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LOWER DEVONIAN BRACHIOPODS AND STRATIGRAPHY OF NORTH PALENCIA (CANTABRIAN MOUNTAINS, SPAIN)

BY

J. G. BINNEKAMP

CONTENTS

ABSTRACT

A continuous sequence of Devonian sediments is exposed in the northern part of the province of Palencia (NW-Spain), on the southern slope of the Cantabrian Mountains. This study concerns the stratigraphy and paleontology of the Lower Devonian formations.

At the base of the sequence a clastic formation is found, called the Carazo Formation. This unit can be sub-divided into three members, from top to bottom: (*c*) alternating shales and sandstones, (*b*) quartzitic sandstones, partly strongly ferruginous, (*a*) shales and micaceous sandstones. Members *a* and *b* did not yield fossils. The upper part of the formation is richly fossiliferous. The main element of the fauna consists of brachiopods, which occur together with tentaculites, trilobites, ostracods, and pelecypods. The well-preserved and characteristic brachiopods are illustrated. The fauna indicates a Lower Gedinnian age for these sediments.

The next lithologic unit, called the Lebanza Formation, consists of some 100 metres of well-bedded limestones with shale intercalations at the base and top of the formation. This formation is extremely fossiliferous. Brachiopods dominate; tentaculites, trilobites, pelecypods, corals, stromatoporoids, bryozoans, and crinoid stems also occur.

The diagnosis and systematic position of 18 of the brachiopods are discussed, viz. 3 dalmanellids; 7 rhynchonellids, including 3 new species; 4 terebratuloids; and 4 rostrospirids. Special attention is paid to the internal structure which was studied in serial sections by means of the peel technique. Drawings of the more important sections are given with each diagnosis.

In total, 25 species were determined in the brachiopod assemblage. Different assemblages occur in the upper and lower parts of the formation. The association in the lower part gives no definite indications about the age of these rocks. With their stratigraphical position taken into account, an Upper Gedinnian to Lower Siegenian age is concluded. The upper part of the formation shows only typical Siegenian species. On account of the correspondence with faunas of the Middle Siegenian formations of the Massif Armoricain (Brittany, France), the age of this part of the formation can be established as Middle Siegenian.

The correlations with sequences in adjacent areas are discussed. There is a marked divergence from the brachiopod succession in other parts of the Cantabrian Mountains, due to different oecological factors.

CHAPTER I

INTRODUCTION

The Iberian peninsula is bordered to the north by the Cantabrian-Asturian Mountains, which extend some 400 km along the coast facing the Atlantic Ocean. The highest points of this mountain chain rise above 2500 m. The eastern part is build up of Mesozoic sediments. In the headwater region of the Rio Pisuerga, Carboniferous rocks are exposed. Further to the west, in the provinces of León and Asturias, large outcrops of Devonian, Silurian, and older strata curve around the Central Asturian basin with its great development of Upper Paleozoic rocks.

Since 1950, the Geology Department of the University of Leiden has been making a study of the geology of the southern slope of this mountain chain. A provisional map scale 1 : 100.000 was published in 1962 by Prof. L. U. de Sitter. The stratigraphy and paleontology of the region is being studied under the direction of Prof. A. Brouwer, with special attention to the richly fossiliferous Devonian and Carboniferous strata.

The present study deals with the stratigraphy and paleontology of the Devonian rocks exposed on the western border of the Pisuerga valley. This area is situated in the northern part of the province of Palencia, approximately between latitudes 43° 02′ and 42° 55′ north and longitudes 0° 56′ and 0° 50′ west. To the south, the Devonian strata are unconformably overlain by Carboniferous sediments (Curavacas conglomerates, Westfalian). The northern and eastern limits of the outcrop are formed by faults which bring the Devonian strata into contact with the Westfalian and Stephanian sediments of the Pisuerga basin. To the west, the area is also limited by a fault and bordered by Curavacas conglomerate. In the south-

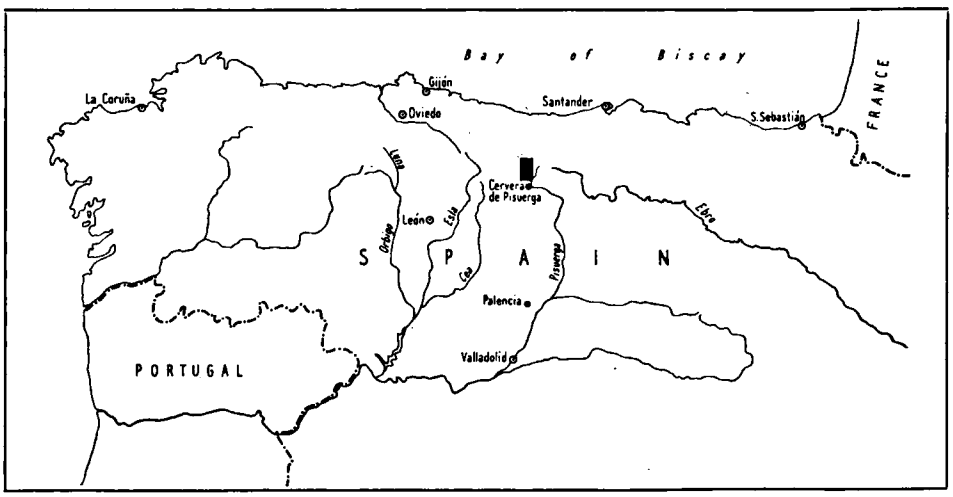

Fig. 1. Map showing location of the area under study.

western direction (Monte Las Huelgas), a continuous outcrop of Upper Devonian quartzites connects the area with a small strip of Devonian sediments north of Cardaño de Arriba.

The highest points in the area are the Peña Carazo and the Horca de Lores, both 2020 m, and in the north the Peña Bistruey of the same altitude. The villages of Polentinos, Lebanza, and Lores are situated at a height of about 1100 m in the eastern part of the area. The western part of the area, formed by the upstream valleys of the Rio Carrion and the Rio Arauz, is unpopulated.

The study of the stratigraphy and paleontology of this area was started by Mr. J. van Hoeflaken (unpublished). I have greatly profited from his report and the fossil material he collected.

I wish to thank Miss A. Renaud, Institut de Géologie, Rennes, for her kindness in showing me the collections of brachiopods from the Massif Armoricain stored in this institute. I have greatly profited from her knowledge of the Devonian brachiopods.

Thanks are due to Prof. R. Kozlowski (Warsaw), Dr. V. Havlíček (Prague), and Prof. A. J. Boucot (Pasadena) for their comments on my assignment of some species.

I also wish to express my gratitude to Mrs. I. Seeger for the correction of the English text, to Mr. T. F. Krans for his assistance in preparing the French summary, to Mr. F. H. Cramer, who translated the Spanish summary, and Mr. B. H. G. Sleumer, who translated the German summary.

I am indebted for the illustrations to Mr. J. F. Hoogendoorn, who made the photographs, and Mr. I. Santa, who prepared the drawings, as well as to Miss Th. H. Sieverts who typed a great part of the manuscript.

CHAPTER II

PREVIOUS INVESTIGATIONS

Since the middle of the last century, much has been published on the geology of the Cantabrian Mountains. Nearly all the studies carried out in the province of Palencia, however deal with the coal basins situated on the southern border of this mountain chain. Only incidental attention has been paid to the Devonian strata.

The geological map (1 : 400.000) published by Casiano de Prado in 1856 is probably the first work to deal with the geology of the Pisuerga basin. Kanis (1956, fig. 4) gives a reproduction of the northern part of this map. Two Devonian areas appear on it, one west of Cervera de Pisuerga and a second north of the village of Vañes. The present paper is concerned with the latter. On later maps (Mapa Geol. de España, 1 : 400.000, hoja 12; Quiring 1939, fig. 2) the extension of this outcrop is restricted to an area between the villages of Arbejal, Vañes, San Salvador de Cantamuda, and the Abadia de Lebanza. On the 1 : 100.000 map of the southern slope of the Cantabrian Mountains published by de Sitter in 1962, the northern limit is about the same as that given by de Prado, namely the watershed at the Peña Bistruey. To the west, however, the outcrop is much larger as compared with de Prado's conception.

Except for these indications of the Devonian on the maps, very few data have been published on the stratigraphy and paleontology of the sequence. Barrois (1882, p. 509) mentions: "M. Casiano de Prado a trouvé une assez riche faune dévonienne inférieure (Sp. hystericus, etc.) au, N. de Cervera de Rio Pisuerga, au confins des provinces de Palencia et Santander". He refers to: "Casiano de Prado: Descripc. geol. de Palencia", which implies that de Prado wrote an explanation for his map in which he also discussed the Devonian strata. Unfortunately, I have been unable to trace this article.

In 1891, Mallada listed in his catalogue of Spanish fossils from a locality L e v a n z a:

Chonetes sarcinulata Schlot.
Leptaena phillipsi Barr.
Spirifer histericus Schlot.
Athyris undata Defr.
Athyris ferronensis Vern. & Arch.
Retzia adrieni Vern. & Arch.
Dalmanites (Gryphaeus) callitellis Green.

It is not clear where he found this data; his source, too, may have been de Prado's description.

Quiring (1939), on Plate I, located the Devonian between Arbejal and Lebanza with the signature of the "Quarzit von Cervera". The age of this quartzite is established by him as middle Lower Devonian (equivalent of the Rhenish Taunusquartzite). This dating is based on the evidence of brachiopods found at a locality 1.8 km southwest of Cervera along the Rivera River and another locality east of Ventanilla. These quartzites are now placed in the Upper Devonian (see Kanis,

1956, p. 395), and therefore represent a much younger and quite different formation than the quartzitic sandstones near Arbejal and Lebanza. Quiring mentions incidentally (p. 11) the Lebanza limestone: "Kalkstein des Mitteldevons mit reicher fauna tritt ferner 2 km nordwestlich von Vañes und am Westrande von Lebanza auf".

A Spanish translation of Quiring's article was published in 1943 by de Alvaredo. In addition to the translation, Alvaredo and Sampelayo (1945) gave a critical review of this article based on their own investigations. They assign a Coblencian—Givetian age to the quartzites of Cervera. Further, they mention outcrops of thickly-bedded limestone along the Lebanza—Abadia de Lebanza road. They named this formation after the nearby village "Caliza de Lebanza" (Lebanza limestone). As far as I have been able to determine, this is the first usage of this term. They list the following fauna:

Favosites polymorpha Gold.
Favosites cervicornis Blam.
Heliolites porosa Gold.
Orthothetes o *Streptorhynchus*
O. hipponyx Schnur
O. aff. *umbraculum* Schl.
Rhynchonella o *Retzia*
Athyris

In the opinion of Alvaredo and Sampelayo, this fauna indicates a Middle Devonian age. They make the remarkable statement that the brachiopods do not dominate in their collection of samples. This is probably due to the fact that they collected their material mainly in the quarry just outside the village of Lebanza. In this quarry the thickly-bedded middle part of the formation is exploited, and in these beds corals and stromatoporoids actually form the dominating element of the fauna. In the fauna of the whole formation, however, the brachiopods dominate.

Recently, Kullmann (1960) studied the stratigraphy of the younger Devonian strata outcropping in the area. By using the main faunal element in this strata, the goniatids, he was able to determine the age of this strata, which ranges from Emsian to Frasnian.

CHAPTER III

STRUCTURAL OUTLINE OF THE AREA UNDER STUDY

The structure of the area is composed of several anticlinal and synclinal units which determine the outcrops of the rocks. The fold axes generally run E-W and plunge westwards. In the southern part of the region these units are rather simple, with only minor complications. In the northern part of the region, however, faults become so numerous that the main trends are difficult to follow. Here the faults determine the outcrops of the rocks. In some places, parts of the sequence are missing or dislocated.

Polentinos anticline

The most southerly unit is a rather simple anticline which is expressed very distinctly on the geological map. The E-W axis plunges to the west. Hence, younger strata crop out successively in this direction and the sequence is extremely clear. The southern limb is disturbed by a rather important thrust-fault, which cuts out the Lebanza limestone. To the north, the structure is limited by another thrust-fault, running along a line between Santa Marina and Lebanza. Due to this fault, the younger strata of the Polentinos anticline are in contact with the older sediments which crop out in the Carazo anticlinorium.

Carazo anticlinorium

In this structure only the older parts of the sequence crop out. The monotonous character of these strata makes it difficult to map the structure in detail. The Peña Carazo and the Horca de Lores form the southern and northern limbs of a minor syncline, easily distinguished in the field because of the shape of the outcrop of hard quartzitic sandstones. North of this syncline follows a sharp anticline, as a result of which the sandstones crop out once again.

Cortes syncline

These quartzitic sandstones, which dip to the north, may also be regarded as the southern limb of this E-W syncline. The structure is crossed by the Arroyo de Arauz which flows N-S. The banks of this river form a perfect exposure of the sequence. The Cortes valley itself is situated in the core of this syncline, in which soft shales and marls crop out. The valley is surrounded by outcrops of Lebanza limestone. In the eastern part of this syncline, west of the village of Lores, the structure becomes complicated.

Coto Redondo anticlinorium

North of the Cortes valley the main structural trends become obscured by a large number of faults. In addition, there is a large strip in which only the monotonous oldest sediments crop out, and which is almost entirely lacking in characteristic

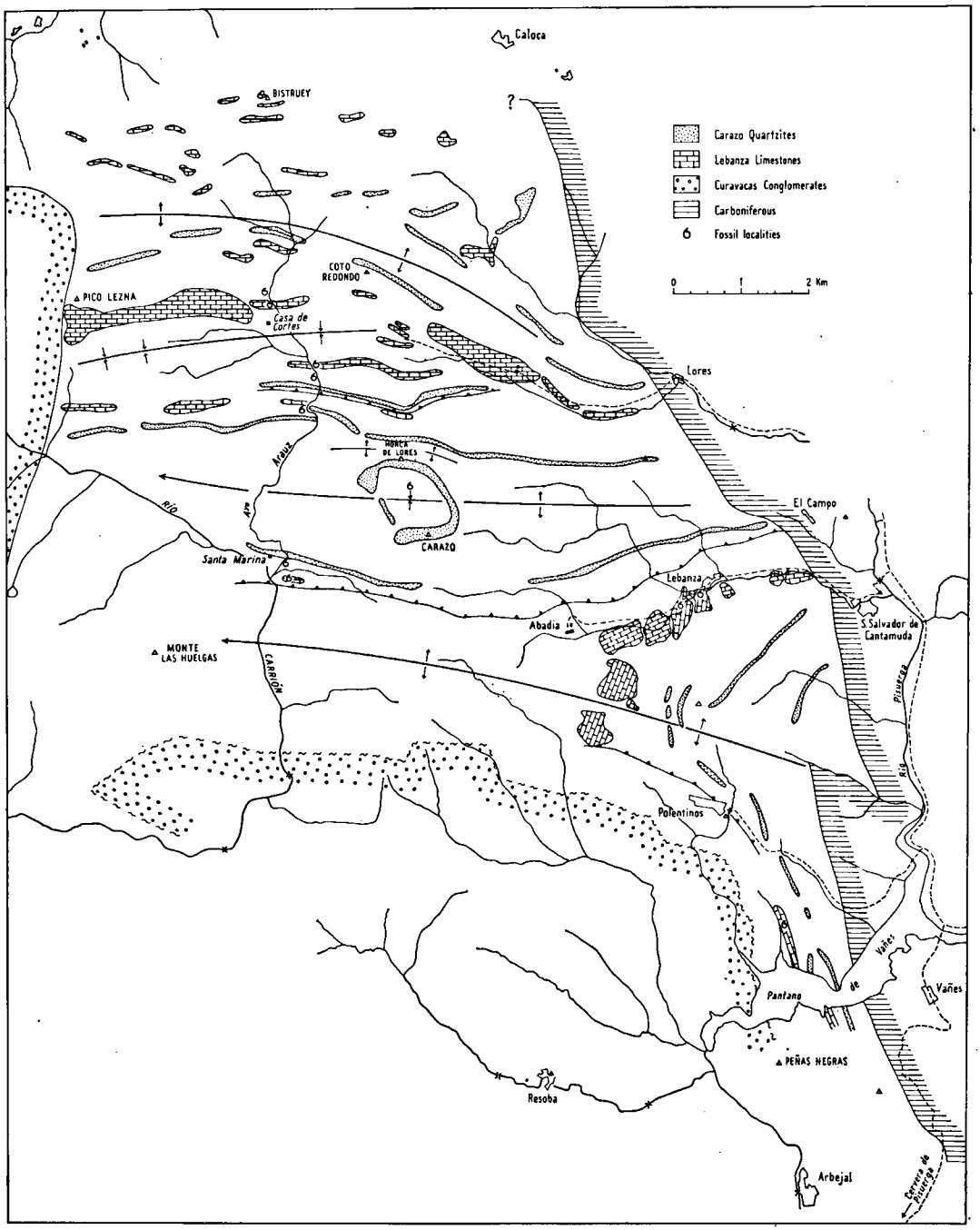

Fig. 2. Geological sketch map of the Devonian in northern Palencia.

strata or useful marker horizons. The quartzitic sandstone beds, which in the Carazo anticline are of some help in mapping parts of the structure, are in this region, unfortunately, not at all or only locally developed.

Bistruey synclinorium

The outcropping of upper parts of the sequence indicates the existence of another synclinal structure around the Peña Bistruey. In detail, however, the structure is very complicated and is not yet fully understood.

CHAPTER IV

OUTLINE OF THE STRATIGRAPHY

General remarks

The strata of this area range in age from Gedinnian to Frasnian. On the basis of its lithological features, the sequence can be provisionally divided into 4 formations; taken from top to bottom:

Carrion Formation: quartzites, dark-grey shales, nodular limestone.
Abadia Formation: shales, sandy shales, limestones, nodular limestones, and marls.
Lebanza Formation: stratified limestones with shale intercalations at base and top.
Carazo Formation: sandstones, quartzitic sandstones, and shales.

The sequence reaches its maximum thickness in the region between Vañes and Lebanza, where it measures some 700 m. To the north, it diminishes considerably. According to Kullmann (1960, p. 11), the strata overlying the Lebanza Formation reach a thickness of 100 m in the Arauz region. Inasmuch as the two lower formations also become thinner to the north, the total thickness of the sequence here can be estimated at approximately 250 m.

The two lower formations constitute the subject of the present study, with emphasis on the brachiopods and the chronostratigraphical position. Both formations are richly fossiliferous, with the brachiopods forming the dominating faunal element. They extend with very little lateral variation over the whole area.

The strata provisionally included in the Abadia Formation are less uniformly developed. Lithologically, great lateral variations occur. A remarkable characteristic of these younger strata is their special faunal assemblage: trilobites and cephalopods dominate, brachiopods are entirely absent. Detailed lithostratigraphical investigation, and a study of the fauna will undoubtedly enable a more detailed subdivision of this formation. Kullmann (1960) made such a study of the strata outcropping in the upstream area of the Arauz River, and designated part of the sequence as "Arauz-Schichten".

The Upper Devonian strata of what is here called the Carrion Formation are exposed further to the west, near Cardaño de Arriba, in a continuous section from Middle Devonian to Carboniferous. Mr. J. van Veen is preparing a publication on this area and will describe these strata and their paleontology.

The Carazo Formation

This formation is build up of clastic sediments, and can be sub-divided into three members, from top to bottom:

(*c*) shales and sandstones, well stratified;
(*b*) quartzitic sandstones;
(*a*) sandy shales and sandstones.

a. The oldest rocks of the region are greenish-grey and brown sandy shales and fine-grained sandstones, all strongly micaceous and ferruginous. Bedding can hardly be distinguished in these sediments. No fossils were found except for one undeterminable graptolite and some questionable organic remains. "Worm-traces" and other irregular structures are frequent, especially in the highly micaceous rock fragments. This part of the formation is well exposed on the slopes of the Peña Carazo and north of Santa Marina along the banks of the Arauz River. It is not known whether the base of the formation is exposed. For this reason, and because of the absence of marker horizons, its thickness is difficult to determine. As a rough guess, it is thought to exceed 75 m.

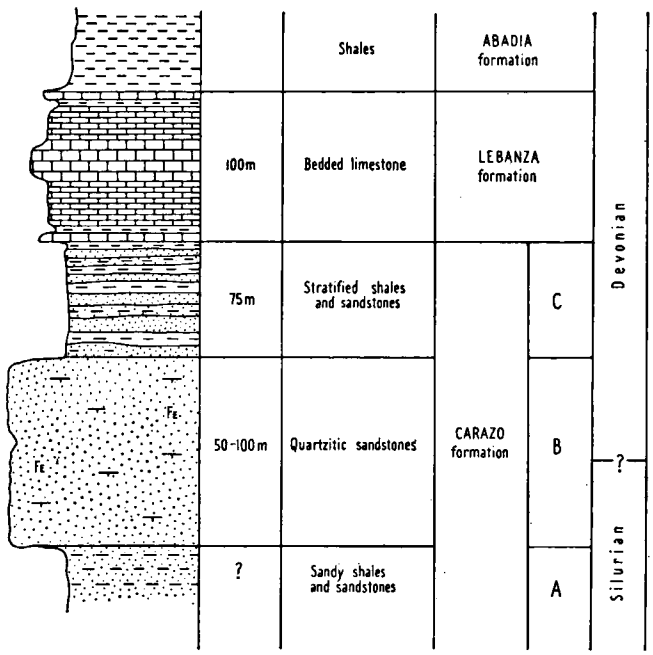

Fig. 3. Litho-stratigraphic column of the Lower Devonian in northern Palencia.

b. The dominating rocks of the middle part of the formation are well-stratified quartzitic sandstones, white on fresh rupture planes and dark grey on weathered surfaces. These rocks stand out very distinctly in the field because of their great resistence to weathering. Parts of these sediments are strongly ferruginous and coloured a dark red-brown. Alternating with these hard rocks are more shaly and sandy beds.

This part of the formation is most clearly exposed on the Peña Carazo itself. Here two quartzitic horizons occur, one some 60 m and the other about 80 m thick, separated by some 30 m of less-resistant shales and sandstones. North of Polentinos and also south of the Pantano de Vañes, in the Peñas Negras, the quartzitic sandstones are present in several horizons of minor thickness; in the Arauz region they are only locally developed.

c. The upper part of the formation is composed of a sequence of alternating sandstones and shales. These soft rocks are only exposed in favourable outcrops; elsewhere

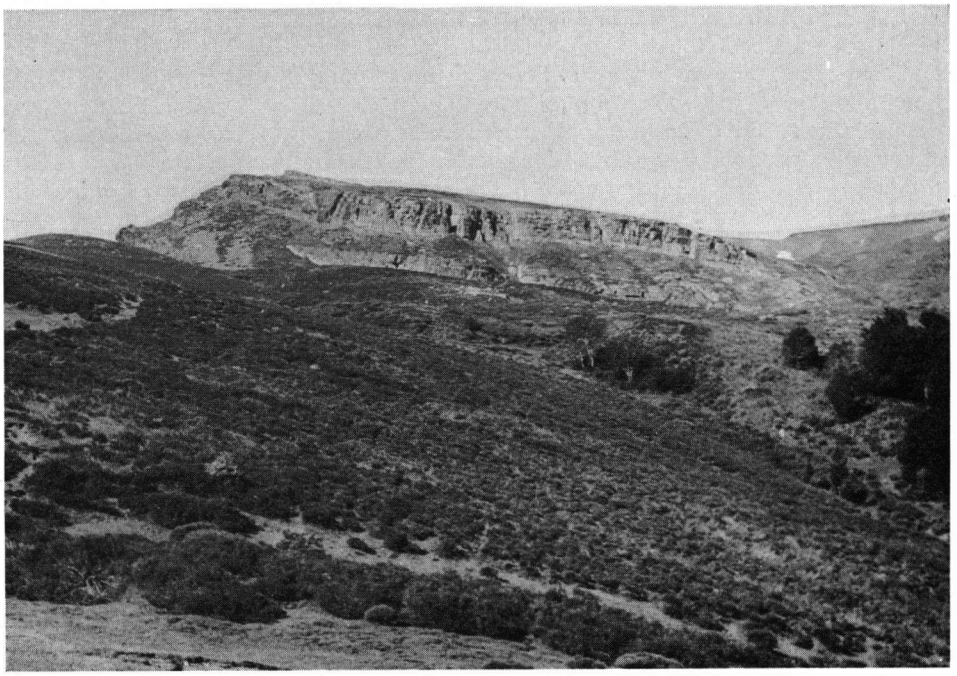

Fig. 4. View of the Peña Carazo.

Fig. 5. Outcrop of the Carazo Formation, Member c along the Arauz River.

they tend to be overgrown. The type-locality was chosen in the southern flank of the Cortes syncline in the exposed section along the Arauz River. Here the quartzitic sandstones are followed by 75 m of well-stratified, thin- to medium-bedded sandstones and shales, yellow-brown in colour. These beds are also found in the northern flank of this syncline, in the small depression between the Peña Carazo and the Horca de Lores and near Santa Marina. In the Polentinos anticline they are not exposed; the places where they could be expected are densely wooded. Examination of the loose-lying rock showed some fossiliferous fragments.

