

A MIDDLE DEVONIAN ATRYPID BRACHIOPOD FAUNA FROM THE CANTABRIAN MOUNTAINS, NORTHWESTERN SPAIN, AND ITS STRATIGRAPHIC SIGNIFICANCE

BY

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ABSTRACT

This paper records for the first time a rich atrypid brachiopod fauna from the Middle Devonian of the Cantabrian Mountains, Spain. A comparison of the Spanish atrypid fauna with that of Germany reveals a close similarity between the two. Even though the species are not identical, yet a comparison and stratigraphic evaluation has been made on the basis of external shape of the shells, ornamentation, etc. It is believed that the development of the Spanish species has been endemic or that the Spanish Middle Devonian sea was supplied with species immigrating from some place other than central Europe. On the basis of the distinct recession of *Atrypa* and the first appearance of the coarse ribbed species of *Spinatrypa* (*Spinatrypa*), a tentative Eifelian/Givetian boundary has been sought in the Portilla Formation of the Alba syncline between the rivers Luna and Bernesga, Prov. León, N.W. Spain. It is hoped that these findings would be correlated with other areas as well in the northwestern Cantabrian Mountains.

The described and figured new species *cantabrica* is the third species of *Spinatrypa* (*Invertrypa*) hitherto known. Questions of its generic and subgeneric assignment and of the taxonomy and morphology of *Spinatrypa* (*Invertrypa*) are discussed. *Sp. (Inv.) cantabrica* (as well as *Sp. (Inv.) fasciplicata* and *Sp. (Inv.) kelusiana*) seems to be an important time marker of late Eifelian. By means of these three species, this time level and the geographic range of *Spinatrypa* (*Invertrypa*) can be traced over a distance of about 2200 km, from Poland over Germany, Belgium, and northern France to Spain.

INTRODUCTION

Field work carried out by the second author in the Portilla Formation (Comte, 1959) of the Alba syncline between the rivers Luna and Bernesga in the province of León, northwestern Spain (Figs. 1 & 2) has revealed

tian University, Sudbury, Canada) during a brief visit to Leiden in September, 1968. Earlier Copper had accompanied the second author on a short field trip. This identification, though rather general and provisional, already showed the stratigraphic importance

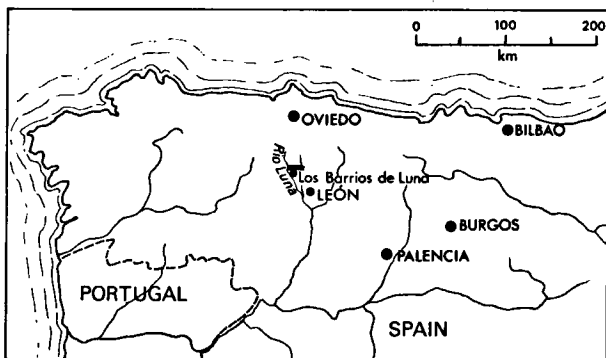


Fig. 1. Situation map: the solid rectangle marks the investigated area.

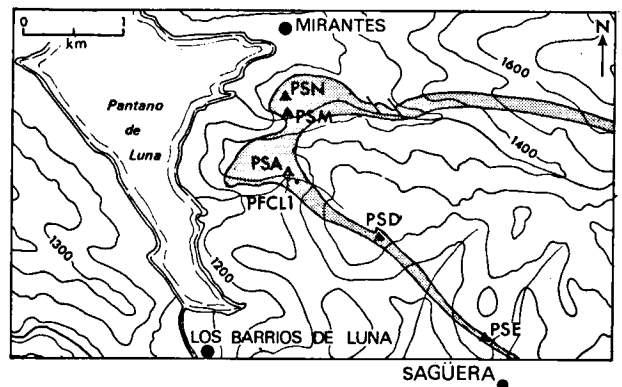


Fig. 2. Westerly part of the outcrop of the Portilla Formation (after van Staaldunin, 1967): solid triangles mark the location of measured sections and the small solid circle fossil collecting locality number 1 (PFCL 1)

an interesting fauna of atrypid brachiopods of Middle Devonian age. A detailed stratigraphic study of this formation has been made by the second author as part of a larger research project in the Cantabrian Palaeozoic under the direction of Prof. Dr. A. Brouwer (Mohanti, in prep.) The collection of atrypid brachiopods was initially identified by Paul Copper (Lauren-

of these atrypids. Later, during the second author's stay in Frankfurt/Main (Western Germany), the collection was examined by the first author who checked the earlier identifications and added some new determinations. The first author contributed the systematic

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part and the second author the stratigraphic part of this paper. Both authors have discussed the stratigraphic importance of the palaeontologic results.

Lithostratigraphic terms (formation and member) have been used in the present paper in accordance both with the practice followed in the Cantabrian Devonian by the Leiden group (see e.g. Brouwer, 1968) and with the proposals of the International subcommission on stratigraphic nomenclature (Hedberg, 1961).

#### ACKNOWLEDGEMENTS

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#### STRATIGRAPHY

The Portilla Formation in the Alba syncline is essentially a carbonate succession with several levels of more argillaceous admixture. The formation thickens as much as up to 246 m at the nose of the syncline whereas eastwards it gradually thins to about 20 m along the northern and southern flanks. The formation is divided into three members informally referred to as A, B, and C. The three members are complete between sections PSD and PSN whereas on either side only member A and the basal few metres of member B are present (Fig. 3). Member A is separated from member

B by a sharp surface of discontinuity marked by lithological and palaeontological changes and local truncation of beds. No sharp boundary is present between member B and member C.

The basal part of member A is generally irregularly bedded and grades gradually into the more massive-bedded light grey limestone of the upper part. The faunal constituents are mostly massive tabulate corals, solitary rugose corals, and stromatoporoids which are associated with echinodermal fragments, brachiopods, bryozoans, trilobites, and gastropods in varying amounts. The basal part of member B is generally formed by fossiliferous calcareous silty shales and argillaceous limestones containing predominantly platy and ramose tabulate corals and brachiopods. It forms the best horizon for brachiopod collecting in the area. The higher part of member B consists of massive to well-bedded limestone containing predominantly massive tabulate corals, compound rugose corals, and stromatoporoids. In a distinct part of the area this alternates with reddish and/or greenish argillaceous limestone beds packed up with the ramose tabulate coral *Thamnopora* and the platy ones *Coenites* and *Alveolites*. Member C is essentially a massive-bedded limestone with a coral-stromatoporoid fauna. The biofacies characters of the Portilla Formation appear to be closely comparable to "Knollen-Block-Riff", "Rasen-Riff und Crinoiden-Wälder" and "Rüben-Riff" facies as described by Struve (1961a, 1963a) in the case of the Middle Devonian biostromal "reefs" in the Eifel region in Germany. The depositional facies has been broadly interpreted as a "reef" facies with developments of "lagoonal" facies, biostromal "reef" barrier facies etc. Slow and prolonged differential subsidence of the depositional basin with possible emergence of marginal areas is believed to be one of the main factors in controlling the thickness and facies changes in the Portilla Formation of the Alba syncline.

