellata* (C. F. Roemer), lower Givetian; *E*, *Desatrypa insquamosa* (Schnur), lower Givetian; *F*, *Desatrypa desquamata* (Sowerby), upper Givetian. The transition between the two genera appears to have occurred about late Freilingen–early Ahbach time

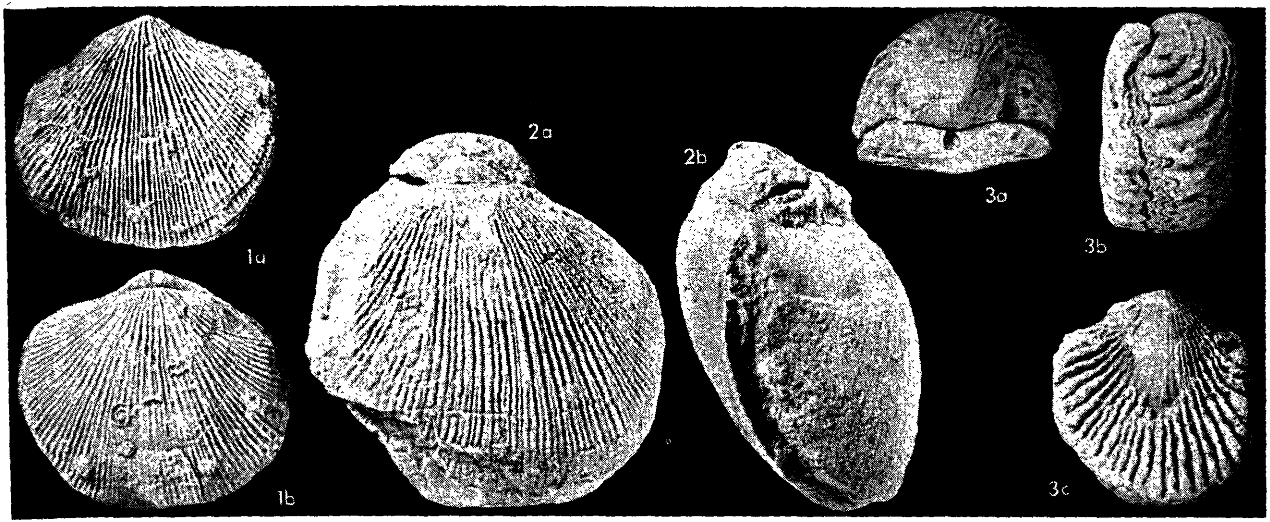

**Fig. 2.** 1*a* and *b*, *Desatrypa insquamosa* (Schnur), lectotype specimen from Schnur's original collection; 2*a* and *b*, *Desatrypa desquamata* (Sowerby), lectotype specimen, Sowerby collection; 3*a*, *b* and *c*, *Desatrypa flabellata* (C. F. Roemer), holotype, Roemer collection. All figures half size

directed spiralia. Deltidial plates are fused medially and are continuous with a pedicle collar or remnant pedicle collar (late Eifelian *Gruenewaldtia* also have monostructural deltidial plates and pedicle collars).

*Member species. Terebratula prisca* var. *flabellata* C. F. Roemer 1844 (ref. 3). *Terebratula insquamosa* Schnur 1853 (ref. 4).

A wide international distribution and long stratigraphic range have commonly been attributed to *Atrypa desquamata* Sowerby, the type species of the new genus *Desatrypa.* Most of the atrypids concealed under this name are, in fact, unrelated to the true *desquamata* of Sowerby, restricted to the upper Givetian. In 1960 Alekseeva[5] established the sub-genus *Desquamatia* and included in this sub-genus many species formerly called "*Atrypa desquamata*". As part of a monographic revision of west European atrypid faunas, I re-examined Sowerby's original material and sectioned topotype specimens of the species *desquamata.* It was then found that the internal structure of *Atrypa desquamata* Sowerby (family Palaferellidae) was very unlike that of the *Desquamatia* (family Atrypidae) described by Alekseeva, although externally they were in part strongly homœomorphic.

The stratigraphical and geographical distribution of the palaferellids is not fully known. Two geographically isolated stocks appear to have existed during late Eifelian–Givetian times. The first, a divergent stock leading to *Desatrypa,* is chiefly concentrated in western Europe and is known from England, France, Belgium and Germany, and probably occurs also in the Carnic Alps of Italy. A second, the root-stock *Gruenewaldtia,* appears to have persisted with little modification to the Upper Devonian at Ober-Kunzendorf near Wroclaw, Poland[6], and is known from the Givetian of the Kutznetsk basin in U.S.S.R.[7]. The emergence, during Givetian time, of massive stromatoporoid-crinoid reefs in north-western Europe coincided with the development of *Desatrypa* n. gen., which is largely restricted to such an environment. It is speculated that *Desatrypa* developed in response to this change in environment. Cementation (and hence strengthening) of the muscle platform probably was advantageous in the more turbid waters of the reefs.