The rocks of this member are characterized by their high fossil content (brachiopods, tentaculites, trilobites, ostracods, pelecypods, and gastropods). The brachiopods are the dominating element in this assemblage. Due to the rather fine grain of the sediment, beautiful internal moulds and impressions of the exterior are plentiful.

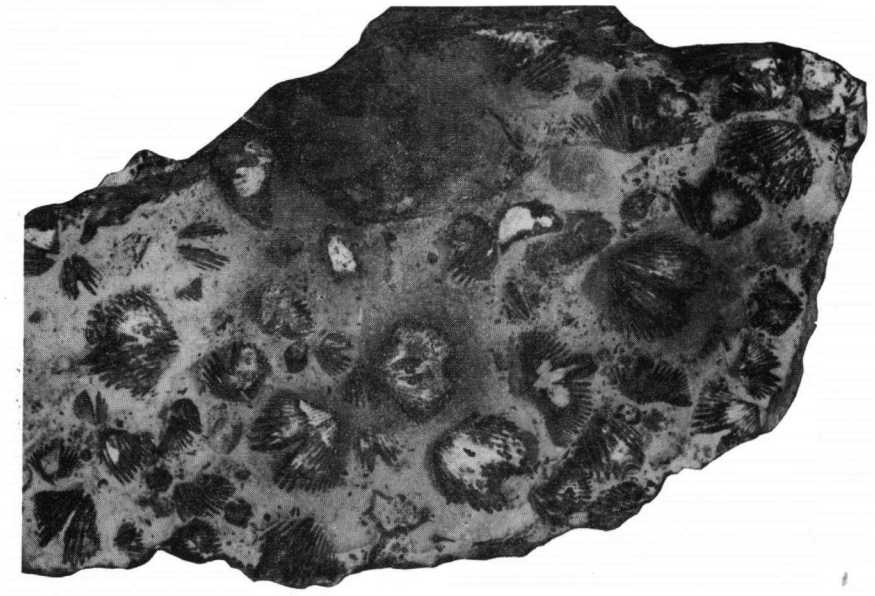

Fig. 6. Rock fragment from the upper beds of the Lebanza Formation.

The Lebanza Formation

The Lebanza Formation was named by de Alvaredo and Sampelayo after the little village of Lebanza, where these limestones are beautifully exposed. This is the most uniformly-developed lithologic unit of the Devonian sequence, and it extends over the whole area. Its outcrops can easily be traced in the terrain and are therefore an important aid to geological mapping. Its maximum thickness is about 100 m in the vicinity of Lebanza, but it decreases considerably to the north.

The most striking character of the rocks of this formation is their extremely high fossil content. Various groups are represented by numerous specimens. The brachiopods exceed all other groups, both in number of species and in number of individuals. In addition, there are tentaculites, trilobites, pelecypods, corals, stromatoporoids, bryozoans, and crinoid stems.

The outcrops just west of Lebanza constitute the type-locality of the formation. Unfortunately, some faults disturb the exposure, but a complete section is easily

reconstructed by using marker horizons. The upper beds and the transition from the limestones to the overlying strata are very well exposed some 500 m west of Lebanza, between the Lebanza—Abadia de Lebanza road and the Rio de Lebanza. The middle and lower part can be easily observed in the little quarry just outside the village and on the right bank of the river in the village itself.

A continuous exposure from the top of the Carazo Formation to the base of the Lebanza Formation is found in the already-mentioned section along the Arauz River. The lower boundary of the Lebanza Formation is taken at the lowest limestone bed in the section. This is somewhat arbitrary, since some calcareous beds occur in the top of the Carazo Formation. In both the top of the Carazo Formation and in the base of the Lebanza Formation, shaly parts are intercalated, and the transition is therefore rather gradual.

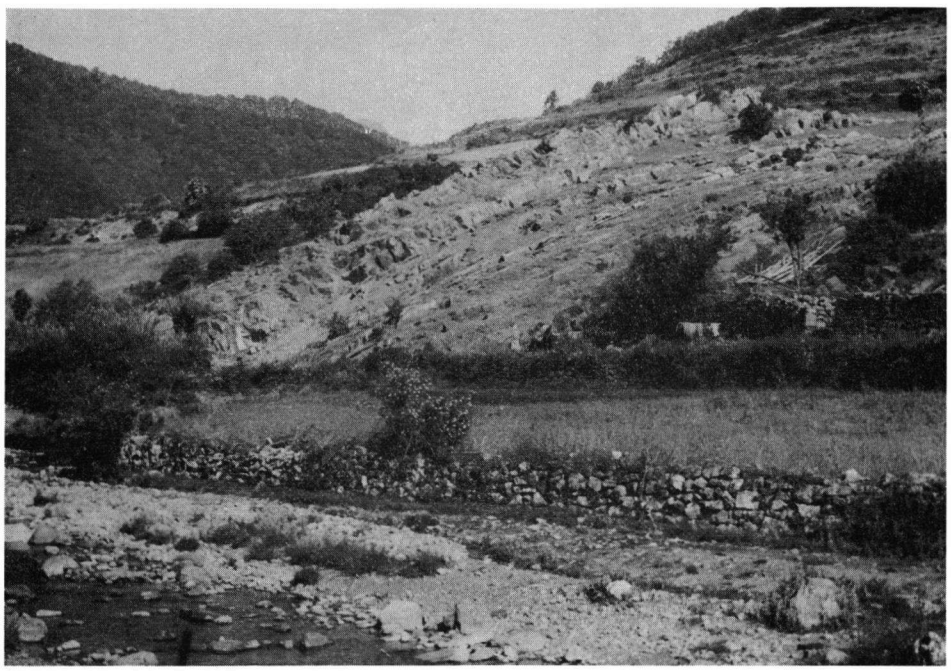

Fig. 7. View of the quarry in the Lebanza limestone west of the village of Lebanza.

The basal strata of the Lebanza Formation are medium-bedded and parallel stratified, sometimes with cross lamination. They are richly fossiliferous, but the shells are often distorted and broken. As a result, the limestone has a detrital appearance. On a fresh surface the rocks are grey, frequently with red-brown spots.

Higher in the section the rocks (the first beds lying next to the last houses of Lebanza) consist of pure, grey, fine-grained limestone. In this part, some of the bedding planes are almost entirely covered with specimens of *Athyris undata*.

The following part of the formation is massive-bedded and less fossiliferous. The brachiopods form a minor part of the fossil content, the dominating groups in this strata being stromatoporoids and corals (Favositidae and small branching Rugosa). West of Lebanza, these beds are exploited in a little quarry for local usage (as building stone). South of the Pantano de Vañes, a large quarry is situated in the

same massive-layered part of the formation. This quarry supplied the rock for the construction of the dam across the Rio Pisuerga near Arbejal and as a result, large bedding planes are exposed, covered with corals and massive stromatoporoids, forming small biostromes (Brouwer 1964, p. 50).

Well-stratified, extremely fossiliferous strata overly this massive part in the vicinity of Lebanza. The most favourable outcrop of this upper part of the formation is situated about 500 m west of Lebanza. The strata dip gently to the north-west. Shale beds alternate with the limestone beds. As a result of the differences in hardness of these alternating strata, combined with their gentle dip, the exposure resembles an amphitheatre or a staircase. On the "steps" of the staircase, fossils freed by weathering are found lying ready to hand. At the base of the exposure the river flows over the hard rocks of the underlying massive part.

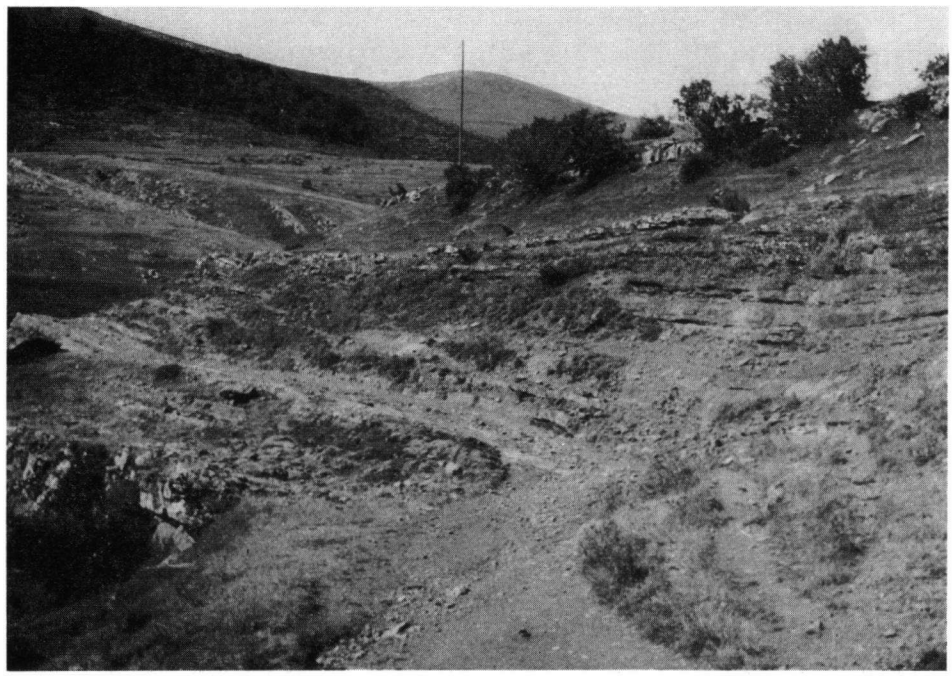

Fig. 8. Outcrop of the upper part of the Lebanza Formation, about 500 m west of the village of Lebanza.

The transition to the overlying sediments is gradual. The intercalated shale beds increase towards the top. The upper boundary of the formation is taken at the uppermost limestone bed, above which a thick sequence of shales follows.

In the section along the Arauz River, these uppermost strata are not developed. The massive-bedded part of the formation is directly overlain by sandy, dark shales. The transition from the limestones to these clastic sediments is rather abrupt.

Further to the north, only the massive part of the formation is found. Some characteristic fossils permit identification of these isolated patches as outcrops of the same formation. Its thickness is greatly reduced, varying here from 30 to 50 m.

CHAPTER V

SYSTEMATIC DESCRIPTION OF THE BRACHIOPODS OF THE LEBANZA FORMATION

General remarks

The rich brachiopod faunas occurring in the upper member of the Carazo Formation and in the Lebanza Formation enable the determination of the age of these formations. For this purpose I have studied the collected material. The fauna occurring in the upper beds of the Carazo Formation has a pronounced Lower Gedinnian character. The assemblage of species is almost completely identical to the Lower Gedinnian fauna from Belgium, recently revised and redescribed by Boucot (1960). Although the Spanish material includes perfectly-preserved internal moulds and impressions of the exterior of nearly all the present species, I can add little that is new to the diagnosis of these species given by Boucot. Consequently, only illustrations of the main elements of this fauna will be given here (pl. XI).

The species present in the Lebanza limestones appeared to be less well known, especially as regards their internal morphological features. The abundant and well-preserved material enabled me to observe these features by grinding down one or more specimens and by preparing internal moulds. This resulted in a more exact determination of the systematic position of these species. The description of some well-known species also present in the limestones has been omitted. The spiriferids, represented by three species, will be described by my colleague, Mr. Th. F. Krans, who is preparing a monograph on the Spanish Devonian spiriferids. A list of all the species found in the formation is given in Chapter VI.

Techniques and methods employed in the study

Most of the specimens in the Lebanza limestone are preserved with both valves still complete and undistorted. The space between the two valves is filled with limestone. In this matrix lies the internal skeleton. In favourable outcrops the specimens have already been freed from the solid rock by weathering. Otherwise, they can nearly always be loosened with a simple chisel and hammer. Thus, although the test is usually strongly exfoliated, the external form, costation, growth lines, etc. are all readily observable.

The preparation of internal moulds was done by heating the specimen to redness and then allowing it to cool. Owing to the heating of the shell, the test and the internal plates are calcined and appear white in contrast to the dark matrix. The soft calcinized material is then readily removed with needles. In this way, artificial steinkerns can be prepared which very clearly show the muscle scars, plates, septa, and sometimes even the pallial markings.

Serial sections prepared by grinding were used to obtain further information about the cardinalia and the brachidia. Grinding can be done by means of a small dental machine, mounted with a small, carborundum-coated steel disc. A slower, but nonetheless preferable, method consists of rubbing the specimen down

by hand on a glassplate, using a very fine carborundum powder. The resulting surfaces are very smooth and almost without grooves; the contrast between shell substance and matrix is brought out more clearly, and this method also provides better peels. Successive planes were routinely ground 0.2 mm apart. The distance from each surface to the front can be used as means of indicating its position. The sections can be copied with a drawing tube. After etching the surfaces with hydrochloric acid, cellulose peels were taken, to serve as a permanent record of the sections. The dry peel technique outlined by Sternberg and Belding (1942) was used. In some cases recrystallization obscured the internal features and prevented the preparation of peels. It is obvious that the orientation has a direct bearing on the appearance of the section. The transverse sections were ground at right angles to the plane of the valves, which usually also means perpendicular to the direction of plates, crura, etc. Longitudinal sections, taken approximately parallel to the plane of the valves, were ground to enable reconstruction of the loop of some terebratuloids (e.g. *Mutationella guerangeri*). Enlarged drawings were made of the peels of the important sections with a drawing tube. These drawings were reduced, and the resulting figures accompany the descriptions of the species.

Terminology

The conventional terminology as given by Shrock & Twenhofel (1953), Cooper (1944), and Roger (1952) has been followed. Cloud (1942) gives a glossary of morphologic terms especially for the terebratuloids and Havlíček (1961) especially for the rhynchonellids.

The descriptions

The diagnosis of each species is a description of the morphological features I observed in the Spanish material. Under "Remarks", the generic assignment of the species is discussed and divergence from descriptions of allied species given in the literature are noted. A list of the most important references is given for each known species. Under "Localities" are listed the places in Palencia where the material was collected. Under "Occurrence" the horizon in which the species was found is given (see also fig. 27). Lastly, the geographical and stratigraphical distribution of the known species is given.

The collected material, including the peels of the sections and the thin sections of some of the species are now stored in the cabinets of the Department of Stratigraphy and Paleontology of the University of Leiden.

Suborder DALMANELLOIDEA Moore 1952

Superfamily DALMANELLACEA Schuchert & Cooper 1931

Family DALMANELLIDAE Öpik 1933

Genus DALMANELLA Hall & Clarke 1892

Dalmanella? fascicularis (d'Orbigny, 1850)

Pl. I, figs. 1, 2

1845 *Orthis orbicularis* de Verneuil & d'Archiac (non Sowerby) - de Verneuil & d'Archiac, p. 478, pl. 15, fig. 9.

1850 *Orthis fascicularis* spec. nov. - d'Orbigny, no. 822, p. 90. Also in Ann. de Paléont., vol. 1 (1906), p. 193, pl. 13, figs. 20, 21.

1850 *Orthis orbicularis* de Verneuil & d'Archiac (non Sowerby) - de Verneuil, p. 161.
1882 *Orthis orbicularis* de Verneuil & d'Archiac (non Sowerby) - Barrois, p. 234.
1884 *Orthis fascicularis* d'Orbigny - Oehlert, p. 434, pl. 18, fig. 1. (The figured specimen is the type-specimen of d'Orbigny!)
1938 *Dalmanella fascicularis* (d'Orbigny) - Comte, p. 10.
1942 *Dalmanella fascicularis* (d'Orbigny) - Renaud, p. 15.
1959 *Dalmanella fascicularis* (d'Orbigny) - Comte, p. 245 and 388.

Description. Medium-sized species. Rounded outline. Length equals width or width slightly greater. Greatest width at midlength or a little anterior to it. Plano-convex (some specimens show a concave brachial valve, others a slightly convex one). Whole surface covered with numerous, irregularly and frequently bifurcating costellae of unequal thickness. The costellae radiate from the umbones and appear to be fasciculated. Costellae crossed by 3 or 4 strong growth-lines. Width of the area about half the width of the valve. The opening of the delthyrium and notothyrium is partly filled with the grooved posterior part of the cardinal process. Brachial valve with a very faint median depression, by which the commissure is hardly inflated.

Recrystallization made it impossible to prepare internal moulds; I was therefore unable to observe the internal features.

Remarks. A description of this species and an excellent summary of its history was given by Oehlert (*loc. cit*). Barrois (1882, p. 235) listed the following points of difference from the Middle Devonian "*Orthis*" *opercularis* Murchison, de Verneuil & Kayserling, 1845:

opercularis	*fascicularis*
transverse	elongated
rounded outline, angle between area and lateral commissure null	rounded outline, angle between area and lateral commissure 125 degrees
width of the area one-third of the width of the valve	width of the area two-thirds of the width of the valve
flat brachial valve	slightly convex brachial valve
greatest width at midlength	greatest width situated one-third of the front

For some of these morphological features the Spanish material is intermediate, but as a whole it links up with d'Orbigny's species. The generic assignment of this species is still uncertain since the internal form is unknown.

Localities. Lebanza.

Occurrence. Upper beds of the Lebanza Formation.

Distribution. Abundant in the Lower Devonian of western France (Massif Armoricain) and in strata of the same age in Spain (La Vid Formation, León).

Family SCHIZOPHORIIDAE Schuchert & Le Vene 1929

Subfamily SCHIZOPHORIINAE Schuchert & Le Vene 1929

Genus SCHIZOPHORIA King 1850

Schizophoria provulvaria (Maurer, 1886)

Pl. II, figs. 1—4; Text-fig. 9

1886 *Orthis provulvaria* spec. nov. - Maurer, p. 21.
1886 *Orthis* (*Hysterolithes*) *vulvarius* Oehlert (non Schlotheim) - Oehlert, p. 53, pl. 5, figs. 1—13.
1904 *Orthis* (*Schizophoria*) *provulvaria* Maurer - Drevermann, p. 267, pl. 30, figs. 29, 30; pl. 31, figs. 11—19.

1930 *Schizophoria provulvaria* (Maurer) - Laverdière, p. 87, pl. 3, fig. 4.
1936 *Schizophoria provulvaria* (Maurer) - Mailleux, p. 53.
1942 *Schizophoria provulvaria* (Maurer) - Renaud, p. 19.
1946 *Schizophoria provulvaria* (Maurer) - Asselberghs, p. 328.
1952 *Schizophoria provulvaria* (Maurer) - Le Maître, p. 102.

Description. Medium-sized to large species. Length biggest specimen 31 mm, width 40 mm. Rounded subcircular outline, slightly transverse. Greatest width at mid-length, maximum thickness near the umbo. Pedicle valve moderately convex near the umbo, concave near the front. Brachial valve strongly convex with a flattened top. In young specimens the pedicle valve is almost flat with a very weak sulcus which becomes accentuated in older specimens and inflates the forward part of the valve. Frontal part of the commissure sulcate. Hinge line straight, about half as wide as the width of the valve. Cardinal area oriented almost perpendicular to the plane of the valves. Open delthyrium. Area of the brachial valve in a direct line with the plane of the valves. In the notothyrium the top of the central part of the cardinal process is visible. Whole surface finely costellate. Costellae bifurcating. Growth-lines rather strong.

Interior pedicle valve with short, strong dental plates, extending forward into two bent ridges surrounding the triangular diductor scars. These are divided by a rather high myophragm.

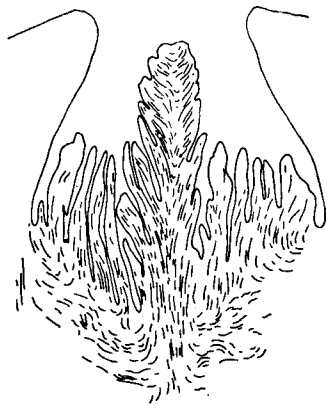

Fig. 9. Transverse section of the cardinal process of *Schizophoria provulvaria*. Drawn from peel nr. 386 (× 20).

Interior brachial valve. Cardinal process lobed with a high median part (text-fig. 9 and pl. II, fig. 4c). Adductor scars medially divided by a low, broad myophragm and transversely by two minor ridges, oblique to the myophragm.

Remarks. These specimens are undoubtedly identical to Maurer's well-known and widespread species. Mailleux (*loc. cit.*) mentions points at which it differs from the younger *Schizophoria vulvaria* (Schlotheim, 1820).

Localities. In nearly every outcrop of the Lebanza limestone.

Occurrence. Abundant in the upper part of the formation.

Distribution. This species is known in strata of Siegenian and Lower Emsian age throughout western Europe and northwestern Africa. Particularly abundant in strata of Middle Siegenian age (Ardennes and Massif Armoricain).

Subfamily ISORTHINAE Schuchert & Cooper 1931

Genus ISORTHIS Kozlowski 1929

Isorthis trigeri (de Verneuil, 1850)
Pl. I, figs. 3—5

1850 *Orthis trigeri* spec. nov. - de Verneuil, p. 782.
1878 *Hysterolithus trigeri* (de Verneuil) - Bayle, Pl. XVII, figs. 7—9.
1886 *Orthis* (*Hysterolithes*) *trigeri* de Verneuil - Oehlert, p. 51, pl. V, figs. 14—32.
1942 *Isorthis trigeri* (de Verneuil) - Renaud, p. 27.
1959 *Dalmanella trigeri* (de Verneuil) - Comte, p. 245 and 388.

For the diagnosis of this species see Oehlert (*loc. cit.*).
For a complete list of references see Renaud (*loc. cit.*).

Remarks. This species shows a strong resemblance to *Schizophoria provulvaria* (Maurer, 1886). The points of difference are:

trigeri	*provulvaria*
subquadrangular outline	subcircular outline
valves of equal convexity	brachial valve more convex
a faint sulcus on the brachial valve	median part of the brachial valve flattened
adductor scars separated by two perpendicular ridges	the transverse ridges oblique to the longitudinal one

It is difficult to distinguish these species on the basis of their external forms only, because the differences are not sharply defined. The internal features are observable only on perfectly-preserved internal moulds. When I attempted to prepare an internal mould, the matrix, which appeared to be recrystallized, fell to pieces. Some extremely quadrangular and biconvex forms from Lebanza are quite certainly identical to de Verneuil's species, but for many intermediate forms the specific assignment remains uncertain.

Localities. Lebanza.

Occurrence. Upper beds of the Lebanza Formation.

Distribution. In western France this species occurs in strata from Siegenian to Lower Couvinian age. Comte mentions it from the top of the La Vid Formation.

Suborder RHYNCHONELLOIDEA Moore 1952

Superfamily CAMAROTOECHIACEA Havlíček 1960

Family UNCINULIDAE Ržonsnickaja 1956

Genus UNCINULUS Bayle 1878
Text-fig. 10

Type-species: *Hemithiris subwilsoni* d'Orbigny, 1850

This genus, mentioned and illustrated by its type-species by Bayle in 1878, was described for the first time and with remarkable accuracy by Oehlert in 1884 (B.S.G.F., 3, XII, p. 427, pl. XII, fig. 1). Oehlert based his diagnosis on d'Orbigny's material (*loc. cit.*, p. 411: "nous avons pu étudier les types du Prodome se trouvant

au Museum dans la collection d'Orbigny, déposée au Laboratoire de Paléontologie"). He noted short dental plates and a deeply-impressed muscle field in the pedicle valve and a median septum with a septalium, its cavity filled by a cardinal process with 8—12 subparallel low ridges on its top.

In 1961 Havlíček redescribed and redefined this genus. His description of the exterior is fully in accordance with the form of the type-species; his description of the interior, however, is based on observations of the morphological features of "*Atrypa*" *maledictus* Barrande, 1879, and *Uncinulus knjaspensis* Chodalevič, 1951, species which he thought to belong to *Uncinulus*. As a result, he ascribed to *Uncinulus* a septalium filled with kallus in the brachial valve — the kallus forming the cardinal process — and a connective band (connectivum) between the anterior ends of the hige plates.

Such a connective band, however, does not exist in specimens of *Uncinulus subwilsoni* from Lebanza (there is no doubt that the Spanish material is identical to the species of western France, see p. 23). The growth lines in the kallus, made visible by etching the ground specimens, and very clearly observable on peels from these ground surfaces, clearly have a V-shaped bend in the septalium cavity in the dorsal direction; hence it follows that a connectivum is not developed in this genus (see fig. 11). I had an opportunity to check these observations on some specimens of *subwilsoni* from Bois-Roux (Ille-et-Vilaine, France) kindly given to me by Miss A. Renaud. Here I noted the same structure of the cardinalia, but with a greater amount of kallus (see fig. 10). Consequently, it seems to me quite certain that where

Fig. 10. Transverse section of the brachial valve of *Uncinulus subwilsoni*. Specimen from Bois Roux (France). Drawn from peel nr. 116 (× 15).

