SPINATRYPA AND SPINATRYPINA (DEVONIAN BRACHIOPODA)

by PAUL COPPER

ABSTRACT. The Eifelian-Givetian (Middle Devonian) sediments of Germany contain a near-continuous suite of brachiopods belonging to the genera Spinatrypa Stainbrook 1951 and Spinatrypina Rzhonsnitskaya 1964. These two allopatric atrypid genera occupy different, mutually exclusive environments: the first is dominant in a brachiopod biotope, and the other is invariably associated with small thamnoporid or disphyllid corals. Several new taxa of limited vertical distribution are briefly described. These are Spinatrypa variaspina, S. aspera meridiana, S. globulina, S. curvirostra, S. orthoclina, and Spinatrypina demissa, S. fabaca, S. girzenensis. Small changes in critical correlations of the Eifel region are suggested. In Germany, and probably elsewhere in Europe, the Spinatrypa–Spinatrypina atrypids of Givetian age predominantly replaced the Atrypa group common to Eifelian rocks, a feature possibly of major significance in marking the Eifelian-Givetian boundary.

A MAJOR part of the Middle Devonian atrypid faunal record consists of species belonging to two genera, *Spinatrypa* and *Spinatrypina*. On the basis of slightly less than 10,000 specimens, mainly from the Devonian synclines of the Eifel region, but also from Bergisches Land east of the Rhine (Germany), fifteen species and subspecies are described, most of them in abridged form and many for the first time. Since these atrypid taxa have a short vertical range, they are especially useful in more detailed Eifelian–Givetian correlations of north-western Europe.

Type and figured specimens are housed for the greater part in the British Museum (Natural History). The remaining collections belong to the author, but substantial portions used in the revisions were also on loan from the Natur-Museum Senckenberg (Frankfurt am Main, Germany) and the Paläontologisches Institut und Museum (Humboldt-Universität, Berlin, Germany). A fine collection from the Paffrath syncline was donated by Dr. Ulrich Jux (Universität Köln, Germany). British Museum specimens are catalogued under the code number BB. Under 'Material' for each specific description, the numbers of specimens collected are cited. Details of grid references reach excessive length and are left for future record. Material was derived from some 600 fossil localities. Where given (e.g. under Stratigraphy and text-figures), the grid references follow the standard German five-digit controls based on the kilometre scale.

Acknowledgements. The author's thanks for the generous loan and use of brachiopod material go particularly to Dr. W. Struve, Dr. Hermann Jaeger (Berlin), and Dr. Ulrich Jux. Financial support for European research came from the Royal Commission for the Exhibition of 1851 and the National Research Council of Canada.

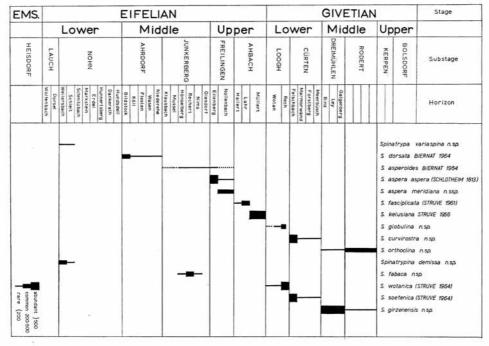
STRATIGRAPHY

The geological sequence in the Hillesheim syncline has become generally accepted by Eifel workers as the type Middle Devonian succession for the Eifel region (text-fig. 1). In this syncline, the Eifelian and Givetian rocks reach a thickness of about 750 m. and from the base to the top are marked by a gradual, much interrupted transition from a brackish water, littoral environment to a fully marine environment rich in brachiopods,

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corals, and reef-forming stromatoporoids (i.e. the Eifel, Normal, or Mischfazies of German workers). Ammonoids are extremely rare in this zone, and therefore of limited value in biostratigraphy on a detailed scale.

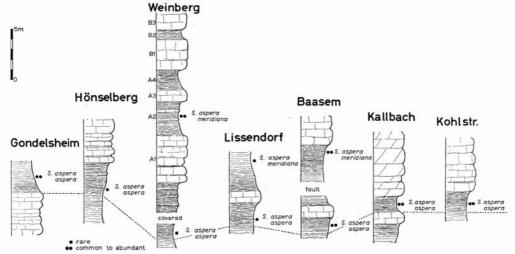
The chief stratigraphical units of the Eifel region are already well known from the sound framework established by Hotz et al. (1955) and Struve (1961). The Eifelian is



TEXT-FIG. 1. Chronologic distribution of individual species of Spinatrypa and Spinatrypina in the Eifel region and Bergisches Land, Germany. The representative stratigraphic section is taken from the Hillesheim syncline (see Struve 1961) and is not to scale. Total thickness of rocks represented c. 750 m.

arbitrarily grouped into lower, middle, and upper divisions. It seems not unlikely that the Eifelian units of the Eifel region, such as the Lauch, Nohn, Ahrdorf, Junkerberg, Freilingen, and Ahbach beds (possibly of substage value), may be recognizable over large areas of north-western Europe. A horizon-by-horizon correlation already appears feasible in part for such widely separated Devonian outcrops as the Lysa Gora of Poland (Biernat 1964) and Devon, England (Copper 1965a), some 1,700 linear kilometres apart. Comparisons are frequently complicated by the dearth of synchronous fossiliferous facies.

One of the important and critical points of correlation in the Eifel synclines is the boundary between the Junkerberg and Freilingen beds, or, more precisely, the separation along the Giesdorf and Eilenberg horizons. The problem has plagued Eifel stratigraphers for several years and is still not wholly solved. Fossils are abundant, but the faunal content of one locality frequently varies strikingly from the next. In the Prüm syncline, the Giesdorf horizon is marked by the conspicuous spiriferid *Spinocyrtia ostiolata* and this horizon has been suitably taken as the top of the Junkerberg beds. Unfortunately, *Spinocyrtia* has a localized distribution and is not common outside the Prüm syncline (viz. Metje 1956, Ochs and Wolfart 1961, Struve 1961). Directly above the *ostiolata*



TEXT-FIG. 2. Critical stratigraphic successions with *Spinatrypa aspera* (Schlotheim) in the Eifel region, Germany. Thicknesses estimated or measured. Grid references—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; Kohlstr., MTB Mechernich r37910: h96450.

horizon on the north flank of the Prüm syncline, specimens of Spinatrypa aspera aspera, sensu restricto, are common.

Spinatrypa aspera (Schlotheim), an index fossil of the Freilingen beds (upper Eifelian) was re-examined. It was found that two different variations, here classed as subspecies, were identifiable, even under the restricted usage of the Schlotheim atrypid in Struve (1956, 1961, 1964). It was also noted that the Spinatrypa aspera aspera of Struve (1961, p. 313) was in fact different from the topotypical S. aspera, and could be called a new type S. aspera meridiana. In two stratigraphic sections (text-fig. 2), this new and different type of aspera was found stratigraphically above the topotypical aspera.

Struve (1961, p. 310) has assumed that the lower part of the Freilingen sequence does not contain *Spinatrypa aspera aspera*, probably because it has not been found with the typical Eilenberg horizon fauna of *Kerpina vineta* Struve. This absence can, however, probably be accounted for by the peculiar biotope complex of the Eilenberg horizon.

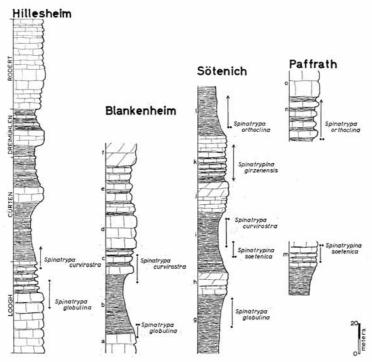
Since Struve concluded that the lower Freilingen beds lacked *aspera*, it was necessary to suppose that there must have been marked stratigraphic hiatuses in the lower Freilingen beds of the Prüm syncline, because here *aspera* lies directly above the top of the Junkerberg beds. As support for such hiatuses Struve (1964, p. 239) cited the presence of an ironstone bed at nearly the same position, and which, it was alleged, 'ist eine typische Transgressions-Bildung'. However, this ironstone bed is not well marked and usually not noticeable in field localities. Other evidence of a sedimentological break (e.g. reworked sediment, shelly debris, mud cracks, ripple marks) is apparently absent. Moreover, there is good evidence that *Spinatrypa* is often strongly indicative of quieter, possibly deeper water (Copper, in press). Proof of a Prüm hiatus is weak.

At the type and neighbouring localities of Spinatrypa aspera aspera, s.r., in the Sötenich syncline, the fossiliferous beds are overlain by sterile limestones or dolomites. At two other localities (Baasem in the Blankenheim syncline, Lissendorf in the Dollendorf syncline), the subspecies aspera is followed by meridiana n.ssp. in well-exposed sections. Predictably then aspera should also be found below meridiana in the Hillesheim syncline. At present this occurrence can be confirmed at Hönselberg and outside the Weinberg quarry (text-fig. 2), though not in outcrop and certainly rare. It seems likely that Spinatrypa aspera aspera occurs in stratigraphic equivalents of the Eilenberg horizon and perhaps even below it, though not in the Junkerberg beds. A change in the definition of the Freilingen beds, previously divided into an upper unit with S. aspera aspera and a lower unit without it (Struve 1961, p. 310), seems required. It also means that the type stratum of the topotypic material of Spinatrypa aspera aspera becomes more or less coeval with the Eilenberg horizon, thereby eliminating the need to postulate hiatuses in the Prüm syncline.

Strong corroboration for this new interpretation was found in the stratigraphic position of two other atrypid species, still undescribed but in part probably predicted by Krömmelbein (1953, pp. 66, 67) as 'eine bezeichnende *Atrypa*-Art'.

Another critical correlation sequence to which the Spinatrypa group makes a contribution is the lower and middle Givetian column of the northern synclines in the Eifel region (text-fig. 3). During this period, the fossiliferous atrypid beds are almost wholly confined to the northern synclines while the southern synclines contain sparse, possibly dwarfed atrypid faunas which are difficult to compare. Correlations on a horizon-byhorizon basis are complicated. The last rich Givetian atrypid fauna of the south (with the exception of the puzzling 'Mühlwäldchen' material) is in the Rech horizon with its Spinatrypina wotanica (Struve). The Wachtberg horizon of the Sötenich syncline (Schmidt and Schröder 1962) and the Neuenbüsch horizon of the Blankenheim syncline (Ochs and Wolfart 1961) are probably roughly coeval and can be correlated with the middle Wotan to middle Rech horizons of the Hillesheim sequence (refer to text-fig. 1). The age of the Spickberg dolomites is tentatively placed as upper Loogh. The Scheid horizon with Spinatrypa curvirostra n.sp. can be dated as upper Rech to Felschbach in age. In 1962 Jux confirmed the Scheid horizon with this same species as middle Eifelian in age, though this was corrected later (Jux 1965, p. 159). Spinatrypina soetenica (Struve) is still uncertainly dated, but is probably restricted to the Felschbach horizon. S. girzenensis n.sp. from the thamnoporid coral rich beds south of Keldenich in the Sötenich syncline is certainly younger than the Scheid horizon, but probably not of Rodert age: it is dated as Dreimühlen.