#### PRINCIPAL ATRYPID TAXA

The atrypid brachiopods in the area have distinct lithologic-faunal associations and are more common in the basal part of member A and the basal part of member B where they are represented by several genera and subgenera. Towards the higher parts of member B and in member C they are represented only by a few genera and species.

The following taxa are recognized in the collection:

*Atrypa* s.l. sp.

*Atrypa* (*Kyrtatrypa*?) sp.

*Atrypa* (*Planatrypa*) sp. aff. *squamifera* (Schnur, 1853)

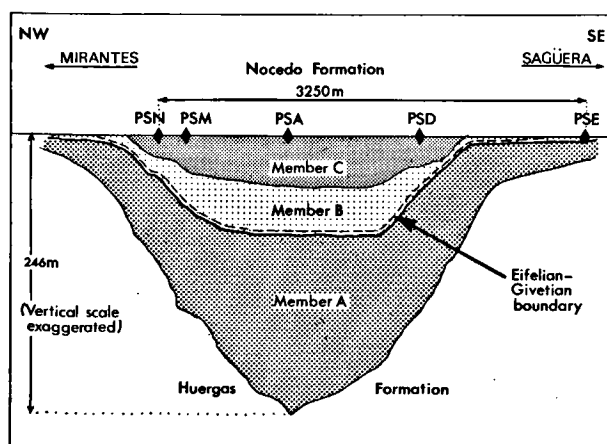


Fig. 3. Schematic stratigraphic cross-section of the Portilla Formation

- Atrypa (Planatrypa?)* sp.  
*Atryparia* sp.  
*Atryparia?* sp.  
*Desquamatia (Synatrypa)* sp. cf. *subzonata* Biernat, 1964  
*Desquamatia (Synatrypa)* sp. cf. *microzonata* Struve, 1966  
*Desquamatia (Synatrypa)* sp. (unusual type, differing by large size)  
*Desquamatia (Variatrypa)* sp.  
*Desquamatia* s.l. sp.  
*Carinatina?* sp. cf. *signifera* (Schnur, 1853)  
*Carinatina?* sp.  
*Gruenewaldtia?* sp.  
*Spinatrypa (Invertrypa) cantabrica* n. sp.  
*Spinatrypa (Isospinatrypa)* sp. cf. *wotanica* Struve, 1964  
*Spinatrypa (Isospinatrypa)* sp. (similar to Upper Givetian forms in Germany)  
*Spinatrypa (Spinatrypa)* sp. (coarse-ribbed specimens; similar to Middle and Upper Givetian forms in Germany)  
*Spinatrypa?* sp.  
*Spinatrypina (Exatrypa)* gr. *explanata* (Schlotheim, 1820)  
*Spinatrypina* sp. cf. *fabaca* Copper, 1967  
*Spinatrypina* sp.  
*Spinatrypina?* sp.

#### RECORD OF A NEW SPECIES OF SPINATRYPA (INVERTRYPA)

With the new species *cantabrica* the third species of *Spinatrypa (Invertrypa)* is introduced. The fortunate discovery from the Cantabrian Mts. is of great importance for the concept of the subgenus. Therefore, revised diagnoses of the three subgenera of *Spinatrypa* are given, and several taxonomic problems of the subgenus *Sp. (Invertrypa)* are discussed. The diagnosis, description, and discussion of *Sp. (Inv.) cantabrica* are elucidated by revised, coordinated diagnoses of *Sp. (Inv.) kelusiana* and *Sp. (Inv.) fasciplicata*.

The new species is also of great stratigraphic importance: As in Poland, Germany, Belgium, and northern France, the subgenus *Sp. (Invertrypa)* seems to mark the late Eifelian in the Cantabrian Mountains, too.

Genus SPINATRYPA Stainbrook, 1951

*Type species: Atrypa hystrix* var. *occidentalis* Hall, 1858.

*Diagnosis:* See Copper, 1967c, p. 494–495.

*Subgenera: Sp. (Spinatrypa)* Stainbrook, 1951, *Sp. (Invertrypa)* Struve, 1961, and *Sp. (Isospinatrypa)* Struve, 1966.

Subgenus SPINATRYPA (SPINATRYPA)  
 Stainbrook, 1951

*Type species: Atrypa hystrix* var. *occidentalis* Hall, 1858.

*Diagnosis:* Species of *Spinatrypa* with medium sized to large, pronouncedly dorsi-biconvex to ventri-resupinate (convexo-concave) shell: pedicle valve with moderately to flatly convex juvenile part and flattened to moderately concave post-juvenile part; brachial valve strongly convex, moderately to much higher than pedicle valve. Ridge-tile sculpture coarse to very coarse, several species with tendency towards obsolescence of sculpture or towards isolation of the individual plications of the ribs.

*Remarks:* The main area of distribution of *Sp. (Spinatrypa)* seems to be North America. In Europe the subgenus is by far less common; characteristically coarsely sculptured representatives as for instance *Sp. (Sp.) longispina* (Bouchard in Rigaux, 1873), *Sp. (Sp.) paffrathi* (Wehrli, 1931), *Sp. (Sp.) curvirostra* Copper, 1967, *Sp. (Sp.) orthoclina* Copper, 1967, and probably also *Sp. (Sp.?) globulina* Copper, 1967 are strongly indicative of Givetian or Frasnian age.

Subgenus SPINATRYPA (ISOSPINATRYPA)  
 Struve, 1966

*Type species: Anomites Terebratulites asper* Schlotheim, 1813.

1966 *Spinatrypa (Isospinatrypa)* Struve, p. 155.

*Diagnosis:* Species of *Spinatrypa* with small to medium sized, aequi-biconvex to somewhat dorsi-biconvex shell: pedicle valve roundish roof-shaped with moderately convex to slightly concave lateral slopes which do not become resupinate marginally (resupination may be simulated by impact); brachial valve commonly moderately arched only (except in globose, extremely gerontic, and pathologic specimens). Ridge-tile sculpture relatively delicate as compared with *Sp. (Spinatrypa)* species; no pronounced tendency towards obsolescence of sculpture.