Havlíček's definition of *Uncinulus* concerns the inner structure of the brachial valve, it must be changed to run as follows:

The inner structure of the brachial valve is very characteristic. The septalium, supported by the median septum, is totally filled with kallus that forms the cardinal process. The ventral side of the cardinal process bears a great many longitudinal ridges that decrease in height towards the front and finally disappear. The secondary filling of the cavity also stretches out on the hinge plates in old specimens. In young specimens the frontal part of the septalium cavity is free of kallus, in gerontic ones even the crura are surrounded with kallus.

Remarks. A definite determination of the morphology of *Uncinulus* requires a study of some syntypes of *subwilsoni* from Néhou, paying special attention to a number of young specimens without much kallus in order to elucidate the original morphological elements.

I sent some specimens of *U. subwilsoni* from Lebanza to Mr. Havlíček. After examining them he fully agreed with my observations and my conclusion that *subwilsoni* and *knjaspensis* belong to different genera. This implies that a new genus name must be chosen for this last species and other species with identical structure.

This revision of Havlíček's diagnosis of *Uncinulus* also has consequences for his system of dividing the superfamily Camarotoechiacea into families. Since *Uncinulus* is the type of the Uncinulidae Ržonsnickaja, 1956, Havlíček's diagnosis of this family should be changed in the same way as his diagnosis of *Uncinulus*, but this means that there would no longer be any difference between the Uncinulidae and the Hebetoechiidae Havlíček, 1960. A new family would have to be established to include the genera that have developed a septalium with a connectivum in the brachial valve.

Uncinulus subwilsoni (d'Orbigny, 1850)

Pl. III, figs. 1—3; Text-fig. 11

1850 *Hemithiris subwilsoni* spec. nov. - d'Orbigny, p. 92.
1878 *Uncinulus subwilsoni* (d'Orbigny) - Bayle, pl. XII, figs. 11—16.
1884 *Uncinulus subwilsoni* (d'Orbigny) - Oehlert, p. 427—430, pl. XII, fig. 1.
1942 *Uncinulus subwilsoni* (d'Orbigny) - Renaud, p. 107.

Description. Small to medium-sized (length biggest specimen 17 mm, most frequently about 12 mm). Rounded subpentagonal outline. Globular form, large specimens more globular than small ones; length equals width. Greatest width at 01 anterior to midlength, greatest thickness on the front side. Lateral and frontal sides perpendicular to the dorsal and ventral side ("abgestützte Seiten- und Vorder-wände" [1]). Frontal region subquadrangular. Both valves convex. Sulcus and fold almost imperceptible. Commissure crenulate, strongly sulcate due to the tongue-like prolongation of the sulcus. Surface covered with about 40—60 rounded costae, seldom bifurcated, showing a groove on the lateral and frontal sides. Marginal spines [1] observable. Beak of pedicle valve small, erect to slightly incurved. Deltidial plates visible in section. Apical angle varying between 90 and 100 degrees. Sulcus shallow, ill defined, beginning at midlength, bearing 8—10 costae. Brachial valve more convex than pedicle valve, fold only visible on the anterior part. Shell thick.

Interior pedicle valve. Short dental plates, mostly fixed to the lateral walls by kallus. Diductor impressions very deep, forming a semi-oval cavity, divided by a low myophragm and surrounding the small adductor impressions. Posterior to the muscle scars is situated a two-lobed calcareous mass surrounding the posterior ends of the adductors.

Interior brachial valve. Septum, supporting a septalium. U-shaped septalium cavity filled by kallus, forming the cardinal process. The posterior part of the cardinal process bears on its ventral side 15 or more subparallel longitudinal low ridges, which disappear towards the front. The kallus also extends on the ventral side of the hinge plates. The frontal part of the septalium is usually free of kallus. The crura arise from the hinge plates (because of their different structure the crura are already observable, especially on peels, very near the umbo as a part of the hinge plates). The septum extends beyond midlength; the lateral cavities may be filled by kallus. Adductor impressions small, divided by the septum.

Remarks. All the essential internal morphological features characters of the Spanish specimens and some of the specimens from Bois-Roux (Massif Armoricain, France)

[1] See H. Schmidt, 1937.

are identical. The only difference is the smaller amount of kallus in the Spanish material.

Localities. Abundant in nearly all the outcrops of Lebanza limestone.

Occurrence. Upper part of the formation.

Distribution. Siegenian of Western France (Massif Armoricain). Comte mentions this species in the La Vid Formation.

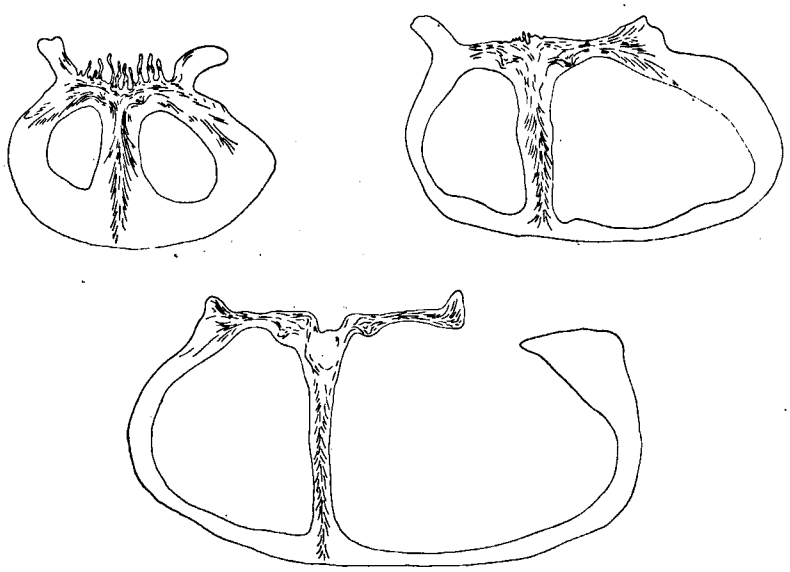

Fig. 11. Transverse serial sections of brachial valve of *Uncinulus subwilsoni*. Drawn from peels nrs. 110, 112 and 113, taken 0.3 mm apart (× 15).

Uncinulus lebanzus spec. nov.

Pl. III, figs. 4, 5; Pl. IV, figs. 1, 2; Text-fig. 12

Holotype. Specimen no 113.

Locus typicus. Lebanza.

Stratum typicum. The top of the Lebanza Formation, corresponding to the Middle Siegenian.

Description. Small to medium-sized, length of biggest specimen 15 mm. Length equals width. Subtriangular outline, apical angle varying about 90 degrees, beak ridges long, greatest width anterior to midlength. Greatest thickness on front side. Dorsibiconvex, lateral and frontal sides perpendicular to the plane of the commissure by the sharp bending of the valves. Commissure crenulate, sulcate due to the subquadrangular prolongation of the sulcus on the front side. Surface covered by about 18—22 rounded costae, grooved on the lateral and frontal sides. Costae not bifurcating; weak or even absent near the beak. Beak of pedicle valve sharp, suberect. Deltidial plates visible on sections. Foramen submesothyrid to mesothyrid. Sulcus vague, shallow, only visible on the anterior part of the shell. Fold only indicated on the front. Two to 4 costae in the sulcus, 3 to 5 on the fold.

Interior pedicle valve. Short, rudimentary dental plates, fixed by kallus to the lateral walls. Diductor scars deep, oval, surrounding the little adductor impressions. Low myophragm divides the muscle field, reaches to midlength.

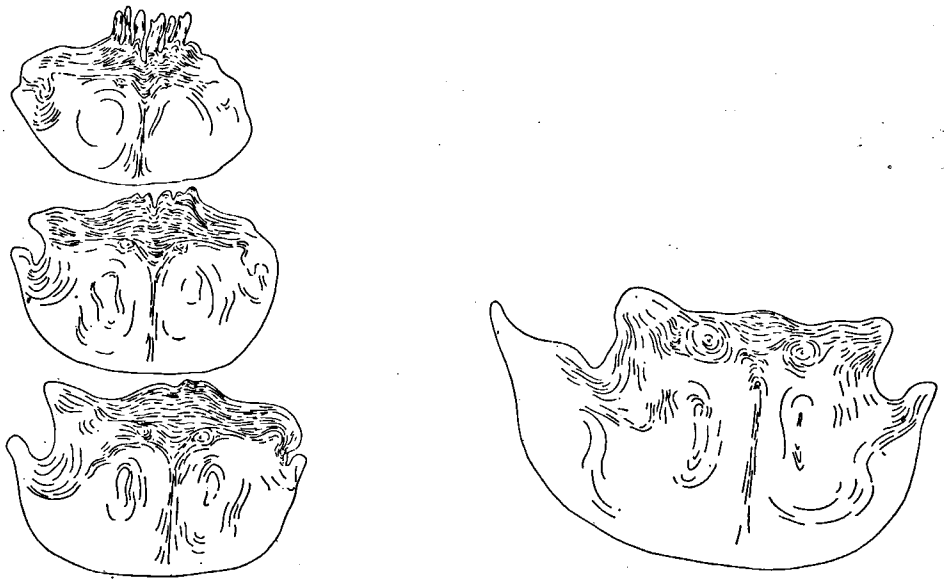

Fig. 12. Transverse serial sections of brachial valve of *Uncinulus lebanzus* spec. nov. Drawn from peels nrs. 104, 105, 106 and 107, taken 0.3 mm apart (× 12).

Interior brachial valve with septum, septalium, and cardinal process of same structure as observed in *Uncinulus subwilsoni* d'Orbigny, 1850. About 8 longitudinal ridges on the cardinal process. All morphological elements markedly thickened with kallus. Adductor impressions also of same configuration as in *U. subwilsoni.*

Remarks. This species undoubtedly belongs to *Uncinulus* Bayle, 1878. To the best of my knowledge it has never been described before.

Genus HEBETOECHIA Havlíček 1959

Hebetoechia cantabrica spec. nov.

Pl. IV, figs. 3—5; Text-fig. 13

Holotype. Specimen no 116.

Locus typicus. Lebanza.

Stratum typicum. The base of the Lebanza Formation, corresponding to the Upper Gedinnian to Lower Siegenian.

Description. Small to medium-sized, length biggest specimen 16 mm. Length greater than width. Subtriangular outline, acute apical angle, greatest width anteriorly. Dorsibiconvex, large specimens almost spherical, smaller ones flat. Commissure crenulated, on the frontal side bent into U-shape by the prolongation of the sinus. About 16—20 broad, rounded costae on flanks and anterior part, umbones smooth. Costae simple and grooved on lateral and frontal sides. Beak pedicle valve small, sharp, suberect. Foramen submesothyrid, delthyrium partly closed by deltidial plates. Sulcus ill defined, only developed anteriorly, bearing 3—5 costae. Fold, only observable anteriorly, with 4—6 costae.

Interior pedicle valve. Dental plates rudimentary, teeth strong. Diductor scars reaching to midlength, elongated oval form, surrounding the triangular adductor scars.

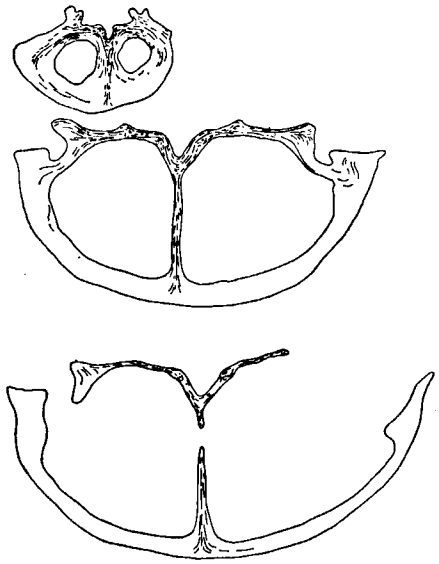

Fig. 13. Transverse serial sections of brachial valve of *Hebetoechia cantabrica* spec. nov. Drawn from peels nrs. 80, 82 and 84, taken 0.6 mm apart (× 7).

Interior brachial valve. Median septum and septalium. Lateral cavities filled in old specimens. Hinge plates and walls of septalium cavity covered with kallus. In the middle of the cavity there is always a groove between the two lobes of kallus. Forward part of septalium cavity free of kallus. Young specimens without this secondary thickening of the elements.

Growth and variation. Small specimens are flat, the commissure lying on a sharp edge and almost without sulcus or fold. Large specimens are nearly spherical. Growth during ephebic and gerontic stages was clearly relatively stronger in thickness than in length, a feature called "bicyclic growth" by Havlíček (1961, p. 18).

Remarks. It is difficult to determine whether this species belongs to *Hebetoechia* Havlíček, 1959 or to *Plethorhyncha* Hall & Clarke, 1894 (diagnosis see Havlíček, 1961, p. 127). Havlíček states that in *Plethorhyncha* the two lobes of kallus form one united mass in the anterior part of the septalium cavity and are divided by a little groove in the posterior part, whereas in *Hebetoechia* the two lobes never unite and are

always divided by a groove; even in ephebic specimens the forward part of the septalium cavity remains free of kallus. In view of this, and taking into account the great resemblance between the sections shown in fig. 13 and the sections of *Hebetoechia compta* (Barrande, 1847) given by Havlíček 1961, fig. 47, the Spanish material is assigned to *Hebetoechia*. It differs from the four known species belonging to this genus in its external form.

Localities. Lebanza, along the Arauz River, and many other outcrops. Also known from the Monte San Julian and the small limestone outcrop north of Revilla.

Genus PLETHORHYNCHA Hall & Clarke 1894

Plethorhyncha polentinoi spec. nov.

Pl. V, fig.s 1—3; Text-fig. 14

Holotype. Specimen no. 119

Locus typicus. The outcrop of Lebanza limestone just south of the Cortes syncline, along the Arauz River.

Stratum typicum. The lowermost part of the Lebanza Formation, corresponding to the Upper Gedinnian to Lower Siegenian.

Description. Large to medium-sized species. Length biggest specimen 25 mm, smallest specimen 14 mm. Subpentagonal outline, length equal to or greater than width, acute apical angle, maximum width about midlength. Greatest thickness at the front, nearly all specimens as thick as wide. Dorsibiconvex, almost spherical, lateral and frontal sides sharply bent. Commissure crenulate, strongly sulcate. Surface covered with about 28—35 costae; costae weak or absent near the umbones. Costae mostly simple, rounded, grooved on the lateral and frontal sides. Pedicle valve shallow, beak sharp, erect to slightly incurved. Delthyrium partly closed by deltidial plates, foramen submesothyrid. Sulcus almost non-existent, only indicated anteriorly and on the frontal side by the the bending of the commissure. Five to 7 costae in the sulcus. Brachial valve twice as deep as pedicle valve, fold only faintly indicated anteriorly.

Interior pedicle valve. Short rudimentary dental plates, in old specimens fixed by kallus to the side walls. Diductor scars very deep, reaching forward from midlength, surrounding the tiny adductor scars.

Interior brachial valve. Medium septum and septalium, septalium cavity filled with kallus, forming one mass, extending over the hinge plates. Posteriorly, the cavity is not completely filled and a groove remains. Anteriorly, the amount of kallus gradually diminishes and becomes divided by a median groove. One pair of oval adductor scars, laterally and posteriorly surrounded by a pair of small and long ones.

Growth and variation. All the specimens in my collection show considerable thickness, so there is little evidence of bicyclic growth.

Remarks. The very subtlety of the differences between the related genera of the Rhynchonellacea, added to the fact that the diagnosis of these genera differs according to various authors, makes it very difficult to determine to which genus this species belongs. It seems to be closely related to *Plethorhyncha* Hall & Clarke, 1894. Havlíček (1961, p. 127) gave a diagnosis of this genus, based, however, on Bohemian species of this genus. He describes a median groove in the posterior part of the septalium,

the anterior part being totally filled with kallus, uniting the hinge plates into a single plate. On the other hand, the original diagnosis given by Hall & Clarke runs as follows: The median pit in the septal cavity becomes obscured with increased age by the deposition of testaceous matter about the bases of the crura until no evidence of it remains but a linear median depression. The groove indicating the line of union of the lateral parts of the hinge plate is never obliterated. Havlíček also distinguishes a genus *Hebetoechia*, differing from *Plethorhyncha* in its more posteriorly-oriented filling of the septalium cavity and the two-lobed character of this filling, the lobes being divided by a "more or less deep groove". This very strongly suggests the original definition of *Plethorhyncha*. Moreover, reliance on such minor differences in defining genera seems to me highly disputable, the more so because the filling of the septalium cavity itself increases during the growth of each individual. Taking into account the original definition of *Plethorhyncha*, I hold the view that this new species may be assigned to this genus.

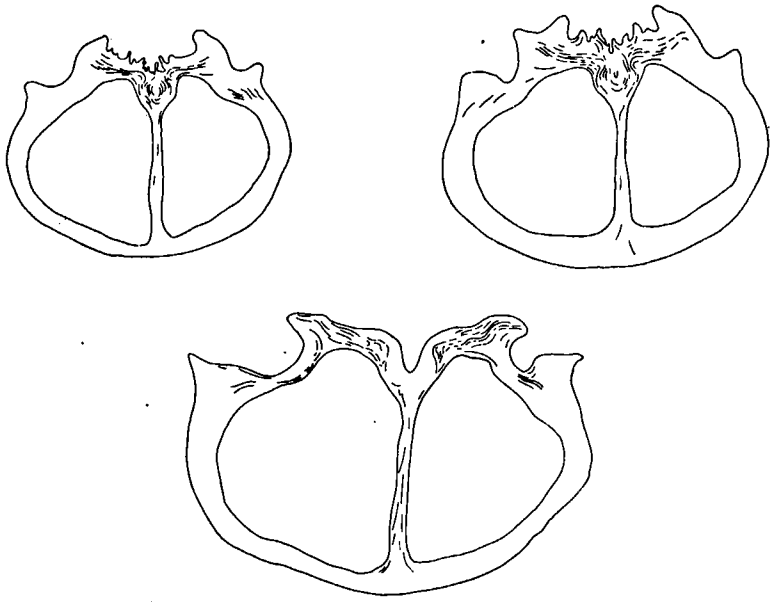

Fig. 14. Transverse serial sections of *Plethorhyncha polentinoi* spec. nov. Drawn from peels nrs. 98, 99 and 100, taken resp. 0.7 and 0.3 mm apart (× 7).

Family CAMAROTOECHIIDAE Schuchert & Le Vene 1929

Genus CAMAROTOECHIA Hall & Clarke 1894

Camarotoechia? cypris (d'Orbigny, 1850)

Pl. V, fig. 4; Text-fig. 15

1850 *Rhynchonella cypris* spec. nov. - d'Orbigny, p. 92, no. 855. Also in Ann. de Pal., vol. I (1906), p. 193, pl. 21, figs. 1—6.
1884 *Rhynchonella cypris* d'Orbigny - Oehlert, p. 412, pl. XIX, fig. 1.
1942 *Camarotoechia cypris* (d'Orbigny) - Renaud, p. 104.
1959 *Camarotoechia* cypris (d'Orbigny) - Comte, p. 246.

Description. An excellent description of this small species is given by Oehlert (*loc. cit.*).

I have attempted to study the internal features by serial sectioning of two specimens from Lebanza and one from the Massif Armoricain (locality Bois-Roux, Ille-et-Vilaine, France). One of the Spanish specimens showed a covered septalium. In the other, the hinge plates were nearly united but did not form one plate (it must be noted that because of the small dimensions and, in this case, also because of recrystallization, it is very difficult to observe the exact nature of these features). In the French specimen I observed a covered septalium. Oehlert mentions that the hinge plates approach each other very closely.

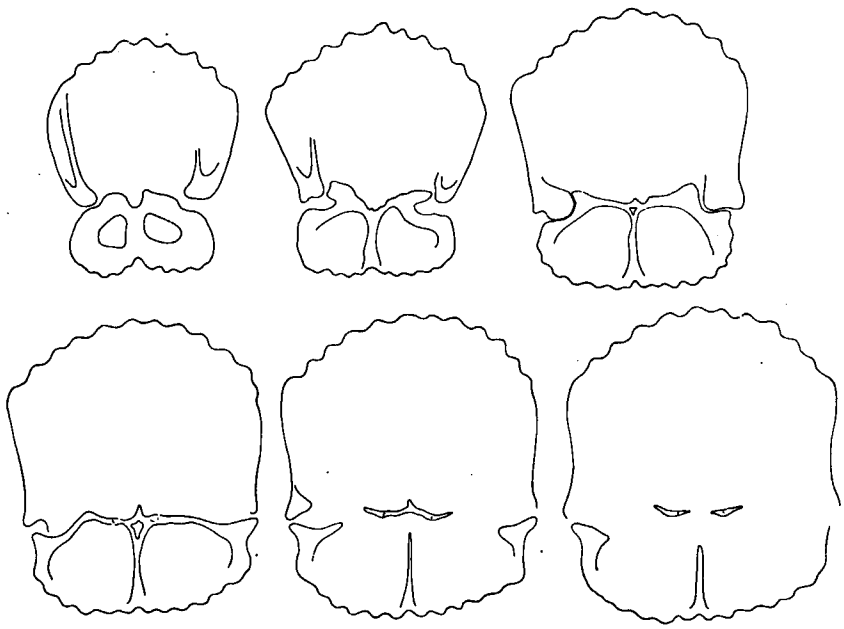

Fig. 15. Transverse serial sections of *Camarotoechia? cypris*, taken 0.3 mm apart (× 8).

Remarks. The generic assignment of this species is still uncertain. A problem lies in the exact nature of its septalium: is the covered or the uncovered septalium characteristic of the species? A second problem is that although Sartenaer revised the definition of *Camarotoechia* Hall & Clarke 1894, our knowledge of this genus is still incomplete. Since its type material consists exclusively of internal moulds, the possible existence of a covering of the septalium cannot be established.

Localities. Lebanza and Arauz.

Occurrence. In limited numbers in the whole formation.

Distribution. Siegenian in western France (Massif Armoricain). In strata of the same age in the Cantabrian Mountains (La Vid Formation, prov. León).

Genus TRIGONIRHYNCHIA Cooper 1942

Trigonirhyncia fallaciosa (Bayle, 1878)
Pl. VI, figs. 1—4a; Text-fig. 16

1878 *Uncinulina fallaciosa* spec. nov. - Bayle, pl. XIII, figs. 13—16.
1884 *Rhynchonella fallaciosa* (Bayle) - Oehlert, p. 420, pl. XVIII, fig. 5.
1928 *Rhynchonella fallaciosa* (Bayle) - Péneau, p. 231.
1942 *Uncinulus? fallaciosa* (Bayle) - Renaud, p. 113.

Description. Size of the specimens varies from small to large. Length smallest specimen 7 mm, biggest specimen 30 mm. Triangular outline, greatest width on the front; length equals width. Dorsibiconvex, large specimens globular, small ones almost flat. Commissure crenulate, strongly sulcate due to the tongue-like prolongation of the sulcus. In young specimens the sulcus is not developed and the commissure lies in one plane. Ornamentation consisting of about 18—24 strong, angular costae, not bifurcating, reaching to the umbo. Palintropes smooth. Pedicle valve shallow. Beak sharp, suberect, resting on the brachial valve. Beak ridges long, apical angle about 90 degrees. Position of foramen and existence of deltidial plates not observable. A shallow, ill-defined sulcus with 4—5 costae begins anterior to midlength. Brachial valve deep, on the front side showing an ill-defined fold with 5—6 costae. Beak strongly curved, thereby hidden under the pedicle valve.

Interior pedicle valve. Short, thin dental plates. Diductor impressions large, oval. Adductor impressions not observable.

Interior brachial valve. Median septum and septalium. Anterior part of the septalium covered by a plate uniting the bases of the crura. Havlíček calls such a plate "Deckplatte" (see Havlíček 1961, p. 17).

Growth and variation. During growth, the external form changes as a result of development of the sulcus and an increase in convexity of the valves.

Remarks. All the specimens from Lebanza are strongly exfoliated; only near the umbones is some shell material left. It appeared impossible to remove this material because heating only left it harder, just the opposite of what normally happens. The muscle scars consequently could not be observed.

