LEIDSE GEOLOGISCHE MEDEDELINGEN, Deel 48, Aflevering 2, pp. 135–205, 4-5-1972

THE PORTILLA FORMATION (MIDDLE DEVONIAN) OF THE ALBA SYNCLINE, CANTABRIAN MOUNTAINS, PROV. LEON, NORTHWESTERN SPAIN: CARBONATE FACIES AND RHYNCHONELLID PALAEONTOLOGY

BY

M. MOHANTI *

ABSTRACT

Three members are informally distinguished in this formation (A, B, and C from base to top). They are present at the western part of the outcrop (thickness ca. 246 m). On the eastern and southeastern part, only member A and basal part of member B are present and the thickness is reduced to ca. 20 m. A sharp surface of discontinuity separates member A from member B. The Portilla Formation abounds in reef-building elements associated with other groups. Five major carbonate facies types are established that belong to a complex biostromal 'reef' facies. Vertical and lateral facies changes are demonstrated. The carbonate facies was deposited in a shallow-marine environment. Towards end of deposition of member A, sharp changes in depositional conditions occurred, soon followed by a notable influx of siliciclastics. A distinctive barrier 'reef' pattern was established during deposition of member B. It protected a back-reef area from the open shallow sea. This back-reef environment was separated from an area of dominantly siliciclastic deposition in the southeast by an extremely shallow marine or shoal area which might have been emergent. During deposition of member B there occurred a rhythmic alternation of the back-reef carbonates and the carbonates continuous with the 'reef' barrier, probably reflecting minor changes in sea level likely due to epeirogenetic movements of the bottom. Eventually organic growth and associated carbonate sedimentation exceeded the rate of subsidence and as a result the 'reefs' laterally shifted seawards, followed by the back-reef facies. The facies pattern suggests an increasingly emergent tendency of the marginal part of the carbonate basin due to bottom movements. The barrier 'reef' pattern of member B probably terminated due to changes in relative subsidence during deposition of member C. A strong supply of siliciclastics during the deposition of the Nocedo Formation brought an end to the carbonate sedimentation of the Portilla Formation. The variation in thickness in the Portilla Formation has been mainly due to a slow and prolonged differential subsidence of the carbonate depositional basin. The absence of a large part of member B and member C in the easterly and southeasterly directions is probably largely due to non-deposition of sediments.

Seventeen species are described of rhynchonellid brachiopods, out of which four species are new. Three new genera are established. Wherever available some critical German rhynchonellid species have been sectioned for comparison. The rhynchonellid and atrypid brachiopod fauna from the Portilla Formation show a great affinity with the Middle Devonian fauna of Eifel region, Germany. The Spanish fauna could be assigned to the mixed or Eifel facies, or close to this type. Striking similarity exists also between the Spanish fauna and the Middle Devonian fauna from the Holy Cross Mountains, Poland. The rhynchonellids and atrypids strongly suggest that the Eifelian – Givetian boundary lies in the basal part of member B. It is suggested that member A is of Eifelian age and that members B and C, apart from the basal part of member B are of Givetian age.