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# A new Middle Devonian atrypid brachiopod from the Eifel, Germany.

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Plate 27, text-figures 1-13.

## Summary.

A new species of atrypid brachiopod, *Desquamatia ajugata* (family Atrypidae) from the lower Givetian of the northern Eifel synclines in Germany, is described. Its distinctive appearance and restricted stratigraphic range make it locally useful as an index fossil. Relatinoships to other *Desquamatia* of the Eifel are discussed. The species shows affinities to some Canadian atrypids, but is rare or absent in synchronous fossiliferous Devonian sediments in the southern Eifel synclines, a few miles away. Significant internal structures are briefly described and their value in atrypid taxonomy and phylogeny evaluated. Crura, cardinal and jugal processes are examined in detail for the first time.

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## Introduction.

The atrypid group of spire-bearing brachiopods, which form an important and major faunal constituent in fossiliferous marine Devonian sediments throughout the world, are undergoing intensive revision. In the period 1960-1965 major works on the atrypid brachiopods have been published by ALEKSEVA, RZHONSNITSKAYA, LJASHENKO and BOUCOT, but, other than in isolated papers, this fossil has as yet received only scant attention in the classical areas of the Devonian of W. Europe, the areas of the Eifel, Givet and Frasne. References to these areas have had to depend on the excellent classical brachiopod works of SCHLOTHEIM, SCHNUR, KAYSER and QUENSTEDT, published in the 19th century. A re-examination of the morphology, distribution and ecology of the Atrypida from these areas is in progress.

Of chief interest in this paper is one species of the genus Desquamatia ALEKSEEVA 1960, a genus found to be particularly useful in the correlation of some of the problematical horizons in the Eifel region of Germany, an area roughly situated between the Belgium-Luxembourg border and the Rhine river (text-fig. 1). In the Eifel, the *Desquamatia*-like atrypids were grouped formerly under the catch-all name *Atrypa zonata* (SCHNUR). This, for example, is the name given by WOLFART (in OCHS & WOLFART 1961: 41) for the new species described in this paper. STRUVE (in HOTZ & KRÄUSEL & STRUVE 1955: 76, 81, 94, 97, 99, 110) previously suggested the possibility of distinguishing besides *Atrypa zonata* sensu stricto several forms of the *zonata* group of specific or subspecific rank, designating them by open nomenclature (ssp. F, ssp. $F_1$, ssp. $F_2$, ssp. H, sp. R). It is not yet clear to what extent these designations coincide with the author's identifications. Nevertheless, the name *zonata* undoubtedly obscures several unnamed, stratigraphically valuable species.

## General.

Specimens were oriented for measurement and sectioning in the manner shown by STRUVE (1955: 209). Shell length in the scatter diagrams (text-fig. 7) refers to the length of the pedicle valve. Rib plans are tabulated as in STRUVE (1955: 210-11, 1956: 391).

To examine internal structures in detail, brachiopods were serially sectioned, and acetate peels, using small sheets of 0·04 mm thick acetobutyratfolie Triafol BN (made by BAYER G.m.b.H., Germany), were taken. This material has the advantage of drying rapidly in roughly 30 seconds, and pressing easily into flat sheets. Text-figures of serial sections were drawn in the style of SIEHL (1962), although slightly modified. Plaster casts were made of each specimen serially sectioned, so that re-identification of the specimen from casts and the remaining $^2/_3$ or $^1/_2$ of the shell is possible.

Abbreviations conform to the style of Senckenbergiana lethaea. Numbers in parentheses refer to the number of specimens from each locality. Type specimens, as well as plaster casts of sectioned specimens, are deposited in the Natur-Museum und Forschungs Institut Senckenberg, Frankfurt am Main, Germany.

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## Genus **Desquamatia** ALEKSEEVA 1960.

Type species: *Atrypa (Desquamatia) khavae* ALEKSEEVA 1960.

Emended diagnosis: Atrypidae with rather high, narrow, linear ribs not arranged in rows, regular growth lamellae and an interarea exposing disjunct, hollow deltidial plates and apical foramen. Internally, distinctive features are prominent lateral cavities or dental nuclei and disjunct, hook-like jugal processes.

Distribution:

The genus has a world-wide distribution although at present it cannot be identified in published research from Australia. Australian atrypids described as *Atrypa desquamata* SOWERBY (e. g. in VEEVERS 1959: 119) belong to the genus *Spinatrypa* STAINBROOK 1951 or *Spinatrypina* RZHONSNITSKAYA 1964.