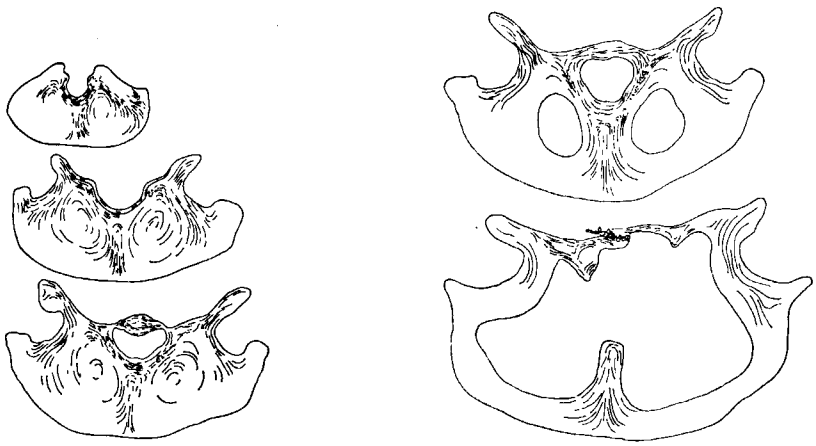

Fig. 16. Transverse serial sections of brachial valve of *Trigonirhyncia fallaciosa*. Drawn from peels nrs. 202, 206, 209, 213 and 221 (× 7).

Discussion of the genus. Bayle assigned his species to a new genus without describing or limiting that genus. Oehlert, unaware of the plate covering the septalium cavity, did not see enough fundamental differences to adopt this genus and therefore included *fallaciosa* in *Rhynchonella.*

Hall & Clarke (1894, p. 199) held the same opinion. They noticed the great resemblance between "*Uncinulina*" *fallaciosa* and "*Terebratula*" *stricklandi* Sowerby, 1820. In American material of this species (now considered as a distinct species, see Cooper 1942, p. 234: *Trigonirhynchia sulcata* spec. nov.) they noticed a uniting of the hinge plates "thus forming an arched and hollow process". They therefore concluded that the term "*Uncinulina*" might have a certain value as a distinctive designation for shells in this condition of development.

In 1925 Muir-Wood compiled a summary of the various opinions on the validity of *Uncinulina* as a separate genus, and proposed to use the generic name of *Uncinulina* to include species agreeing in external shape and ornament with *U. fallaciosa* and *U. stricklandi.* In her definition she does not mention a covered septalium as a distinguishing character.

In 1942 Cooper replaced the name *Uncinulina* by *Trigonirhynchia,* the former being a younger homonym of an echinoderm genus. He includes two species, namely *Uncinulina fallaciosa* Bayle, 1878 and *Trigonirhyncia sulcata* Cooper, 1942.

Renaud suggested in 1942 that Bayle's species belonged to *Uncinulus* Bayle, 1878.

In view of my observations of the internal features of *fallaciosa,* it seems to me justified to separate *Trigonirhynchia* as a distinct genus. Miss Renaud (Rennes) showed me ground specimens from the Bois-Roux locality (Massif Armoricain) with the same internal structure as I observed in the Spanish specimens. In my opinion *Trigonirhynchia* should include all species with the same external form and ornamentation (triangular outline; sulcus and fold only developed in later growth stages; strong, angular costae) and the brachial valve showing a septalium, its anterior part covered by a rather strong plate.

Sartenaer (1961), revising the type species of *Camarotoechia* Hall & Clarke, 1893, erected a new genus *Cupularostrum,* which shows a great resemblance to *Trigonirhynchia.* Many others species formerly assigned to *Camarotoechia* appear to have a covered septalium.

Localities. Lebanza.

Occurrence. Quite abundant in the upper beds of the Lebanza Formation.

Distribution. This species is known from the Middle Siegenian limestones from the Massif Armoricain.

Suborder TEREBRATULOIDEA Muir-Wood 1955

Superfamily TEREBRATULACEA Waagen 1883

Family DIELASMATIDAE Schuchert & Le Vene 1929

Subfamily MUTATIONELLINAE Cloud 1942

Genus MUTATIONELLA Kozlowski 1929

Mutationella guerangeri (de Verneuil, 1850)

Pl. V, figs. 5, 6; Pl. VI, fig. 4b; Text-figs. 17, 18

1850 *Terebratula guerangeri* spec. nov. - de Verneuil, p. 780.
1878 *Trigeria guerangeri* (de Verneuil) - Bayle, pl. 12, figs. 9—12.
1882 *Rhynchospira guerangeri* (de Verneuil) - Barrois, p. 264, pl. 10, fig. 1.

1883 *Centronella guerangeri* (de Verneuil) - Oehlert, p. 59—69, pls. I & II.
1931 *Trigeria guerangeri* (de Verneuil) - Maillieux, p. 32.
1938 *Trigeria guerangeri* (de Verneuil) - Comte, p. 22.
1942 *Trigeria guerangeri* (de Verneuil) - Renaud, p. 191.
1942 *Mutationella?* cf. *"Trigeria" guerangeri* (de Verneuil) - Cloud, pl. 20, figs. 23—29.
1946 *Trigeria guerangeri* (de Verneuil) - Asselberghs, p. 330.
1959 *Trigeria guerangeri* (de Verneuil) - Comte, p. 246.

Description. Small to medium-sized. Length smallest specimen 6 mm, length biggest specimen 14 mm. Subquadrangular outline. Length equals width, greatest width at midlength. Biconvex to planoconvex, without fold or sulcus, the crenulated commissure lying in one plane. Surface entirely covered by about 22—30 simple costae, the two median ribs often being a little more strongly developed and a little more widely separated.

Pedicle valve convex, ordinarily carinate. Beak sharp, suberect, beak ridges long and straight. Foramen submesothyrid to mesothyrid, conjunct deltidial plates.

Brachial valve slightly convex to almost flat.

Interior pedicle valve. Short, but distinct dental plates. Muscle field poorly impressed, consisting of small adductor impressions, enclosed by long oval diductor scars. Anterior part of the adductor impressions separated by a low myophragm.

Fig. 17. Transverse serial sections of brachial valve of *Mutationella guerangeri*. Drawn from peels nrs. 226, 229—1, 229—2 and 230, taken at distances of 0.7, 0.2 and 0.4 mm respectively (× 7).

Interior brachial valve. Hinge plates free, sometimes anteriorly united by a transverse, ventrally convex band, thus forming a perforate cardinal plate. Loop relatively long (about one-half to two-thirds as long as the valve), narrow, with a well-developed median lamella. The muscle scars are divided by a low myophragm.

Remarks. Oehlert was the first to describe this species in full detail. He stated as his opinion that this species could be assigned to *Centronella* Billings, 1859. In fact, the loop of this species has the same form, but otherwise there are great differences. Cloud (1942, p. 71—73) defines this North American genus as:

Shell small, smooth.

Ventral interior with obsolete dental plates.

The greatly swollen hinge plates rest upon the slightly thickened posterior margin of the dorsal valve and are separated by a deep medial cleft, however they are believed to be parts of a true cardinal plate which is completely sessile upon the floor of the valve and fused to it.

Obviously, de Verneuil's species cannot be placed in this genus. Bayle had in 1878 created a new genus named *Trigeria* to which he assigned "*Terebratula*" *adrieni* de Verneuil, 1845 and "*Terebratula*" *guerangeri* de Verneuil, 1850, without designating either as the type-species. The first species was taken by King in 1850 as the type of a new genus named *Retzia*. In 1879 Douvillé, presenting Bayle's work to the Geological Society of France, drew special attention to the new genera, mentioning *Terebratula adrieni* as the type species of *Trigeria* (Bull. Soc. Géol. de France, série 3, tome 7, p. 91). Thus, according to the International Code of Zoological Nomenclature, *Trigeria* became an objective and younger synonym of *Retzia*.

This poses the problem of what should be done with the species already assigned to "*Trigeria*", apparently because of their external resemblance with *guerangeri*, and to what genus *guerangeri* itself must be assigned. The distinguishing characteristics of

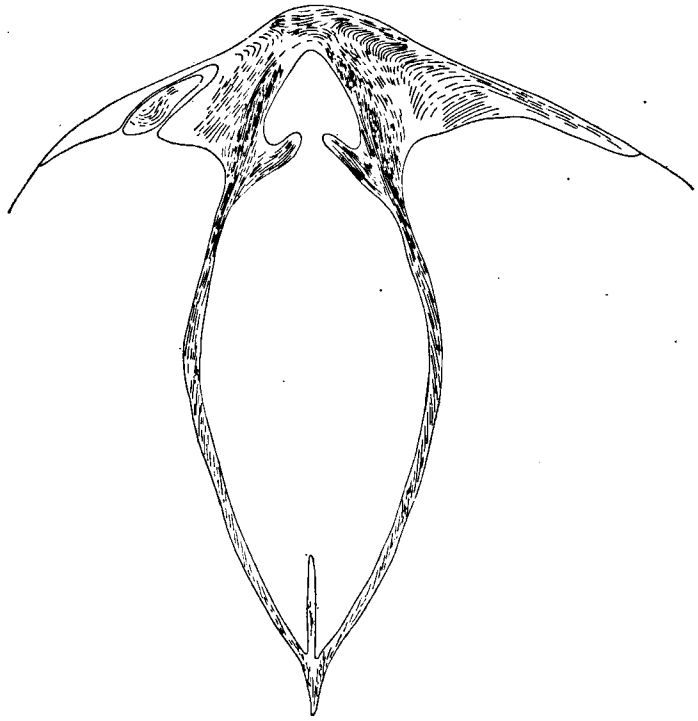

Fig. 18. Reconstruction of the loop of *Mutationella guerangeri* from a longitudinal section parallel to the plane of the valves. Drawn from peel nr. 237—4 (× 15).

adrieni (and therefore of *Retzia*) are a hinge plate supported by a strong median septum and an athyroid brachidium (see Hall & Clarke, 1894, Report of the State Geologist, p. 981), so "*Terebratula*" *adrieni* and "*Terebratula*" *guerangeri* even belong to different suborders.

Cloud (1942, p. 119) noted that the morphological features of *guerangeri* and other species of "*Trigeria*" are in general very similar to those of *Mutationella* Kozlowski, 1929 (p. 236—243, text-figs. 89B and 92—94, pl. 12, figs. 7—25). This genus also possesses a perforate cardinal plate. The loop of *guerangeri*, as illustrated by

Oehlert in 1883 and as I reconstructed it in the Spanish material, resembles figure 94C of Kozlowski. Therefore, it seems to me that *guerangeri* can be assigned to *Mutationella*. According to Kozlowski, the loop of *Mutationella podolica*, the type-species of *Mutationella*, shows great variability in its form and structure. In *guerangeri* it seems to be always relatively long and narrow with a long median lamella.

As regards the other species assigned to "*Trigeria*", Cloud has remarked that these are a polyglot lot at best and probably include not only terebratuloids but coelospirids and rhynchonellids as well.

Localities. Lebanza.

Occurrence. Abundant in the upper beds of the Lebanza limestone.

Distribution. Siegenian and Emsian in the Ardennes. Siegenian in western France (Massif Armoricain). La Vid Formation of the Cantabrian Moutains (prov. León).

Genus PODOLELLA Kozlowski 1929

Podolella rensselaeroides Kozlowski, 1929

Pl. VII, figs. 1—4; Text-fig. 19

1929 *Podolella rensselaeroides* spec. nov. - Kozlowski, p. 233, text-figs. 89, 90 en 91, pl. 12, figs. 1—6.
1942 *Podolella rensselaeroides* Kozlowski - Cloud, p. 114, pl. 20, figs. 6—10.

Description. Small species. (Length smallest specimen 2 mm, biggest specimen 13 mm; average specimen 7 mm). Subovate outline, length equal to or greater than width, maximum width at midlength. Biconvex without sulcus or fold. Commissure rectimarginate, crenulate. Ornamentation consisting of some 30 simple costellae, restricted to the anterior part of the shell. The smaller specimens lack these costellae altogether. Growth lines strong. Pedicle valve deeper than brachial valve. Beak suberect to erect. Beak ridges rather conspicuous. Apical angle varying from 85 to 100 degrees. Tiny deltidial plates, basally conjunct. Foramen situated mesothyrid. Some of the larger specimens show a much deeper pedicle valve with an almost incurved beak. The pedicle valve of this specimens has a rounded subcircular outline (cover-like). The brachial valve is commonly only a little less deep than the pedicle valve.

Thin, short dental plates in the pedicle valve.

Brachial valve with free, unsupported hinge plates, sometimes anteriorly united by a thin transverse band. Loop moderately long, about half as long as the valve, with a rather long median lamella. Muscle scars difficult to distinguish because of the small dimensions of the specimens; separated by a low myophragm.

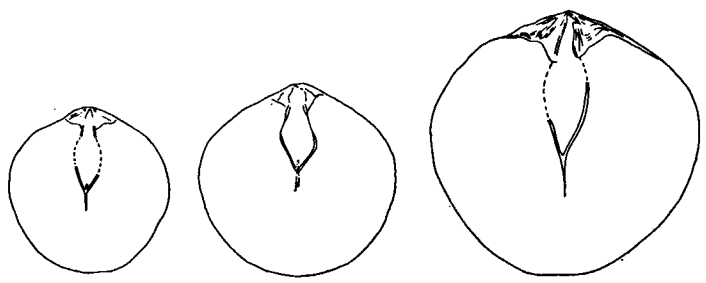

Fig. 19. Reconstruction of the loop of *Podolella rensselaeroides* from longitudinal sections parallel to the plane of the valves. Drawn from thin sections nrs. 3, 6 and 8 (× 3).

Transverse lamellae. Some specimens give the impression that the hinge plates are not united although they approach each other very closely at their anterior parts. In Kozlowski's opinion, a uniting band always existed, but due to its fragility it had a little chance of being preserved. "*Trigeria*" *guerangeri* (de Verneuil, 1850) has an analogous structure (see p. 32); here I noted some specimens with united hinge plates, while in others the hinge plates were certainly free and discrete and, in my opinion, had never been united. For example, in the case of the specimen depicted with its loop in fig. 18 and plate VI, fig. 4b, it is difficult to imagine that the transverse band was lost because of its fragility while the even more fragile loop is perfectly preserved. This could be an interesting case of intraspecific variation, since it concerns an important element of the structure.

Remarks. Mr. Kozlowski has been kind enough to give his opinion on my assignment of this Spanish material to the Podolian species. He came to the conclusion that the material from Lebanza cannot be distinguished either externally or internally from the Podolian material.

In Podolia this species occurs in the Borszczów Formation, which Boucot regards as an equivalent of the Lower Gedinnian (see Boucot 1960, p. 288, Tab. 1). In the Lebanza Formation it occurs in the lower part in strata to which I attribute a Lower Siegenian age because of their position in the stratigraphical column and their brachiopod assemblage (see Chapter VI).

Localities. Lebanza, along the Arauz and the Monte San Julian near Barruelo.

Occurrence. Lower part of the Lebanza limestone.

Distribution. Borszczów Formation (Gedinnian) in Podolia. Boucot (1960) reports *Podolella* without specific determination from strata of Gedinnian age in Belgium.

Subfamily CRYPTONELLINAE Thomson 1926

Genus CRYPTONELLA Hall 1861

Cryptonella? inornata (d'Orbigny, 1850)

Pl. VIII, figs. 1—5; Text-figs. 20, 21

1850 *Atrypa inornata* spec. nov. - d'Orbigny, p. 92, no. 860. Also in Ann. de Paléont., vol. 1 (1906), p. 194, pl. 21, fig. 11.
1886 *Meganteris inornata* (d'Orbigny) - Oehlert, p. 20, pl. 2, figs. 1—10.
1889 *Megalanteris inornata* (d'Orbigny) - Barrois, p. 152, pl. 10, fig. 5.
1928 *Megalanteris inornata* (d'Orbigny) - Péneau, p. 247.
1930 *Megalanteris inornata* (d'Orbigny) - Laverdière, pp. 34 en 96.
1942 *Meganteris inornata* (d'Orbigny) - Renaud, p. 188.
1944 *Meganteris inornata* (d'Orbigny) - Le Maître, pl. A, figs. 5—7.
1952 *Meganteris inornata* (d'Orbigny) - Le Maître, p. 143, pl. 16, figs. 1—3.

Description. Externally, the specimens from Lebanza show great morphological variation. Differences in outline, location of the maximum thickness, and the course of the convexity from this point towards the margins, make it possible to distinguish three different forms.

Form A. Rounded subcircular outline. Length equals width. Valves of equal depth varying to deeper pedicle valve. Greatest thickness halfway between mid-length and the umbones. From that point the convexity decreases rapidly (especially in the brachial valve); consequently near the margins the shells are very thin and

the commissure lies on a very sharp edge. Cardinal margin characteristically terebratuloid. Beak pedicle valve suberect to erect.

Form B. Rounded subpentagonal outline. Length equals width, greatest width at midlength. Valves of equal depth varying to deeper brachial valve. Greatest thickness at midlength. From the umbones to the margins, the course of the convexity is quite regular (i.e. the greatest thickness is less prominent than in form A) and the commissure lies on a blunt margin.

Form C. Elongated outline; length exceeds the width by about $1\frac{1}{2}$ to 2 times. Otherwise, the same characteristics as Form B.

Because all intermediate forms between Forms A and B and between Forms B and C can be found and because of the absolute identity of internal shape, muscle scars, and vascular markings, it is impossible, and in my opinion unjustified, to separate the material into distinct species. All forms are large, smooth, show concentric growth-lines, lack fold or sulcus, and have a rectimarginate commissure. The beak of the pedicle valve is sharp, mostly suberect, the delthyrium partly closed by deltidial plates (see fig. 20) and the foramen situated mesothyrid.

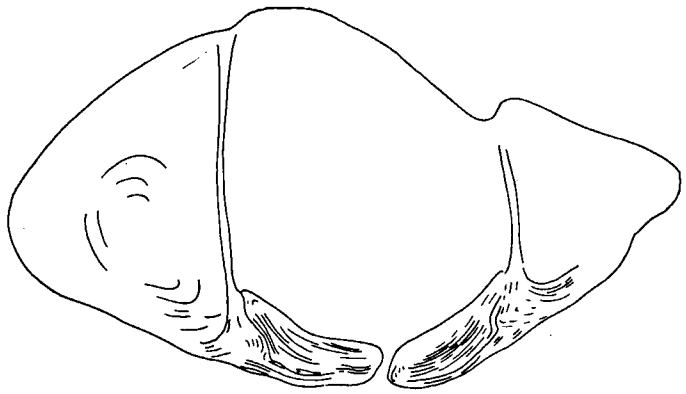

Fig. 20. Transverse serial section of the umbo of the pedicle valve of *Cryptonella? inornata*, showing the deltidial plates. Drawn from peel nr. 68 (× 30).

In the pedicle valve the teeth are supported by well-developed dental plates. Muscle field one-third as long as the valve, subovate outline. A low myophragm is present.

In the brachial valve the hinge plates are united, thus forming a cardinal plate, perforated posteriorly. The loop could not be reconstructed. The muscle field is about one-fourth as long as the valve. The scars are divided by a myophragm. On internal moulds the pallial markings are sometimes visible as low ridges. Most specimens are strongly exfoliated and retain some shell material only near the umbones.

Remarks. This terebratuloid, under the name of "*Atrypa*" *inornata* d'Orbigny, 1850, is well-known from the Massif Armoricain. Oehlert described this species very accurately in 1886 and also noted the variation in proportions described here as Forms B and C. Up to the present, this species has been thought to belong to *Meganteris* Suess, 1855. Cloud (1942, p. 109) in his definition of this genus, mentions a swollen, imperforate, sessile cardinal plate with a large boss-like cardinal process. Therefore, *inornata* with its free, perforate cardinal plate without cardinal process

cannot be assigned to this genus. The cardinalia indicate that it might belong to *Cryptonella* Hall, 1861. Cloud (1942, p. 127) suggested such a generic assignment, based on Oehlert's description. Oehlert's observations were completely confirmed by the Spanish material. For a definite assignment, a reconstruction of the loop is needed.

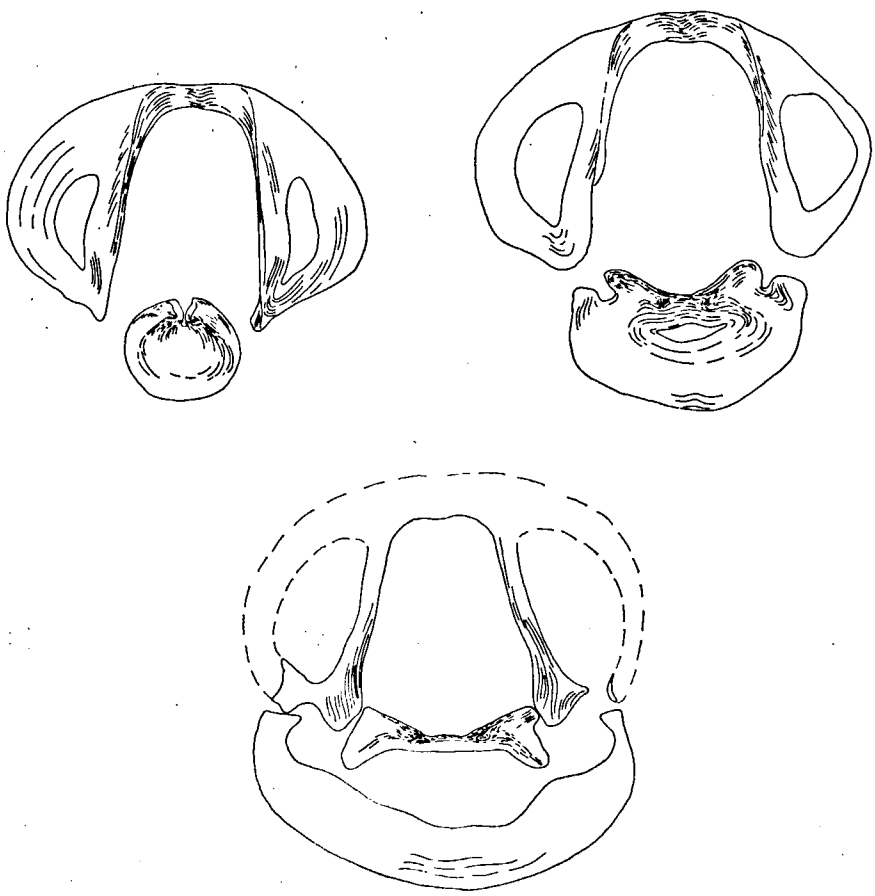

Fig. 21. Transverse serial sections of *Cryptonella? inornata.* Drawn from peels nrs. 37c, 73 and 78, taken 1.2 mm apart (× 5).

Localities. Lebanza.

Occurrence. Quite abundant in the upper beds of the formation.

Distribution. This species is known from the Siegenian formations of the Massif Armoricain and from the Siegenian of the Saoura (South Oran) and of the western Pyrenees.

Cryptonella? cf. *minor* Dahmer, 1931
Pl. VII, figs. 5, 6; Text-fig. 22

1904 *Dielasma rhenana* Drevermann (non Drevermann, 1902) - Drevermann, p. 259.
1931 *Cryptonella rhenana* (Drev., 1904), n. mut. minor - Dahmer, p. 107, pl. 9, figs. 3 and 4.
1931 *Cryptonella rugosa* spec. nov. - Mailleux, p. 27, pl. 1, fig. 12.
1936 *Cryptonella minor* Dahmer - Mailleux, p. 113.
1942 *Cryptonella minor* Dahmer - Renaud, p. 198.
1946 *Cryptonella minor* Dahmer - Asselberghs, p. 330.

Description. Medium-sized species. Length biggest specimen 24 mm, average length 18 mm. Oval subpentagonal outline, length greater than width, greatest width posterior to midlength. Biconvex, greatest thickness posterior to midlength. Commissure rectimarginate. Surface smooth, except for some growth-lines. Beak pedicle valve suberect. Delthyrium partly closed by deltidial plates, foramen situated submesothyrid. Brachial valve slightly deeper than the pedicle valve.

Interior pedicle valve with long, thin dental plates. Diductor scars subovate, broadening anteriorly, one-third as long as the valve.

Interior brachial valve with a perforate cardinal plate. Anterior adductor scars laterally and posteriorly surrounded by long, narrow posterior adductor scars. Muscle field divided by a myophragm.

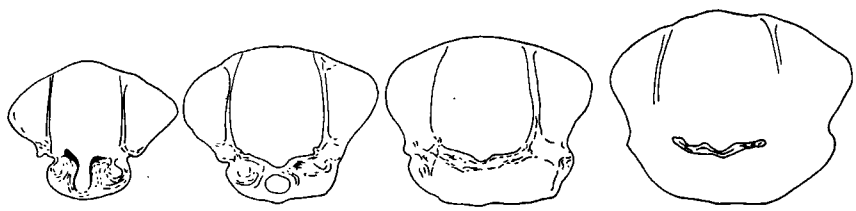

Fig. 22. Transverse serial sections of *Cryptonella?* cf. *minor*, taken about 0.5 mm apart (× 4).

Remarks. The loop of this species could not be reconstructed because of the recrystallized matrix. The generic assignment is therefore doubtful, but in all likelihood should be to *Cryptonella* Hall, 1861.