SAMENVATTING

Er zijn drie laagpakketten ('members') onderscheiden (A, B, en C, van onder naar boven), die aanwezig zijn in het westelijke gedeelte van de dagzoom (dikte ca. 246 m). In het oostelijke en zuidoostelijke gedeelte zijn alleen laagpakket A en het basale gedeelte van laagpakket B aanwezig; de dikte is hier gereduceerd tot 20 m. Een scherp discontinuïteitsvlak scheidt laagpakket B van laagpakket A. De Portilla-Formatie bevat zeer veel potentieel rifbouwende elementen, geassocieërd met vertegenwoordigers van andere groepen. Er zijn vijf hoofdtypen van carbonaat-faciës onderscheiden, die behoren tot een biostromale 'rif'-faciës. Verticale en laterale faciësveranderingen worden beschreven. De carbonaat-faciës is afgezet in een ondiep marien milieu. Tegen het eind van de afzetting van laagpakket A traden sterke veranderingen op in de afzettingsomstandigheden, spoedig gevolgd door een aanmerkelijke toevoer van siliciklastisch materiaal. Een duidelijk barrière-'rif' werd gevormd gedurende de afzetting van laagpakket B. Dit schermde een lagune af van de ondiepe, open zee. Dit lagunaire milieu was in het zuidoosten gescheiden van een gebied met voornamelijk siliciklastische afzettingen door een zeer ondiep, marien gebied of een zandbank, die boven water gelegen kan hebben. Tijdens de afzetting van laagpakket B trad ritmische afwisseling op van lagunaire carbonaten, en carbonaten die een geheel vormen met het barrière-'rif'. Waarschijnlijk is dit het gevolg van kleine veranderingen in het zeeniveau, vermoedelijk veroorzaakt door epirogenetische bewegingen van de bodem. Mettertijd overtrof de organische groei en de daarmee samenhangende carbonaatsedimentatie de daling, waardoor de 'riffen' zich lateraal, zeewaarts verplaatsten, gevolgd door de lagunaire faciës. Het faciëspatroon doet een meer en meer oprijzende tendens van het marginale gedeelte van het carbonaatbekken vermoeden, wat te wijten is aan bodembewegingen. De barrière'rif'-faciës kwam waarschijnlijk aan zijn eind door veranderingen in de relatieve daling gedurende de afzetting van laagpakket C. Een sterke aanvoer van siliciklastisch materiaal tijdens de afzetting van de Nocedo-Formatie maakte een eind aan de carbonaatsedimentatie van de Portilla-Formatie. De variatie in dikte van de Portilla-Formatie is hoofdzakelijk veroorzaakt door een langzame en langdurige differentiële daling van het carbonaatbekken. De afwezigheid van een groot deel van laagpakketten B en C in oostelijke en zuidoostelijke richting is waarschijnlijk grotendeels primair.

Zeventien soorten van rhynchonellide brachiopoden worden beschreven, waarvan vier soorten nieuw zijn. Drie nieuwe genera worden ingevoerd. Wanneer deze beschikbaar waren, zijn ter vergelijking enkele soorten uit Duitsland eveneens gebruikt voor seriesecties. De rhynchonellide en atrypide brachiopoden fauna van de Portilla-Formatie vertoont grote verwantschap met de fauna uit het Midden-Devoon van de Eifel in West-Duitsland. De Spaanse fauna kan gerekend worden tot de gemengde of Eifel-faciës, of een faciës hier dichtbij. Opvallende gelijkenis bestaat ook tussen de Spaanse fauna en de middendevonische fauna uit de Góry Swietokrzyskie in Polen. De rhynchonellide associatie is gedateerd als Boven-Eifelien tot Onder-Givetien. Zowel de rhynchonelliden als de atrypiden doen sterk vermoeden dat de Eifelien/Givetien-grens in het onderste gedeelte van laagpakket B ligt. Er wordt geopperd, dat laagpakket A een Eifelien-ouderdom heeft en dat de laagpakketten B en C, behalve het onderste gedeelte van laagpakket B, een Givetien-ouderdom hebben.

---

* Dept. of Geology, Utkal University, Ravenshaw College, Cuttack-3 (Orissa), India – Temporary address: Dept. of Stratigraphy & Palaeontology, University of Leiden, The Netherlands.

CONTENTS

Drawing of text figures (Figs. 1–5 & Figs. 11, 12) and enclosures (A & B) by Mr. B.G. Henning. Figure above chapter I and text figure 10 by Mr. J. Bult. Drawing of text figures (Figs. 13–37) by Miss C. Roest.
Photographs by Mr. W.C. Laurijssen and Mr. W. Devilé.

Panoramic view of the Portilla Limestone outcrop of the Alba syncline. View looking east.

CHAPTER I

INTRODUCTION

Since the last century, geologists have evinced keen interest in the study of the Devonian sediments of the Cantabrian Mountains, Spain (Fig. 1). The completeness of the Devonian succession, its varied facies, prolific fauna, availability, and accessibility of well-exposed sections truly provide a splendid opportunity for geological and palaeontological studies. Van Adrichem Boogaert (1967) gives a concise review of the important works concerning the Devonian of this mountain chain. Brouwer (1968) provides a stratigraphic synthesis of the Devonian sediments.