Paulus (1959, p. 359) and Schmidt and Schröder (1962, p. 37) give the fossiliferous shales of Urfey valley a Kerpen age, mainly on the basis of trilobites. Indirectly, however, the brachiopod evidence suggests an older age. The Urfey beds carry a coral and brachiopod fauna with *Spinatrypa orthoclina* n.sp. which is similar, if not identical, to the fauna of the Torringer beds in the Paffrath syncline outside the Eifel. Jux (1964,



TEXT-FIG. 3. Critical stratigraphic successions of the lower and middle Givetian in the Eifel region and Bergisches Land, Germany. Data compiled from Hotz et al. 1955, Ochs and Wolfart 1961, Schmidt and Schröder 1962, Jux 1964. Code: a—Pierensberg horizon, b—Neuenbüsch horizon, c—Buir horizon, d—Ermberg 'horizon', e—Kerpen beds, f—dolomite unit, g—Wachtberg horizon, h—Zilckens horizon, i—Scheid horizon, j—Spickberg beds, k—unnamed unit (herewith), l—Urfey beds, m—Odenthal quarry, n—Torringer beds, o—Büchel beds.

p. 164) has dated the Torringer beds as Rodert, and followed the interpretation of Hotz et al. (1955, p. 151). This correlation concurs with the atrypid evidence. Moreover, it seems possible that the upper part of the Urfey beds (locality 17 in Paulus 1959, p. 359) can be separated from the lower part (locality 16, ibid.) on the basis of differences in S. orthoclina n.sp., here still regarded as infraspecific.

Near Odenthal in the Paffrath syncline (Bergisches Land), a small atrypid-rich sequence can be correlated with basal portions of the Felschbach horizon (or Scheid

horizon of the Sötenich syncline) on the presence of *Spinatrypina soetenica* (Struve). This correlation makes the Odenthal beds considerably older than given in Jux (1964) who placed the Odenthal strata level with the *quadrigemina* beds of Hand.

SYSTEMATIC DESCRIPTIONS

Order Atrypida Rzhonsnitskaya 1960 Superfamily Atrypacea Gill 1871 Family Atrypidae Gill 1871

At the present time very few developmental series have been established for the atrypid brachiopods and many postulated generic or specific links are weakened because of the lack of internal structure information. The true relationship between *Spinatrypa* and *Spinatrypina*, for example, is far from clear. The two genera obviously inhabited different environments, but whether their morphology is due to divergence from a single stock or to later convergence from an *Atrypa* ancestor, remains doubtful. Both genera appear to show a number of iterative clines during Devonian time (particularly of rib structure), but it does not appear justified at the moment to classify each cline as a separate taxon, e.g. of subgeneric status. The appearance and disappearance of such clines may be due to periods of widespread migration in Devonian history. It may also be debated if strong breeding barriers in palaeontological 'species' or stocks of Palaeozoic age really existed.

Size change may be a measure of phylogenetic development, though this characteristic must be tempered with ontogenetic and ecological observations. In *Spinatrypa* all the Eifelian species of north-western Europe, and from available published data also those of the Ural Mountains and the Kuznetsk basin (see Lyashenko 1959, Alekseeva 1962), were small, with a width rarely exceeding 20 mm. The first large *Spinatrypa* are found in Givetian rocks. Similarly, nearly all *Spinatrypina* of Eifelian age are small; larger size in this genus is not reached until much later in Givetian time. This factor may be useful in broad faunal comparisons, but it is not axiomatic that small size is indicative of Eifelian age.

Terminology is after Siehl (1962) and Struve (1955); internal structures are described according to techniques used in Copper (1965a, 1965b).

Genus Spinatrypa Stainbrook 1951

Type species. Atrypa aspera var. occidentalis Hall 1858, p. 515, pl. 6, figs. 3a-d.

Range. Wenlockian (Silurian) to Frasnian (Upper Devonian). Spinatrypa infrequens (Weller 1914, pp. 285-6, pl. 35, figs. 1-5) is reported as lower Carboniferous but may be Frasnian.

Distribution. World-wide.

Diagnosis. Biconvex through dorsibiconvex and planoconvex spinose atrypids with small interareas and small deltidial plates of primitive type, and ortho-hypercline beaks. Ribs are coarse, undulose-shallow, and raised at each growth lamella. Internally, thick pedicle layers are absent, fibrous and columnar layers limited. Deltidial plates minute, undeveloped, rarely hollow. Teeth bear dental nuclei or lateral cavities. Cardinal process

small, few-stranded, frequently amorphous. Crural bases round, thick; crura often feathered. Jugal plates straight, bulky, and relatively long.

Remarks. The original definition of the genus given in 1945 by Stainbrook is still largely valid. The name *Hystricina* which Stainbrook selected for this group of spinose atrypids was pre-occupied and replaced by *Spinatrypa* in 1951.

Spinatrypa is easily distinguishable superficially from the genus Atrypa Dalman 1828 by its undulose ribs arranged in interrupted rows: ribs are also coarser and shallower, growth lamellae more widely separated. Internally, Spinatrypa is even more dissimilar in lacking numerous interlayers of fibrous and columnar test, thick pedicle constrictions without differentiation into deltidial structures, and solid teeth of Atrypa. Jugal plates also are distinct: in Atrypa they are longer, bent, and more U-shaped and in Spinatrypa more irregular, smaller, and stubbier.

The diagnostic characters of *Invertrypa* Struve (1961, p. 334), which are a ventribiconvex shell, small area, and loss of ribs but distinct mid-rib pair, are well developed only in one species, the type *Spinatrypa kelusiana* Struve 1956, and are hereby judged not to be of sufficient value to warrant separate generic status (viz. Biernat 1964, p. 315). There is also evidence that '*Invertrypa*' reverted to typical *Spinatrypa* in Givetian time, a feature difficult to explain in terms of normal zoosystematic taxonomy.

Spinatrypa differs from Spinatrypina Rzhonsnitskaya 1964 in its undulose, instead of tubular-imbricate ribs, in its minute area, and small deltidial plates, rather than relatively large area and plates, and in its development of spines which are prominent and abundant when preserved. Spinatrypa also reaches a far greater size and shows a more prominent anterior fold. Spinatrypa is chiefly sedentary as its size, beak structure, ribs, and convexity indicate, and inhabited a clayey, muddy base. Spinatrypina is an elevated, attached atrypid brachiopod confined to a thicket reef or Rasenriff type of environment with thamnoporid or disphyllid corals.

Spinatrypa variaspina n.sp.

Plate 76, figs. 1-12

Name. Latin, variate, variable, changeable; spina, thorn, spine. Where observed, the spines are highly variable in direction.

Type locality. Road cut Lissingen-Büdesheim, MTB Gerolstein r44890:h64630 (locality C398). Type stratum, Schleit horizon or slightly higher, Nohn beds, Eifelian. Source sediment. Brownish green to dark brownish grey calcareous shales and thin limestone interbeds rich in fine bioclastic debris. Associated fauna: Atrypa sp., Desquamatia ovata Copper, Gruenewaldtia sp.aff. rhenana (Spriestersbach). Mainly brachiopods.

Diagnosis. Small, generally flattish, biconvex shells with a prominent protruding, orthocline beak, small but sharp-edged area. Specimens are somewhat roundish in outline but the hinge is well defined: there is a marked variation in dimensions from wider than long to longer than wide. Ribs are small, flat, spaced at nine to eleven per 10 mm. and terminate in disarrayed spines where these were observed. Growth lamellae spaced at about 1 mm. Fold weak.

Remarks. This species differs from Spinatrypa dorsata Biernat (1964, pp. 307-9) which is somewhat younger, in being more distinctly ribbed, in a much larger area and

prominent, orthocline beak, and in its flatter dimensions. S. variaspina is already more reminiscent of S. aspera aspera (Schlotheim 1813) but can be separated by finer, more delicate ribs and wider area as well as its shape.

Material. The species is scarce and makes up only a very minor fraction of the Nohn atrypid fauna at any locality. It is overshadowed by Atrypa and Desquamatia and appears to be more common on the southern and eastern fringes of the southern Eifel synclines. Total 103 specimens.

Spinatrypa cf. dorsata Biernat 1964

Plate 76, figs. 13-19

1964 Spinatrypa dorsata Biernat, pp. 307-9, pl. 3, figs. 1-8.

Remarks. Polish specimens of this species compare most closely with Spinatrypa found in the Bildstock horizon of the Ahrdorf beds in the Eifel. But the identification is still not positive. In the Bildstock horizon, Spinatrypa becomes abundant for the first time in the Eifel region, locally even outnumbering small Atrypa. Specimens of the Bildstock niveau are not wider than 15 mm., but somewhat higher up in the sequence (Niederehe horizon), the Spinatrypa become rare yet larger in size. The Eifel S. dorsata are small, rather rotund, somewhat longer than wide, and very flat-ribbed with prominent rib interruptions.

The serial sections figured by Biernat (1964, p. 309) are difficult to compare and sketchy. Biernat shows the delthyrial cavity plugged by solid calcite, a feature absent in Eifel specimens and not typical of *Spinatrypa* as a whole. Biernat also shows remarkable joined jugal plates not present in Eifel material sectioned (text-fig. 4). The Eifel specimen showed small deltidial plates, an elongated dental nucleus (but no cavity), short and stubby teeth, a prominent inner socket ridge, slightly feathered crura, a thick jugal plate, and spiralia with about ten whorls.

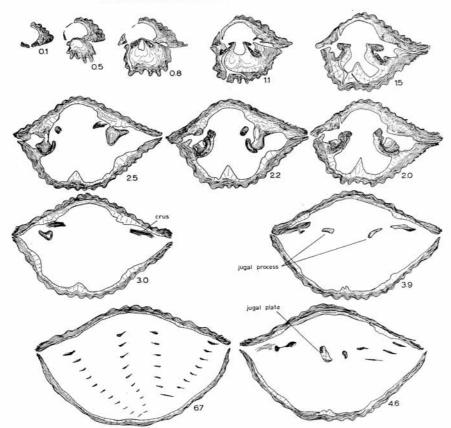
Material. Total about 250 specimens, some not yet catalogued. This species is particularly common in the Ahrdorf and Hillesheim synclines.

EXPLANATION OF PLATE 76

Figs. 1–12. Spinatrypa variaspina n.sp. Lower Eifelian, Weilersbach-Schleit horizons. 1–4, MTB Gerolstein r44890:h64630 (C398); 5–12, MTB Dollendorf r57000: h78230 (H252). 1–4, holotype BB55145, a small, slightly deformed specimen; 5–8, paratype PC62, wide coarsely ribbed shell with damaged umbo; 9–12, paratype PC63, elongate shell with prominent area.

Figs. 13–19. Spinatrypa cf. dorsata Biernat 1964. Middle Eifelian. 13–17, Bildstock horizon; 18–19, Flesten-Niederehe horizon. 13–17, MTB Dollendorf r56340: h83560 (C252); 18–19, r55790–61100: h78000–90 (C249). 13–15, hypotype BB55150, typical small shell; 16–17, hypotype BB55149, more coarsely ribbed specimen; 18–19, hypotype BB55148, larger variety more common to higher horizons.