*Remarks:* Apparently the bulk of the European *Spinatrypa* species belongs to *Sp. (Isospinatrypa)*, for instance *Sp. (Isosp.) aspera aspera* (Schlotheim, 1813), *Sp. (Isosp.) aspera meridiana* Copper, 1967, *Sp. (Isosp.)*

*asperoides* Biernat, 1964, *Sp. (Isosp.) variaspina* Copper, 1967, *Sp. (Isosp.) orthoclina* Copper, 1967, and several others. The generic assignment is obscured by homeomorphy with species of *Spinatrypina* Ržonsnickaja, 1964. Especially the spines of *Spinatrypa* shells are preserved rarely. This is the case in the species *wotanica* Struve, 1964 which is referred to *Spinatrypina* by Copper (1967c, p. 517–518). However, few exceptionally well preserved specimens show well developed spines so that either *wotanica* belongs to *Sp. (Isospinatrypa)* yet or the generic diagnosis of *Spinatrypina* has to be changed.

Subgenus SPINATRYPA (INVERTRYPA)  
Struve, 1961

*Type species: Spinatrypa kelusiana* Struve, 1956.<sup>1</sup>

- 1956 Formen um *Spinatrypa kelusiana*. – Struve, p. 384–385.
- \* 1961b *Invertrypa*. – Struve, p. 324, 325, 334.
- ± 1964 *Spinatrypa*. – Biernat, p. 306, 315 (as far as the species *kelusiana* and *fasciplicata* are concerned).
- 1965 *Invertrypa*. – Boucot, Johnson & Staton, p. 639–640.
- 1966 *Spinatrypa (Invertrypa)* Struve, p. 153–155.
- ± 1967c *Spinatrypa*. – Copper, p. 495 (as far as the species *kelusiana* and *fasciplicata* are concerned).

*Diagnosis* (see: Struve, 1956, p. 384–385; Struve, 1961b, p. 334; Boucot, Johnson & Staton, 1965, p. 639–640; Struve, 1966, p. 155): Species of *Spinatrypa* with small or, at most, medium-sized, markedly to extremely ventri-biconvex or plano-convex, exceptionally faintly dorsi-resupinate (concavo-convex) shell (resupination may be simulated by impact). Ridge-tile sculpture relatively delicate as compared with *Sp. (Spinatrypa)*; faint to distinct reduction of ribs or isolation of the individual plications, proceeding from the posterolateral parts of the shell towards the central field.

*Discussion*

Though the bulk of species of the Atrypidae has “normal”-arched, aequi-biconvex, dorsi-biconvex, or convexo-plane shells, there are several genera which have brought forth species with “inverse” arching: *Anatrypa* Nalivkin, 1941, *Spinatrypa* Stainbrook, 1951, *Kerpina* Struve, 1961, and *Spinatrypina* Ržonsnickaja,

<sup>1</sup> Explanation of the symbols used in the synonymy lists.

\* By this description in literature the name of the taxon has been introduced in accordance with the IRZN.

● The description and/or figuration in literature may be ascribed reliably to the taxon named in the heading.

v (= vidimus) The author has seen (at least an essential part of) the original material.

∅ The description and/or figuration in literature does not refer to the taxon named in the heading.

± Only a part of the description and/or figurations in literature refers to the taxon named in the heading.

1964. The new species *Spinatrypa (Invertrypa) cantabrica* is an excellent example of “*Invertrypa*”. This is displayed by the general shape of the shell, the character of the pedicle interarea and beak region, and the possession of well developed spines. Thus, *cantabrica* is in the first author’s opinion another support for his taxonomic concept.

Since *Invertrypa* has been established (Struve, 1961b, p. 334) with a generic rank, it was subject of several discussions. G. Biernat (1964, p. 315) and P. Copper (1967c, p. 495) treated it as a junior synonym of *Spinatrypa* Stainbrook, 1951 and conceded it not even a subgeneric rank. Boucot, Johnson & Staton (1965, p. 639–640) retained it as a genus. Struve (1966, p. 153–155) has discussed the taxonomic problems about *Invertrypa* on the background of present standards of generic and subgeneric calibers in Atrypidae. It is a legitimate procedure in taxonomy to evaluate species lineages as for instance the *fasciplicata-kelusiana* branch at least as a subgenus. Therefore, Struve (1966, p. 155) divided *Spinatrypa* into three subgenera: *Sp. (Spinatrypa)* Stainbrook, 1951, *Sp. (Isospinatrypa)* Struve, 1966, and *Sp. (Invertrypa)* Struve, 1961. This “compromise” allows to respect differing opinions of other authors as well as to make clear by nomenclatoric means the affinities among species.

Unfortunately, the discussion about “*Invertrypa*” is burdened by prejudiced and erroneous statements. This needs correction.

*Arching of valves:* Undoubtedly some percentage of *Sp. (Invertrypa)* shells approaches considerably the external shape of *Sp. (Isospinatrypa)*. This has been already expressed in the diagnosis (Struve, 1956, p. 386: pedicle valve in general considerably higher than brachial valve) and the description (Struve, 1956, p. 388: thickness of pedicle valve : thickness of brachial valve varying between 1.25:1 and 3.4:1, most of the ratios lying between 1.3:1 and 2.0:1) of *Sp. (Inv.) kelusiana*. The actual percentage of distinctly inverse specimens is obscured by imperfect preservation, especially by impact which for example, the material from the marly sediment of the type horizon of *kelusiana* has sustained; furthermore by intermixture with *Sp. (Isospinatrypa)* itself: *Sp. (Inv.) fasciplicata* as well as *Sp. (Inv.) kelusiana* occur together with representatives of the *Sp. (Isosp.) aspera* stock as pointed out in detail by Struve (1961b, p. 315, 324–325). Thus, biostatistical evaluations might be obscured by material not belonging to *Sp. (Invertrypa)*. In some publications the number of *Sp. (Invertrypa)* specimens approaching the shape of

*Sp. (Isospinatrypa)* is overvalued in the first author's opinion so that the reader may even gain the impression that such forms prevail and that the inverse arching of *Sp. (Invertrypa)* has no taxonomic value at all. This impression might be strengthened by a hypothesis of P. Copper (1967c, p. 495) who writes: "There is also evidence that '*Invertrypa*' reverted to typical *Spinatrypa* in Givetian time, a feature difficult to explain in terms of normal zoosystematic taxonomy." Such a phenomenon is imaginable only if the inverse arching of the *Sp. (Invertrypa)* shells were not fixed genetically or if the gene that caused the inverse arching was barred by some gene effective before. The easiest explanation would be the first one, that is the arching of the shells has been a reversible characteristic controlled merely by environmental factors. However, there is no evidence that *Sp. (Invertrypa)* has been especially stenoeic. On the contrary, its shells occur in very different types of rocks as there are marls, argillaceous limestones, light grey organodetritic limestones, dark grey-brownish to almost blackish limestones, and carbonatic siltstones. Though the source sediments give no absolute evidence of the environment, they reflect to an essential degree the variability of the physiotope.