This thesis deals with a detailed stratigraphic study of the Portilla Formation (Comte, 1959) (mainly Middle Devonian in the area of study) of the Alba syncline (de

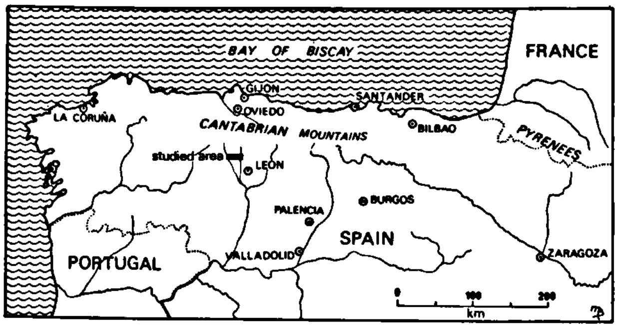


Fig. 1. Index map of Spain: solid rectangle marks the area of study.

Sitter, 1962) between the rivers Luna in the west and Bernesga in the east in the province of León, northwestern Spain (Fig. 2). Besides stratigraphy, systematic palaeontology of rhynchonellid brachiopods is another major part of this thesis. This work is part of a larger research project on the Cantabrian Palaeozoic directed by Prof. Dr. A. Brouwer (Dept. of Stratigraphy & Palaeontology, University of Leiden). The previous regional stratigraphic and tectonic survey by the members of staff and students of the Geological Institute of the University of Leiden has greatly aided in undertaking this work.

ACKNOWLEDGEMENTS

I am grateful to several persons who have helped me ungrudgingly in completing this research. I would like to extend my most cordial thanks to Dr. P. J. M. J. Sartenaer (Institut royal des Sciences naturelles de Belgique, Bruxelles) for giving me an opportunity to visit his laboratory and providing me valuable informations on systematic and stratigraphic aspects of rhynchonellid brachiopods. I am very grateful to him for his warm hospitality during my stay in Bruxelles. Prof. Dr. A. Vandercammen has been kind enough to discuss general problems pertaining to work on brachiopods. I am greatly indebted to Dr. W. Struve and Dr. Herta Schmidt (Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt/Main) for having enabled me to take full advantage of a two months' stay in Frankfurt/Main, West Germany, to compare my own material with that of the excellent collection of German Middle Devonian rhynchonellids at Senckenberg. I have had the great benefit of the expert guidance of Dr. Herta Schmidt in this study. Dr. Struve enlightened me on problems of Middle Devonian biostratigraphy and helped in the identification of atrypid brachiopods in my collection. I am very grateful to Prof. Dr. H. K. Erben, Dr. A. Siehl, and Dr. G. Plodowski (Institut für Paläontologie, Rhein. Friedrich-Wilhelms-Universität, Bonn) for their genuine courtesy and cordiality during a short visit to Bonn. My grateful thanks are also due to Dr. V. Havlícek (Ústredni Ústavu Geologický, Praha) who very kindly showed me the Czechoslovakian collection of rhynchonellids and discussed problems pertaining to rhynchonellids. Dr. P. Copper (Laurentian University, Sudbury, Canada) has kindly given his time in the preliminary identification of atrypids during a short visit to Leiden in 1968 fall. This research has been largely possible through a scholarship awarded to me by the