Figs. 20–28. Spinatrypa aspera aspera (Schlotheim 1813). Upper Eifelian, base of the Freilingen beds. 20–27, MTB Mechernich r37910: h96450 (C475); 28, MTB Mechernich r38020: h96980 (C468). 20–22, hypotype BB55153, large, straight, and wide-hinged variety; 23–24, hypotype BB55152, smaller, wide variety; 25–27, hypotype BB55155, normal elongate shell; 28, hypotype BB55151, large coarsely ribbed shell reminding of S. semiorbis latecostata Havliček 1956.



TEXT-FIG. 4. Transverse serial sections of *Spinatrypa* cf. *dorsata* Biernat 1964. The brachial umbo of this specimen is fractured. Bildstock horizon, lower Eifelian; MTB Dollendorf r54800: h79180. Hypotype BB55223. \times 4.

Spinatrypa aspera aspera (Schlotheim 1813)

Plate 76, figs. 20-28; Plate 77, figs. 1-9

- 1813 Anom. Terebratulit. asper Schlotheim, pl. 1, figs. 7a-c.

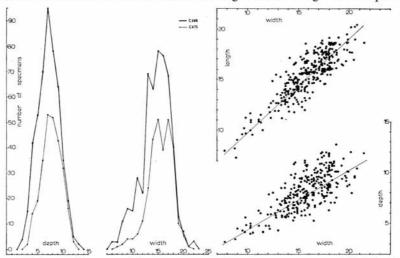
- Anom. Terebratulit. asper Schlotheim, pl. 1, lngs. 7a-c.
 Terebratulites asper Schlotheim; Schlotheim, p. 363.
 Terebratulites asper Schlotheim; Schlotheim, pl. 18, figs. 3a-b.
 Terebratulia aspera Schlotheim; Koenig, p. 3, pl. 4, fig. 44.
 Spinatrypa aspera aspera (Schlotheim); Struve (partim), p. 387, pl. 1, figs. 2a-c.
 Spinatrypa aspera (Schlotheim); Biernat, pp. 309-12, pl. 4, figs. 1-5- pl. 5, figs. 1-12.
 Spinatrypa aspera aspera (Schlotheim); Struve (partim), pp. 527-9, figs. 4a-c.

Type horizon (revised). Low Eilenberg horizon, Freilingen beds, upper Eifelian.

Range. Eilenberg through lower Nollenbach horizons.

Diagnosis. A full diagnosis of topotypic material is given in Struve (1956, p. 387).

External form. Specimens are small; maximum observed width 22 mm., maximum depth 13 mm., average width between 15 and 17 mm. (text-fig. 5). Shell valves are nearly equally convex. Anterior fold weak. The pedicle valve is slightly less convex and a bit flatter than the brachial valve. Shoulder lines straight. Lateral margins are sub-parallel,



TEXT-FIG. 5. Scatter diagrams and frequency curves of *Spinatrypa aspera aspera* (Schlotheim 1813). Scatter diagrams plotted from locality C475, MTB Mechernich r37910: h96450. Locality C468, r38020: h96980. Approximately Eilenberg horizon, upper Eifelian.

EXPLANATION OF PLATE 77

Figs. 1–9. Spinatrypa aspera aspera (Schlotheim 1813). Upper Eifelian, base of the Freilingen beds. MTB Mechernich r37910: h96450 (C475). 1–2, hypotype BB55157, globose elongate variety; 3–4, hypotype BB55158, normal shell with early growth pause; 5, hypotype BB55159, brachial valve of wide variety—note elevated notothyrial pit; 6, hypotype BB55160, brachial valve of elongate variety with damaged apex; 7, hypotype BB55161, pedicle valve elongate variety—muscle scar deeply impressed; 8, hypotype BB55162, pedicle valve wide variety—small delicate tips of the crura just visible (bv); 9, hypotype BB55163, pedicle valve of elongate variety—crura visible (bv). Figs. 10–15. Spinatrypa aspera meridiana n.ssp. Upper Eifelian, Nollenbach horizon. MTB Dollen-

Figs. 10–15. Spinatrypa aspera meridiana n.ssp. Upper Eifelian, Nollenbach horizon. MTB Dollendorf r51000: h75720 (C343). 10–12, paratype BB55165, small specimen; 13–15, holotype BB55166, mature form.

Figs. 16–18. Spinatrypa cf. asperoides Biernat 1964. Upper Eifelian, Eilenberg horizon. MTB Dollendorf r50930: h75720 (C345). Hypotype BB55156.

Figs. 19–22. Spinatrypa fasciplicata (Struve 1961). Upper Eifelian, Lahr horizon. MTB Dollendorf r55530–70: h77390 (C279f). 19–20, hypotype BB55170, small elongate, nearly biconvex form; 21–22, hypotype BB55171, somewhat flattened shell—no prominent mid-ribs; 23–25, hypotype BB55172, elongate shell with damaged umbo.

All figures $\times 2$.

hinge corners may be marked and angular. Hinge angles from 125 to 145 degrees. A blunt, small anacline beak normally stays free from the brachial umbo. A foramen and small delthyrium are exposed in maturity. The brachial valve is more rounded and convex but not gibbous. The dorsal apex is not exposed.

Ribs. The coarse, undulose ribs show advanced stage of disintegration and planation. Spacing of ribs at the margins is 5–6 ribs per 10 mm., favouring 5. Distally growth lamellae are thick and crowded, tending to blot out rib structure. Ribs do not show much bifurcation and intercalation and expand greatly distally.

Growth lamellae. Maximum space between lamellae in coarsely ribbed specimens is about 2 mm., but average is about 1.5 mm. Distal crowding is typical. Spines are rare, even on well-preserved material.

Growth and variation. Biernat (1964, p. 312) remarked that Polish specimens of this species, almost certainly conspecific, showed only limited variation. In the Eifel region, especially near the type locality, a broad dichotomy into wide, flat, and long, globose specimens seems to exist, though this did not come out in a biometrical study (text-fig. 5). Wide forms have longer and thinner areas, more orthocline than anacline beaks, a definable hinge corner, and lack globosity. Narrow forms have short areas and are gibbous in late maturity. All gradations between the two occur. However, this dichotomy is apparently absent higher in the Freilingen beds, and *Spinatrypa aspera meridiana* n.ssp., which possibly was derived from the wide variety, shows no partition of forms.

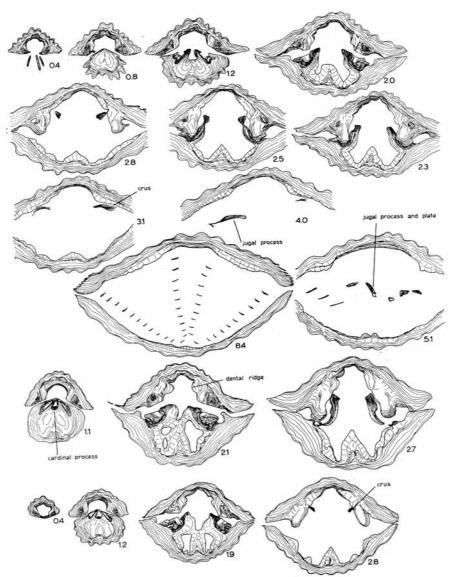
Neanic specimens are shield-shaped, with orthocline beak, a relatively much greater area, and ventribiconvexity.

Internal structure. 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. The delthyrial cavity is lined by rather thick columnar calcite. A dental nucleus broadens out into a small lateral cavity in some specimens. Teeth are short, stubby with the main lobe twisted inwardly and outer lobe strongly crenulated. A four to five stranded cardinal process caps the notothyrial pit and part of the hinge plate. Socket plates are moderately thick, outer socket ridges well marked. Thick crural bases give strong support to delicate crura which are partially feathered distally. Jugal processes are thick and distally contain nodules or small spine bases (refer to text-figs. 6–8). Jugal plates short, with small distal hooks. Spiralia with about ten whorls.

Remarks. Like Atrypa reticularis (Linne 1758), Spinatrypa aspera has gained a reputation as a catch-all species. It seems to have been found everywhere. The name aspera was even fixed by Koenig (1825, fig. 219) to a species of Acanthothiris, a spinose Jurassic rhynchonellid brachiopod. However, Koenig (1825, fig. 44) was also among the first to recognize the validity of the Schlotheim spinatrypid species.

Spinatrypa aspera aspera, sensu restricto, is rare in the Hillesheim syncline but very common on the western margins of the Devonian synclines of the Eifel region. It can be distinguished from the subspecies meridiana in its coarser, much flatter and shallower ribs, its smaller area, greater convexity, and lack of strongly protruding orthocline beak. Struve (1964, p. 529) placed the tota species in the Rasenriff, Crinoidenwald, Knollenblockriff milieu, but this applies only to the subspecies meridiana, and not to topotypical material of aspera aspera.

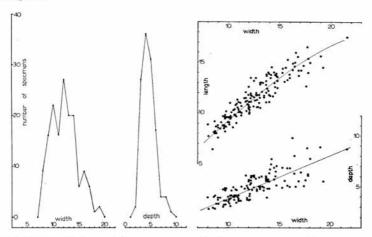
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TEXT-FIGS. 6-8. Transverse serial sections of three different specimens of *Spinatrypa aspera aspera* (Schlotheim 1813). About Eilenberg horizon, upper Eifelian; MTB Mechernich r37910: h96450. Top BB55224, middle BB55225, bottom BB55226. Note the simulated 'septalium' in the lower two globose specimens caused by angle of serial sectioning. ×4.

In the Eifelian of the Prague area (Czechoslovakia), there are spinatrypids which bear a strong likeness to rare varieties of *Spinatrypa aspera aspera* from the Sötenich syncline. These Czech atrypids, *S. semiorbis* (Barrande 1847) and *S. semiorbis latecostata* (Havliček 1956) show coarse, flattened ribs and strong wide-spaced growth lamellae reminiscent of some *S. aspera* (see Pl. 76, fig. 21). In the Eifel this variety is rare.

Material. Total 3,218 specimens. The richest localities are in the Sötenich syncline and the west corner of the Blankenheim syncline and the species is virtually confined to western and northernmost parts of the Eifel sigmoid.



TEXT-FIG. 9. Scatter diagrams and frequency curves of *Spinatrypa aspera meridiana* n.ssp. Combined data from locality St621, St621a; MTB Dollendorf r52030: h77310. Nollenbach horizon, upper Eifelian.

Spinatrypa aspera meridiana n.ssp.

Plate 77, figs. 10-15

Name. Latin, meridianus, southern. It is a reference to the abundance of the subspecies in the southern Eifel synclines.

Type locality. Weinberg quarry near Kerpen, Hillesheim syncline, MTB Dollendorf r53030: h77310 (locality C343). *Type stratum*. Bohnert subhorizon (A2), Nollenbach horizon, Freilingen beds, upper Eifelian (viz. Struve 1961, p. 313).