**The "double keel":** According to Copper (1967c, p. 495) one must conclude that Struve values a "distinct mid-rib pair" as a "diagnostic character" of *Invertrypa*. Self-evidently, this is not correct, as the reader can easily learn from the generic diagnosis given by Struve (1961b, p. 334) to which Copper (1967c, p. 495) refers, too. The marked double keel has been described by Struve (1956, p. 385, 386, 388, 390) from *Sp. (Inv.) kelusiana*. Furthermore, also some specimens of *Sp. (Inv.) fasciplicata* show this double keel. Disregarding such exceptions, Struve (1961b, p. 335) has stated in the diagnosis of *fasciplicata* that there is no significant development of a double keel in this species. Absolutely correct, the double keel is not at all mentioned in the quoted diagnosis of *Invertrypa* (Struve 1961b, p. 334).

**Crura:** P. Copper (1967c, p. 504) has criticized that in Struve (1956, p. 396) the "extended crural bases are wrongly interpreted to be crura". However, as becomes clear from the description of these "crura" in Struve 1956 this term was used in a more extensive sense, as it is in common usage in German literature. Even in the "Treatise" terminology (Williams *et al.*, 1965, p. 142) the "crural bases" are defined as "Parts of crura" (spaced type not in the original text).

**Jugum:** In the opinion of P. Copper (1967c, p. 504), the "jugal plates" of *kelusiana* "are not connected as

claimed by Struve (1956, p. 396, Pl. 2, Fig. 14a)". Coalesced jugal processes, i.e. juga in a strict sense, are well known from several illustrations of Atrypacea interiors already in last century publications. Alexander (1949, p. 211, text-fig. 2/letter H) has figured such a V-shaped jugum from *Atrypa reticularis* with the two branches fused. In the text she has stated: "the primary lamellae give off the arms of the jugum which are directed antero-dorsally and which may or may not join". In agreement with Alexander the first author assumes that conjunct as well as disjunct jugal branches may occur even within one species. The first author sees no fundamental but only a gradual difference between coalesced and disjunct jugal branches especially if the two branches come so closely together as in many Atrypacea. Very probably the two branches were connected with some special kind of tissue during life, necessary because of the function of this supporting structure. The degree of calcification might have been a matter of strain or age as it is the same in bones, or merely a question of housing a surplus production of calcium carbonate (this might be the same with the fimbria, see below). Several serial sections of *kelusiana* made by the first author give no clear evidence of fused jugal branches and might be readily interpreted to show disjunct ones. The *kelusiana* interior given by Struve (1956, Pl. 2, Fig. 14a) suggests that the jugal branches are conjunct. Of course, this is not provable because the "jugum" is coated by diagenetic calcite; but for the same reason it cannot be proved that they are disjunct. In the opinion of P. Copper (1965, p. 315), it is "likely that disjunct jugal processes are characteristic of all atrypids". He thinks the interpretation of the already discussed *kelusiana* "jugum" (Struve, 1956, Pl. 2, Fig. 14a) as well as the jugum in the reconstruction of *Gruenewaldtia* sp. (Struve, 1955b, Pl. 1, Fig. 2) to be incorrect. This reconstruction is the result of many hours of preparation and of many hours of scrupulous drawing. It is founded on observations on numerous burnt specimens the preparations of which are much easier to understand than acetate peels. Undoubtedly, the specimen SMF XVII 3080 (mentioned already in the explanation of Pl. 1, Fig. 2 in Struve, 1955b; see also Pl. 1, Fig. 2 in the present paper) shows coalesced jugal branches, i.e., a jugum in a strict sense! Several brachiopod specialists have seen this specimen and fully agree with the first author. Thus, Copper's criticism of the reconstruction lacks every foundation.

**Fimbria:** Without special reference to Struve's observations on a *Sp. (Inv.) kelusiana* interior, P. Copper

(1967c, p. 504) stated, "No spines were noticed on the coils of the spiralia and none was seen in prepared specimens with the shell wall removed". In the specimen figured by Struve (1956, Pl. 2, Fig. 13) the calcite spines are arranged rather regularly and restricted to the external edges of the adaxial branch of the first to third coil of the spiraliium. This suggests that the calcite spines do not result from diagenetic processes but must be interpreted as "fimbria". Such fimbria are well known also from other brachiopods, e.g. from *Atrypacea* (see Boucot, Johnson & Staton, 1965, text-fig. 525/5a). The specimen SMF XVII 4025 is hitherto the only one which shows this peculiarity, and in Struve, 1956, p. 396, the observation was expressly referred to this specimen "Fig. 13". Clearly under certain conditions fimbria have developed in *kelusiana*.

*Species assigned:* *Spinatrypa (Invertrypa) kelusiana* Struve, 1956, *Spinatrypa (Invertrypa) fasciplicata* (Struve 1961), and *Spinatrypa (Invertrypa) cantabrica* n. sp.

*Vertical range:* As far as affirmed until now, late Eifelian (Ahbach beds and their time equivalents).

*Geographic range:* Poland (Holy Cross Mountains), Germany (Sauerland, Eifel), Belgium and northern France (southern flank of Dinant syncline), and Spain (Cantabrian Mountains), the extreme points being 2200 km apart.

#### *Spinatrypa (Invertrypa) kelusiana* Struve, 1956

- v\* 1956 *Spinatrypa kelusiana* n. sp. – Struve, p. 385–407 [except the specimens subsequently assigned to *Sp. (Inv.) fasciplicata*], text-figs. 1–6; Pl. 1, Figs. 1, 3–5; Pl. 2, Figs. 7–14; Pl. 3, Figs. 15–19, 21, 22.
- 1964 *Spinatrypa fasciplicata*. – Biernat, p. 315–316 (partim), Pl. 6 Figs. 9–11 [Pl. 6, Figs. 6–8 do not show *Sp. (Inv.) fasciplicata* but a variant close to *Sp. (Inv.) kelusiana*; see also Struve, 1966, p. 155].
- 1967c *Spinatrypa kelusiana*. – Copper, p. 503–505, text-figs. 12–14, Pl. 78, Figs. 1–8.