*Desquamatia* is abundant in the fossiliferous lower Middle Devonian (Eifelian) sediments of the southern Eifel, that is, the area including the Hillesheim, Ahrdorf, Prüm, Gerolstein and Salmerwald synclines (text-fig. 1). The first representatives of the genus are found in the lower Eifelian (Schleit horizon, Nohn beds), and the last appear to have become extinct or to have migrated in upper Eifelian time (Müllert horizon, Ahbach beds). The group reached their zenith in late middle Eifelian time in the brachiopod and coral rich Junkerberg beds. *Desquamatia zonata* (SCHNUR 1853: 182-3, pl. 24 fig. 6), sensu stricto, which is limited to the Klausbach and Mussel horizons (Junkerberg beds), commonly forms more than 80% of local brachiopod faunas. *Desquamatia* is absent in fossiliferous lower Givetian rocks of the southern Eifel and its ecological niche appearrs to have been captured by the *Mimatrypa* group. The decline of *Desquamatia* is associated with the advent of a reefoid environment.

By comparison with the northern Eifel, the area including the Rohr, Blankenheim, Dollendorf and Sötenich synclines, *Desquamatia* and atrypids in general are a rare element of the Eifelian fauna, with some exceptions. This is particularly noticeable in the Junkerberg beds, so abundant in atrypids to the south, of the railroad section NW Blankenheim. Here, spiriferids, schellwienellids, orthids, athyrids and chonetids are numerous, but atrypids are virtually absent. A few *Desquamatia* appear late in Junkerberg time, but the genus reaches its first, and also its last peak in the Neuenbüsch horizon of the lower Givetian. W. STRUVE (written communication) has advanced the view that the Neuenbüsch horizon appears to be of Rech-Felschbach age, i. e. that it occurs higher in the stratigraphic column than supposed by WOLFART (in OCHS & WOLFART 1961: 40, 69). I endorse this view, and also suggest that the lowest part of the Neuenbüsch horizon is probably ageequivalent to middle and high parts of the Rech horizon, Loogh beds, lower Givetian.

There is a possibility that some of the faunas of the northern Eifel, not containing *Spinatrypa aspera* (SCHLOTHEIM 1820) and previously given a Freilingen age, are somewhat older and correlate with the Nims and Giesdorf horizons (Junkerberg beds). The following localities are probably mainly of Nims-Giesdorf age: in Paulus 1961: 438 (BP 8, BP 24 MTB Münst. r 4746 : h 0173; BP 204 MTB Mech. r 4094 : h 9698; BP 204 MTB Mech. r 4690 : h 0154), WOLFART in OCHS & WOLFART 1961 : 38 (? RW 200: MTB Blank. r 4541 : h 8961). Similarly, it is thought that some of the faunas designated by GLINSKI (1961) as lower Freilingen, possibly also are of high Junkerberg age. This applies to GLINSKI's localities AG. 32 and AG. 33 (GLINSKI 1961: 284), which probably are of Nims-Giesdorf age. GLINSKI's horizon 8 (Rohr *Hexagonaria* horizon) is believed to be of Rechert age.

The geographic distribution of *Desquamatia ajugata* n. sp. is shown in text-fig. 13. Possible conspecific members of the species, which are older than the typical forms, are plotted separately. The early appearance of the latter is somewhat puzzling because intervening species do not show the marked loss of growth lamellae of the new species. It is suggested that the species may have migrated northwards in Eifelian time to become restricted locally around the Blankenheim area in the lower Givetian. It is striking that the species (and genus) should not be present in fossiliferous lower Givetian of the southern Eifel, with the exception of 2 crushed specimens of Cürten age (see Material: St. 95, St. 96). This can probably largely be attributed to the strong facies preference of *Desquamatia* to argillaceous sub-strades and the dissociation with colonial and tabulate coral growth. Faunal isolation in the Eifel is lso typical of other brachiopods.

## Basic inernal elements:

A brief description of several internal structures, important in the identification of atrypids and possibly useful in determining phylogenetic trends, is given. Some of these structures are new, others have not been examined in detail before and still others appear to have been misinterpreted.

Great weight has been attached to the presence or absence of dental plates in atrypid genera, and in the present literature it is very often assumed automatically that dental plates are present only if there is a lateral cavity to separate them from the shell wall. This assumption is misleading and leads to confusion in identification as well as to nomenclatorial difficulty when these lateral cavities are absent, embryonic or filled in with calcite. It the latter instances, acetate peels of transverse sections immediately reveal that the dental plate is present irregardless of the presence of lateral cavities. It is suggested that the trem dental plate be so redefined as to include all tooth supporting structures. Such a redefinition is important because the presence or absence of lateral cavities or dental nuclei (where lateral cavities are embryonic, the term dental nucleus is used) is a vital, generic-level form of dinstinction for many atrypids, and should not be confused with the presence of dental plates.