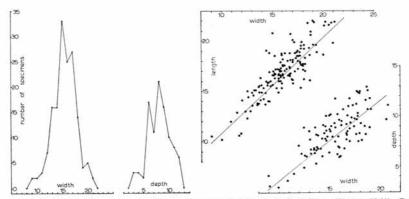
Range. Nollenbach horizon, Freilingen beds. Source sediment. Pale green to yellowish-brown calcareous shales and limestone interbeds. Associated fauna. Atrypa spp., Kerpina vineta Struve, Carinatina plana (Kayser), Atryparia stabilia Copper, Gruenewaldtia apsaklina Struve, Desquamatia sp.

Diagnosis. Small, flattish, strongly ribbed shells with well-rounded outline and wider than long. Beaks orthocline, areas small but defined, shoulder line indented. Ribs spaced at six to seven per 10 mm. marginally, imbricate (somewhat *Spinatrypina*-like), and not as interrupted as most spinatrypids. Shell somewhat flattish, with weak fold.

Remarks. There are many gradational specimens leading to an aspera aspera type of morphology but end members of both subspecies are distinctive (refer to Pl. 76 and Pl. 77). The new subspecies appears to be restricted to slightly younger beds. Scatter diagrams and distribution curves accentuate the differences in size and width/length/ depth proportions (text-fig. 9). Compare the optimum width of 12 mm. and depth of 4 mm. with those of S. aspera aspera.

A striking resemblance is formed by Spinatrypa semilukiana (Lyashenko 1951) figured in Lyashenko (1959, pl. 51, figs. 1-2), a species of Frasnian age. The external differences between the subspecies meridiana and the atrypid from the Russian platform are slight.

Material. This subspecies is much scarcer in the Eifel region and only 286 specimens were examined. It is known from the Blankenheim, Dollendorf, and Hillesheim synclines.



TEXT-FIG. 10. Scatter diagrams and frequency curves of Spinatrypa fasciplicata (Struve 1961). Combined data from locality C279f, C279fa; MTB Dollendorf r55580: h77390, Lahr horizon, upper Eifelian.

Spinatrypa fasciplicata (Struve 1961)

Plate 77, figs. 19-22

1961 Invertrypa fasciplicata Struve, pp. 334–5, pl. 2, figs. 7–8.
 1964 Spinatrypa fasciplicata (Struve); Biernat, pp. 315–16, pl. 6, figs. 6–11.

Type locality, type stratum. In Struve 1961.

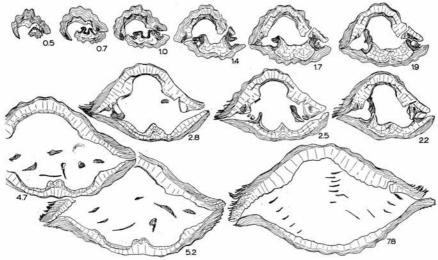
Range. Hallert and Lahr horizons (chiefly Lahr), Ahbach beds, upper Eifelian.

Remarks. An adequate diagnosis is cited in Struve (1961). No material has previously been sectioned. In a trench near Nohn in the Hillesheim syncline (through the type locality of the Müllert horizon), a small but decisive fasciplicata fauna of some 184 specimens was found (locality C279f, C279fa). Many of the specimens were crushed or deformed. Struve's original diagnosis is supplemented by statistics and serial sections.

Average width is from 15 to 17 mm. (text-fig. 10) and average depth 8 mm., thus slightly greater than for S. kelusiana Struve. Most specimens are longer than wide. Internal morphology compares with S. aspera (Schlotheim). Teeth are short, lateral cavities absent. Crura are distal in location and supported by lengthy crural bases. Jugal processes tipped by spinose ends and thin jugal plates. About six spiralial whorls were counted.

The species on the whole is nearly equally convex, though the pedicle valve tends to be deeper. Ribs are finer, not as flattened, and interrupted by more growth lamellae than in *S. kelusiana*. Beaks are not as hypercline. Refer to text-fig. 11.

Material. Total 191 specimens. In the Eifel region, the species is virtually confined to the Hillesheim syncline, but has been reported from the Sötenich syncline (Paulus 1961) and Prüm syncline (Struve 1961).



TEXT-FIG. 11. Transverse serial sections of *Spinatrypa fasciplicata* (Struve 1961). Lahr horizon, upper Eifelian; MTB Dollendorf r55580: h77390. Specimen slightly skew and fractured. BB55227. ×4.

Spinatrypa kelusiana Struve 1956

Plate 78, figs. 1-8

1956 Spinatrypa kelusiana Struve, pp. 383-409, pl. 1-3, figs. 1, 3-24.

1961 Invertrypa kelusiana (Struve); Struve, p. 334, pl. 2, figs. 9-11.

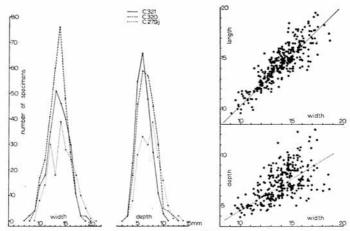
Type locality, type stratum. In Struve 1956.

Range. Müllert horizon, Ahbach beds, upper Eifelian.

Diagnosis, external form. These are given in great detail in the original description. Scatter diagrams and frequency curves confirm Struve's findings about shape variation (text-fig. 12).

Internal structure. Struve (1956) omitted details of internal shell structure except in generalized 'blacked' transverse sections. Slight deviations from the earlier descriptions are noted.

Small, minute, apparently solid deltidial plates are obscured by the ventral umbo (text-figs. 13–14). 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 only two small strands were noted in the notothyrial pit. Crural bases are elongated and crura are bent laterally only very close to the ventral wall. In Struve (1956, p. 396) these extended crural bases are wrongly interpreted to be crura. Crura are long, thin and compact. Jugal plates are thin, subvertical, and rather straight. They



TEXT-FIG. 12. Scatter diagrams and frequency curves of *Spinatrypa kelusiana* Struve 1956. Scatter diagram data from locality C320, MTB Dollendorf r54620: h75700. Frequency curves C279j, r55460: h77380; C321 r54550: h75730. Müllert horizon, upper Eifelian.

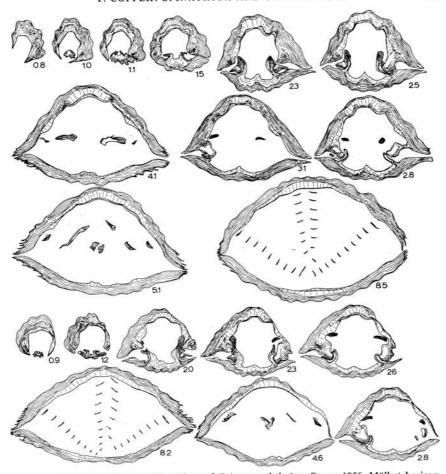
are not connected as claimed by Struve (1956, p. 396, pl. 2, fig. 14a). Flatly conical spires bear nearly ten whorls. No spines were noticed on the coils of the spiralia and none was seen in prepared specimens with the shell wall removed.

Remarks. The ventribiconvex shell and coarse ribs make this species easily identifiable

EXPLANATION OF PLATE 78

Figs. 1–8. Spinatrypa kelusiana Struve 1956. Upper Eifelian, Müllert horizon. 1–2, 6, MTB Dollendorf r55460: h77380 (C279j); 3–4, r55480: h77390 (C279i); 5, 7, 8, r54620: h75700 (C320). 1–2, hypotype BB55183, large shell with planate ribs; 3–4, hypotype BB55177, small, elongate shell with planate ribs; 5, hypotype BB55179, ventral valve showing sturdy spines; 6, hypotype BB55182, brachial valve with attached auloporid coral colony; 7, hypotype BB55180, ventral valve with broken distal spines; 8, hypotype BB55181, ventral valve with few preserved spines.

Figs. 9–10. Spinatrypa aff. globulina n.sp. Upper Eifelian, Müllert horizon. MTB Dollendorf r54550: h75730 (C321). Hypotype BB55184, typical specimen of this rare atrypid associated with S. kelusiana.
Figs. 11–24. Spinatrypa globulina n.sp. Lower Givetian, Neuenbüsch horizon (high Wotan-low Rech). MTB Blankenheim r46410: h90050. 11–12, paratype BB55187, elongate specimen—note mid-ribs; 13–16, paratype BB55185, small shell; 17–20, holotype BB55186, typical mature, rather globose shell; 21–24, paratype BB55188, large shell of maximum width.
All figures × 2.



TEXT-FIGS. 13-14. Transverse serial sections of *Spinatrypa kelusiana* Struve 1956. Müllert horizon, upper Eifelian; MTB Dollendorf r54620: h75700. Top, BB55228; bottom, BB55229. ×4.

in the field. It has not been traced into the overlying, Givetian Wotan horizon but its absence there may be at least partly a feature of biotope development. The Wotan horizon contains beds rich in *Spinatrypina*, which are typical of a Rasenriff environment, and would not be expected to show a *Spinatrypa* fauna (see Copper, 1966). This biofacies change at the Eifelian–Givetian boundary detracts from the certainty that *S. kelusiana* may be confined everywhere to Eifelian rocks.

Material. Total 1,026 specimens. The species is especially abundant in the Hillesheim syncline, but rare elsewhere. Struve (1961, p. 327) has plotted its European distribution.

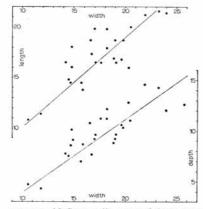
Spinatrypa globulina n. sp.

Plate 78, figs. 11-24

Name. Latin, globus, round ball; ina, diminutive, small. The shell is small and round.

Type locality. Road cut NE. Blankenheim, Blankenheim syncline, MTB Blankenheim r46410: h90050. Type stratum. Neuenbüsch horizon (equivalent to high Wotan-middle Rech), Loogh beds, lower Givetian.

Range. Loogh beds. Rare related specimens found in the upper Eifelian Müllert horizon (Pl. 78, figs. 9–10). Associated fauna. Desquamatia ajugata Copper, Spinocyrtia sp., small horn corals (Lythophyllum?), small athyrids. Fauna dominantly of Spinatrypa and Desquamatia. Source sediment. Greyish-green, pale brown weathering calcareous shales poor in coral fauna.



TEXT-FIG. 15. Scatter diagrams of Spinatrypa globulina n.sp. Loogh beds, lower Givetian; MTB Blankenheim r46410: h90050.

Diagnosis. Small- to medium-sized, rather circular and globose shells with coarse ribs (four to five per 10 mm.) and prominent ventral midrib pair. Beak anacline-hypercline. Growth lamellae wide spaced. Strong anterior fold in late maturity. Internally there are distinct lateral cavities, slender teeth, and hinge plates.

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. 15). Shell outline rounded, rarely elongate transversely or longitudinally (rare shells remind of S. kelusiana, e.g. Plate 78, figs. 10–11). Brachial valve slightly more convex. Beak blunt, broad, anacline to hypercline. Shoulder line weakly indented. Apical angle 125–130 degrees. Area not

well exposed except in smaller specimens, though shells from the Wachtberg horizon of the Sötenich syncline show a somewhat larger area and more anacline beak. Foramen minute, not marked. Deltidial plates usually not observed superficially. Fold narrow, incised, U-shaped. Dorsal apex covered.