As regards the specific assignment, there is some resemblance to *Cryptonella minor* Dahmer, 1931. The characteristics of this species (small dimensions, no sinus or fold, rather strong growth-lines, and posteriorly broadened muscle scars in the pedicle valve) are not very distinctive. Moreover, the photographs published by Dahmer and Mailleux are not very clear. Cloud (1942) places *Cryptonella rhenana minor* as a "species to be investigated" with *Cryptonella* and rejects "*Cryptonella*" *rugosa* as a species of this genus. The deviations from *Cryptonella inornata* (d'Orbigny, 1850) are the smaller dimensions and the more oval and elongated outline.

Localities. Arauz and Lebanza.

Occurrence. Lower part of the formation.

Distribution. Siegenian in Belgium and Germany. Lower Siegenian in western France (Massif Armoricain).

Suborder SPIRIFEROIDEA Allan 1940

Superfamily ROSTROSPIRACEA Schuchert & Le Vene 1929

Family MERISTELLIDAE Hall & Clarke 1895

Subfamily HINDELLINAE Schuchert 1894

Genus WHITFIELDELLA Hall & Clarke 1893

Whitfieldella spec.

Pl. IX, figs. 1—4a; Text-fig. 23

Description. Large species. (The smallest specimen of the collection measures one millimeter in length, the largest 27 mm.) Subpentagonal outline, maximum width at midlength, greatest thickness a little posterior to midlength. Length equals width or width slightly greater (ratio varing from 0.9 to 1.0). Biconvex with a faint sinus on both valves. The commissure is rectimarginate, the straight frontal part is slightly curved inward by the sinuses of the valves. Smooth surface with concentric growth-lines, especially near the margins. The exfoliated specimens show fine radiating

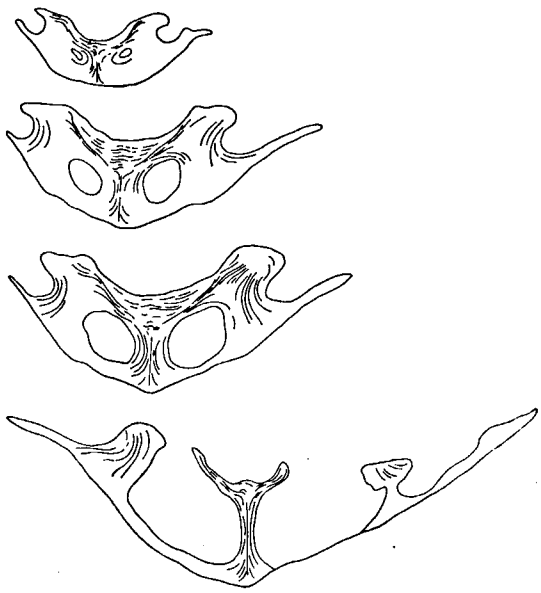

Fig. 23. Transverse serial sections of brachial valve of *Whitfieldella* spec. Drawn from peels nrs. 243, 248, 250 and 253 (× 7).

lines, probably vascular markings. Beak pedicle valve suberect in small specimens to slightly incurved in large specimens. Foramen situated mesothyrid, delthyrium partly closed by deltidial plates, which in large specimens are hidden under the beak. Apical angle about one hundred degrees, beak ridges long and straight from beak to the place of maximum width. Pedicle valve slightly deeper than brachial valve.

Interior pedicle valve with strong, short dental plates In larger specimens they become attached to the walls. Muscle field not observable.

Interior brachial valve with a concave hinge plate supported by a median septum. The hinge plate cavity is partially filled with secondary deposited material ("Kallotest"). The amount of filling diminishes anteriorly. The septum extends forward to half the length of the valve. The crural basis, already observable in the walls of the hinge plate cavity, become free as short, tape-like crura. The primary lamellae are attached to them at an acute angle, directed outward and backward, then curve towards the front and form two spiral cones with about 10—12 volutions at maturity. The jugum has a simple Y-shape. Muscular impressions faint.

Remarks. This species has all the diagnostic properties of *Whitfieldella* Hall & Clarke, 1893. Its cardinalia, brachidium, and jugum are identical to those of the type-species of *Whitfieldella.* Hall and Clarke mention in their definition (47th Report of the New York State Museum, 1894, p. 960); "In the typical forms there is a faint sinus on both valves near the anterior margin". Thus, the Spanish material resembles the type of the North American genus externally, too. In Europe only one species of *Whitfieldella* is known to me, namely *Whitfieldella ypsilon* (Barrande, 1847) (see Siehl 1962, p. 220, pl. 32, fig. 2). But the internal form of most of the species commonly assigned to *Meristella* Hall, 1859 is not known. It is quite possible that some of these species belong to other genera of the Rostrospiracea. In this connection it is interesting to note the great external resemblance of this Spanish material to a species from Erbray, described by Barrois as *Meristella recta* (Barrois, 1889, p. 107, pl. VI, fig. 6). Barrois himself (*loc. cit.*, p. 105) noted that knowledge of the brachidium might cause transfer of this species to *Whitfieldia* Davidson, 1882, a younger synonym of *Meristina* Hall, 1867. This genus has about the same jugum as *Whitfieldella* and seems to me difficult to distinguish from it.

Localities. Lebanza.

Occurrence. Upper beds of the formation.

Family ATHYRIDAE Davidson 1884

Subfamily ATHYRINAE Waagen 1883

Genus ATHYRIS McCoy 1844

Athyris undata (Defrance, 1828)

Pl. IX, fig. 4b; Pl. X, figs. 1—3; Text-figs. 24, 25

1828 *Terebratula undata* spec. nov. - Defrance, p. 155.
1886 *Athyris undata* (Defrance) - Oehlert, p. 32, pl. III, figs. 1—20.
1942 *Athyris undata* (Defrance) - Renaud, p. 178, pl. I, fig. 4.
1952 *Athyris undata* (Defrance) - Le Maître, p. 136, pl. XVII, figs. 25—29.

Description. Large species (length biggest specimen 35 mm, width 34 mm), subquadrangular outline, length equals width or length slightly greater. Maximum width situated anterior to midlength. Biconvex with a strong sulcus and fold, anterior commissure strongly sinuous due to the prolongation of the sulcus. Greatest thickness at or slightly posterior to midlength. Whole surface covered with irregular lamellar and imbricate growth-lines, regularly distributed.

Pedicle valve with erect beak. Foramen situated hypothyrid; deltidial plates were not observed. Median sulcus large, well defined, with a low longitudinal fold on both sides. The sulcus extends into an anteriorly directed tongue supporting the fold of the brachial valve.

Brachial valve with a subtriangular hinge plate, perforate at its apex (just beneath the beak). The plate is divided into three parts, the median part flat or concave, the lateral parts thickened and elevated. In the raised borders of the median part lie the bases of the crura. They become free and form very long crura to which the primary lamellae are joined at an acute angle. The primary lamellae first extend posteriorly, then reverse direction and follow the curvature of the brachial valve. The number of whorls may reach 16. The jugum consists of a saddle-shaped central part (saddle) with a convex upper surface, united by two links (lateral branches) with the primary lamellae. From the posterior part of the saddle rises a postero-ventrally directed, long, thin process (stem). Near the extremities of the crura, the stem bifurcates and gives rise to two branches (accessory lamellae). These accessory

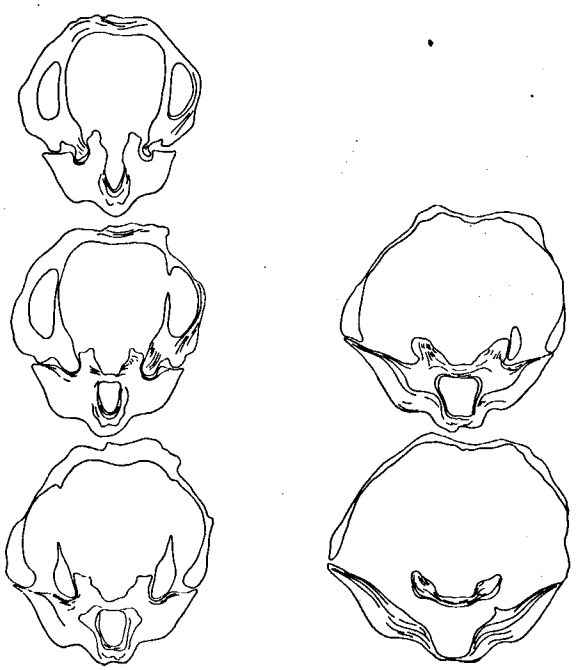

Fig. 24. Transverse serial sections of *Athyris undata*, taken at distances of 0.3, 0.4, 1.0 and 1.7 mm respectively (× 1.5).

lamellae follow the curvature of the spiral and lie between the primary lamellae and the first whorl of the secondary lamellae. An extremely low myophragm, leaving a groove on the internal moulds, divides the long adductor scars which lie in the fold.

Remarks. All the morphological features, exterior as well as interior, are in accordance with those of the genus *Athyris* Mc Coy, 1844. For a description of this genus and the here followed terminology for the various parts of the jugum see Hall & Clarke 1894, 47th Report of the State Geologist, p. 971—973, text-fig. 311.

This species is widespread and has long been known in western France (Massif Armoricain), the western Pyrenees, and northern Spain. In Belgium and Germany a slightly different species, *Athyris avirostris* (Krantz, 1857) occurs in strata of the same age. In this species the sulcus continues to the beak, while in *A. undata* the sulcus

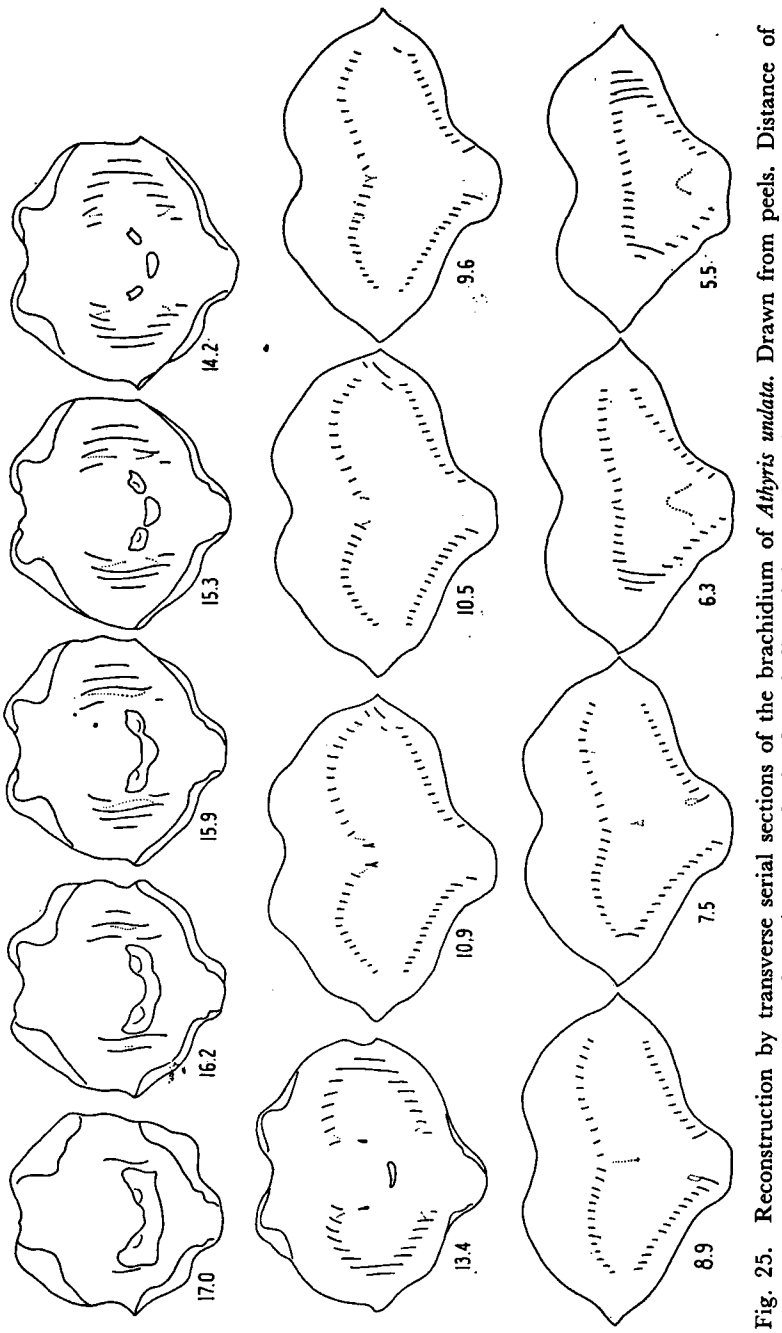

Fig. 25. Reconstruction by transverse serial sections of the brachidium of *Athyris undata*. Drawn from peels. Distance of each section towards the front indicated for each section (× 1.5).

is obscure near the beak. I think it doubtful to base a specific distinction on such a difference.

Localities. Abundant in all the outcrops of Lebanza limestone.

Occurrence. The upper part of the Lebanza Formation.

Distribution. Siegenian of southwestern Europe. Especially abundant in the Middle Siegenian formations ("calcaires à *Athyris undata*") of the Massif Armoricain.

Athyris spec. cf. *concentrica* (von Buch, 1834)

Pl. X, figs. 4, 5

1834 *Terebratula concentrica* spec. nov. - von Buch, p. 103.
1840 *Terebratula concentrica* von Buch - Murchison, de Verneuil & d'Archiac, p. 251, pl. 2, fig. 1.
1864 *Athyris concentrica* (von Buch) - Davidson, p. 14, pl. 3, figs. 11—15, 24.
1886 *Athyris concentrica* (von Buch) - Oehlert, p. 32.
1930 *Athyris concentrica* (von Buch) - Laverdière, p. 106.
1938 *Athyris concentrica* (von Buch) - Comte, p. 39.
1938 *Athyris concentrica* (von Buch) - Mailleux, pp. 12, 24.
1942 *Athyris concentrica* (von Buch) - Renaud, p. 180, pl. 14, figs. 11—12.
1952 *Athyris concentrica* (von Buch) - Le Maître, p. 137, pl. 19, figs. 41—42.
1959 *Athyris concentrica* (von Buch) - Comte, pp. 247, 251, 404.

Description. Medium-sized species. Rounded subquadrangular outline. Length equals width. Greatest width at midlength. Biconvex. Greatest thickness at midlength. Anterior part of the commissure sulcate. Surface covered with overlapping lamellae. Pedicle valve with suberect beak. Apicle angle varies about 95 degrees. Beak ridges long and straight from beak to place at which the valve reaches its greatest width. At midlength, an ill-defined, flat-bottomed sulcus starts. Pedicle valve moderately convex near the beak, nearly flat at the margins. Brachial valve more convex, carinated by the inconspicuous fold. Near the front, the fold is more distinct.

Interior pedicle valve with short, strong dental plates.

Interior brachial valve with a perforate hinge plate and an athyroid spiralium.

Remarks. Recrystallization obscures the interior of the specimens I collected. I was therefore unable to reconstruct the spiralium in detail. Nearly all the specimens are strongly exfoliated, so the lamellose surface is also poorly preserved. For this reasons doubt remains as to whether this material is identical to *concentrica.*

Localities. Arauz and Lebanza.

Occurrence. Lower part of the Lebanza Formation.

Distribution. A. concentrica is known throughout western Europe and northwestern Africa, in strata ranging from Siegenian to Frasnian age.

Genus PRADOIA Comte 1938

Pradoia? cf. *P. torenoi* (de Verneuil & d'Archiac, 1845)

Pl. XI, figs. 1, 2; Text-fig. 26

1845 *Terebratula toreno* spec. nov. - de Verneuil & d'Archiac, p. 469, pl. 14, fig. 8.
1938 *Pradoia torenoi* (de Verneuil & d'Archiac) - Comte, p. 44, pl. 4, fig. 14.
1959 *Pradoia torenoi* (de Verneuil & d'Archiac) - Comte, pp. 247 and 405.

Description. Medium-sized species. Length biggest specimen 16 mm. Rounded subpentagonal outline. Length slightly exceeds width. Greatest width anterior to mid-length. Biconvex, greatest thickness near the umbones. Commissure rectimarginate, crenulate. Whole surface covered with subangular costae, bifurcating and reaching a total number of about 30 to 45 at the margin. Pedicle valve slightly deeper than the brachial valve. Beak incurved, beak ridges long and straight. A vague, ill-defined sulcus reaches to the umbo. The lateral borders of this sulcus are slightly elevated. On the brachial valve an inconspicuous fold, sometimes with a faint median depression.

Interior pedicle valve with tiny, long dental plates. Muscle field faintly impressed, not observable.

Interior brachial valve with hinge plates united at their anterior ends, thus forming a perforate hinge plate. Attached at an acute angle to the crura are the primary lamellae of the athyroid spiralium. Between the primary lamellae, a Y-shaped jugum. Each spiral of the spiralium consists of about 10—12 turns.

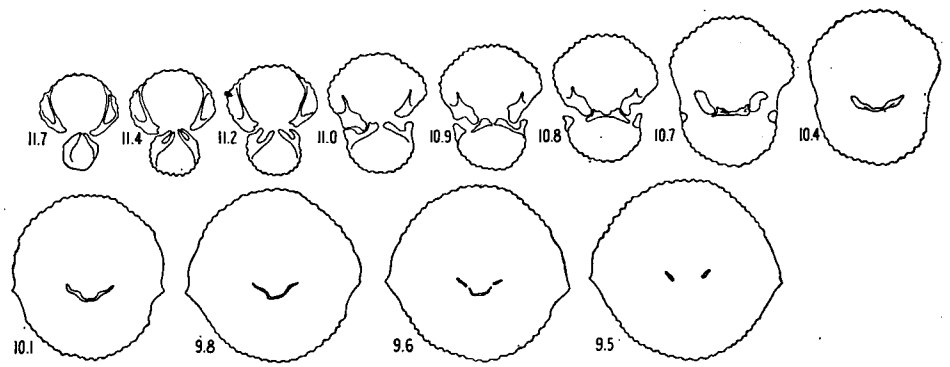

Fig. 26. Transverse serial sections of *Pradoia?* cf. *P. torenoi*. Distance of each section towards the front indicated for each section (× 2).

Remarks. This species shows a resemblance to *Pradoia torenoi*, especially as it appears in the photographs given by Comte. The remarkable papillate surface of *torenoi* is not observable on my material because of the strong decortication of the shell. *Pradoia torenoi* is one of the two species assigned by Comte to his new genus *Pradoia*. Concerning *Pradoia*'s interior, little more is known than its athyroid spiralium. This lack of information makes it impossible to assign my material with certainty to this genus. I have tried to reconstruct the interior of *Pradoia collettei* (de Verneuil, 1850). I had at my disposal specimens from Colle (near Sabero, prov. León), the locality where de Verneuil collected his material. I observed a perforate hinge plate and an athyroid spiralium. Unfortunately, the jugum could not be distinguished because of the recrystallization of the matrix. Consequently, the diagnosis of *Pradoia* is still incomplete and a revision of the type material is needed.

Assuming that my material and *torenoi* are identical, there is a remarkable difference in the stratigraphical occurrence of Verneuil's material and mine. Both species of *Pradoia* are, according to present knowledge, of Lower Emsian age, *P. torenoi* occurring mainly in the northern part of the Cantabrian Mountains (top of

the Ferroñes Formation, prov. Asturias) and *P. collettei* being much more common in the southern part (top of the La Vid Formation, prov. León). The strata in which I collected my material are, in my opinion, of Upper Gedinnian to Lower Siegenian age (see Chapter VI).

Locaties. Arauz.

Occurrence. Lower part of the Lebanza Formation.

Distribution. See under remarks.

CHAPTER VI

AGE OF THE FORMATIONS

Carazo Formation

The oldest sediments that crop out in the area under study totally lack determinable fossils, which prevents an exact determination of their age. I found one fragment of a graptolite, and this might be considered an indication of a Silurian age. Another indication comes from their position in the sequence: because these sediments are overlain by strata containing a typically Gedinnian fauna, they must be of a pre-Gedinnian, and thus possibly Silurian, age. But a precise definition of the Silurian-Devonian boundary is not possible.

The upper member of the Carazo Formation, to the contrary, is richly fossiliferous and its age rather easily established. The brachiopod fauna contains diagnostic forms common to the Lower Gedinnian of Belgium and other regions. *Platyorthis verneuili* (de Koninck, 1876) and *Douvillina* (*Mesodouvillina*) *triculta* (Fuchs, 1919), both considered to be typical Gedinnian forms, occur in abundance. Present but less abundant are *Proschizophoria torifera* (Fuchs, 1919), *Schuchertella euzona* (Fuchs, 1919), *Protathyris* spec. cf. *praecursor* Kozlowski, 1929, and *Howellella* spec. cf. *mercuri* (Gosselet, 1880), all species considered to be of Gedinnian age or younger. The fauna contains no Silurian or older forms, so the age of this part of the formation can be established as Lower Gedinnian.

Lebanza Formation

The Lebanza limestones yield a well-preserved brachiopod fauna which allows an exact determination of its age. The assemblage occurring in the lower part of the formation differs from that in the upper part.

From the basal limestones I collected:

Hysterolites hystericus Schlotheim, 1820
Cryptonella? cf. *minor* (Dahmer, 1931)
Podolella rensselaeroides Kozlowski, 1929
Pradoia? cf. *P. torenoi* (de Verneuil & d'Archiac, 1845)
Athyris spec. cf. *concentrica* (von Buch, 1834)
Hebetoechia cantabrica spec. nov.
Plethorhyncha polentinoi spec. nov.
Douvillina (*Mesodouvillina*) *triculta* (Fuchs, 1919).

Of these forms, *H. hystericus* is commonly considered to be diagnostic for the Siegenian. *C. minor* is also recorded from Siegenian strata. *A. concentrica* is known from Siegenian and younger strata. The genus *Pradoia* has only been found in Emsian strata in León and Asturias. *D. triculta* is a widespread Gedinnian form, while *P. rensselaeroides* is only known from Lower Gedinnian strata in Podolia. The assemblage is thus of a rather mixed character and has no great diagnostic value. Taking the stratigraphical position of these beds into account as well, I think we are justified to establish their age as Upper Gedinnian to Lower Siegenian.

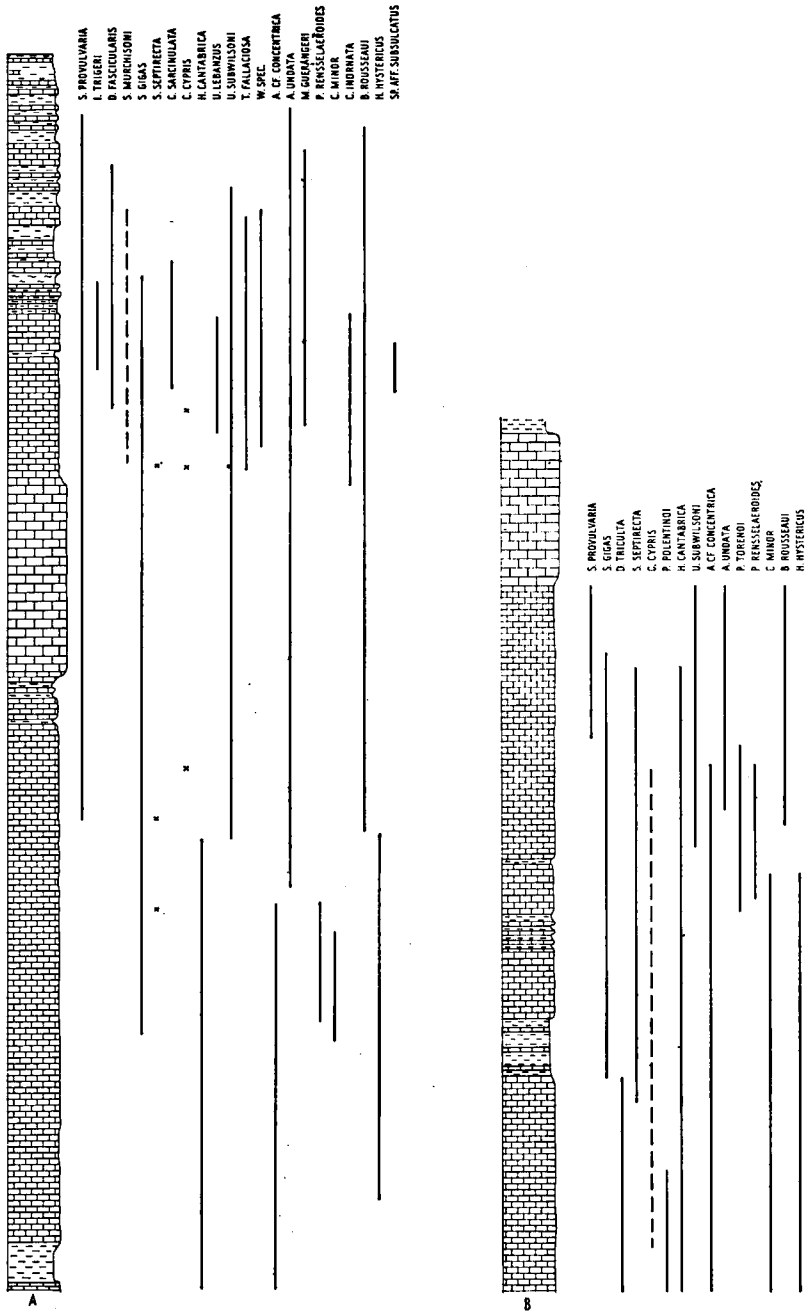

Fig. 27. Distribution of the brachiopods in the Lebanza Formation.
A. Section near Lebanza.
B. Section along the Arauz River.
(Scale 1 : 1.000).