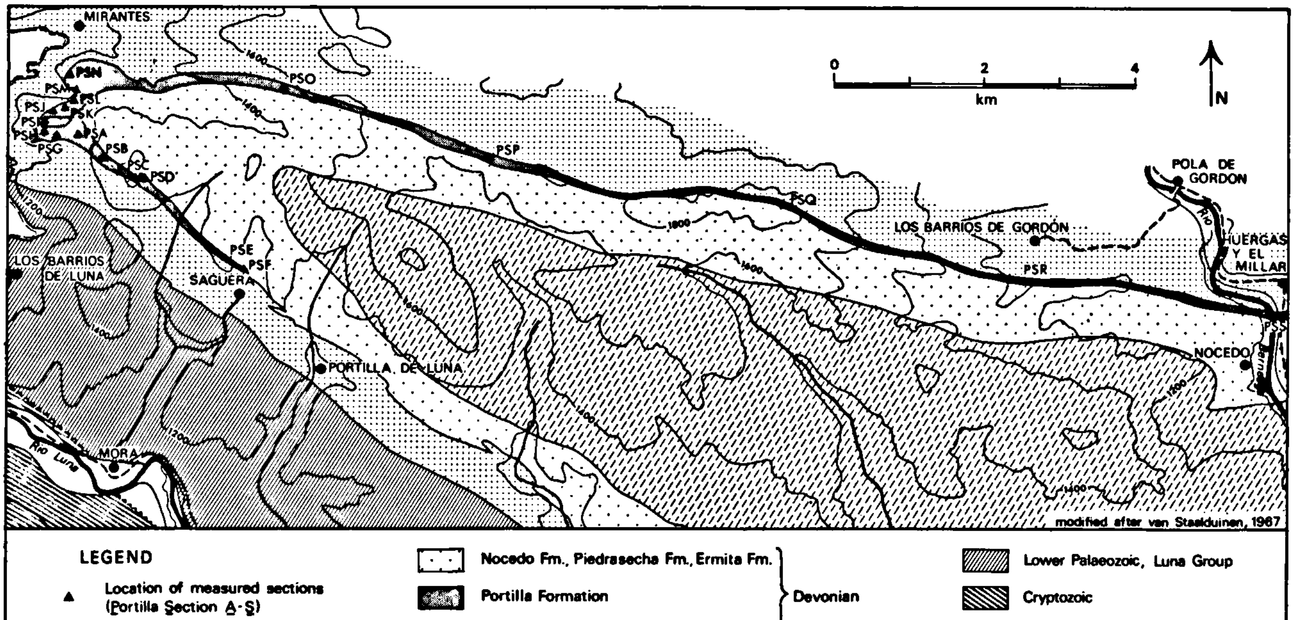


Fig. 2. Map showing among other things the outcrop of the Portilla Formation in the area of study: solid triangles mark the location of measured sections.

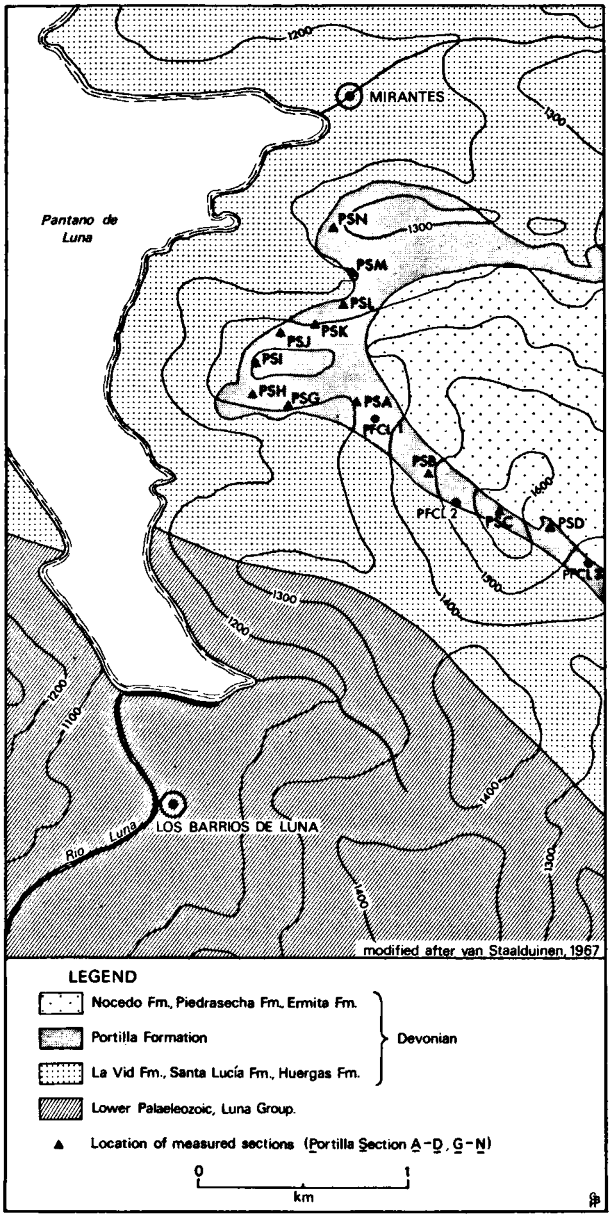


Fig. 3. Suggested reference area of the Portilla Formation between sections PSD and PSN: solid triangles mark the location of measured sections and small solid circles indicate fossil collecting localities.