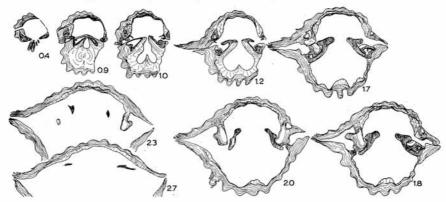
Ribs. Rounded, undulose, and broad ribs cover the shell. At the margin they have a wave length of 2·0-2·5 mm.; most are about 2·5 mm. In appearance the ribs span the variation between S. kelusiana (though lacking the extreme planation of some of those) and S. curvirostra n.sp. (but not as well defined as this form). Ribs show strong row arrangement; fragmented shells or decorticated shells give a prominent nodose appearance. Rare spines were observed: these are thick basally (1·0-1·5 mm. diameter), but their full length is not known. From the elevation of the ribs at each lamellar intersection, the spines appear to be strongly deflected, perhaps from 60 to 90 degrees on the brachial valve. Spines do not reach the abundance or prominence of S. curvirostra n.sp.

Growth lamellae. Growth lamellae are spaced widely at 3.5-4.5 mm. No distal crowding

was noted. Spines appear to begin at 1–2 mm. away from the shell surface. The lamellae are not extended as frilly margins like in *S. curvirostra* n.sp. and some *S. orthoclina* n.sp. but tend to hug the shell surface.

Growth and variation. Smaller specimens are biconvex or ventribiconvex, with orthocline-anacline beaks. Small delthyrium and apical foramen are exposed. Incurvature to the epicline stage is common in maturity. Rare specimens retain an anacline beak.

Variation is rife. Some specimens are similar to S. kelusiana in their elongate shape, ventribiconvexity, and strong mid-rib pair, but already show more 'advanced', undulose



TEXT-FIG. 16. Transverse serial sections of *Spinatrypa globulina* n.sp. Loogh beds, lower Givetian (Neuenbüsch horizon); MTB Blankenheim r46410: h90050. Spiralia missing in this specimen. BB55230. ×4.

rib-structure. Others show strong links to the younger S. curvirostra in beak incurvature, size, and dimensions.

Internal structure. Small deltidial plates are retracted inside the delthyrial cavity, and are hollow. Lateral cavities are clear-cut. Teeth long, flanked by small lateral lobes. A broad notothyrial pit divides thin hinge plates. Inner socket ridges thick. Crural bases and crura small, shortened. Jugal processes and spiralia not observed.

Remarks. Comparisons with S. kelusiana and S. curvirostra have been discussed. S. globulina is almost certainly a forerunner of S. curvirostra.

The species is nearly twice as coarsely ribbed and much larger and globose than *S. aspera* (Schlotheim). With its robust size and shape it is also easy to distinguish from the *S. semiorbis* (Barrande) group of Czechoslovakia, and *S. bifidaeformis* (Chernyshev).

In size, and also nearly in shape, the best comparison is with specimens illustrated by Lyashenko (1959, pl. 6, figs. 8–11) and tentatively identified by that author as *Spinatrypa* ex. gr. *bifidaeformis* (Chernyshev 1887). However, the rib structure of the Russian specimens is already advanced to a *S. curvirostra* type.

Material. The species is rather rare in the Eifel region and cannot be confirmed yet from east of the Rhine. Total 104 specimens, all from the Blankenheim and Sötenich synclines.

Spinatrypa curvirostra n.sp.

Plate 79, figs. 1-13; Plate 80, figs. 1-4

1962 Atrypa aspera (Schlotheim); Jux, pp. 505-13, figs. 1 a-c.

Name. Latin, curvus, curved, bent, arched; rostra, 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 (about equivalent to Felschbach horizon), Cürten beds, lower Givetian. Associated fauna. Spinatrypina soetenica (Struve) which is rare, Yunnanella cf. custos Schmidt, Bornhardtina sp., Stringocephalus sp., rare horn corals. Source sediment. Dark grey to brownish-weathering shales, sometimes almost black shales, with limestone interbeds.

Range. Higher parts of the Rech horizon probably through Cürten beds, lower Givetian.

Diagnosis. Medium- to large-sized, dorsibiconvex, longer than wide shells with coarse, undulose ribs and 3-4 mm.-spaced growth lamellae. Spines are commonly preserved. Beak pointed, hypercline. Anterior fold moderate. Internally, teeth are strongly crenulated with elongate lateral cavities. Jugal plates thick; spiralia with up to fifteen whorls.

External form. Average shell width is about 25 mm., average depth 14 mm., maximum observed width 35 mm. (text-fig. 17). Shells are usually longer than wide, somewhat roundish in outline. Hinge corners not well marked. Anterior fold moderate to deep. The ventral valve, slightly less convex, flattens distally and may even be slightly concave at the margins. The shell is reasonably stable, with the brachial valve nearly twice as deep as the pedicle valve. The beak is sharp, flat, slightly angularly crested, strongly incurved, and pressed against the dorsal umbo. Areas are not visible; the foramen is minute or obscured. The dorsal apex is covered for the first 2 mm.

Ribs. Ribs are gently, evenly undulose, strongly interrupted by growth lamellae. Shallow ribs are nearly ironed out just in front of each lamella, then gradually expand in height

EXPLANATION OF PLATE 79

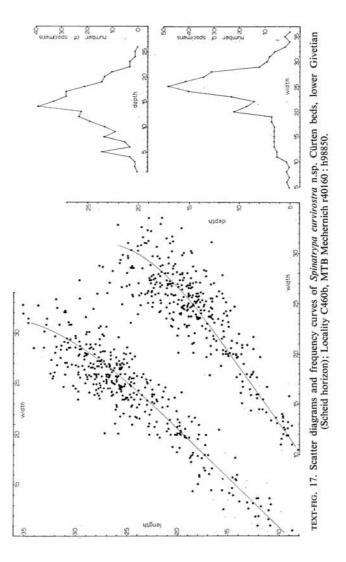
Figs. 1–13. Spinatrypa curvirostra n.sp. Lower Givetian, Scheid horizon (approx. Felschbach). MTB Mechernich r40160: h98850 (C460b). 1–2, paratype BB55194, small shell with prominent lamellar fringes; 3–4, paratype BB55191, elongate immature shell; 5–8, holotype BB55197, mature shell with a few anterior spines partially preserved; 9–10, paratype BB55193, broad-ribbed variety; 11–13, paratype BB55195, large shell showing irregular spine growth.

EXPLANATION OF PLATE 80

Figs. 1-4. Spinatrypa curvirostra n.sp. Lower Givetian, Scheid horizon (approx. Felschbach). MTB Mechernich r40160: h98850 (C460b). 1, paratype BB55192, loose pedicle valve; 2-4, paratype BB55196, wide ribbed shell with short lamellar fringes and spines.

Figs. 5–15. Spinatrypa orthoclina n.sp. Middle Givetian, Rodert beds (approx.). 5–10, 12–14, MTB Mechernich r44000: h00370 (C454); 15, r45020: h00840 (C453); 11, MTB Mülheim/Rhein r76800: h51120 (C228). 5–6, paratype BB55200, immature flattish shell with broken umbo; 7–10, holotype BB55202, immature shell with typical ribs and orthocline beak; 11, paratype BB55198, decorticated pedicle valve exposing ovarian and muscle impressions; 12–14, paratype BB55203, mature broad shell with damaged umbo; 15, paratype BB55201, large shell with tongue (this variety slightly higher stratigraphically).

All figures $\times 2$.



until at maximum amplitude a spine is given off. Some specimens have extremely shallow ribs (Pl. 79, figs. 1–2). Ribs are normally 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 6–7 ribs per 10-mm. arc; at the margins, more than 4 ribs per 10 mm. is rare.

Growth lamellae. Growth lamellae are wide spaced at 3 mm. or more. Distal crowding is rare. Small portions of the lamellae are free and deflected at 10–20 degrees between rib crests; these give the illusion of frilly extensions. Spines are more common in the deeper troughed variety of shell. Distally there may be some disorder of spine array. On the pedicle valve, there are few spines on the apical mid-field. In the trough of the anterior fold, spines are better preserved, thicker and longer, and sub-parallel to the horizontal plane. Apically, short delicate spines about 3–5 mm. long are deflected at 40–60 degrees. The anterior side fields of the pedicle valve are more sparsely spinose with 10–30-degree deflected spines.

On the brachial valve, small areas about the hinge corners show short, laterally inclined spines deflected at 30–50 degrees. Anterior side fields contain spines at 20–40 degrees. The crest and mid-field of the brachial valve is devoid of spines.

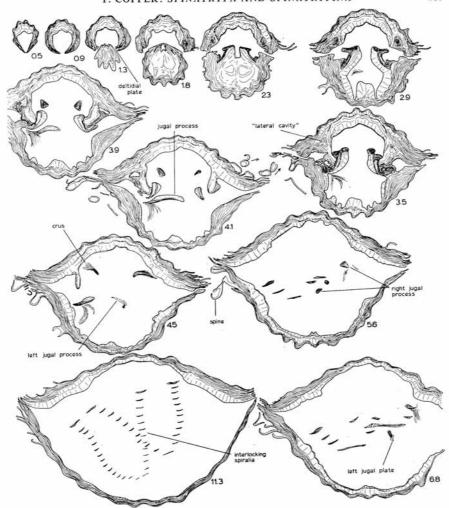
Jux (1962) dealt specifically with specimens of this species from the Sötenich syncline and reconstructed a view showing spines parallel to the commissural plane, and even some forked spines. Unfortunately, none of the nearly 800 specimens here examined, many of them well preserved, showed the spine direction portrayed by Jux (1962, fig. 1c). There is adequate evidence that the spine deflection differs sharply on the same valve and on opposing valves, and that only the spines located in the anterior trough are parallel to the commissural plane. A filter-feeding function appears unlikely.

Growth and variation. About 80 per cent. of the specimens are longer than wide and have well-defined ribs. Less common varieties include wider than long specimens (usually with flattened ribs). Some specimens show a stronger mid-rib pair than others, a feature possibly remaining from S. kelusiana derivatives.

Small shells (immature) are ventribiconvex, with orthocline beak, small foramen and area, and short deltidial plates. Young forms have strongly deflected spines. The foramen is obscured at an early stage.

Internal structure. Deltidial plates are small, retracted, and do not touch in maturity (text-fig. 18). Lateral cavities are rather small, elongated distally. Long teeth show centrally directed main lobes, corrugated and long lateral lobes. A small notothyrial pit contains six to eight strands of a cardinal process also overlapping the hinge plates. Crura distal, strongly feathered. Jugal processes not nodose at tips; jugal plates long and straight.

Remarks. This species has usually gone under the name Spinatrypa longispina (Quenstedt) in the literature of the Eifel region. As such it has been listed by Paulus (1961), Ochs and Wolfart (1961), and Hotz et al. (1955). From examination of topotypical material of S. longispina, which occurs in the Frasnian of the Boulonnais region, France, the Eifel species is seen clearly to be a distinct and separable form. This is brought out in its smaller size, finer ribs, spinose covering, and beak structure. S. longispina under the I.C.Z.N. should properly be referred to its Bouchard in Rigaux (1873) authorship. It was Klähn (1912, p. 31) who invalidly designated Quenstedt as the author though



TEXT-FIG. 18. Transverse serial sections of *Spinatrypa curvirostra* n.sp. Cürten beds, lower Givetian (Scheid horizon); MTB Mechernich r40160: h98850. BB55231. Note that the spines consist of only partially closed tubes. \times 3.