The assemblage found in the middle and upper part of the Lebanza Formation comprises the following species:

"*Spirifer*" spec. aff. *subsulcatus* Barrois, 1889
Brachyspirifer rousseaui (Rouault, 1846)
Cryptonella? inornata (d'Orbigny, 1850)
Mutationella guerangeri (de Verneuil, 1850)
Athyris undata (Defrance, 1828)
Whitfieldella spec.
Trigonirhynchia fallaciosa (Bayle, 1878)
Uncinulus lebanzus spec. nov.
Uncinulus subwilsoni (d'Orbigny, 1850)
Camarotoechia? cypris (d'Orbigny, 1850)
Chonetes sarcinulata (Schlotheim, 1820)
Schellwienella septirecta (Wolf, 1930)
Stropheodonta gigas (Mac Coy, 1852)
Stropheodonta murchisoni (d'Archiac & de Verneuil, 1842)
Dalmanella? fascicularis (d'Orbigny, 1850)
Isorthis trigeri (de Verneuil, 1850)
Schizophoria provulvaria (Maurer, 1886).

All these species are diagnostic Siegenian forms (some forms are also known from Emsian strata). The same characteristic assemblage of species is known from the "Schistes et calcaires à *A. undata* et *Sp. rousseaui*" in the Massif Armoricain (Brittany, France). This formation is regarded as equivalent to the Middle Siegenian of the Ardennes (Renaud 1942, p. 58). Therefore, it is concluded that the upper part of the Lebanza Formation is also of Middle Siegenian age.

CHAPTER VII

CORRELATION WITH ADJACENT AREAS

General remarks

Lower Devonian sediments are widespread throughout the whole of western Europe and western North Africa. This chapter will discuss the correlations between the Lower Devonian sequence cropping out in the northern part of the province of Palencia and sequences in adjacent areas where the faunal succession has affinities to the faunal succession in the area under study. The brachiopods are the most appropriate group for correlative purposes, since this group of fossils is widespread and common in marine strata of Lower Devonian age.

Other parts of the Cantabrian Mountains

Along the southern slope of the Cantabrian Mountain chain, large outcrops of Devonian sediments occur. With the exception of the Upper Devonian their development is quite constant from the Valsurvio Dome in the east to the Luna river in the west, a distance of nearly 100 km. Fossils found in these strata were already studied by de Verneuil and Oehlert in the middle of the last century. In 1934—1939 Comte (1959) made a comprehensive study of the stratigraphy and paleontology of the province of León. His work gives a fairly exact general picture of the Devonian stratigraphy (fig. 28B) and the brachiopod succession in this area.

To the west, the strata can be followed to the regions around the pass of Ventana and the pass of Somiedo. Here the strip of outcropping Devonian sediments bends to the north, thus lying in a great arc around the Carboniferous of the central Asturian basin. The stratigraphic sequence and the faunal succession in Asturias were worked out by Barrois (1882), whose work ("Recherches sur les terrains anciens des Asturies et de la Galice") has become a classic study in stratigraphy. Recently, German investigators under the direction of Prof. F. Lotze (Münster) have undertaken a revision of the Devonian in this area. Some provisional results have been published by Radig (1961, 1962) and Poll (1963). The lithostratigraphic units distinguished by these authors are those of Barrois; only their time-stratigraphic position has been changed. The stratigraphical column of the Lower Devonian rocks is represented in fig. 28C.

The Devonian of León and Asturias being directly connected, it is not surprising that the sequences show great resemblances. According to Comte, the Lower Devonian formations distinguished in the two areas correspond as follows:

Calcaires de Santa Lucia	Calcaires de Moniello
	Calcaires d'Arnao
Calcschistes et calcaires de La Vid	Calcaires de Ferroñes
	Calcaires de Nieva
Grès de San Pedro	Grès de Furada

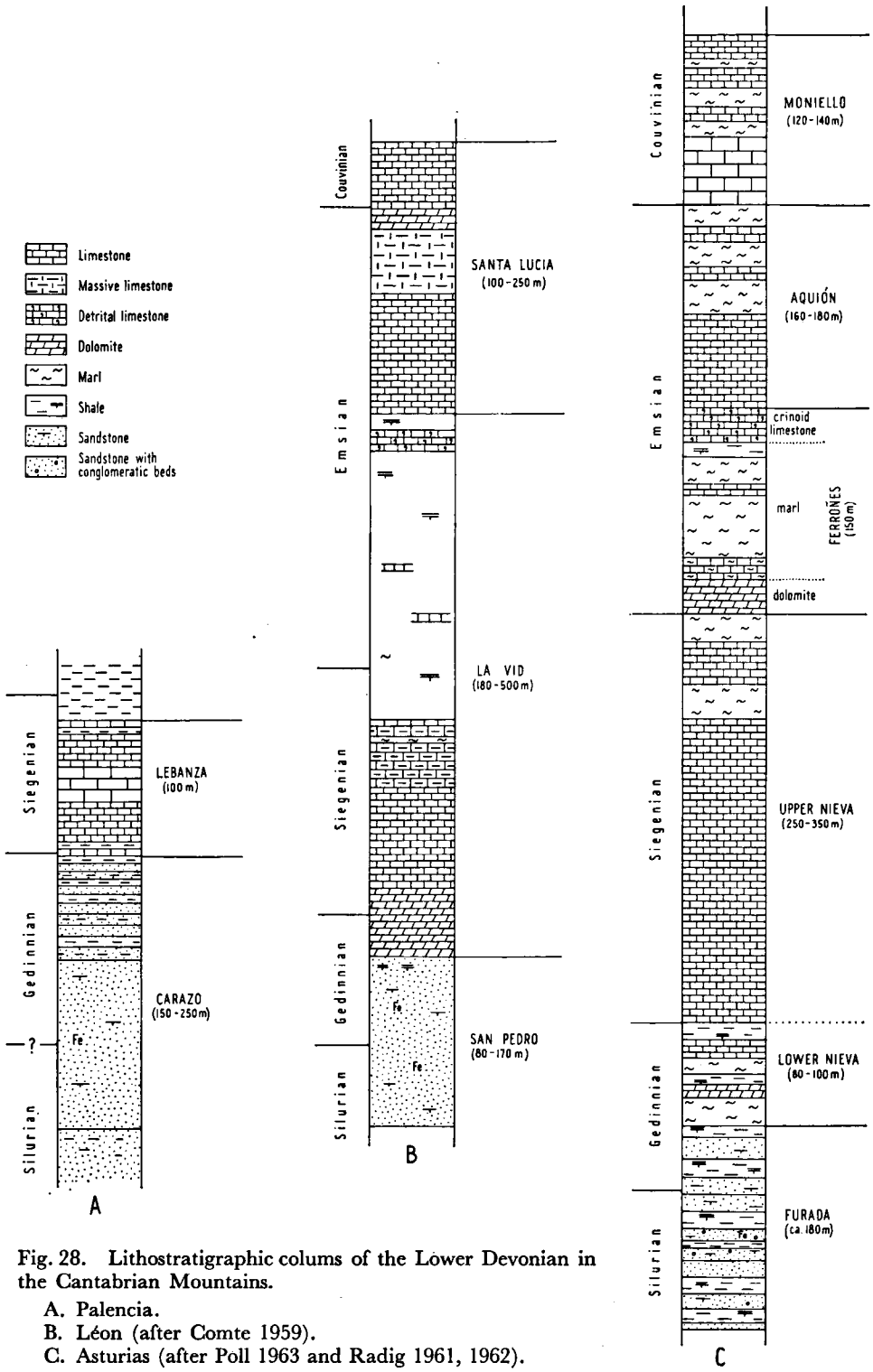

Fig. 28. Lithostratigraphic colums of the Lower Devonian in the Cantabrian Mountains.

A. Palencia.
B. Léon (after Comte 1959).
C. Asturias (after Poll 1963 and Radig 1961, 1962).

Carazo Formation

At the base of the sequence in north Palencia I have found a formation of clastic rocks, sandstones, and shales, in part strongly ferruginous. Similar sediments occur at the base of the Devonian in León (San Pedro Formation) and in Asturias (Furada Formation). Comte (p. 141) remarked with respect to the identity of these last formations: "Ce sont les similutides de faciès et d'identité de position qui rendent cette équivalence évidente, mais on n'a pas trouvé jusqu'ici d'espèces communes à ces deux formations, ce qui s'explique par le fait qu'elles sont peu fossilifères". The same applies to the similarity between the Carazo Formation and the San Pedro and Furada Formations. The lithology of all three formations, clastic ferruginous sediments with furrows and trails as common features, indicates the same facies. I have already noted the identical position of the formations in the lowermost part of the sequences.

A restriction must be made for the upper part of the Carazo Formation. As described, the upper member consists of 75 m of alternating shales and sandstones which contain a rich and well-preserved fauna. This part of the formation does not seem to have its direct counterpart in León and Asturias. Comte (1959, p. 142 and p. 243) indeed mentions a rich fauna in the upper beds of the San Pedro Formation. The characteristic brachiopods in this fauna are the same species I found in the upper member of the Carazo Formation. In León this fossiliferous horizon is very thin, however, and found at only a few localities.

According to Poll (1963, p. 243), the upper part of the Furada Formation is formed by alternating shales and sandstones. Some of these beds contain fossils, mainly brachiopods belonging to the genera *Howellella*, *Mesodouvillina* and *Platyorthis*. Unfortunately, Poll gives no specific assignment, but the genera are the same as those which occur in the upper member of the Carazo Formation. Mainly on the evidence of *Platyorthis*, Poll concluded a Lower Gedinnian age for the upper 30 metres of the Furada Formation. In my opinion, the upper member of the Carazo Formation is of the same age (see Chapter VI).

Summarizing, I note a strong lithological resemblance between the three formations. The brachiopod assemblages present in the upper beds of the formations have species or genera in common, an indication of the chronological equivalence of the formations. A marked difference is that the fossiliferous strata in León and Asturias are much thinner than those in northern Palencia.

Boundary Carazo Formation — Lebanza Formation

The clastic formations are overlain in all the three areas by carbonate rocks (limestones, dolomites, calcareous shales, etc.). In León these rocks are united in the La Vid Formation. The lower part of this formation, about 60 metres of stratified dolomites, yields no fossils.

In Asturias the rocks pass gradually from sandstones and shales to limestones. Barrois named this part of the sequence the Nieva Formation, which is divided by Radig into a lower and upper part. From the lower part, consisting of about 50 to 100 m of dolomites and marls, he mentions a rich fauna without any further determination. He assigns a Gedinnian age to these sediments; Poll places them in the Upper Gedinnian.

The same age is given by Comte to the dolomites at the base of the La Vid Formation. He does so because of their stratigraphical position, for they are overlain by limestones in which *Hysterolites hystericus* occurs. This species is also found in the

basal beds of the Upper Nieva Formation. It indicates a Siegenian age, so the underlying strata must be placed in the Gedinnian.

In Palencia I found *Hysterolites hystericus* in the basal beds of the Lebanza Formation, i.e. immediately above the Carazo Formation with its characteristic fauna of *Douvillina triculta* and other brachiopods. Comparing the three sequences we see:

Palencia	Asturias and León
limestones with *Hysterolites hystericus*	
75 m sandstones and shales with *D. triculta*	50 to 100 m dolomites and marls a few meters of shales with *D. triculta*

Taking the horizon with *Hysterolites hystericus* as being of the same age over the whole area, I conclude the chronological equivalence of the dolomites and marls in León and Asturias to the upper part of the sandstones and shales in Palencia since the sequences are continuous. This also explains the difference observed in the thickness of the beds containing *Douvillina triculta* in the Asturo-Leonesian region and in Palencia.

Lebanza Formation

Lithologically, the beds with *Hysterolites hystericus* and the overlying strata show a strong resemblance. Stratified limestones dominate in all the three areas. Paleontologically, however, we find less resemblance. Even in the field a remarkable difference can be observed in the fossil content of the beds. The rocks of the Lebanza Formation are abundantly fossiliferous and sometimes even built up of fossils. The strata of the La Vid Formation contain fossils, but they are scattered through the sediment. According to Radig (1961, p. 253), the fossils of the Upper Nieva Formation are "insgesamt dürftig" (altogether scarce).

The same groups of fossils occur in all three areas. Brachiopods dominate, and besides this group there are trilobites, pelecypods, tentaculites, corals, stromatoporoids, and crinoid fragments. Lack of determinations make it impossible to say whether there are any differences or similarities in the species of these last groups.

Even comparison of the species of the best-known group, the brachiopods, is hindered by incomplete knowledge. For Asturias we have only the determinations made by Barrois about hundred years ago. For León, Comte gives an extensive list of species found in the La Vid Formation but, judging from my own observations of material collected by students from Leiden, this list seems to me somewhat too extensive. For example, the occurrence of typical Bohemian species (*Uncinulus princeps, U. henrici*, and others) seems highly doubtful. But in spite of all these handicaps, I still note some remarkable differences between the species of the La Vid and Lebanza limestones.

Comte gives the following list of species occurring in the limestones of the La Vid Formation (in his tableau II, p. 245, Comte subdivides the formation into three members; member α and part of β represent the limestones):

P. personata, S. vulvaria, D. circularis, paillata, gervillei, fascicularis, L. rhomboidalis, S. sedgwicki, herculea, murchisoni, cf. *elegans, davousti, explanata, S. hipponyx, C. sarcinulatus* var., *P. davyi, C. cypris, daleidensis, W. subwilsoni, U. princeps, frontecostatus, henrici, M. spec., T. oliviani, guerangeri, Sp. primaevus, fallax, hystericus, subsulcatus, cabanillas, baylei, rousseaui, cabedanus, togatus, subspeciosus, arduennensis, trigeri, A. avirostris, undata, subconcentrica.*

On the evidence of this fauna and its affinities to the fauna of the Ardennes, Comte concludes a Lower and Middle Siegenian age for the limestones.

If we compare this list of 40 species with the 25 species found in the Lebanza limestones (see Ch. VI) we see that the two assemblages have only ten species in common. Of these common species, *Brachyspirifer rousseaui*, *Athyris undata*, and *Uncinulus subwilsoni* form only a minor element of the La Vid fauna but dominate among the species of Lebanza.

Summarizing, I may conclude:

(1) chronologically, the Lebanza and La Vid limestones are equivalent; lithologically, the formations are also identical.

(2) the faunas are composed of the same groups, but the number of specimens in the Lebanza Formation exceeds by far the number in the La Vid Formation.

As for the brachiopods, the two formations have nearly no species in common in spite of their identical age. For the other groups of fossils, specific resemblance or difference has still to be examined.

Massif Armoricain (Brittany, France)

The Devonian of the Massif Armoricain transgressively overlies strata of Lower Paleozoic age. The main outcrops of the very thick Lower Devonian are found in the cores of three E-W synclinoriums, namely, from north to south, the "Synclinorium médian", the "Synclinorium d'Angers—St.-Julien-de-Vouvantes", and the "Synclinorium d'Ancenis". Péneau (1962) demonstrated a transgression from north to south, reaching the synclinorium of Angers in the Siegenian and the synclinorium of Ancenis in the Emsian.

A continuous sequence from Silurian to Devonian is found in the synclinorium médian. A comprehensive study of the stratigraphy and paleontology was made by Renaud (1942). The strata are very rich in fossils, with the brachiopods as the dominating element of the fauna. The oldest strata are the most constantly developed. Higher in the sequence the thickness decreases and the sediments show great lateral variation.

Péneau (1962) gives the following stratigraphy for the synclinorium médian and the synclinorium of Angers:

	Syncl. médian	Syncl. d'Angers
Emsien	Schistes et calcaires à Sp. decheni	Calcaires d'Angers (= calcaires d'Erbray) à Sp. decheni
Siegenien	Schistes et calcaires à Athyris undata et Sp. rousseaui	Schistes et calcschistes d'Angers (= calcaires de Vern) à Athyris undata et Sp. rousseaui
	Grès à Dalmanella monnieri	Grès à Dalmanella monnieri
Gedinnien	Schistes et quartzites de Plougastel	Hiatus

Schistes et quartzites de Plougastel

This formation reaches the greatest thickness of all the formations of the Massif Armoricain. It has the same lithology as the Carazo Formation, namely shales and hard quartzites standing out in the field because of their great resistance. A difference is the absence of Fe in the formation of Plougastel. Since both the Carazo and Plougastel quartzites lack fossils there are no paleontological data for correlation. The two formations do have the same position, namely at the base of the Devonian.

Grès à Dalmanella monnieri

This formation is widespread in the whole Massif Armoricain. Its lithology — quartzitic sandstones, sometimes ferruginous — and its rich fossil content are similar to the lithology and fossil content of the upper member of the Carazo Formation. However, the fauna of the Grès à *Dalmanella monnieri* indicates a Lower Siegenian age, whereas the fauna of the Carazo Formation is of a Lower Gedinnian age.

Schistes et calcaires à Athyris undata

In a complete succession, the Grès à *Dalmanella monnieri* are followed by a richly fossiliferous formation of shales and limestones. This formation is found in the whole Massif Armoricain. The limestones, developed as lenses in the shales, vary in thickness.

Among the fossils the brachiopods are especially abundant; Renaud gives long lists of species. It appears that all the species I was able to determine in the upper part of the Lebanza limestones also occur in these "schistes et calcaires à *Athyris undata*". This remarkable resemblance is strengthened by the fact that some of these species are only known from the Massif Armoricain and Palencia (*Dalmanella fascicularis*, *Isorthis trigeri*, *Uncinulus subwilsoni*, *Trigonirhynchia fallaciosa*, and *Cryptonella inornata*). In addition, the abundance of *Brachyspirifer rousseaui* and *Athyris undata* among the brachiopods is very similar in the two regions, as I observed during a visit to Rennes and Nantes, where large collections of fossils from the Massif Armoricain are stored. The number of species occurring in the "schistes et calcaires à *A. undata*" greatly exceeds the number of species in the Lebanza limestones. This difference can be explained by the greater size of the French collections, which were assembled over many years and have been studied by many famous paleontologists.

Pyrenees

In various parts of the Pyrenees, Devonian strata crop out. Laverdière (1930) studied the succession of Devonian sediments and their paleontology in the western part of this mountain chain. The Lower Devonian, following the Silurian without any discontinuity, consists mainly of detrital sediments ("grauwackes", shales, and quartzites). Higher in the succession (Emsian and Middle Devonian), calcareous shales and limestones also occur. The Gedinnian age of the lowest strata is ascribed mainly on the basis of the occurrence of *Douvillina triculta*. A second fossil horizon is characterized by *Hysterolites hystericus*, indicating a Siegenian age. Laverdière places this strata in the Upper Gedinnian. This part of the sequence shows both lithologically and paleontologically a rather marked similarity to the oldest Devonian strata in the Cantabrian Mountains, both in the Asturo-Leonesian region and in northern Palencia. The strata to which Laverdière assigns an Upper Siegenian and Emsian age show great affinities to the succession in the Asturo-Leonesian region, as has

	LEÓN	ASTURIAS	PALENCIA	MASSIF ARMORICAIN
Emsian	SANTA LUCIA	AGUION		
	red detrital limestone	crinoid limestone	ABADIA	Schistes et calcaires à Sp. decheni
	shales and marls	limestones and marls		
		FERRONES		
Siegenian	LA VID	dolomite		Schistes et calcaires à A. undata et Sp. rousseaui
	limestones	UPPER NIEVA	LEBANZA	Grès à D. monnieri
	dolomites	LOWER NIEVA		
Gedinnian			c	Schistes et quartzites de Plougastel
Silurian	SAN PEDRO	FURADA	CARAZO b	
			a	

Fig. 29. Correlation of the Lower Devonian Formations in León, Asturias, Palencia, and the Massif Armoricain.

already been mentioned by Laverdière (1930, p. 57) and Comte (1959, p. 322). The facies of limestones alternating with shales, and the fauna of brachiopods, corals, and stromatoporoids is very similar to the facies and fauna of the Nieva, Ferroñes, and La Vid Formations. Among the brachiopods are various species that are characteristic for the Asturo-Leonesian region and none of the species characteristic for the Lebanza limestone.

Mirouse (1962) studied the Devonian strata of the western part of the axial zone of the Pyrenees. The strata in this area are also detrital in character, with only locally intercalated limestones. Gedinnian has not been proven, since the lowest strata have so far yielded no fossils. Hence, it is still doubtful whether the Devonian follows the Silurian with no hiatus. The brachiopod species mentioned by Mirouse higher in the sequence show a similarity to the faunas of the La Vid Formation and the Ferroñes Formation.

North Africa

Marine Lower Devonian is found in the western parts of North Africa. General summaries of the stratigraphy and paleontology have been published by Termier (1936), Choubert (1952), Alimen c.s. (1952), and Hollard (1960).

Gedinnian has not yet been proven. A continuous sedimentation from Silurian

to Devonian does seem likely at some places, but the age of these sediments could not be determined because they have yielded no fossils so far.

The Siegenian and Emsian strata, however, are richly fossiliferous. We will discuss only the Siegenian outcrops.

Along the southern border of the Anti-Atlas, Hollard distinguishes two regions with a different facies: in the western part a facies with shales and sandstones with a brachiopod fauna showing great affinity to the Spanish brachiopods of the Asturo Leonesian region; in the east (Maïder—Tafilalelt region) the sequence is build up of carbonate rocks with trilobites as the main constituent of the fauna. Hollard compares the western facies with the Ardennes-Rhine facies and the eastern with the Bohemian-Hercynian facies.

Lower Devonian sediments also crop out in South Oran in the mountain chain of Ougarta and along the Oued Saoura. Le Maitre studied the rich faunas from this region (Le Maitre 1952; also in Alimen c.s. 1952). The succession starts with unfossiliferous detrital sediments (shales and reddish micaceous sandstones, sometimes ferruginous). Some limestone beds on top of this series contain fossils indicating a Siegenian age. Next follows an alternation of limestones and shales with a fauna of brachiopods, corals, and trilobites, of Siegenian age. The brachiopod assemblage is very similar to the assemblage found in the Siegenian strata in León and Asturias.

South of this region, at the western edge of Erg Djemel, however, sandy limestones contain a brachiopod fauna which resembles the Lebanza fauna. The main elements are *Brachyspirifer rousseaui*, *Athyris undata*, and *Cryptonella inornata*. The first two species occur abundantly.

In Central Morocco, Termier (1936) mentions Siegenian strata resembling the equivalent strata in León and Asturias both lithologically and paleontologically.

Conclusions

From the preceding correlation of the sequences in Palencia and other parts of the Cantabrian Mountains we may conclude that during the Devonian there must have been two important facies zones in this part of Spain.

During the transition from Silurian to Devonian, the lithological and paleontological characteristics of the sediments were identical in the whole mountain chain. Llopis Lladó (1958) interpreted these clastic, ferruginous sediments as deposited under continental or littoral conditions. According to Comte (1959, p. 79), the deposition of the detrital sediments of the San Pedro Formation took place at no great depth. The occurrence of similar sediments and identical faunas indicate that the same facies prevailed during those times in all of western Europe and northwestern Africa.

The Siegenian strata still show a uniform lithology throughout the whole Cantabric Mountain chain. The presence of different species, however, indicates a differentation into two regions: an Asturo-Leonesian region and a Palencian region.

The strata of Emsian and younger age are lithologically entirely different in the Asturo-Leonesian region and in Palencia. In León and Asturias the succession is build up of an alternation of sandstones and shales on the one hand and of limestones on the other. Paleontologically, the succession is characterized by brachiopods, bryozoans, crinoids, stromatoporoids, and corals. The main elements of the sequence in Palencia are shales, fine-grained argillaceous limestones, and marls with a fauna consisting of ammonoids, tentaculites, pelecypods, trilobites, and conodonts. Brouwer (1962, 1964) named these two areas the Asturo-Leonesian facies and the Palencian facies. All the characters of the Asturo-Leonesian facies are indicative of deposition in

shallow water (benthonic fauna, potentially reef-building), while the Palencian succession probably developed in somewhat deeper water further away from the shore (pelagic fauna). Brouwer compared these two facies types with the Rhenish facies and the Bohemian (or Hercynian) facies, long known in the Variscan geosyncline. Erben (1962) made an analysis of these two facies types and suggested as a possible explanation a difference in distance to the shore with consequent differences in sedimentation of terrigenous material, resulting in the occurrence of different faunas.