In some genera such as *Desquamatia* ALEKSEEVA and *Spinatrypa* STAINBROOK there is a strong phylogenetic development towards widening and expansion of the lateral cavities. In others, e. g. *Gruenewaldtia* CHERNYCHEV, the reverse is true. Some authors (BIERNAT 1964: 289; ALEKSEEVA 1962) have advanced the opinion that dental plates serve as attachment for the pedicle muscle. Although atrypid genera with well exposed foramen and delthyria often have prominent lateral cavities which possibly served as attachment, there also are genera with large delthyria which lack lateral cavities (*Gruenewaldtia* CHERNYCHEV in late Eifelian time, all *Mimatrypa* STRUVE). Furthermore, there is direct evidence in many *Spinatrypa* and *Atrypa* of the presence of a pedicle layer (or rarely a pedicle collar), which does not extend beyond the teeth. In some *Gruenewaldtia*, the pedicle muscle leaves a large circular scar in the delthyrial cavity.

Pedicle collars and pedicle layers, internal structures of the pedicle valve related in function to deltidial plates, have been found in *Atrypa, Spinatrypa, Anatrypa, Desquamatia, Mimatrypa* and *Kerpina*. Some of these genera show peculiar associations of collars and deltidial plates which may be of value in classification, and, on an infrageneric level, may serve to distinguish between species. Pedicle collars commonly were developed late in ontogeny (small specimens rarely have them) and also late phylogenetically (in *Desquamatia* of the Eifel region, they appear to be absent or rudimentary in early Eifelian species). It should be noted that the „Kragen“ in a species of *Gruenewaldtia* described by STRUVE (1955: 215) is not an internal pedicle collar, but simply a calcite rim around the foramen, a feature typical of many atrypids. Development of a pedicle collar is usually associated with the presence of an exposed delthyrium, but rarely also takes place when the beak is fully incurved.

In *Desquamatia*, one of the distinctive features of the deltidial plates is their hollowness (text-figs. 3-5). None of the Eifelian-Frasnian species from Germany show any fusion of the deltidial plates, although many show interlocking plates. A syndeltarium, a single unified deltidial plate, is therefore absent. The deltidial plates of *Desquamatia* are similar to those of *Gruenewaldtia* of middle Eifelian age, and to most *Spinatrypa* of Givetian age.

Distinctive cardinal processes, structures which served as attachment for the diductor muscles, are common to most, if not all, atrypids. They are located in the notothyrial pit and overlap onto the hinge plates (text-figs. 3-5). According to ALEXANDER (1948: 208) atrypids lack these processes, and in the literature they are only rarely mentioned (VANDERCAMMEN & LAMBIOTTE 1962: 12; BIERNAT 1964). The processes consist of up to 15 minute ridges, roughly parallel or sub-radiate, commonly with a brownish colour due to their fine crystallinity. On the portions overlapping the hinge plates, there is little arrangement of the ridges, and in transverse section they resemble mushroom-like growths. Cardinal processes are particularly well developed in *Desquamatia* from the Eifel region. Their appearance in different species is variable.

Crura, fibres connecting the spiralia and jugal processes to the hinge plates in the brachial valve, are not solid and clearly defined structures in *Desquamatia*. In this genus, although not in all Atrypida, crura consist of closely packed, fine calcite fibres at the base and extremely feathery and diffuse crystals distally. The distal fibres radiate in many directions, but chiefly towards the ventral valve. The term primary lamellae, which appears first to have been used by ALEXANDER (1948: 211), is abandoned because there is no means of determining where these structures, supposedly uniting crura to spiralia, begin and end. The feathery structure of the crura is mentioned by IVANOVA (1962: 80).

In some species of atrypids there appears to be a complete lack of connection between the crura and spiralia, and some species even lack spiralia, at present the only means of distinction between rhynchonellid and atrypid brachiopods. The lack of spiralia cannot be wholly attributed to breakage or destruction by scavengers, since for such material preservation is nearly ideal and associated species of spire-bearing brachiopods (e. g. athyrids, spiriferids) bear a full complement of spires. Some atrypids which lack spiralia also show minute degenerate or vestigial crura. The feathery structure of the crura may be significant. Firstly, a solid calcite connection would be more liable to breakage than a fibrous, loose connection. Secondly, it is possible that the focal point between crura and spiralia was the generating zone for the growth of the brachidia, and may have been replaced by a muscular connection. Thirdly, the filamentous crura may be phylogerontic features, although evidence for this is sparse.