Quenstedt (1871, p. 215, pl. 42, fig. 104) never described the species and did not even figure a complete specimen.

Spinatrypa mosolovica (Lyashenko 1952), re-illustrated in Ljashenko (1959, pl. 4, figs. 1-7), is the most similar foreign species. The Eifel form is only somewhat more

finely ribbed (with less prominent mid-ribs) and more spinose, but very likely almost coeval with the Russian species. The Eifel species may approach specimens called *S. ex. gr. bifidaeformis* (Chernyshev) by Lyashenko (1959, pl. 6, figs. 8–11) in rib structure.

Spinatrypa coriacea Crickmay (1960), from the Hume formation of north-west Canada, is larger, more flatly ribbed, and has a much more anacline beak. This Canadian species is probably of Cürten age or younger. S. hornensis Norris (1964) is biconvex, more deeply and less undulose ribbed, and lacks the epicline beak of Eifel forms.

Material. Total 775 specimens, mainly from the Sötenich syncline, but also from eastern parts of the Dollendorf and Hillesheim synclines. This species is also abundant east of the Rhine, near Hagen.

Spinatrypa orthoclina n.sp.

Plate 80, figs. 5-15

Name. Latin, ortho, straight; clinatus, inclined, leaning. This refers to the orthocline position of the beak in maturity.

Type locality. Road cut Urfey-Keldenich, Sötenich syncline, MTB Mechernich r44000: h00370. Type stratum. Probably equivalent to the quadrigeminum-ramosa horizon (Hotz et al., 1955) of the Rodert beds. Possibly as low as the Binz horizon, Dreimühlen beds. Middle Givetian.

Range. Tentatively assigned as Dreimühlen-Rodert, possibly more restricted or younger. Associated fauna. Large colonies of Hexagonaria, numerous Spinocyrtia sp., trilobites, rare thamnoporids. Source sediment. Greenish-grey calcareous shales weathering pale brown and soft.

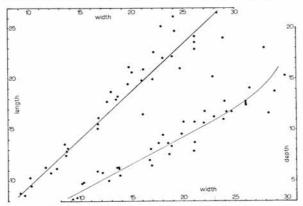
Diagnosis. Medium- to rather large-sized, coarse, and flatly ribbed shells with long projecting, orthocline beak and low anterior fold. Shell relatively flat and round-outlined, biconvex-dorsibiconvex. Internally, large lateral cavities are common, feathery crura characteristic.

External form. Average specimen width is from 23 to 25 mm., rarely up to 35 mm. (text-fig. 19). Both valves are weakly convex. Width exceeds length; width/depth ratio 2·1:1. On the pedicle valve, elevated mid-ribs are lacking though the mid-rib pair may be wider. Side areas are flattish and gently convex. Hinge corners poorly defined. The orthocline beak points out about 2 mm. and exposes a narrow, triangular area with deeply indented shoulder lines. Deltidial plates are small, about 1·5 mm. high and wide. The foramen very commonly expands through the apex, and is about 1 mm. in diameter. Apical angles range through 130–135 degrees. The dorsal apex is incurved and the first 1–1·5 mm. covered. The brachial valve is slightly more convex but rarely globose.

Ribs. Rib wave length is moderate: at 10 mm. from the apex, 5-6 ribs per 10 mm., at 15 mm. from the apex 4-5 ribs per 10 mm. Apical ribs are rather sharp, with steeper crests and deeper troughs. Distal ribs tend to broaden out. Large varieties may have a rib coarseness of 3 per 10 mm. Growth interruptions are marked by expansion and contraction of rib crests. At the ventral apex, a single mid-rib is flanked by 3 side 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 marginal crowding. Spines are rarely preserved: where present, distal spines are near-horizontal, apical spines strongly deflected. Spines are thicker and more common on the brachial valve. The longest observed spines reached 6·5 mm. They were commonly bent or twisted.

Growth and variation. Neanic specimens have a large and expansive interarea, with orthocline, weakly apsacline beak and a flat shell. They are wider than long, the brachial valve is nearly flat, and the pedicle valve slightly convex. Spines are strongly deflected. Mature specimens become more dorsibiconvex, coarse-ribbed (a lack of rib increase), and flattened. The fold is broad and may form a tongue (Pl. 80, fig. 15).



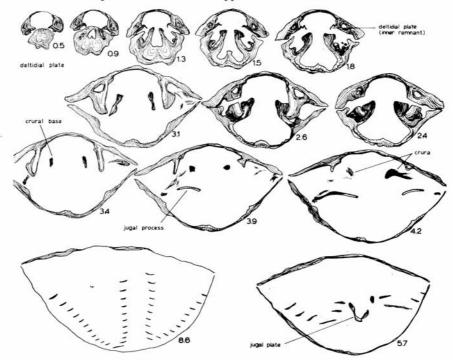
TEXT-FIG. 19. Scatter diagrams of *Spinatrypa orthoclina* n.sp. Data combined from available Urfey valley localities: C454, MTB Mechernich r44000: h00370, C453 r45020: h00840 and BP48, BP143 (see Paulus 1961).

Internal structure. Deltidial plates hollow, with distal inner and outer portions widely apart (text-fig. 20). Inner deltidial margins are crenulated. Lateral cavities are large and oval. Teeth long, with short, thick lateral lobes. Notothyrial pit wide and broad. Cardinal process small, apparently amorphous. Hinge plates long, subvertical, evenly thickened. Socket plates bulky, crural bases elevated, crura elaborately feathered. Jugal processes are thin, weakly convex. Jugal plates long, thick, and inwardly directed. Spiralia flattened, with about ten or twelve whorls.

Remarks. There are numerous differences with S. curvirostra n.sp. which is an older atrypid. S. orthoclina is planar, with more deeply incised rib and lamellar structure, a strong, pointed and orthocline beak, and lacks a marked anterior fold. Internally, S. orthoclina is marked by large lateral cavities, long slender teeth and highly feathered crura, but particularly by its prominent hollow deltidial plates.

In 1931 Wehrli described Atrypa aspera var. paffrathi from the Paffrath syncline east of the Rhine and used material collected by a Revd. Wendland. Illustrations of this atrypid bear some resemblance to coarsely ribbed varieties of S. orthoclina though the poor material and scant description make exact comparison unreliable. An attempt was made to collect topotypic material but this was unsuccessful. Jux (personal communication) also made a fruitless attempt to collect material at the site mentioned by Wehrli and concluded that an error had been made in the source locality designation, and that the atrypids probably came from Hand in the Paffrath syncline (where S. orthoclina is

common). However, this seems unlikely for several reasons. Wehrli (1931, p. 429) mentioned that specimens were imbedded in a fine-grained dolomite, a rock type absent at Hand. Moreover, both Wehrli and Wendland later tried to find additional specimens at the locality they so precisely defined, and met with no success. It seems possible then that this atrypid was of a very local, pocket-type occurrence, a feature not uncommon for other brachiopod occurrences in the upper Givetian of this area.



TEXT-FIG. 20. Transverse serial sections of *Spinatrypa orthoclina* n.sp. Rodert beds (approximately), middle Givetian; MTB Mechernich r44000: h00370. BB55232. ×3.

There is a likelihood that the *Spinatrypa squamosa* (Sowerby 1840) of the upper Givetian in England is conspecific with Wehrli's variety in that both are of nearly the same size and show strong rib planation. The Sowerby species is to be re-examined.

Material. Common to the middle Givetian shales east of the Rhine, but in the Eifel region can only be verified from the Sötenich syncline. Total 253 specimens.

Genus Spinatrypina Rzhonsnitskaya 1964

Type species. Spinatrypina margaritoides Rzhonsnitskaya 1964, pp. 101–3, pl. 1, figs. 1–8. Range. Lower to Upper Devonian (Gedinnian–Frasnian).

Distribution. World-wide. Acme. Givetian-Frasnian.

Diagnosis. Small- to medium-sized, ventribiconvex-dorsibiconvex atrypids with orthocline beaks, small areas, and disjunct deltidial plates in a small delthyrium. Ribs are tubular-imbricate, deep-troughed, and embryonically spinescent. Frills lacking. Internally, pedicle layers are thin. Teeth have small to large lateral cavities. Jugal processes show short, stumpy jugal plates without spinosity or nodosity. Spiralia rarely preserved.

Remarks. The relationship of Spinatrypina to Spinatrypa is comparable to that of Desquamatia-Atrypa. Spinatrypina and Desquamatia show a parallel development of deeper, more tubular ribs and expansion of the interarea and deltidial plates, and internally an enlargement of dental nuclei into lateral cavities.

Spinatrypina, with its tubular-imbricate ribs and prominent beak and interarea, is readily separable from Spinatrypa. It also inhabits a different environment, being restricted to thamnoporid or disphyllid coral associates in a Rasenriff biotope. Rare occurrences of Spinatrypa in this environment are recorded (e.g. S. aspera meridiana n.ssp.), and these can result in deceptive homoemorphy. Spinatrypina itself does not occur outside a Rasenriff environment.

Spinatrypina demissa n.sp.

Plate 81, figs. 1-12

Name. Latin, demissus, low-lying, low down. This species is the oldest member of the genus in the Eifel synclines, occurring towards the base of the Eifelian sequence.

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, approximately equivalent to the Schleit horizon, Nohn beds, lower Eifelian. Associated fauna. See Paulus (ibid.). The new species is probably described as Atrypa reticularis by Paulus. Gruenewaldtia sp., and thamnoporid corals are abundant. Source sediment. Brownish-green, chippy bioclastic calcareous shales rich in broken coral debris and some crinoidal fragments.

Diagnosis. Small, flat, biconvex shells with fine ribs (sixteen to eighteen per 10 mm.), interrupted by 2 mm. or more spaced lamellae. Margins are adpressed. A weak fold flexes the commissure. The beak is small, angular, and heads a narrow interarea. Shoulders are round-edged, shoulder lines indented. Shells are roundish, wider than long, with the pedicle valve slightly more covex. Internally (text-figs. 21–22), thin teeth are built about relatively large lateral cavities. Cardinal process thick and bushy. Columnar shell layer is thin.

Remarks. This species is not abundant in the Eifel synclines except locally, e.g. the type locality. This is probably because of the general absence of thamnoporid thicket reefs in lower Eifelian time in the Eifel. It can be distinguished from younger species by its fine ribs, flatness and wideness, and pointed beak. The nature of the rib-lamellae structure causes a greater affinity with some specimens of the Atrypa type than Spinatrypa type. The growth lamellae in this form are very prominent and even slightly frilly and free from the surface.

Biernat (1964, p. 317, pl. 7, figs. 1-6) described a somewhat comparable species

Desquamatia varistriata which possibly also can be referred to Spinatrypina, rather than Desquamatia. There are, in the Eifel region, older Devonian species of Desquamatia which do not show the trigeneric convergence (Atrypa, Desquamatia, and Spinatrypa) claimed by Biernat for the Polish species. A clear example is Desquamatia ovata Copper.