*Note:* The synonymy list includes only references of major importance.

*Diagnosis (revised):* A *Sp. (Invertrypa)* of medium size, length and width approaching 17 mm, arching of shell noticeably to distinctly "inverse". Pedicle valve with a median pair of ribs usually forming a prominent "double keel", accompanied on each side by 2 to 3 distinct, continuous ribs; remainder of lateral fields covered with isolated, partly flattened plications in which file-shaped patterns are hard to recognize; tendency of splitting of ribs and flattening of plications

also distinct anteriorly in large specimens; total of ribs + supposed "files" of isolated plications up to approximately 20. Ornamentation of brachial valve correlative to that of pedicle valve.

#### *Spinatrypa (Invertrypa) fasciplicata* (Struve, 1961)

- v\* 1961b *Invertrypa fasciplicata* n. sp. – Struve, p. 334–335, Pl. 2, Figs. 7–8.
- ∅ 1964 *Spinatrypa fasciplicata*. – Biernat, p. 315–316, Pl. 6, Figs. 6–11 [Figs. 6–8 = *Sp. (Inv.) kelusiana* var.; Figs. 9–11 = *Sp. (Inv.) kelusiana*].
- 1967c *Spinatrypa fasciplicata*. – Copper, p. 502–503, text-figs. 10–11, Pl. 77, Figs. 19–22.

*Note:* The synonymy list includes only references of major importance.

*Diagnosis (revised):* A *Sp. (Invertrypa)* of considerable size, length and width approaching 21 mm; arching of shell noticeably to moderately "inverse", scarcely extremely "inverse". Central field and adjacent parts of the lateral fields of pedicle valve with 8–12 distinct ribs resembling each other and being slightly and well graded in width and height, only little divergent and typically even more or less clearly parallel to one another; remainder of lateral fields covered with a more or less large number of narrower ribs; "double keel" developed only in few specimens; splitting of ribs into isolated plications and flattening of sculpture at the anterior margin as well at the posterior margin scarcely indicated. Total of ribs 20 to 36. Ornamentation of brachial valve correlative to that of pedicle valve.

*Remarks:* Among the species of *Sp. (Invertrypa)*, the inverse arching of the shell is developed the least in *fasciplicata*. As the material is generally somewhat deformed and not well preserved, exact numerical values for the proportions are difficult to find out. Thickness of pedicle valve : thickness of brachial valve ranges from about 1.2:1 to somewhat more than 2:1. About 40% of the specimens show a ratio close to 2:1 (more or less). The average seems to be about 1.5:1. As Copper states (1967c, p. 503), the "species on the whole is nearly equally convex, though the pedicle valve tends to be deeper".

#### *Spinatrypa (Invertrypa) cantabrica* n.sp.

Pl. 1, Fig. 1

*Name:* *Cantabricus*, Latin, = Cantabrian, referring to the type area.

*Holotype:* Complete specimen (St. P. 6802001), Pl. 1, Fig. 1.

*Type locality:* N. W. Spain, Cantabrian Mountains, Province of León, Alba syncline, between the rivers Luna and Bernesga, PFCL 1, about 80 m southerly of section PSA.

*Type horizon:* Middle Devonian, Upper Eifelian, basal dusky yellow calcareous silty shale of member B.

*Paratype:* 1 complete specimen, somewhat flattened by impact (St. P. 6802002), topo- and stratotypic.

*Diagnosis:* A *Sp. (Invertrypa)* of small size, length and width approaching 10 mm; arching of shell distinctly "inverse". Pedicle valve with about 20 to 22 moderately divergent, very delicate, well graded ribs resembling each other closely in width and height; "double keel" scarcely indicated; maximum wave length of ribs at anterior margin of central field about 0.8 mm; splitting of ribs into isolated plications imperfect, restricted to the postero-lateral parts of the valve. Ornamentation of brachial valve correlative to that of pedicle valve; about 20 ribs.

#### *Description of holotype*

Shell small, length and width approaching 10 mm; arching extremely ventri-biconvex ("inverse"), thickness of pedicle valve: thickness of brachial valve about 3.1: 1.

Pedicle valve a little longer than wide, width: length about 0.95: 1, outline resembling a truncated circle with a flat triangle on top; maximum width at about half the valve length. Cross-section definitely roof-shaped with narrowly rounded crest and faintly convex lateral slopes in the posterior half of the valve; central field broadly flattened in the anterior half, tangents at the lateral slopes intersecting with about 100°. Strongest longitudinal curvature close to posterior end, at about 1/5 length of valve. Beak small, pointed, not inflated, projecting about 1 mm beyond the umbo of the brachial valve (length of pedicle valve: length of brachial valve about 1.1: 1), its tip hanging a little onto the side of brachial valve and pressed against it. Posterior contour of the valve ("shoulder-line") faintly concave, tangents at it intersecting with about 125°. No sulcus; tongue scarcely indicated, anterior commissure only slightly convex.

Brachial valve slightly wider than long, width: length about 1.05: 1. Cross-section gently convex, small marginal parts flattened. Maximum longitudinal curvature at about half the valve length; small part at anterior end flattened. Cardinal extremities somewhat angular

in outline, tangents at the posterior contour ("shoulder-line") intersecting with about 165°. Umbo concealed by ventral beak.

Sculpture somewhat asymmetrical, on the right half a few more ribs (=ridge-tile shaped plication-files) than on the left half. Ribs delicate, maximum wave length (transv.) about 0.8 mm, plications and interspaces ("ribs" and "troughs") of similar cross-section. About 20 to 22 ribs<sup>2</sup> on the pedicle valve, newly added ribs distinctly narrower in the central field, too. Splitting of ribs into isolated plications imperfect, restricted to the postero-lateral extremities. Margins of the partly broken off spinose growth lamellae spaced 1.1 mm at most. Length of spines about 2 mm. Sculpture of brachial valve correlative to that of pedicle valve; about 20 ribs.

*Measurements:* Width of pedicle valve = 9.2 mm, length of pedicle valve = 9.6 mm, length of brachial valve = 8.7 mm, width of ventral interarea approximately 4.8 mm, thickness of pedicle valve = 4.3 mm, thickness of brachial valve = 1.4 mm; about 5.5 ribs/ 5 mm at the anterior margin.