As stated above, such differences were not so markedly developed during Siegenian and Gedinnian times. However, an initial differentation during Siegenian times is apparent. It therefore seems justified to explain the occurrence of different brachiopod species in the Asturo-Leonesian region and the Palencian region as due to a difference in water depth and other oecological features. The occurrence of a "Palencian" assemblage in other parts of western Europe and North Africa favours such an explanation. Apparently, the distribution of species was not controlled by geographical factors but by oecological features. Unfortunately, very little is known about the dependence of brachiopods on environmental conditions. Erben (1962, p. 47) mentions for the brachiopods not only a difference in species but also a more frequent occurrence of smooth forms in the Hercynian facies (deep water) in contrast to a more frequent occurrence of strongly costated forms in the Rhenish facies (shallow water). The same phenomenon can be observed in the Middle Siegenian faunas in Spain (*C. inornata*, *C. minor*, *Whitfieldella* spec., and *A. undata* abundant in the Lebanza limestones and scarce or unknown in the La Vid limestones).

RESUMÉ

Dans le Nord de la province de Palencia (Espagne) affleure une succession continue, constituée des sédiments devoniens. L'objet de ce travail est l'étude de la stratigraphie et de la paléontologie des assises du Dévonien inférieur. On peut distinguer dans ces sédiments deux formations, la Formation de Carazo et la Formation de Lebanza.

La Formation de Carazo, comprenant des sédiments clastiques se divise, de haut en bas, en trois parties: (*c*) une alternance des lits grèseux et schisteux; (*b*) grès quartzitiques, sur place très ferrugineux; (*a*) schistes et grès micacés. Les parties *a* et *b* n'ont pas fournit de fossiles, tandis que la faune de la partie *c* est très riche. On y trouve surtout des Brachiopodes, d'autres des Tentaculites, Trilobites, Ostracodes et Lamellibranches. Les Brachiopodes indiquent un âge du Gédinnien inférieur. Quelques exemplaires caractéristiques et bien conservés ont été figurés.

La Formation de Lebanza est constituée des calcaires stratifiés, atteignant une épaisseur d'une centaine de mètres. Au sommet et à la base de la formation on rencontre des couches schisteuses. Cette assise est extrêmement riche en fossiles. Les Brachiopodes sont les plus abondants, on y trouve aussi des Tentaculites, Trilobites, Lamellibranches, Coraux, Stromatopores et articles de Crinoïdes.

Les diagnoses et les positions systématiques de 18 des espèces de Brachiopodes ont été étudiées: 3 Dalmanelles, 7 Rhynchonelles, parmi lesquels 3 espèces nouvelles, 4 Terebratules et 4 Rostrospirides. Une attention spéciale a été consacrée aux caractères internes, étudiés par des sections successives et par la technique des "peelings". Chaque diagnose est accompagné par des figures montrant les sections les plus importantes.

La faune comprend 25 espèces de Brachiopodes. La partie inférieure de la formation renferme une association peu indicative pour l'âge de ces couches. La position stratigraphique montre que ces couches appartiennent au Gédinnien supérieur et au Siegenien inférieur. La faune de la partie supérieure comporte des espèces caractéristiques pour le Siegenien. Cette faune offre d'étroites relations avec celles des formations du Siegenien moyen ("Calcaires à *Athyris undata* et *Spirifer rousseaui*") des Régions Armoricaines. Ces relations permettent de préciser l'âge de cette assise comme Siegenien moyen.

Les relations du Dévonien de Palencia avec le Dévonien des régions adjacentes ont été discutées. On trouve une différence nette avec la succession des Brachiopodes des autres régions des Montagnes Cantabriques, probablement due à une différence de facies.

SUMARIO

Una serie contínua de capas devónicas aflora en la parte norte de la provincia de Palencia, en las laderas meridionales de las montañas cantábrico-asturianas. El presente artículo trata la paleontología y estratigrafía de las dos formaciones más viejas en esta serie.

En la base de la serie se halla una formación clástica, llamada la Formación de Carazo, que se puede ser subdivida en tres miembros (de arriba a abajo): (*c*) pizarras y areniscas alternantes; (*b*) areniscas cuarzosas, en parte ferruginosas; (*a*) pizarras y areniscas. Los miembros *a* y *b* no han rendido fósiles. La parte superior de la formación contiene abundante cantidad de fósiles. El elemento mas importante son Braquiópodos, que ocurren juntos con Tentaculites, Trilobites, Ostracodas y Pelecipodas. La fauna indica una edad del Gediniense inferior para estas capas. Aquí se reproducen los Braquiópodos característicos y bien conservados.

La siguiente unidad litológica, llamada la Formación de Lebanza, se compone de unos cien metros de calizas con intercalaciones de pizarras en las partes inferior y superior de la formación. Las rocas de esta formación son extremadamente fosilíferas; dominan los Braquió-

podos y además ocurren Tentaculites, Trilobites, Briozoarios, Pelecipodos, Corales, Estromatoporoideos y troncos de Crinoideos.

La diagnosis y la posición sistematica de 18 especies de los Braquiópodos ha sido tratado. Atención especial ha sido centrada a la estructura interna que fué estudiada con secciones seriales con uso de la técnica de los "peels". Se presentan dibujos de las secciones mas importantes en cada diagnosis.

En total 25 especies fueron determinadas. En la parte inferior y superior de la formación distintas asociaciones ocurren. La asociación que se halla en la parte inferior no presenta precisas indicaciones sobre la edad de estas rocas. Tomando en cuenta tambien la posición estratigráfica puede concluirse una edad del Gediniense superior y Siegeniense inferior. En la parte superior ocurren especies típicos para el Siegeniense. Esta fauna corresponde a las faunas del Siegeniense medio de las regiones armoricanas (Francia).

Una correlación del Devónico con las zonas adyacentes enseña una diferencia marcada con la repartición de los Braquiópodos en regiones vecinas en las Montañas Cantábricas. Probablemente estas diferencias pueden explicarse como debidas a factores ecológicos.

ZUSAMMENFASSUNG

Eine lückenlose Abfolge devonischer Sedimente ist im nördlichen Teil der Provinz Palencia (Spanien) an den Südhängen des Kantabrischen Gebirges aufgeschlossen. Die vorliegende Arbeit behandelt die Stratigraphie und Paläontologie der beiden ältesten Schichtkomplexe dieser Abfolge.

An der Basis befinden sich die klastischen Carazo-Schichten. Diese Einheit kann in drei Schichtglieder unterteilt werden (von oben nach unten): (*c*) Wechselfolge von Tonschiefern und Sandsteinen; (*b*) quarzitische Sandsteine, manchmal stark eisenhaltig; (*a*) Tonschiefer und Glimmersandsteine. Die Schichtglieder *a* und *b* ergaben keine Fossilien. Der obere Teil des Komplexes ist dagegen sehr reich an Fossilien. Brachiopoden sind sehr zahlreich. Sie kommen zusammen mit Tentaculiten, Trilobiten, Ostracoden und Pelecypoden vor. Nur die Brachiopoden werden abgebildet. Die Fauna weist für diese Schichten auf das Unter-Gedinne hin.

Die nächste lithologische Einheit sind die Lebanza-Schichten. Diese bestehen aus ungefähr 100 m gut geschichteten Kalken mit Tonschiefereinlagerungen im unteren und oberen Teil. Diese Schichten sind sehr fossilreich. Brachiopoden herrschen vor; ausserdem kommen Tentaculiten, Trilobiten, Pelecypoden, Korallen, Stromatoporen und Crinoidenstielglieder vor.

Beschreibung und systematische Stellung von 18 der vorkommenden Brachiopoden werden behandelt: 3 Dalmanelliden, 7 Rhynchonelloiden, davon 3 neue Arten, 4 Terebratuloiden und 4 Rostrospiriden. Besondere Aufmerksamkeit wird der inneren Struktur gewidmet, die in Serienschnitten mit Gebrauch der "peel" Technik studiert wurde. Zeichnungen der wichtigsten Schnitte werden jeder Beschreibung hinzugefügt.

Insgesamt wurden 25 Brachiopodenarten bestimmt. Es kommen verschiedene Gemeinschaften im oberen und unteren Teil des Komplexes vor. Die Artengemeinschaft im unteren Teil gibt keine definitiven Hinweise für das Alter dieser Schichten. Unter Berücksichtigung ihrer stratigraphischen Lage wird auf ein Ober-Gedinne bis Unter-Siegen Alter geschlossen. Im oberen Teil kommen nur Arten vor, die charakteristisch für das Siegen sind. Auf Grund der Ähnlichkeit mit Faunen vom Mittel-Siegen des Armorikanischen Massifs (Bretagne, Frankreich) kann das Alter dieser Schichten als Mittel-Siegen festgestellt werden.

Die Korrelationen mit Abfolgen in benachbarten Gebieten werden besprochen; hierbei hat sich ein markanter Unterschied mit den Brachiopoden in angrenzenden Teilen des Kantabrischen Gebirges herausgestellt. Diese Unterschiede müssen ökologischen Faktoren zugeschrieben werden.

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PLATES

PLATE I

a = pedicle view
b = brachial view
c = lateral view

Figs. 1—2 *Dalmanella? fascicularis* (d'Orbigny, 1850) . . . . . p. 18
Both specimens from Lebanza. Siegenian.
fig. 1 specimen 101
fig. 2 specimen 102

Figs. 3—5 *Isorthis trigeri* (de Verneuil, 1850) . . . . . p. 21
All the specimens from Lebanza. Siegenian.
fig. 3 specimen 103
fig. 4 specimen 104
fig. 5 specimen 105

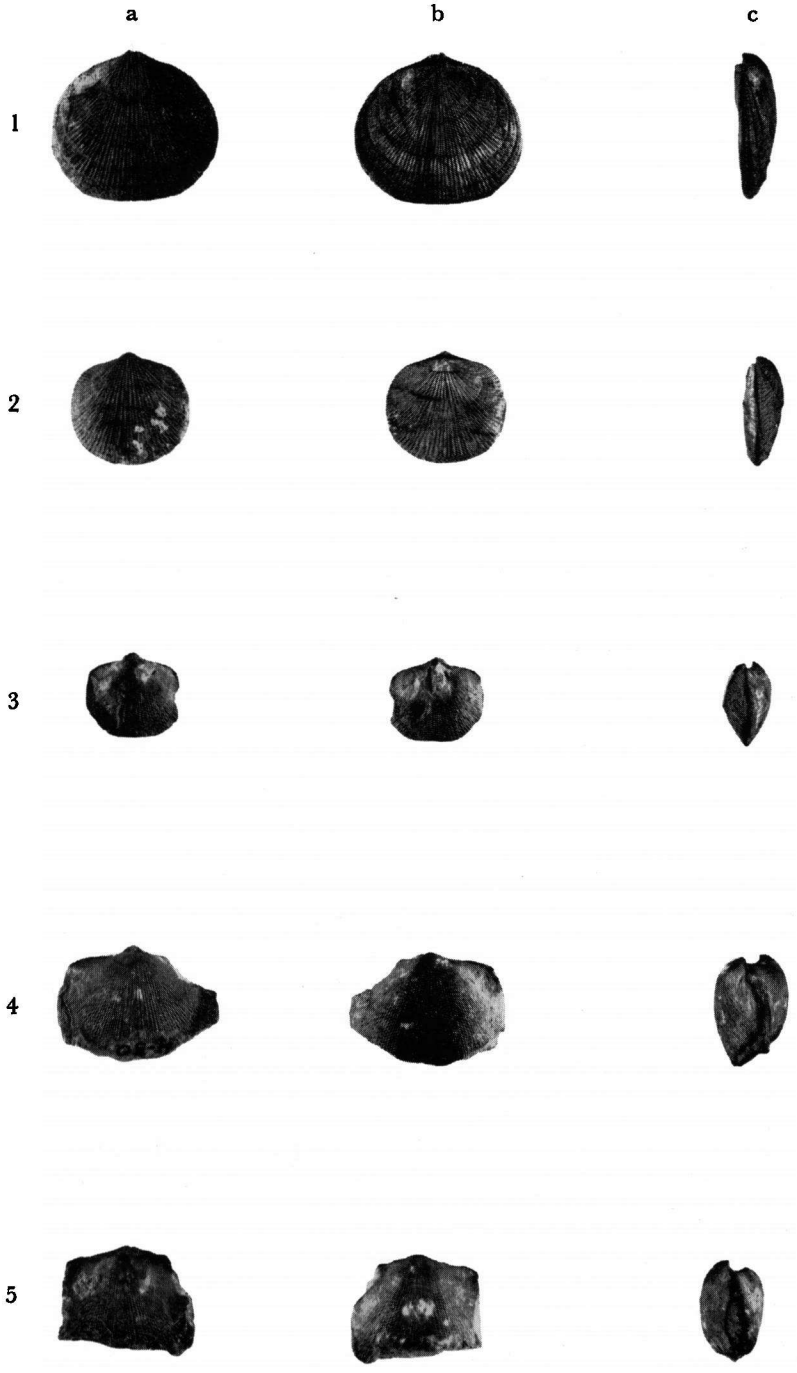
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PLATE II

a = pedicle view
b = brachial view
c = frontal view

Schizophoria provulvaria (Maurer, 1886) . . . . . p. 19

All the specimens from Lebanza. Siegenian.

fig. 1 specimen 106
fig. 2 specimen 107
fig. 3 specimen 108 (shell removed)
fig. 4 specimen 109 (shell removed)
fig. 4c transverse section of cardinal process; photograph from peel nr. 386 (about 15 ×)

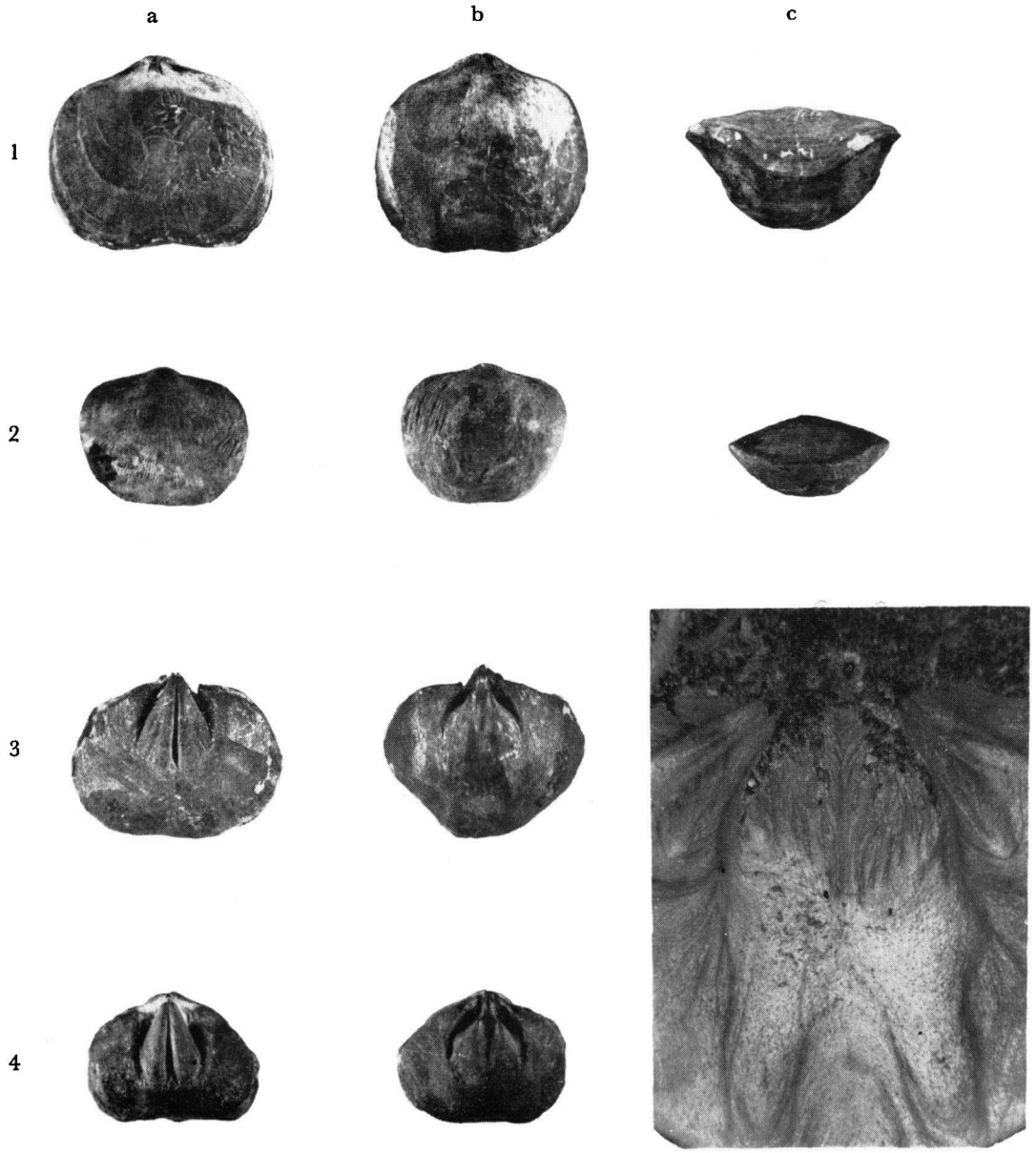
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PLATE III

a = pedicle view
b = brachial view
c = lateral view
d = frontal view

Figs. 1—3 *Uncinulus subwilsoni* (d'Orbigny, 1850) . . . . . p. 23
All the specimens from Lebanza. Siegenian.
fig. 1 specimen 110
fig. 2 specimen 111
fig. 3 specimen 112 (shell removed)
fig. 3c transverse section of brachial valve, showing the cardinal process; photograph from peel nr. 110—14.1 (about 25 ×)

Figs. 4—5 *Uncinulus lebanzus* spec. nov. . . . . p. 24
Both specimens from Lebanza. Siegenian.
fig. 4 specimen 113 (holotype)
fig. 5 specimen 114

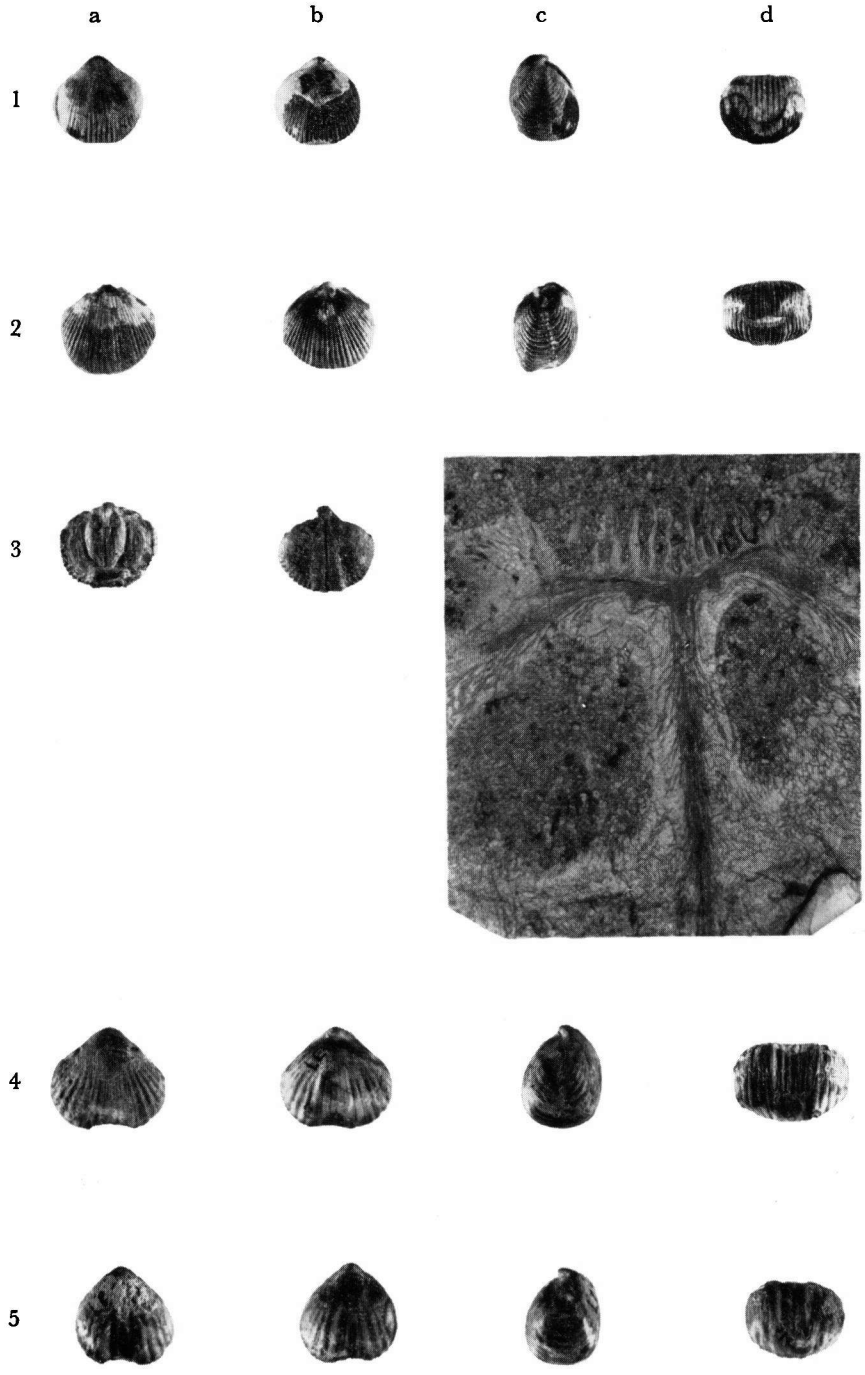
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PLATE IV

a = pedicle view
b = brachial view
c = lateral view
d = frontal view

Figs. 1—2 *Uncinulus lebanzus* spec. nov. . . . . p. 24
fig. 1 specimen 115 (shell removed). Lebanza. Siegenian.
fig. 2 transverse section of brachial valve, showing the cardinal process; photograph from peel nr. 104—11.0 (about 25 ×)

Figs. 3—5 *Hebetoechia cantabrica* spec. nov. . . . . p. 25
All the specimens from Lebanza. Lower Siegenian - Upper Gedinnian.
fig. 3 specimen 116 (holotype)
fig. 4 specimen 117
fig. 5 specimen 118 (shell removed)

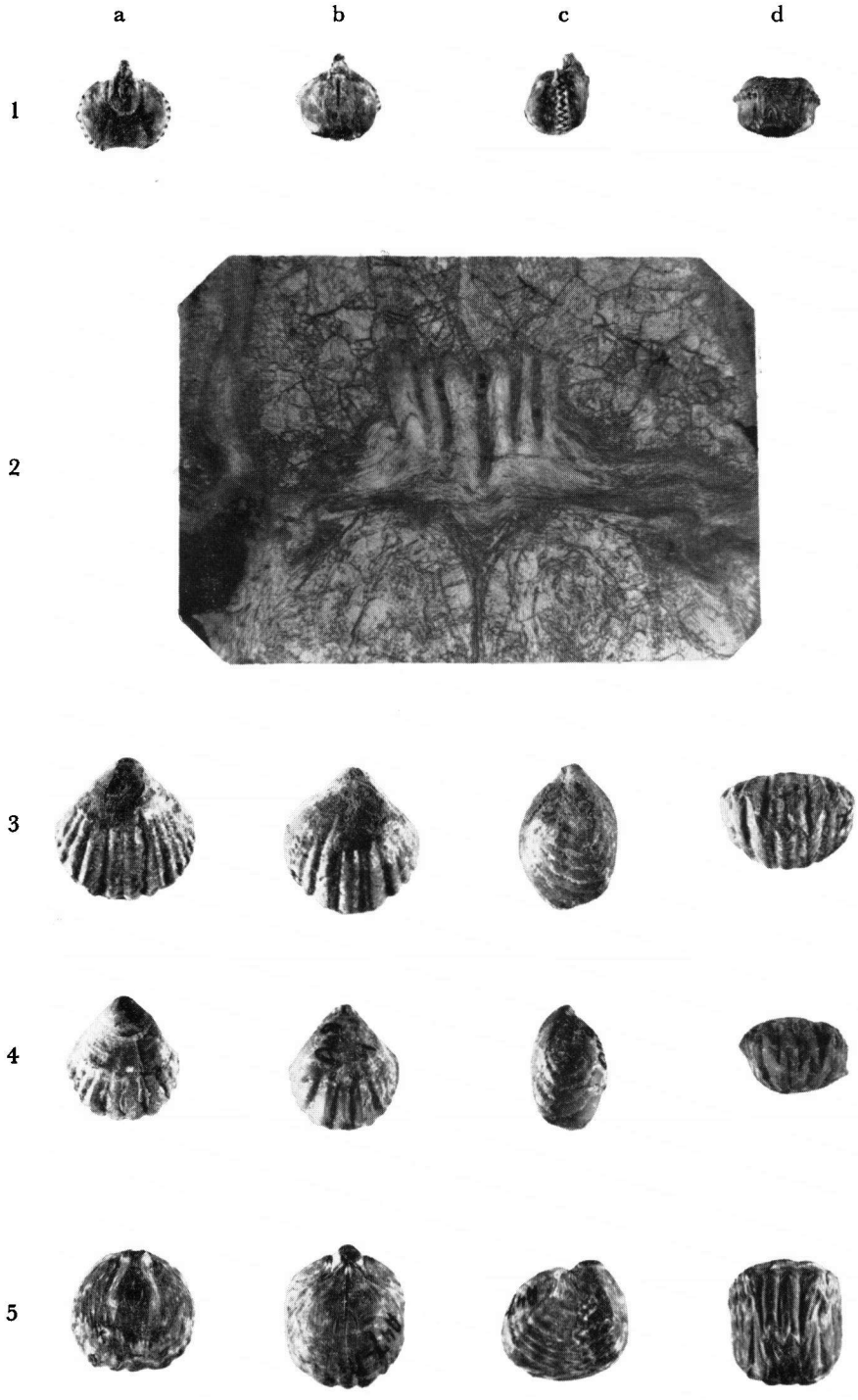
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PLATE V

a = pedicle view
b = brachial view
c = lateral view
d = frontal view

Figs. 1—3 *Plethorhyncha polentinoi* spec. nov. . . . . p. 27
All the specimens from the locality Arauz. Lower Siegenian - Upper Gedinnian.
fig. 1 specimen 119 (holotype)
fig. 2 specimen 120
fig. 3a specimen 120a (shell removed)
fig. 3b specimen 121 (shell removed)

Fig. 4 *Camarotoechia? cypris* (d'Orbigny, 1850) . . . . . p. 28
Specimen 122. Lebanza. Siegenian.