The nature of the jugal processes, whose function is uncertain, is debated and relatively unstudied. They are said to be sometimes connected, sometimes disjunct. DAVIDSON (1865: pl. 6 fig. 7, 1882: pl. 1 fig. 15) showed both disjunct and connected processes in the same species *Mimatrypa desquamata* (SOWERBY). Detailed serial sections of specimens of *Gruenewaldtia matutina* STRUVE and *Spinatrypa kelusiana* STRUVE 1955: pl. 1 fig. 2, 1956: pl. 2 fig. 14a), which are said to have united jugal processes, are shown, in fact, to have distinctive, disjunct processes. Similar results were obtained in the examination of more than 15.000 acetate peels taken from 142 sectioned specimens of Devonian and Silurian atrypid genera. It is likely that disjunct jugal processes are characteristic of all atrypids. The function of the processes is still problematical, but it is suggested that instead of uniting the spiralia, they served to keep the spiralia away from the diductor muscles or as a fulcrum in levering the spiral cones into elevated or lowered positions.

In *Desquamatia*, as in some other atrypid genera but not *Atrypa* or *Spinatrypa*, small hook-like plates called jugal plates, are attached to the ends of jugal processes (text-fig. 6). The position and shape of the jugal plates is distinctive in many genera and is useful in determinations. This structure alone is probably sufficient to group ALEKSEEVA's *Spinatrypa waterlooensis canadiensis* (WEBSTER) (ALEKSEEVA 1962: 132) under *Desquamatia*.

It is also likely that the shell structure may be used to distinguish atrypid genera, because there is considerable variability in the development of the different layers of the shell wall. In *Desquamatia*, five different types of crystal growth are present. The outer cryptocrystalline layer is thin and usually not preserved. The two chief layers are the outer prismatic layer, with crystals oriented obliquely to the shell surface, and the inner columnar layer with coarse crystals at right angles to the surface. These layers may interfinger. The cardinalia consist of thick, closely layered calcite distinct from the shell wall. The last type of growth is the thinly layered lalcite which makes up the pedicle layer, and deltidial plates.

## Shell sculpture:

The genus is characterised by straight ribs relatively undisturbed by growth lamellae. Frills are not uncommon. Well etched microscopic growth lines are best seen in the rib troughs (pl. 27 fig. 4). This type of micro-ornament is typical of the genus and is not present in *Atrypa*. It may, however, also be found in distantly related genera such as *Gruenewaldtia* and *Mimatrypa*.

## Ecological setting:

As are many other atrypid genera, *Desquamatia* is particularly abundant in one type of sediment; in this case the group thrived in argillaceous sediments. It is associated with non-arenaceous, calcareous shales, often black but rarely reddish and with a notable absence of detrital debris. The associated fauna includes brachiopods and some simple rugosans, but almost never colonial and tabulate corals or stromatoporids. The group probably favoured a muddy bottom, undeep (10-50 m?), non-reefoid environment. This is not true of all the Atrypida, many of which are highly specialized eco-genera, genera restricted to certain faunal associations. Beds with a rich *Spinatrypa* fauna rarely contain *Desquamatia*, which would suggest tht the two, although contemporaneous, were incompatible.

## *Desquamatia ajugata* n. sp.

Pl. 27 figs. 1-2; text-figs. 3-12.

v 1961 *Atrypa zonata.* — Wolfart in Ochs & Wolfart, Geologie der Blankenheimer Mulde: 41.

Name: *a-* (Latin) = absent, without; *jugatus* (Latin) provided with a yoke or jugum. It brings attention to the disconnected jugal processes. — Holotypus: The complete specimen pl. 27 fig. 1, SMF 19972. — Locus typicus: Road cut and adjacent field about 300 m ENE Blankenheim station, MTB Blankenheim r 4641 : h 9005. The locality area is shown in Wolfart 1956: 491. — Stratum typicum: Neuenbüsch horizon, lower Givetian. Source sediment: At the type locality in yellowish-brown calcareous shales directly above a resistant weathering, reddish-green stained, slightly bituminous, 2-4 m limestone unit (? Pierensberg horizon); specimens commonly are closely packed. — Associated fauna: *Spinatrypa* sp. aff. *S. squamosa* (Sowerby 1840), common *Spinocyrtia* cf. *S. ascendens* (Spriestersbach 1935), rare *Bornhardtina* sp., small horn corals, *Aulopora* and rare *Thamnopora.* Wolfart (1961: 41) reports *Stringocephalus.* — Paratypes: 164 specimens (4 specimens figured, SMF 19973-19976); for detail see „Material".

Occurrence: Frequent in the Neuenbüsch horizon of the Blankenheim syncline. Possibly (?) in the Cürten beds of the Hillesheim syncline. Very similar, but not conspecific, specimens in the range of the Nims-Giesdorf horizons, Junkerberg beds, high Eifelian.