*Paratype:* This almost complete specimen lacks the tip of the beak. Its outline differs from that of the holotype because the specimen is somewhat flattened by impact. Despite this deformation the shell is distinctly ventri-biconvex, thickness of pedicle valve: thickness of brachial valve still being 2.5: 1. Before deformation the shell might have had a length of pedicle valve of about 7.5 mm. The sculpture is rather well preserved. A few spines are still visible, protected by matrix supporting them. The "double keel" is slightly better indicated than in the holotype. The total of ribs is about 22 on the pedicle valve and about 20 on the brachial valve.

*Comparison:* The delicacy of the sculpture might suggest that *Sp. (Inv.) cantabrica* belongs to *Spinatrypina*, Ržonsnickaja, 1964; however, *cantabrica* has small but well developed spines and lacks the distinct interarea. It is a typical representative of the subgenus *Sp. (Invertrypa)*. This is displayed by its markedly inverse arching and by the characteristics of the beak and interarea region. The holotype of *cantabrica* is a mature specimen. This is proved by the decreasing space between the growth-lamellae at the anterior end of the shell. This allows to conclude that *cantabrica* is a species of small size. By this it differs distinctly from *Sp. (Inv.) kelusiana* and *Sp. (Inv.) fasciplicata*. By the overall

<sup>2</sup> Sculpture partially covered by matrix which was not completely removed because its peculiarities might facilitate tracing the exact type layer.

shape of its shell, *cantabrica* closely approaches *kelusiana*. However, equally sized (young) specimens (and of course mature and gerontic ones) of *kelusiana* show distinctly coarser ribs (2 to 5 ribs per 5 mm, 10 mm distant from posterior end measured along curvature of pedicle valve; see text-figs. 4a-b), a distinct "double keel", and an advanced splitting of ribs into individual plications on the lateral fields; this splitting may be so extreme that there may be only 1 to 2 more continuous files of plications ("ribs") besides the double keel.

*Sp. (Inv.) fasciplicata* differs from *cantabrica* by its much larger size, lesser convexity, and coarser ribbing (3 to 5.5 ribs per 5 mm, 10 mm distant from posterior end measured along curvature of pedicle valve; see text-figs. 4a-b).

STRATIGRAPHIC EVALUATION

The Portilla atrypids show great similarities with the central European atrypids. However, specific or sub-specific identifications have not been possible in the present stage of research. In several cases, even an exact generic or subgeneric determination is impossible. Many specimens are flattened or badly crushed. As

such most of the Portilla material gives no reliable base for a precise study, judging the present stage of knowledge on atrypids.

Arranged in stratigraphic order (as far as the material of the present collection is concerned) the Spanish "species" show no distinct trend in the development of characters comparable with the observed trends in the central European material. This probably suggests that the development of species in Spain was endemic or that Spain was supplied with species immigrating from some place other than central Europe.

The presence of some distinct genera or subgenera, however, allows only a broad stratigraphic approximation. The atrypid fauna could be grouped into two assemblages.

The first assemblage, indicating the possibility of at least a late Eifelian age, includes forms identical or closely similar to *Atrypa (Kyratrypa)*, *Atrypa (Planatrypa)*, *Atryparia*, *Desquamatia (Synatrypa)*, *Spinatrypa (Invertrypa)*, *Carinatina* and *Gruenewaldtia*, some of which are rather common and largely confined to the basal part of member A and the basal part of member B. These genera and subgenera are largely confined to the Eifelian stage in Germany. The presence

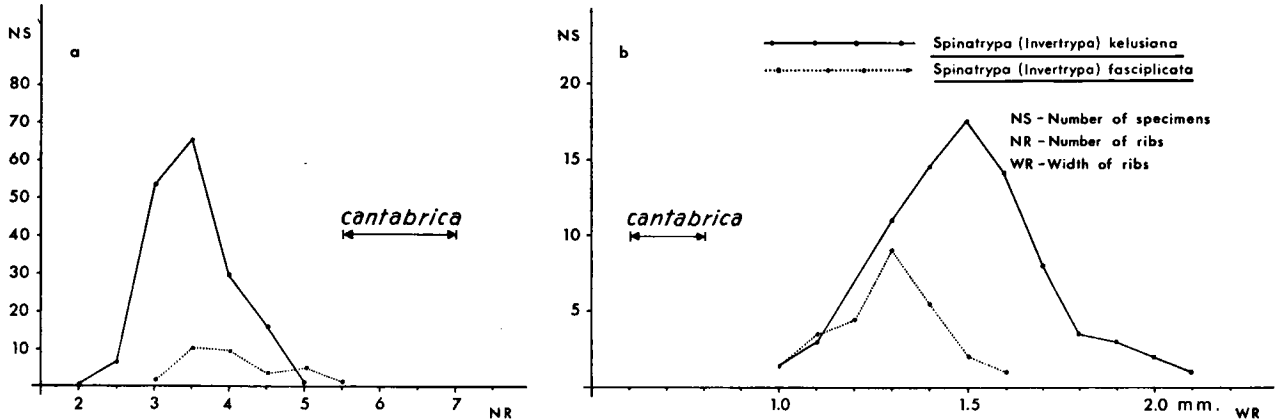


Fig. 4a-b. Variation diagrams of the sculpture of *Spinatrypa (Invertrypa)* species. Continuous line = *Sp. (Inv.) kelusiana*, Müllert horizon, locality "Im Lahr" near Niederehe (St. 950), Hillesheim syncline, Eifel. Dotted line = *Sp. (Inv.) fasciplicata*, Lahr horizon, several localities in the eastern end of the Hillesheim syncline, Eifel. Arrows = variation range of *Sp. (Inv.) cantabrica* deduced from the holotype and the paratype.

a) Number of ribs per 5 mm width in the central sector of the pedicle valve, measured 10 mm from the tip of the beak (along the curvature of the shell).

b) Average width of one of the ribs of the "double keel", measured 10 mm from the tip of the beak (along the curvature of the shell).

PLATE 1

Fig. 1. *Spinatrypa (Invertrypa) cantabrica* n. sp.; holotype, complete adult specimen, St.P. 6802001; × 5. Middle Devonian, Portilla Formation, basal part of member B, Upper Eifelian; N.W. Spain, Cantabrian Mountains, Province León, Alba syncline, between the rivers Luna and Bernesga, PFCL 1. Specimen whitened with ammonium chloride vapour before photographing. 1a) Ventral view. 1b) Dorsal view. 1c) Posterior view. 1d) Anterior view. 1e) Lateral view.