Figs. 5—6 *Mutationella guerangeri* (de Verneuil, 1850) . . . . . p. 31
Both specimens from Lebanza. Siegenian.
fig. 5 specimen 123
fig. 6 specimen 124


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PLATE VI

a = pedicle view
b = brachial view
c = lateral view
d = frontal view

Figs. 1—4a *Trigonirhynchia fallaciosa* (Bayle, 1878) . . . . . p. 30
Series of three specimens showing development of sulcus during ontogeny.
All specimens from Lebanza. Siegenian.
fig. 1 specimen 125
fig. 2 specimen 126
fig. 3 specimen 127
fig. 4a transverse section of brachial valve, showing the covered septalium; photograph from peel nr. 213 (about 14 ×)

Fig. 4b *Mutationella guerangeri* (de Verneuil, 1850) . . . . . p. 31
Reconstruction of the loop by a longitudinal section parallel to the plane of the valves; photograph from peel nr. 237-4 (about 7 ×)

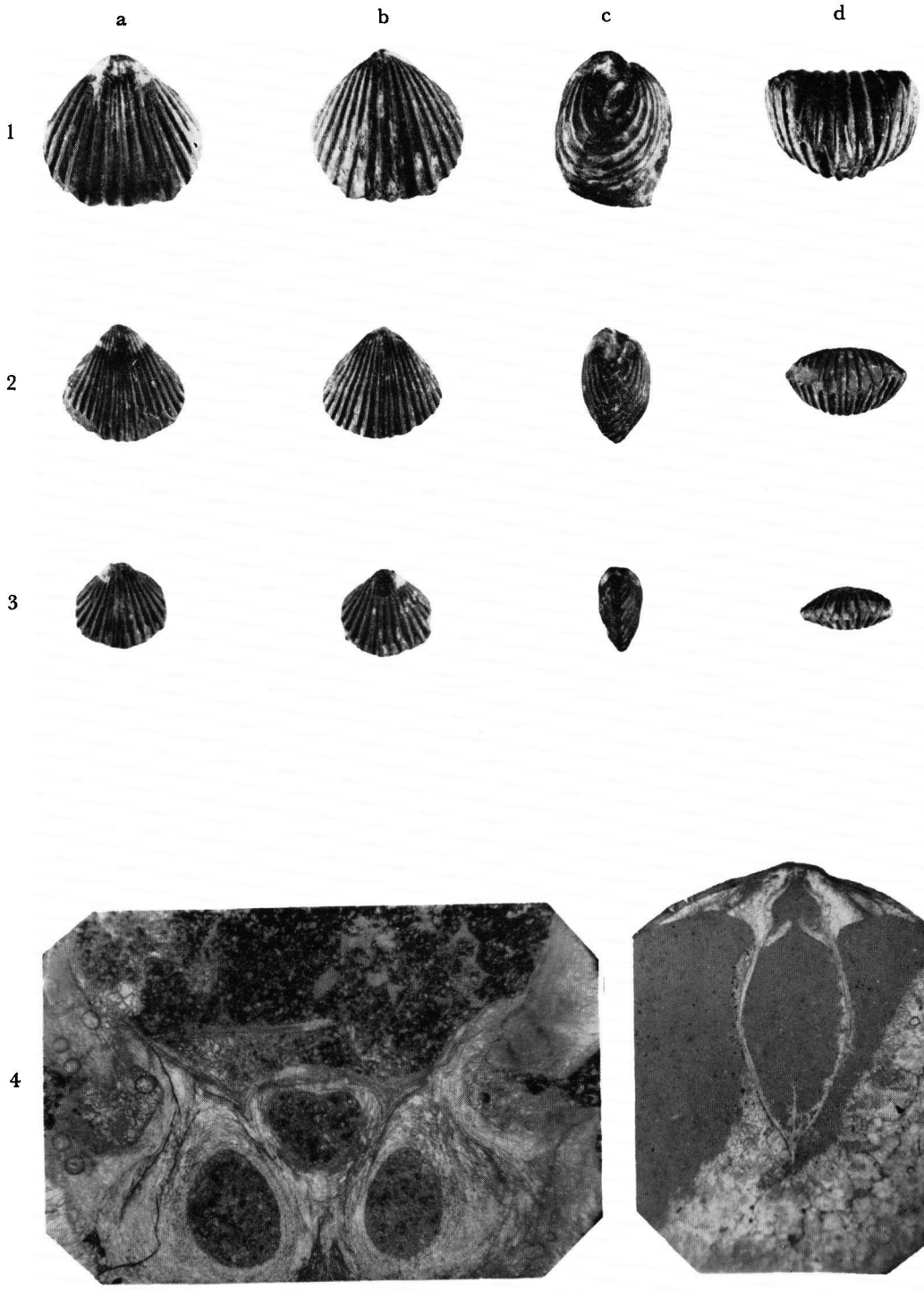
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PLATE VII

a = pedicle view
b = brachial view
c = lateral view

Figs. 1—4 *Podolella rensselaeroides* Kozlowski, 1929 . . . . . p. 34
Series of four specimens showing increasing depth of pedicle valve. All the specimens from Lebanza. Lower Siegenian - Upper Gedinnian.
fig. 1 specimen 128
fig. 2 specimen 129
fig. 3 specimen 130
fig. 4 specimen 131

Figs. 5—6 *Cryptonella?* cf. *minor* Dahmer, 1931 . . . . . p. 38
Both specimens from the locality Arauz. Lower Siegenian - Upper Gedinnian.
fig. 5 specimen 132
fig. 6 specimen 133

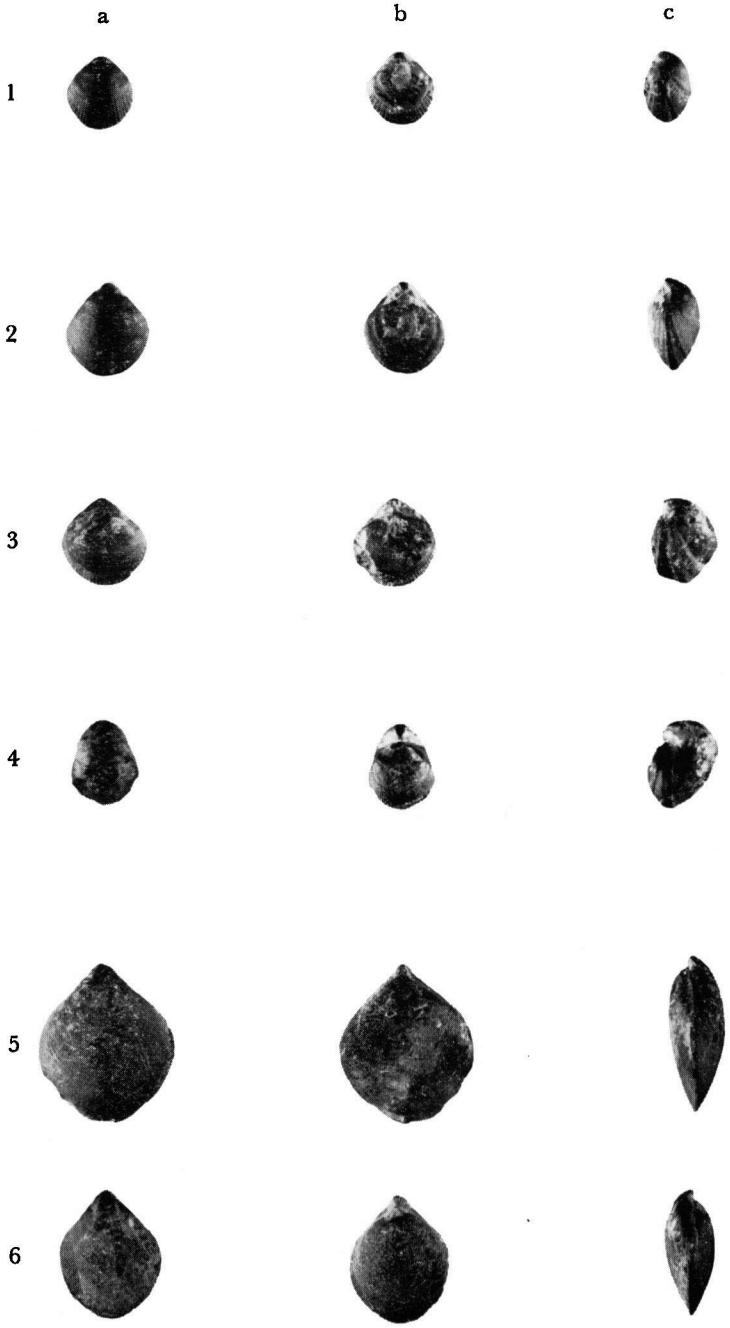
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PLATE VIII

a = pedicle view
b = brachial view
c = lateral view

Cryptonella? inornata (d'Orbigny, 1850) . . . . . p. 35

Series of five specimens showing the variation in form of this species. All specimens from Lebanza. Siegenian.

fig. 1 specimen 134 form A
fig. 2 specimen 135 intermediate form
fig. 3 specimen 136 form B
fig. 4 specimen 137 intermediate form
fig. 5 specimen 138 form C

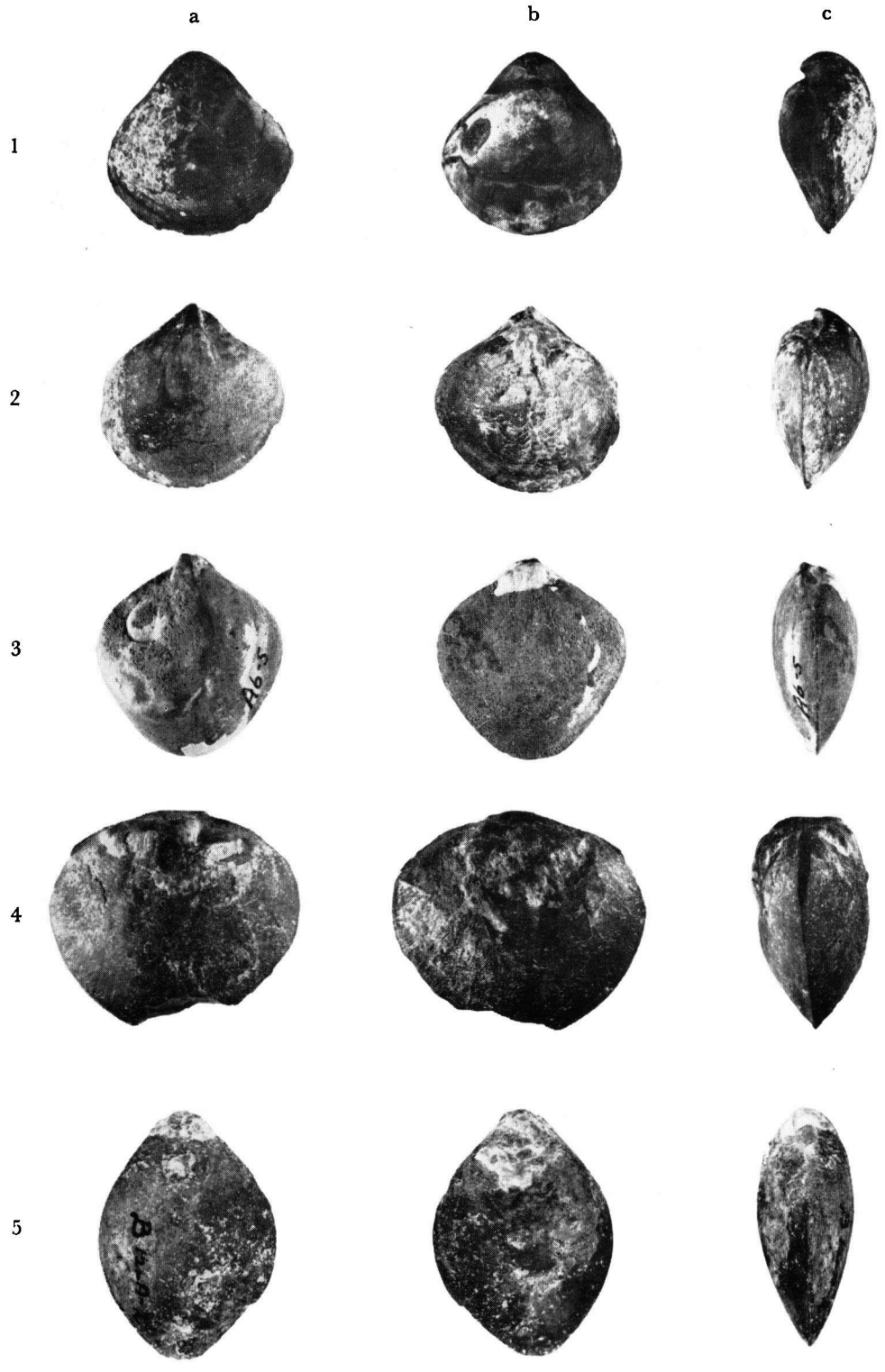
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PLATE IX

a = pedicle view
b = brachial view
c = lateral view

Figs. 1—4a *Whitfieldella* spec. . . . . p. 39
All the specimens from Lebanza. Siegenian.
fig. 1 specimen 139
fig. 2 specimen 140
fig. 3 specimen 141
fig. 4a transverse section of brachial valve showing the concave hinge plate with secondary filling; photograph from peel nr. 287 (about 13 ×)

Fig. 4b *Athyris undata* (Defrance, 1828) . . . . . p. 40
Transverse section of brachial valve showing the hinge plate; photograph from peel nr. 324-19.0 (about 7 ×)

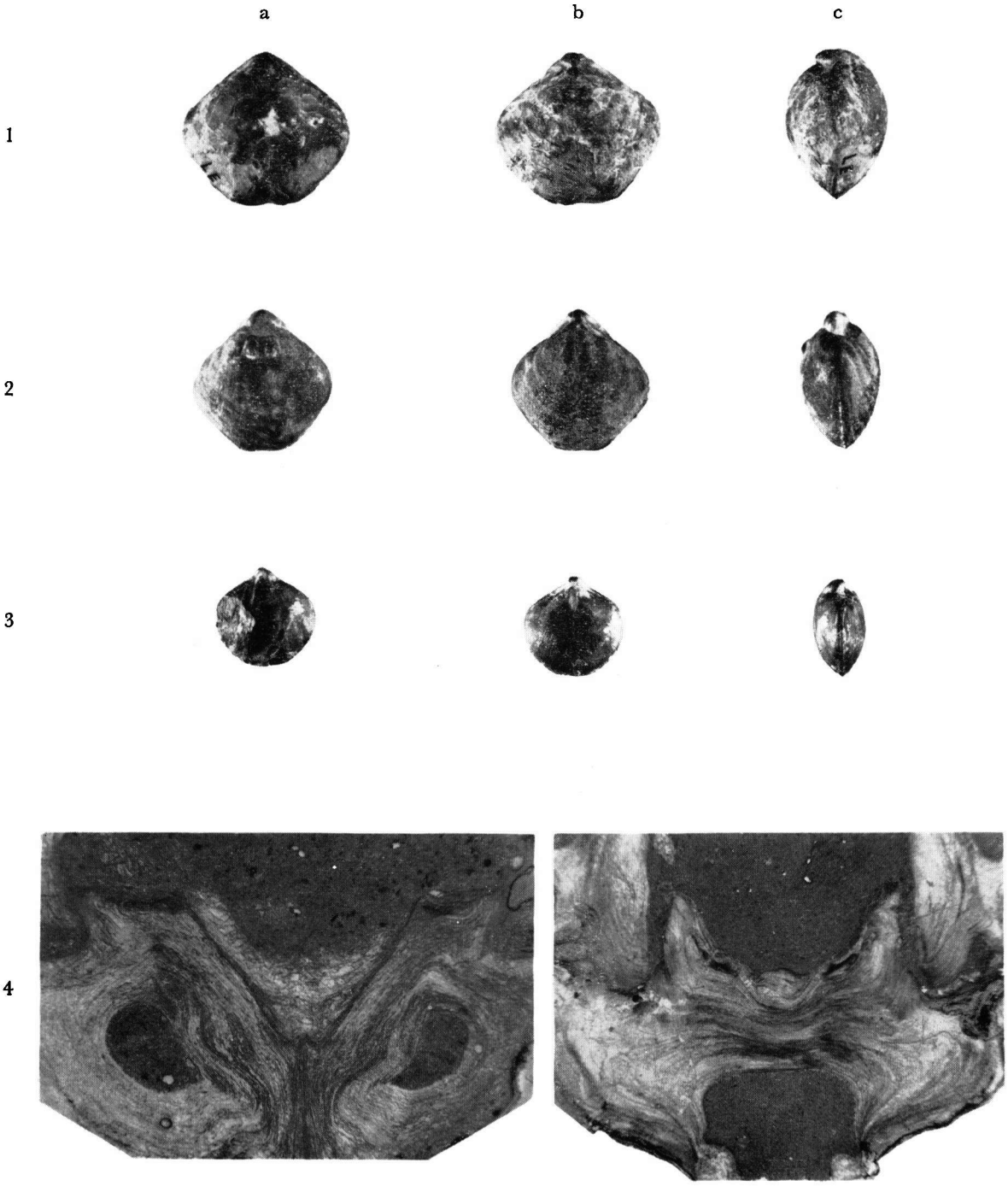
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PLATE X

a = pedicle view
b = brachial view
c = lateral view

Figs. 1—3 *Athyris undata* (Defrance, 1828) . . . . . p. 40
All the specimens from Lebanza. Siegenian.
fig. 1 specimen 142 (note the growth lamellae)
fig. 2 specimen 143 (surface wholly decorticated)
fig. 3 specimen 144 (shell removed)

Figs. 4—5 *Athyris* spec. cf. *concentrica* (von Buch, 1834) . . . . . p. 43
Both specimens from the locality Arauz. Lower Siegenian - Upper Gedinnian.
fig. 4 specimen 145
fig. 5 specimen 146


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PLATE XI

Figs. 1—2 *Pradoia?* cf. *P. torenoi* (de Verneuil & d'Archiac, 1845). . . . . p. 43.
a = pedicle view b = brachial view c = lateral view
Both specimens from the locality Arauz. Lower Siegenian - Upper Gedinnian.
fig. 1 specimen 147
fig. 2 specimen 148

Main elements of the brachiopod fauna of the upper member of the Carazo Formation

Fig. 3 *Douvillina* (*Mesodouvillina*) *triculta* (Fuchs, 1919)
a = impression of interior pedicle valve
b = impression of interior brachial valve
c = impression of exterior

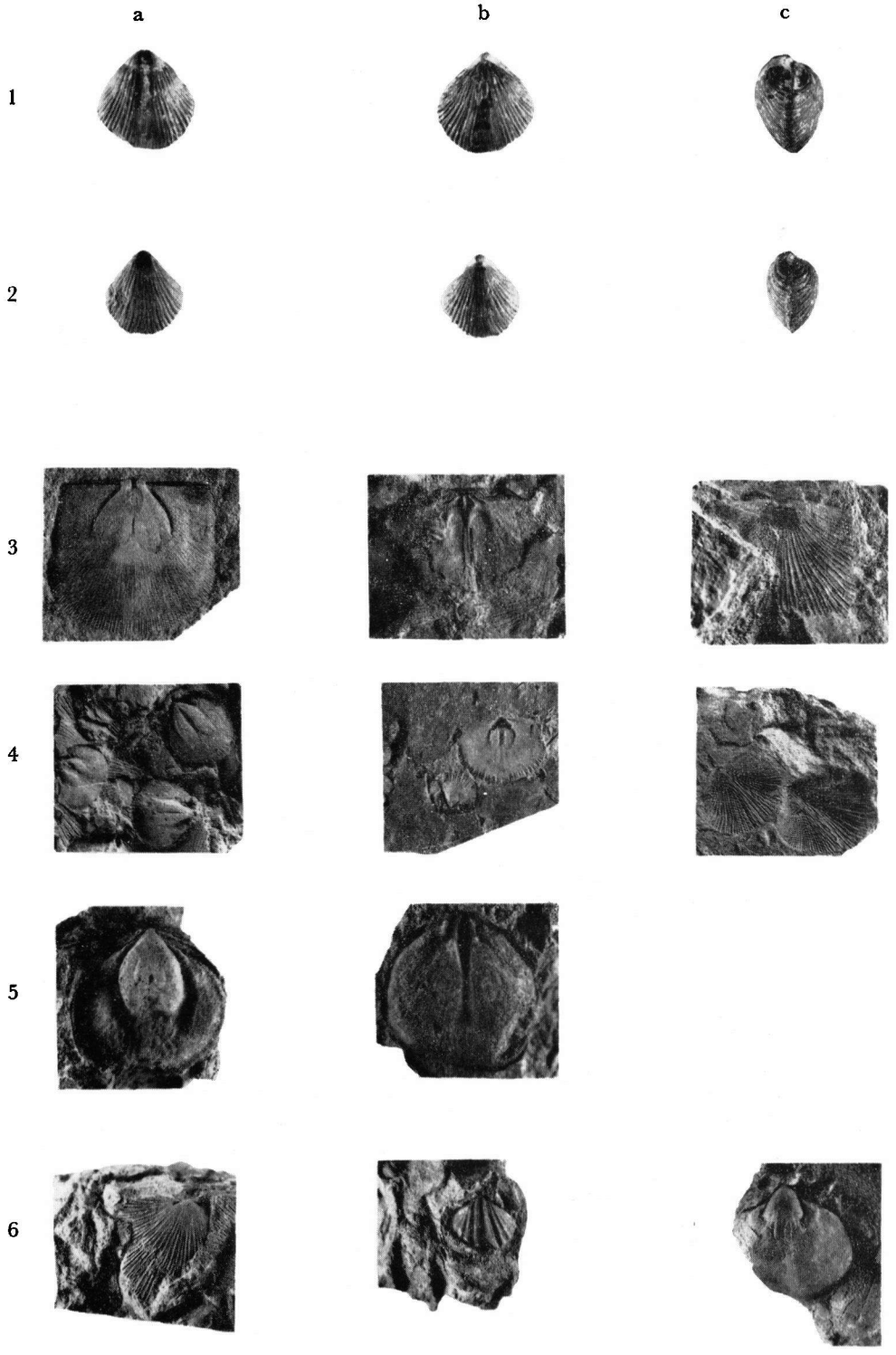
Fig. 4 *Platyorthis verneuili* (de Koninck, 1876)
a = impression of interior pedicle valve
b = impression of interior brachial valve
c = impressions of exterior

Fig. 5 *Proschizophoria torifera* (Fuchs, 1919)
a = impression of interior pedicle valve
b = impression of interior brachial valve

Fig. 6a *Schuchertella euzona* (Fuchs, 1919)
impression of interior brachial valve

Fig. 6b *Howellella* spec. cf. *mercuri* (Gosselet, 1880)
impression of interior pedicle valve

Fig. 6c *Protathyris* spec. cf. *praecursor* Kozlowski, 1929
impression of interior pedicle valve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