Dutch Ministry of Education and Sciences. The University of Leiden provided a grant from the 'Van Vollenhoven-Fonds' for undertaking trips to Bruxelles, Frankfurt/Main, and Praha and also a grant from the 'Van Aalst Arntzenius-Fonds' towards the preparation of the manuscript. The Dutch Ministry of Education and Sciences have partly defrayed the costs of printing this thesis. These are most gratefully acknowledged. I am also delighted to thank the inhabitants of the village Los Barrios de Luna for their friendly help and hospitality during field work in their country.

Sincere thanks are due to the authorities of the Utkal University (Orissa), India for their due consideration of my leave of absence.

PREVIOUS INVESTIGATIONS

Fundamental work on the Devonian stratigraphy of northern León was done by P. Comte (1959) who had clearly distinguished the different lithological units of the Devonian. Comte's work provided the base for subsequent work on the Devonian by the Leiden group. The lithological units of Comte have since been refined by the Leiden group and are being used now in the sense of lithostratigraphic units in accordance with the principles formulated by the International Subcommission on Stratigraphic Terminology (Hedberg, 1961). The geological map (1 : 50,000) of the area between the rivers Luna and Bernesga was prepared by Van Staalduinen (thesis in prep.).

METHOD OF INVESTIGATION

To complete this project, field work was carried out in the summers of 1966, 1967, and 1968. Nineteen stratigraphic sections were measured over the outcrop of the Portilla Formation (PSA–PSS, Fig. 2). Generally brachiopod samples were collected from the stratigraphic sections. Some additional material, however, was obtained from three separate localities numbered as PFCL 1, 2, and 3 (Fig. 3). The outcrop between sections PSF and PSO has been delimited for description and interpretation of facies types. Rock samples were collected at each significant lithologic change. Generally, for the lithologically monotonous units one sample was collected from an interval of 2 m or more. Approximately 1000 hand specimens were collected from different sections.

In the laboratory, carbonate samples were studied on polished surfaces, acetate peels and in thin sections. Several polished samples approximately of a size of 20 cm x 10 cm were made in order to observe the internal structure and such polished surfaces exhibited large frame-building organisms that are not easily seen on the surface of the outcrop. Alizarine Red-S and potassium ferricyanide were used for staining. The techniques were mainly after Friedman (1959) and Evamy (1963). Selected samples were dissolved in HCl for estimating the amount of insoluble residues. X-ray analysis was done for silt and clay fraction of some insoluble residues.

Rhynchonellid brachiopods were chosen for systematic palaeontological study. The internal structures of the rhynchonellids were studied by serial grinding. Polished surfaces were etched with 10% HCl and the etched surfaces were recorded by the dry peel method using acetophane sheet and acetone. In few cases, Acetobutyratfolie Triafol NB (Bayer AG) paper and methyl

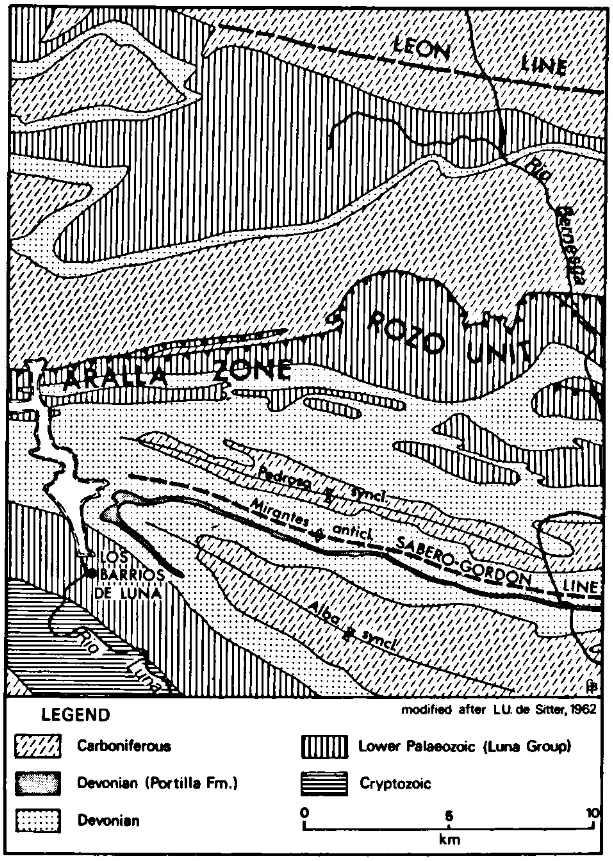


Fig. 4. Structural setting of the area.