Diagnosis: Medium to large size, thin and wide rimmed shells, with planar to concave pedicle valves (obscure in side and posterior views), moderately convex pedicle valves, a strongly projecting umbo and relatively large interarea. Small aural extensions produce a rather straight hinge line and give a shield-like shape. Ribs are long, straight and uninterrupted, deep and wide troughed. Lateral shell margins commonly curve ventrally. Internally the species has thin crural bases and hinge plates, prominent feathery crura. Jugal processes are disjunct. Lateral cavities are large; a pedicle collar is absent. The shell wall typically is thin.

### Description.

External form:

A statistical summary of normal dimensions is given in scatter diagrams of text-fig. 7.

Shells are medium to large sized; maximum size, with frills or marginal rim, does not exceed 52 mm; the thin, appressed shell margins (which form a type of frill, and which may give a false impression of size) commonly are broken. The outline is elliptical transversely, but shield-shaped in smaller specimens. Shell width is roughly twice shell depth; globose forms are rare. Width is commonly greater than length. Maximum width occurs near the hinge line.

Asymmetrically deformed specimens are common, with beaks and ribs twisted and margins depressed inwardly. At the type locality, 20% of the specimens were skew; 85% of these were skew on the right-hand side (in ventral view). It is not known if this hight ratio of uni-directional skewness is incidental. It may be a post-depositional feature of deformation.

The pedicle valve is convex angularly towards the umbo; maximal convexity occurs apically. The beak projects 2-3 mm over the brachial apex, has gently sloping sides and is acutely angled in ventral view. As a result, the shoulder line is deeply indented. Hinge corners are planar to gently concave, bevelled in ventral view. Side areas and anterior margins are ventrally curved to make the pedicle valve concave in appearance. The interarea is wide and long, sharp-edged apically, round-edged medially and sharp-edged laterally. The beak is deflected ventrally or erect, leaving the plane of the interarea roughly in line with the horizontal plane. The small foramen (about 1 mm across), with a weak deltidial rim, is hypothyrid (sensu Buckman) and occupies the apex of the delthyrium. The delthyrium is large and somewhat angular at the apex, with two long and wedge-like deltidial plates (length 517 mm, height 1-2 mm), which abut, but do not fuse medially. The fold on the anterior commissure is very weak or absent.

The brachial valve is moderately to deeply convex. The apex is exposed, with the shoulder line slightly indented to expose portions of the interarea. The umbonal area is rather flattened, rarely with a slight median furrow. Side areas are well-rounded, dropping steeply, and, towards the hinge corners, somewhat curled. Maximum convexity comes about mid-length.

Ribs:

These are fine, long and continuous, bifurcating on the pedicle valve and intercalating on the brachial valve. They are straight in the mid-areas but curved in the side areas, although not greatly. Ribs are very well-defined, high, narrow and deep-troughed with round crests and round troughs. Ribs on the brachial valve are not as deeptroughed and high-crested as on the pedicle valve. Rib increase is gradual and remains steady at a concentration of about 16 per 10 mm of arc in maturity. A typical view is seen in pl. 27 fig. 4.

Rib concentration:

At 10 mm from the apex, 16-21 ribs per 10 mm of arc; average 19.
At 15 mm from the apex, 16-20 ribs per 10 mm of arc; average 18.
At 20 mm from the apex, 15-19 ribs per 10 mm of arc; average 16.

Rib plan:

| | pv. | bv. |
|---|---|---|
| apex | 4-3:1:3-4 | 3:0:3 |
| 1 mm | 5-4:(1)1-2(1):4-5 | (2)3:(1)1(1):3(2) |
| 2 mm | 7-5:(1)2-3(1):5-7 | (3)5:1(1)1(1)1:5(3) |
| 5 mm | 14-10:(2)2(1)2(2):10-14 | 15-13:2(1)2(1)2:13-15 |

Two slightly enlarged mid-ribs are rarely found towards the apex oft he pedicle valve, and are accommodated by a faint groove on the brachial valve. This is common to nearly all atrypids. Rib plans were found to be highly variable, and an almost countless number of combinations could be made up. The plan presented is generalized.

Growth lamellae:

The species is particularly distinctive in its few or totally absent concentric growth lamellae. A few scattered lamellae may appear at wide intervals, or may be developed as incipient ridges on the shell surface. There is no evidence that surface frills were developed and subsequently eroded. Shell margins, which commonly consist of thinly appressed lamellae, are delicate and tend to be kroken; when preserved they form a rim around the shell. This rim or „frill" is unlike the frills portrayed by Ivanova (1962: 60), which completely cover the shell surface.

Microscopic growth lines, as in pl. 27 fig. 4, crowd the rib troughs at a concentration of about 7-9 per millimeter, with rare smaller lines between.