The holotype and paratype are deposited with the Department of Stratigraphy and Palaeontology of Leiden University indicated by "St.P."

Fig. 2. *Gruenewaldtia* sp., cf. *latilinguis* (Schnur 1851); specimen SMF XVII 3080; × 2. One of the preparations of the interior which served as a model of the drawing in Struve, 1955b, Pl. 1, Fig. 2, showing the coalesced jugal branches, i.e., a jugum in a strict sense. Middle Devonian; Eifel. 2a) Posterior view. 2b & 2c) Oblique views of dorsal side with different angles of inclination. All Figs. unretouched.





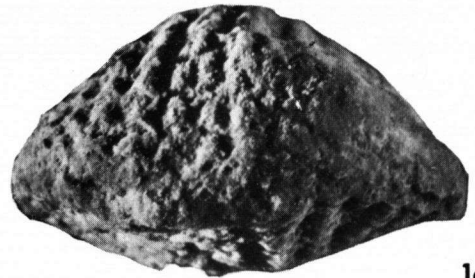
1a



1c



1b



1d



1e



2a



2b



2c

of *Spinatrypa* (*Invertrypa*) in this assemblage is interesting.

Though it were a mistake to assert apodictically that *Spinatrypa* (*Invertrypa*) is restricted to the late Eifelian, it has to be stated that all guaranteed and exactly dated specimens of this subgenus come from the Ahabach beds or their time equivalents.

There is no proved record from below or above this late Eifelian level. Records from "Freilingen beds" (Biernat, 1964, p. 316) are caused by a mistake in spelling (for the old stratigraphic term "Fleringen beds" the lower portion of which are the Ahabach beds).

Records from the Lower Givetian are caused by deviating correlations or by different opinions about the position of the Eifelian/Givetian boundary (e.g., Herm. Schmidt & Trunko, 1965; Herm. Schmidt, 1965).

The Ahabach beds were transferred from the Givetian down into the Eifelian about ten years ago (see Struve, 1961b, p. 323–330). This procedure aroused some unpleasant controversy which culminated in the opinion that the first author has invented a new Eifelian/Givetian boundary and that the phylogeny of *Sp. (Inv.) kelusiana* were his only proof for this "new" boundary. In fact, many years of comparative studies on faunal assemblages and stratigraphic sections in the Eifel area and Belgium led to the conclusion that the Ahabach beds and the Couvinien Co2d are contemporaneous. Consequently, the Eifelian/Givetian boundary had to be pushed upwards into the "Fleringen beds" of the Eifel area, which then became assigned partially to the Eifelian (Ahabach beds) and partially to the Givetian (Loogh and Cürten beds) (see also Bultynck, 1970).

In the opinion of P. Copper (1967c, p. 505), the "biofacies change at the Eifelian/Givetian boundary detracts from the certainty that *S. kelusiana* may be confined everywhere to Eifelian rocks". Unfortunately, little attention seems to have been paid to the remarks of the first author on the strata transitional from Ahabach beds to Loogh beds (see Struve, 1963 b, p. 347; Struve, 1964 a, p. 523; Boucot, Johnson & Struve, 1966, p. 1355). Therefore, the most important facts are to be summarized again: The lowest part of the Loogh aged Wotan horizon, i.e., the early Givetian "Eowotanian", containing important index fossils as *Sp. (Isosp.) wotanica* Struve, 1964 [= *Spinatrypa* sp. G. in Struve, 1963, p. 347] and *Stringocephalus*, and lacking *Sp. (Inv.) kelusiana* Struve, 1956, is ecologically and lithologically very similar to the upper Eifelian Müllert horizon of Ahabach age being the type horizon of *Sp. (Inv.) kelusiana*. The more resistant layers in the Eowotanian are Müllert type marls with

a somewhat higher content in calcium carbonate, intercalated in Müllert type marls. If there were no change of important index fossils, i.e., using prostratigraphical methods, one would assign the Eowotanian undoubtedly to the late Eifelian Müllert horizon. Furthermore it was already mentioned above (p. 159) that *Sp. (Inv.) kelusiana* occurs in very different kinds of sediments (see also Struve, 1970, p. 167–169).

The second assemblage, strongly indicating a Givetian age, is constituted of the coarse-ribbed specimens of *Spinatrypa* (*Spinatrypa*), *Spinatrypa* (*Isospinatrypa*) sp. cf. *wotanica* Struve, 1964, and *Spinatrypina* (*Exatrypa*) gr. *explanata* (Schlotheim, 1820) which is present higher in member B in the area between section PSD and PSN (Fig. 3). The coarse-ribbed form of the subgenus *Spinatrypa* (*Spinatrypa*) is so far not known from the Eifelian strata of Europe but seems to be restricted to the Givetian strata.

*Spinatrypa* (*Isospinatrypa*) *wotanica* Struve, 1964 [= *Spinatrypina wotanica* (Struve, 1964), Copper, 1967c, p. 517–518, Pl. 82, Figs. 1–4; Pl. 83, Figs. 9–10] is known from the Lower Givetian of Germany (Struve, 1964a, p. 530, 1966, text-fig. 13; Copper, 1967c, p. 490, text-fig. 1).

According to Struve (1964a, p. 524, 1964b, p. 232) and Copper (1967a, p. 126), *Spinatrypina* (*Exatrypa*) *explanata* (Schlotheim, 1820) could be limited to the Lower Frasnian of Europe. The *explanata*-group might as well be Givetian as we do not know the vertical range of the different species of *Spinatrypina* (*Exatrypa*).

There is no other atrypid in our collection which would indicate a Frasnian age. The very distinctive *Atrypa* (*Neatrypa*) and *Desquamatia* (*Seratrypa*) which are characteristic of Frasnian strata in Germany are lacking in the Spanish collection from the Alba syncline. Thus, it is highly improbable that beds of Frasnian age are represented in the Portilla Formation of the Alba syncline.

If a specialist in atrypids were urged to place an Eifelian/Givetian boundary in the Portilla section of the Alba syncline, he would undoubtedly place it roughly between the A and B member of the Portilla Formation. As already stated, the A member contains an atrypid assemblage of Eifelian tinge and the B member of largely Givetian tinge.

The type level of *Sp. (Inv.) cantabrica* as affirmed by the second author lies in the very basal part of the member B containing an atrypid assemblage of Eifelian type!<sup>3</sup>

<sup>3</sup> *Carinatina* and *Gruenewaldtia* are not indicative of Eifelian age because they are also present in the Givetian!