acetate were used for peeling. Drawings of selected peels were made mostly by means of a Wild M5 binocular microscope. For observing details under higher magnification, a Wild M20 microscope was employed. For photography, the specimens were at first thinly smeared with Indian ink and later whitened with ammonium-chloride vapour.

GENERAL GEOLOGICAL SETTING

The investigated area belongs to the Luna unit (de Sitter, 1962) in the Leonides. It is a complicated synclinorium with Cryptozoic on its southern flank, Lower Cambrian on its northern flank, and Carboniferous in the centre. It consists of the Alba syncline, Mirantes anticline, Pedroso syncline, and the Aralla zone (Fig. 4). The Alba syncline trends south of the Sabero-Gordón line. The Devonian succession of the Bernesga Group is very well-developed in the southerly Leonides. The most complete succession of the Devonian is found in the Bernesga valley which has been adequately described by Comte (1959, p. 33–43). Fig. 5 presents a generalized stratigraphic division of the Devonian in northern León.

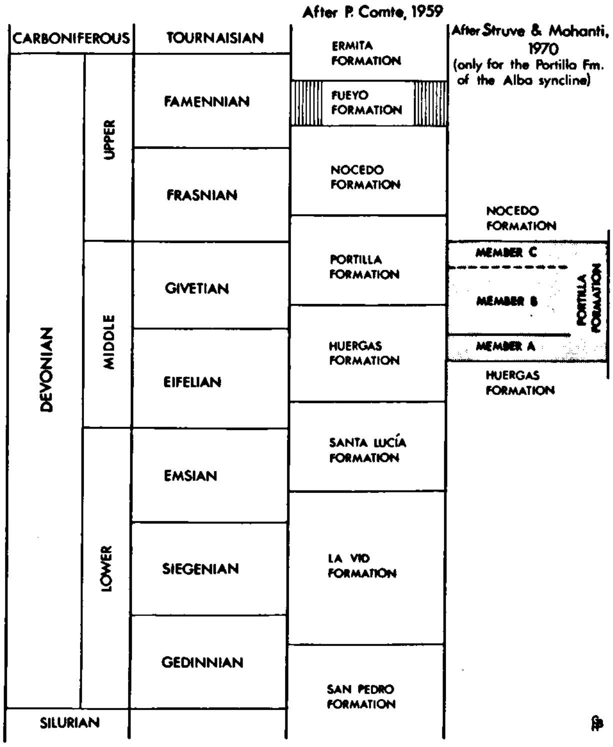


Fig. 5. Generalized stratigraphic division of the Devonian in the Prov. León.

LITHOSTRATIGRAPHIC UNITS

The Portilla Formation is largely a carbonate succession between two siliciclastic formations: the Huergas Formation (below) and the Nocedo Formation (above).

The Huergas Formation

Shales and some sandstones dominate the lithology of the Huergas Formation. Generally, a thickness of 200–300 m has been attributed to this formation (Brouwer, 1968, p. 41). In the southern flank of the Alba syncline, the Huergas Formation gets thinner and near the village Sagüera it measures about one meter in thickness. Comte assigns (1959, p. 41, 310, 311, 317) a late Eifelian to early Givetian age to this formation. The contact of the Huergas with the Portilla Formation is conformable and gradational. The Huergas deposits were probably laid down in a low-energy, shallow marine environment as the dominant shaly lithology, occasional presence of bioclastic limestone lenses and marine fossils may suggest.