Growth and variation:

Small specimens lack ventrally directed frills, are somewhat planar, with convex brachial and plane to slightly concave pedicle valves, and show more acute apical angles and proportionally larger interarea and delthyria. Commissures are straight. Shell outline changes from near circular to shield-shaped to elliptical. The incurvature of the beak remains constant.

In maturity, three main variations may occur (see text-figs. 8-11). Firstly, frills which are horizontally extended (rare); secondly, frills ventrally curved (very common), and, lastly, skew specimens (common). No abnormal trends towards globosity were observed; there was no binary population. No other *Desquamatia* are present in the Neuenbüsch horizon.

Internal markings:

No loose valves were examined; the thinness of the shell wall makes valves very fragile. Muscle scars, pallial markings and ovarian markings, are as a result only thinly impressed.

Internal structures:

Enlarged transverse sections based on a study of about 300 acetate peels are shown in text-fig. 12. Serial sections of the Canadian specimen (pl. 27 figs. 3a-b) were found to be identical in nearly every respect.

A pedicle collar is absent. The umbonal cavity is rounded to sub-quadrate in section and lacks a strong median groove. Deltidial plates, which are solid, and somewhat squared apically, become hollow and split distally (text-figs. 3-5), with a thin inner edge and a thicker, brushlike outer edge which extends laterally. Lateral cavities are large and prominent; in section they appear thin and elliptical apically, and triangular distally. Dental plates are thin and nearly vertical; the dental buttress plate is stout. A dental ridge is only weakly developed. Teeth are strong, inwardly directed, with a thick and rounded inner lobe and crenulated small outer lobe.

The notothyrial pit is mall and shallow and contains a weak cardinal process with up to 8 minute ridges (text-figs. 3-5). The cardinal process is rarely extended over the hinge plates. Hinge plates are thin and show a brushlike inner socket ridge, and a prominent middle socket ridge, but lack an outer ridge. A thick cardinal block is absent. Crural bases are thin; crura are well-developed, thick and quite straight, and are directed ventro-laterally at about 30° to the horizontal plane. Distal crural fibres are not elaborate. Jugal processes are long and thin, fairly straight and horizontal; medially they curve sharply dorsally and laterally to terminate in small, hooked jugal plates (text-fig. 6). They do not unite. A median septum is weakly developed; it is round and humped posteriorly, and, anteriorly, it becomes broad-based and sharp-edged to finish as two weak, rounded ridges. Spiralia have up to 10 whorls.

## Comparison.

The species is readily distinguishable from other *Desquamatia* in the Eifel by its very few growth lamellae, its long and continuous ribs, and in shape by the somewhat concave pedicle valve and the thin ventrally-turned marginal rims.

A strong resemblance between *Desquamatia ajugata* n. sp. and a species from the Kee Scarp formation, Snake River, Yukon, NW Canada, is evident. A specimen of this Canadian species is figured (pl. 27 figs. 3a-b) and has been tentatively assigned to *Desquamatia aperanta* (Crickmay 1960). The internal resemblance between *D. ajugata* n. sp. and the figured Canadian specimen is also striking. The thinness of the shell, the large lateral cavities, the deltidial plates and jugal processes are only slightly different.

*Desquamatia ajugata* n. sp. differs from type specimens of *D. aperanta* (Crickmay 1960: pl. 8 figs. 2-15) in having straighter ribs, a concave pedicle valve and marginal frill. The specimens figured in McClaren & al. 1962: pl. 8 figs. 13-15, and said to come from the Hume formation of NW Canada, are more similar to specimens listed in this paper under Giesdorf-Nims (Eifelian) age. It is, however, premature to judge the relative age of species so widely separated geographically.

Some immature specimens of *D. snakensis* (McCammon 1960: 54-55) are similar to small specimens of *D. ajugata* n. sp. but there appears to be less resemblance in older forms.

## Material.

164 specimens, chiefly from the type locality, where the species is most abundant. Material from the Cürten beds is doubtful. Specimens listed under Nims-Giesdorf horizons possibly belong to a new species, closely related to *Desquamatia ajugata* n. sp. Additional material must be collected and examined to certify such a new species.

Neuenbüsch horizon, lower Givetian: RW 39 (1) MTB Aremberg r 5173 : h 9445; RW 198 (1) MTB Blankenheim r 4656 : h 8992; C 115 (9), C 183 (5) coll. Herta Schmidt, r 4630 : h 8990; C 499 (148) locus typicus r 4641 : h 9005.