In its rib structure and general shape *Spinatrypina demissa* also is reminiscent of the genus *Kerpina* but internally shows none of the morphological peculiarities of deltidial plates, collars, and solid teeth of that later Eifelian atrypid.

Material. Total 162 specimens. The Sötenich syncline, Ahrdorf syncline, and Hillesheim syncline (central and eastern Eifel) have provided the bulk of material.



TEXT-FIGS. 21–22. Random transverse umbonal sections of two specimens of *Spinatrypina demissa* n.sp. About Schleit horizon (Urft horizon, Paulus 1959), lower Eifelian; MTB Blankenheim r44690: h94770. Left BB55233; right, BB55234. ×4.

Spinatrypina fabaca n.sp.

Plate 81, figs. 13-22

Name. Latin, faba, bean; acus, pertaining to. These small atrypids distantly resemble beans at rich localities.

Type locality. Exposure on the north flank of Leukersberg in the town of Rohr, Rohr syncline, MTB Aremberg r52360: h91090. Locality temporarily exposed during construction work, 1963. Type stratum. Directly above the Rohr Hexagonaria horizon, even imbedded among large coral colonies (equivalent to Rechert horizon. Note that previously the Rohr horizon has been correlated with the Giesdorf horizon), Junkerberg beds, middle Eifelian.

Range. Junkerberg beds. Associated fauna. Colonies of Hexagonaria, thamnoporids, rare Desquamatia sp., small athyrids. Source sediment. Light brown or yellowish calcareous shales.

EXPLANATION OF PLATE 81

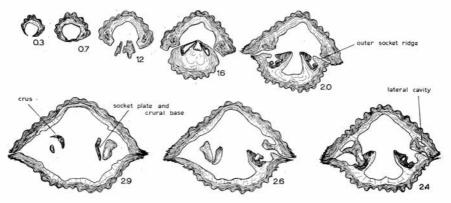
Figs. 1–12. Spinatrypina demissa n.sp. Lower Eifelian, Weilersbach–Schleit horizons. 1–4, MTB Blankenheim r44690: h94770 (C451); 5–8, MTB Dollendorf r56950–7020: h78210–50 (Fp1262); 9–12, MTB Dollendorf r56900: h78130. 1–2, holotype BB55204, damaged specimen from type locality; 3–4, paratype BB55207, larger damaged shell; 5–8, paratype PC136, partly damaged shell, displaying tubular-imbricate ribbing; 9–12, paratype BB55206, Spirorbis attached to normal shell.

Figs. 13–22. Spinatrypina fabaca n.sp. Middle Eifelian, about Rechert horizon. MTB Aremberg r52360: h91090 (C340). 13–15, holotype BB55208, well-preserved mature form; 16–19, paratype BB55209, long and globose shell with anacline beak; 20–22, paratype BB55210, mature shell with damaged umbo.

Figs. 23–28. Spinatrypina wotanica (Struve 1964). Lower Givetian, Wotan-Rech horizons, 23–24, MTB Dollendorf r52550–620: h76745–800 (St739); 25–28, r54855–730: h77060–310 (St805). 23–24, hypotype PC143, coarsely ribbed specimen of Wotan age; 25–28, hypotype PC144, finely ribbed shell of Rech age.

All figures $\times 2$.

Diagnosis. Small, less than 20 mm. wide, ventribiconvex-biconvex globose shells with a weak anterior fold. Beaks pointed, orthocline: foramen commonly expanded, with small anterior rim. Areal edges rounded. Shell roundish, longer than wide. Pedicle valve swollen, slightly more convex or equally convex than the opposite valve. Ribs spaced at ten per 10 mm., constant. Growth lamellae at 1–1·5 mm., crowded anteriorly. Internally (text-fig. 23) the lateral cavity is elongated, teeth long, sub-vertical with minor lateral lobe. Crura thick. Spiralia and jugal processes still unknown.



TEXT-FIG. 23. Transverse serial sections of *Spinatrypina fabaca* n.sp. About Rechert horizon, middle Eifelian; MTB Aremberg r52360: h91090. BB55235. \times 4.

Remarks. The species can be distinguished by its shape, outline, and rib size from the older Spinatrypina demissa and the younger S. wotanica.

The most similar morphology belongs to *Spinatrypina sinensis* (Kayser 1883) from Ta-kwan, China. Kayser's collection of this species, which is stored in the Paläontologisches Museum der Humboldt Universität, Berlin, was examined. The Chinese atrypid is larger, more distinctly ventribiconvex, almost planoconvex, and has a smaller, less distinctive beak and area.

Spinatrypina bodini (Mansuy 1912) from North Vietnam, is larger and more coarsely ribbed than the Eifel species.

Material. Total 404 specimens. The species is common in the Rohr, Hillesheim synclines but rare elsewhere in the Eifel.

Spinatrypina wotanica (Struve 1964)

Plate 82, figs. 23-28; Plate 83, figs. 1-4

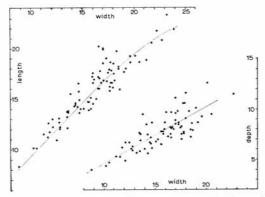
1964 Spinatrypa aspera wotanica Struve, pp. 529-30, figs. 2a-c.

Diagnosis. Refer to Struve 1964.

Remarks. The structure and form of the ribs and growth lamellae of this atrypid is typical of Spinatrypina. Ribs are imbricate-tubular and the area is well defined and sharp.

Resemblances to Spinatrypa aspera are apparently superficial but can give rise to confusion. Dimensions are summarized in text-fig. 24.

Material. Total 442 specimens. This species is only known abundantly from the Hillesheim syncline, where it is found in beds showing current-oriented lumachelles (see Pl. 83, figs. 9-10). Rarer occurrences are from the Blankenheim syncline.



TEXT-FIG. 24. Scatter diagrams of Spinatrypina wotanica (Struve 1964). Locality St739, Rechhorizon, lower Givetian; MTB Dollendorf r52550: h76745, r52620: h76800.

EXPLANATION OF PLATE 82

Figs. 1–4. Spinatrypina wotanica (Struve 1964). Lower Givetian, Rech horizon. MTB Dollendorf r54815: h77240 (St804). Hypotype PC142, smaller immature shell (compare figs. 13–20). Figs. 5–12. Spinatrypina soetenica (Struve 1964). Lower Givetian, Felschbach horizon. MTB

Mechernich r40160: h98860 (C460a). 5-8, hypotype BB55217, typical immature form; 9-12, hypotype BB55218, adult shell.

Figs. 13-20. Spinatrypina cf. soetenica (Struve 1964). Lower Givetian, Felschbach horizon. MTB Mechernich r40160: h98860 (C460a—accompanying typical S. soetenica). 13-16, hypotype BB55215, flattish immature shell; 17-20, hypotype BB55216, mature shell of ribbing intermediate to Spinatrypa.

Figs. 21–28. Spinatrypina girzenensis n.sp. Middle Givetian, about Dreimühlen beds. MTB Mechernich r41650: h99220 (C459b). 21–24, paratype BB55220, small specimen with deformed beak; 25–28, holotype BB55219, specimen slightly smaller than average mature size.

All figures ×2 unless otherwise stated.

EXPLANATION OF PLATE 83

Figs. 1-8. Spinatrypina girzenensis n.sp. Middle Givetian, about Dreimühlen beds. MTB Mechernich r41650: h99220 (C459b). 1-4, paratype BB55221, rare large variety showing trend towards S. tubaecostata (Paeckelmann 1913); 5-8, paratype BB55222, globose and wide variety.

Figs. 9-10. Spinatrypina wotanica (Struve 1964). Lower Givetian, Rech horizon, Loogh beds, MTB Dollendorf r54550: h77780. BB55287. 9, upper side of a 3.5 cm.-thick limestone slab with a coquina of loose pedicle and brachial valves, washed into a convex-side up stable position. Note a few small athyrid brachiopods, crinoid ossicles, and fenestellate bryozoans; 10, underside of the same slab with concave side of the shells oriented upwards. $\times 1$.

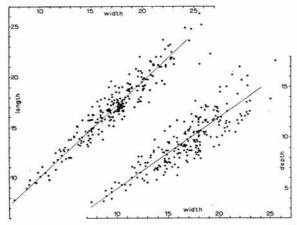
All figures × 2 unless otherwise stated.

Spinatrypina soetenica (Struve 1964)

Plate 82, figs. 5-12

1964 Spinatrypa aspera soetenica Struve, pp. 530-1, fig. 3.

Remarks. As for the older species wotanica, this atrypid has only a distant superficial resemblance to the Spinatrypa aspera (Schlotheim) group. At the Wachtberg quarry



TEXT-FIG. 25. Scatter diagrams of Spinatrypina soetenica (Struve 1964). Locality C460a, lower Scheid horizon, Cürten beds, lower Givetian; MTB Mechernich r40160: h98860.

where it was found in great numbers a crude separation into a larger, coarsely ribbed type and a smaller, finely ribbed type is possible. But the two varieties are presently still classed under the same name. The more coarsely ribbed form is possibly a remnant of the older *S. wotanica* (Struve). Statistically, the two types do not appear separable (text-fig. 25).

Internally (text-fig. 26: a finely ribbed, holotypic specimen), deltidial plates are small, hollow. Teeth long, lateral cavities elongated. Jugal processes not observed. Spiralia extremely scarce, and often dwarfed (e.g. text-fig. 26, section 6·2 mm.). Another specimen showed two interlocking, upside-down spiralia (text-fig. 27).

Material. Total 1,059 specimens. This species is common in the northern Eifel and east of the Rhine, but very rare in the south Eifel.

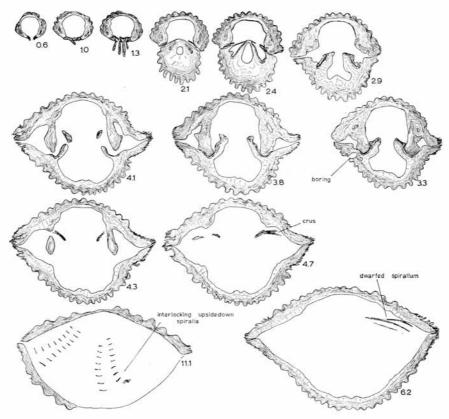
Spinatrypina girzenensis n.sp.

Plate 82, figs. 21-28; Plate 83, figs. 1-8

Name. After Girzenberg, a small hill about 100 m. south-west of the type locality in the Sötenich syncline.

Type locality. Road cut 1 km. south of Keldenich, Sötenich syncline, MTB Mechernich r41660: h99230. Type stratum. Shaly interbeds between Hexagonaria-rich horizons, directly overlain by coarse-grained

dolomites, probably Dreimühlen beds, middle Givetian (Binz horizon?). Associated fauna. Small athyrids, spiriferids, numerous Thamnopora, Aulocystis, and Roemeria tabulate corals. Also Hexagonaria. Source sediment. Yellowish-brown calcareous shales with lumachelle heaps of brachiopods and corals (no horn corals).