Furthermore, the atrypid assemblage above *cantabrica* level contains the coarse-ribbed *Spinatrypa* (*Spinatrypa*) species and *Sp. (Isosp.)* sp. cf. *wotanica* which are definitely Givetian species, and *Spinatrypina* (*Exatrypa*) sp. which might even be younger. This fact strongly supports the boundary concept. Our proposal for the Eifelian/Givetian boundary is further strengthened by Copper's views who thinks that the large scale recession of the *Atrypa* group in passage from Eifelian to Givetian strata and the preponderance of the *Spinatrypa*-*Spinatrypina* group in Givetian strata is possibly a significant event in marking the Eifelian/Givetian boundary (Copper, 1967b, 1967c).

We are fully aware of the lithotope and biotope conditions while comparing the Spanish atrypid succession with that of Germany. To us, the lithotope and biotope conditions appear to be broadly comparable. According to the survey of the second author, the members A and B of the Portilla Formation are separated by a "sharp surface of discontinuity". Though this discontinuity offers itself as a prostratigraphic boundary, the biostatigraphic boundary should be placed between the *cantabrica* level and the level with coarse-ribbed *Sp. (Spinatrypa)* species in the very basal part of member B.

In connection with this, it is very interesting that a discontinuity corresponding to an hiatus is recorded also between middle and upper parts of the Eifelian

of the Eifel area in Germany, i.e., between Junkerberg beds and Freilingen beds (Struve, 1955a, p. 294-295; 1961b, p. 312; 1964b, p. 239). P. Copper (1967c, p. 492) has denied this idea as in his opinion, necessary evidence of a sedimentological break such as for instance reworked sediments are absent. However, reworked sediments, truncation and corrosion surfaces have already been recorded (Struve, 1955a, 1961b, 1964b). These observations are also supported by evidence of stratigraphic gaps (sedimentation breaks and/or erosion) [Struve, 1961a, text-fig. 9, and 1963a, text-fig. 18 (signatures 1)]. Furthermore, reworked sediments of Eilenberg (early Freilingen) age are described by Winter (1968) from the Gerolstein syncline, and still more recent, yet unpublished investigations are clear evidence that the statement of P. Copper lacks every foundation.

Thus, viewed in the light of the new informations on atrypid biostratigraphy, the most likely chronostratigraphic conclusion would be that member A of the Portilla Formation of the Alba syncline represents an Eifelian age and greater part of member B and member C a Givetian age; the Givetian sequence being complete or largely complete between sections PSD and PSN whereas farther on the southerly and the northerly flanks a large part of the Givetian is probably missing, suggesting probably a greater hiatus in this direction.

#### SUMARIO

En el este presente artículo se registra por primera vez una fauna rica en braquiópodos atrípidos del Devónico medio de la Cordillera Cantábrica. Tras una comparación de esta fauna atrípida española con la de Alemania, se descubre que existe una estrecha semejanza entre ambas. Aunque las especies no son idénticas, se ha hecho una comparación y una evaluación estratigráfica tomando como base la forma exterior de las conchas, su ornamentación, etc. Se cree que el desarrollo de las especies españolas ha sido endémico, o bien que el mar existente en el Devónico medio español fue abastecido de especies inmigradas desde algun otro lugar que no fue Europa central. Tomando como base la clara recesión de *Atrypa* y la primera aparición de la especie *Spinatrypa* de estructura plicada gruesa, se ha buscado el límite Eifeliense/Givetiense en la formación de Portilla del sinclinal de Alba, situada entre los ríos

Luna y Bernesga, prov. de León. Se espera que en la Cordillera Cantábrica, en su parte noroccidental, exista una correlación de estos hallazgos, así como en otras regiones.

La nueva especie *cantabrica*, aquí descrita, es la tercera especie de *Spinatrypa* (*Invertrypa*) hasta ahora conocida. Se discuten cuestiones de asignación genéricas y subgenéricas, así como la taxonomía y la morfología de *Spinatrypa* (*Invertrypa*). *Sp. (Inv.) cantabrica* (así como *Sp. (Inv.) fasciplicata* and *Sp. (Inv.) kelusiana*) parece ser un indicador cronológico importante del Eifeliense tardío. Con *cantabrica* pueden ser trazados este nivel cronológico y el alcance geográfico de *Spinatrypa* (*Invertrypa*) sobre una distancia de aproximadamente 2200 km, desde Polonia, pasando por Alemania, Bélgica y el norte de Francia, a España.

## ZUSAMMENFASSUNG

Mit vorliegender Veröffentlichung wird erstmals eine reiche Fauna von Atrypidae (Brachiopoda) aus dem Mittel-Devon des Kantabrischen Gebirges (NW-Spanien) gemeldet. Zwischen den spanischen Atrypidae und solchen aus dem Rheinischen Schiefergebirge bestehen grosse Ähnlichkeiten, jedoch keine artlichen Übereinstimmungen. Es ist zu vermuten, dass die spanischen Arten endemisch sind oder dass das spanische Mitteldevon-Meer aus anderen Gebieten mit Arten beschickt worden ist als aus Mittel-Europa. Aufgrund des deutlichen Zurückgehens der Gattung *Atrypa* und des ersten Auftretens von grobrüppigen Arten von *Spinatrypa* (*Spinatrypa*) lassen sich Vermutungen über die Lage der Grenze Eifelium/Givetium in der Portilla-Formation der Alba-Mulde (zwischen den Flüssen Luna und Bernesga, Provinz León) an-

stellen. Es ist zu hoffen, dass sich diese Ergebnisse auch auf andere Gebiete im NW-Teil des Kantabrischen Gebirges übertragen lassen.

Mit *cantabrica* n. sp. wird nunmehr die dritte Art von *Spinatrypa* (*Invertrypa*) bekannt gemacht; Fragen ihrer Gattungs- und Untergattungs-Zuordnung sowie Fragen der Taxonomie und Morphologie von *Spinatrypa* (*Invertrypa*) werden erörtert. *Sp. (Inv.) cantabrica* scheint – wie auch *Sp. (Inv.) fasciplicata* und *Sp. (Inv.) kelusiana* – eine wichtige Zeitmarke des späten Eifeliums zu sein; durch die genannten 3 Arten lässt sich dieses stratigraphische Niveau und die räumliche Verbreitung von *Spinatrypa* (*Invertrypa*) nunmehr über eine Entfernung von etwa 2200 km verfolgen, von Polen über Deutschland, Belgien und N-Frankreich nach NW-Spanien.

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