Cürten beds, lower Givetian: St. 95 (?1) MTB Dollendorf r 5378 : h 7559; St. 96 (?1) r 5381 : h 7559. This material from the Hillesheim syncline is very uncertainly grouped under *Desquamatia.*

Nims-Giesdorf horizons, Junkerberg beds, Eifelian: C 455 (?2) MTB Mechernich r 4650 : h 0149; C 456 (?3) MTB Münstereifel r 4736 : h 0180; C 508 (?1) MTB Hallschlag r 3524 : h 8089; RW 119 (?1) MTB Aremberg r 5185 : h 9465; St. 673 (?1) MTB Dollendorf r 52225-45 : h 76445-60 (impure locality?); C 108 (?1) MTB Schönecken r 3159 : h 5926; C 125 (?1) r 3226 : h 6066; C 128 (?1) r 3175 : h 5955; C 370 (?3) r 3220 : h 6033.

## Conclusions.

*Atrypa (Desquamatia)* Alekseeva 1960, with its distinctive external sculpture and delthyrial development, and internally with lateral cavities and hook-like jugal processes, is a readily recognizable species-group of atrypid brachiopods fully deserving of generic rank. *Desquamatia ajugata* n. sp. is, at present, the only known Givetian species of the genus in the Eifel area of Germany. Here, the genus is abundant only in the lower Middle Devonian (Eifelian).

The new species shows a striking development of rib pattern and loss of growth lamellae, which is not present in its Eifelian relatives, and which appears to be distinctive of Givetian species. The distribution of *Desquamatia ajugata* n. sp. is chiefly restricted to the northern Eifel synclines (text-fig. 13), although related specimens of Eifelian age show a wider distribution in the Eifel (text-fig. 13).

Correlations of some of the stratigraphic horizons in the northern synclines are slightly changed. The Neuenbüsch horizon becomes slightly younger (Loogh-Cürten age) and there is a possibility that some of the brachiopod rich beds previously dated as Freilingen age, may be somewhat older and of Junkerberg age.

Text-fig. 1. Location map of the Eifel synclines in Germany (SW corner)

Text-Fig. 2. Stratigraphic section at the type locality of *Desquamatia ajugata* n. sp. after Ochs & Wolfart 1961: 35-45. The Neuenbüsch horizon is probably thicker than previously indicated.

Text-figs. 3-5. The cardinal process and deltidial plates in three different specimens of *Desquamatia ajugata* n. sp.; transverse sections; ×10. The position of the cardinal process as seen in section corresponds to the angle and interval of the section. — All specimens from lower Givetian, Neuenbüsch horizon, MTB Blankenheim r 46410 : h 90050 (locus typicus). — 3: SMF 19974. — 4: SMF 19975. — 5: SMF 19976 (same as in text-fig. 6, 12).

Text-fig. 6. The jugal process and jugal plates of *Desquamatia ajugata* n. sp.; transverse sections; ×13·3. Specimen SMF 19976 (same as in text-fig. 12). — Lower Givetian, Neuenbüsch horizon, MTB Blankenheim r 46410: h 90050 (locus typicus).

Text-fig. 7. Scatter diagrams of three major shell dimensions of *Desquamatia ajugata* n. sp. — All specimens from Lower Givetian, Neuenbüsch horizon, MTB Blankenheim r 46410: h 90050 (locus typicus); stratigraphic interval roughly 2 m.

Text-figs. 8-11. Common morphological variations in *Desquamatia ajugata* n. sp.; ×1. Ribs are not shown. — Drawn from topotypic material.

Text-fig. 12. Transverse serial sections of *Desquamatia ajugata* n. sp.; ×4. Specimen SMF 19976 (same as in text-figs. 5, 6). — Lower Givetian, Neuenbüsch horizon, MTB Blankenheim r 46410 : h 90050 (locus typicus).

Text-fig. 13. Geographic distribution of the Eifelian *Desquamatia* sp. aff. *D. ajugata* (13a) and the *Givetian D. ajugata* n. sp. (13b) in the Eifel region, Germany. The brachiopod biotope is stippled; fossil localities in black circles. The Neuenbüsch brachiopod biotope is modified from Struve 1963: text-fig. 19.

## Plate 27.

Figs. 1-2. *Desquamatia ajugata* n. sp. — Neuenbüsch horizon, lower Givetian; locus typicus MTB Blankenheim r 4641 : h 9005, Blankenheim syncline, Eifel.
1. Holotypus, SMF 19972; × 1. — Views: a) ventral, b) lateral, c) dorsal, d) oblique dorsal, e) posterior, f) anterior.

Fig. 3. *Desquamatia* sp. aff. *D. aperanta* (Crickmay 1960). — Kee Scarp formation, Snake River, Yukon, NW Canada. — SMF 19971; × 1. — Views: a) ventral, b) lateral.

Fig. 4. *Desquamatia ajugata* n. sp. — Neuenbüsch horizon, lower Givetian; locus typicus MTB Blankenheim r 4641 : h 9005. — Paratypus, SMF 19973 (see also fig. 2); × 16. — Enlarged view of the ribs on the ventral side showing the characteristic ornament preserved in the troughs.

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