TEXT-FIGS. 26–27. Transverse serial sections of *Spinatrypina soetenica* (Struve 1964). Scheid horizon, Cürten beds, lower Givetian; MTB Mechernich r40160: h98860. One completely sectioned specimen (0·6–6·2 mm.) with a dwarfed, three-whorl spiralium, BB55236. Single section (11·1 mm.) of specimen with upside-down interlocked spiralia, BB55237. ×3.

Diagnosis. Small- to medium-sized atrypids with rather coarse ribs spaced at seven to nine per 10 mm., round-outlined, frequently globose. Interareas relatively large, round-edged; beaks blunt, orthocline, strongly jutting. Growth lamellae hug the shell and are barely deflected; imbrication not noticeable. Anterior folds weak. Shells wider than long, equally convex.

Remarks. A few specimens show affinities with the Spinatrypina tubaecostata (Paeckelmann)-S. explanata (Schlotheim) group in being much wider than long, rather flat, and in having larger areas (e.g. Pl. 83, figs. 1-4).

This species is distinct from S. soetenica in its much coarser ribbing, its convexity, and shell-hugging growth lamellae with lack of imbrication.

Material. The species is confined to the northern Eifel and east of the Rhine in its presently known distribution. Total 1,047 specimens.

CONCLUSION

A great deal of systematic work remains to be done to refine the present species for the purpose of more detailed biostratigraphy. Internal structures need to be more thoroughly examined and interrelationships of Spinatrypa and Spinatrypina clarified. It is questionable if Spinatrypina represents an off-shoot from a Spinatrypa stock. It may well have been an independent lineage showing convergence towards characteristics of spinose atrypids. The earliest Spinatrypina may well have been derived from a form like Atrypa reticularis var. lonsdalei Alexander (1949, pl. 9, figs. 3 a-d). Spinatrypa, on the other hand, was already well established in the Silurian as the illustrations of Poulsen (1943, pl. 2, fig. 14), Chapman (1913, pl. 11, fig. 15), and Davidson (1882, p. 112) show. Alexander's Atrypa reticularis var. davidsoni (1949, pl. 10, figs. 1a-d) probably also can be referred to Spinatrypa.

A number of Devonian European nomina dubia remain to be investigated. Among these are Atrypa squamosa Sowerby 1840, Terebratula insperata Phillips 1841, Atrypa trigonella Davidson 1884, Atrypa reticularis var. sagittata Maurer 1885, and Atrypa aspera var. paffrathi Wehrli 1931, all of which may probably be grouped under Spinatrypa.

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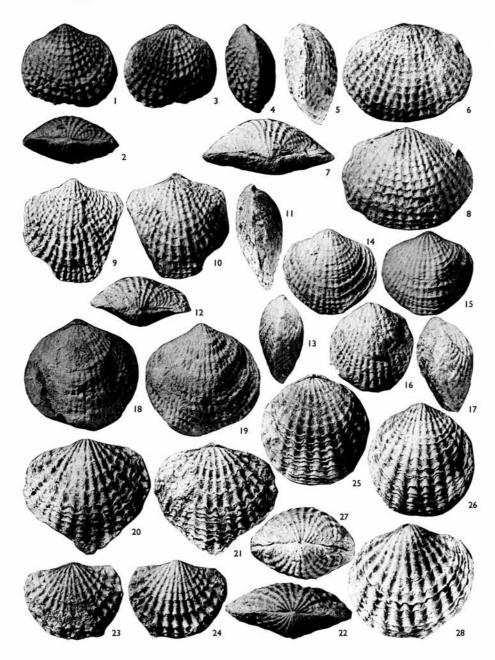
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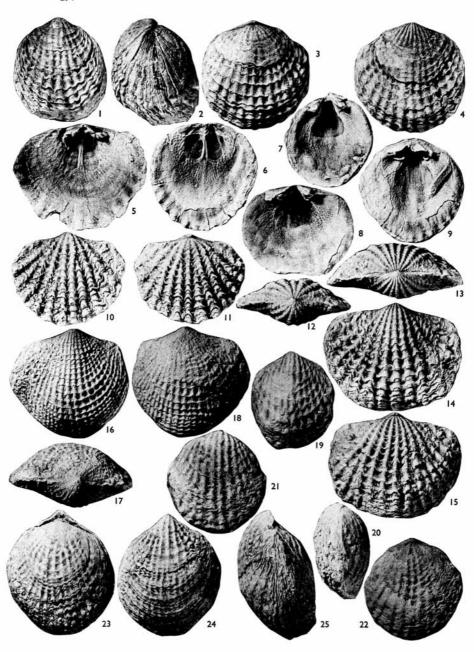
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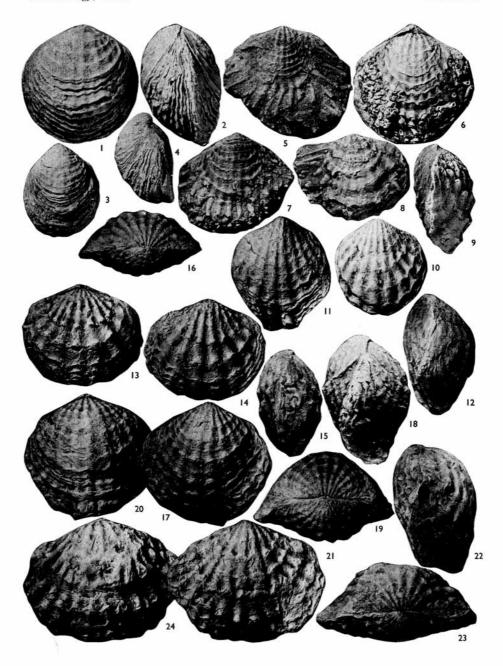
COPPER, Spinatrypa from the German Devonian

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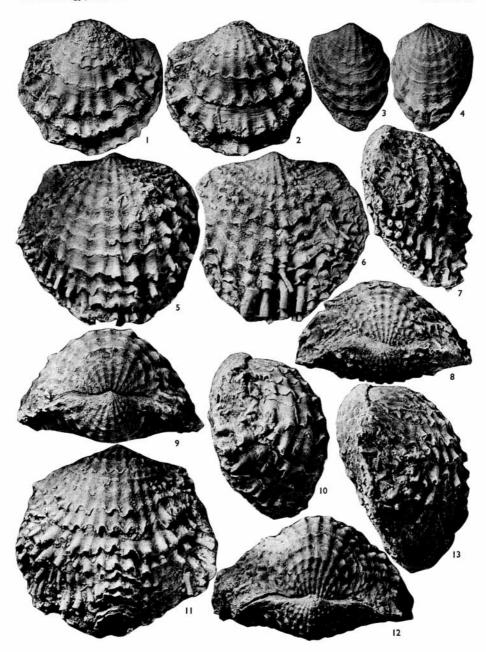
COPPER, Spinatrypa from the German Devonian

PLATE 78



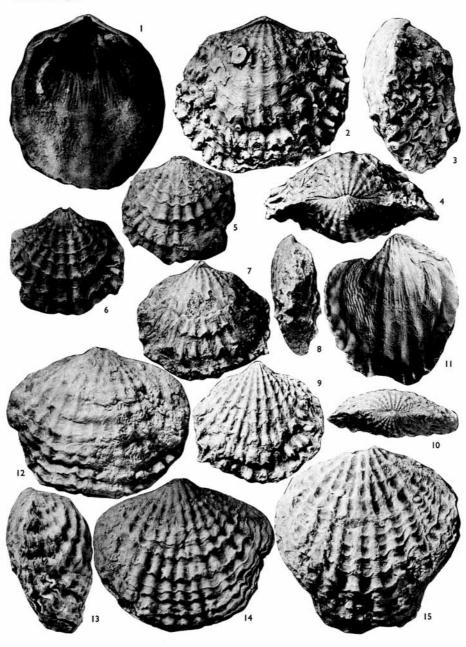
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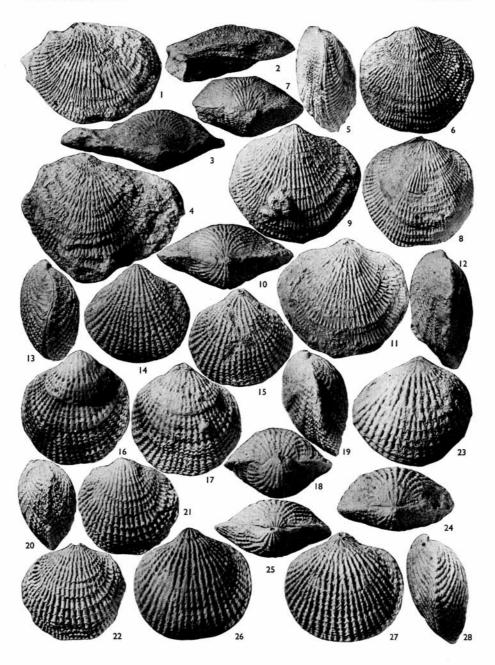


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PLATE 80

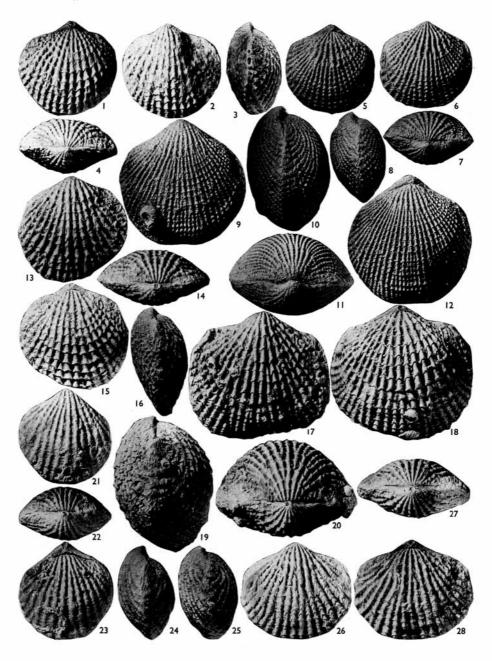


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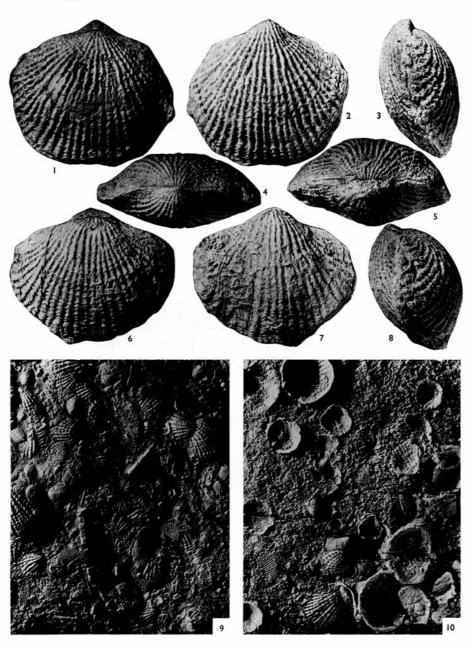
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PLATE 82



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