The Portilla Formation

The Portilla Formation was introduced by Comte (1959) as 'Calcaires de la Portilla' for the limestones overlying his 'Grès et schistes de Huergas' and underlying his 'Grès de Nocedo'. Seemingly, Comte (1959, p. 199) has chosen the type locality of the Portilla Formation on the right bank of the Portilla creek about one kilometer northwest of Matallana-Estación close to the confluence of Portilla creek and river Torío in the neighbourhood of the village Orzonaga. The Portilla Formation has a dominant carbonate lithology. Brouwer (1968, p. 41) assigned a thickness of 60–200 m to the Portilla Formation.

The age of the Portilla Formation according to Comte (p. 41, 311, 317) ranges from late Givetian to early Frasnian.

Stratigraphic division in the Alba syncline. – It seems suitable to extend a three-fold lithostratigraphic division to the Portilla Formation of the Alba syncline (Fig. 6), informally distinguished as member A, member B, and member C from base to top. Member A and member C are formed by more resistant cliff-forming limestones whereas member B is relatively more recessive principally due to the presence of prominent argillaceous limestone beds. The contact of member A and member B is sharp, while that between member B and C is rather gradational and is arbitrarily placed at the base of the prominent massive-bedded limestones of member C. The contact between the Portilla and the Huergas Formation is taken at the first appearance of medium grey to dark grey argillaceous limestones. The contact with the Nocedo Formation is the top of the massive-bedded limestones of member C between sections PSD and PSN. At section PSE, this contact is placed at the top of medium-bedded limestones and at section PSO and further east it is placed at the top of the fossiliferous calcareous silty shales or argillaceous limestones.

Since the type locality of the Portilla Formation is poorly chosen, in this thesis a reference area will be introduced to provide a comprehensive impression of the lithostratigraphic features of the Portilla Formation. Thus, this reference area is chosen between sections PSD and PSN (Fig. 3) and in this area sections PSA and PSM are chosen as the principal reference sections.

The Nocedo Formation

Sandstones mainly constitute the lithology of the Nocedo Formation.

Comte (1959) recorded a thickness of 515 m for the Nocedo Formation in the Bernesga valley where it is interrupted by a red limestone member (Brouwer, 1968, p. 42). Comte assigns (1959, p. 41, 312, 317) a late Frasnian to early Famennian age to the Nocedo Formation. The contact of the Nocedo with the Portilla Formation in the Alba syncline is generally unconformable. The Nocedo sediments were probably deposited in a very shallow marine environment with sediment transport from north or north-east.

A FEW TERMS AND THEIR USAGE

As regards the terms 'biostrome' and 'bioherm', I follow the definition of Cumings (1932) in a morphologic sense.

The term 'reef' is used in a broad genetic sense. In view of the composition and abundance of the fauna and the general facies pattern, the Portilla carbonate facies is referred to as a complex biostromal 'reef' facies.

The term 'facies' is used for the gross lithologic and palaeontologic features of a particular sedimentary deposit (see Schieferdecker, 1959, p. 148; Laporte, 1967).

CHAPTER II

STRATIGRAPHIC AND PALAEONTOLOGIC FIELD OBSERVATIONS

GENERAL REMARKS

North of the village Los Barrios de Luna, at the nose of the Alba syncline, the Portilla Limestone Formation shows a remarkable development in thickness and facies. The informally designated three members A, B, and C (Fig. 6) are present here between the measured sections PSD and PSN (see eclosures A & B) where the thickness of the formation varies from 102–246 m. However, when this formation is traced farther towards the northern and southern flanks, a gradual attenuation in thickness is observed; the thickness is reduced to ca. 20 m. As is clearly seen, this attenuation is due to appreciable reduction in thickness of member A as well as absence of member C and a large part of member B. Only at section PSS in the Bernesga valley, the thickness again rises to ca. 50 m.

The Portilla Formation is highly fossiliferous abounding in potentially reef-building elements like corals and stromatoporoids. The lithology and associated fauna vary in the stratigraphic sequence; both laterally and vertically and admirably so in member B which, therefore, is the most interesting stratigraphic unit from an ecological point of view. In this chapter, a description of the three members will be given and finally a few major facies will be introduced on basis of field observations.

MEMBER A

Contact, thickness, and distribution

The contact of member A with the underlying Huergas Shales is gradational. The shales of the Huergas Formation become increasingly calcareous towards the higher

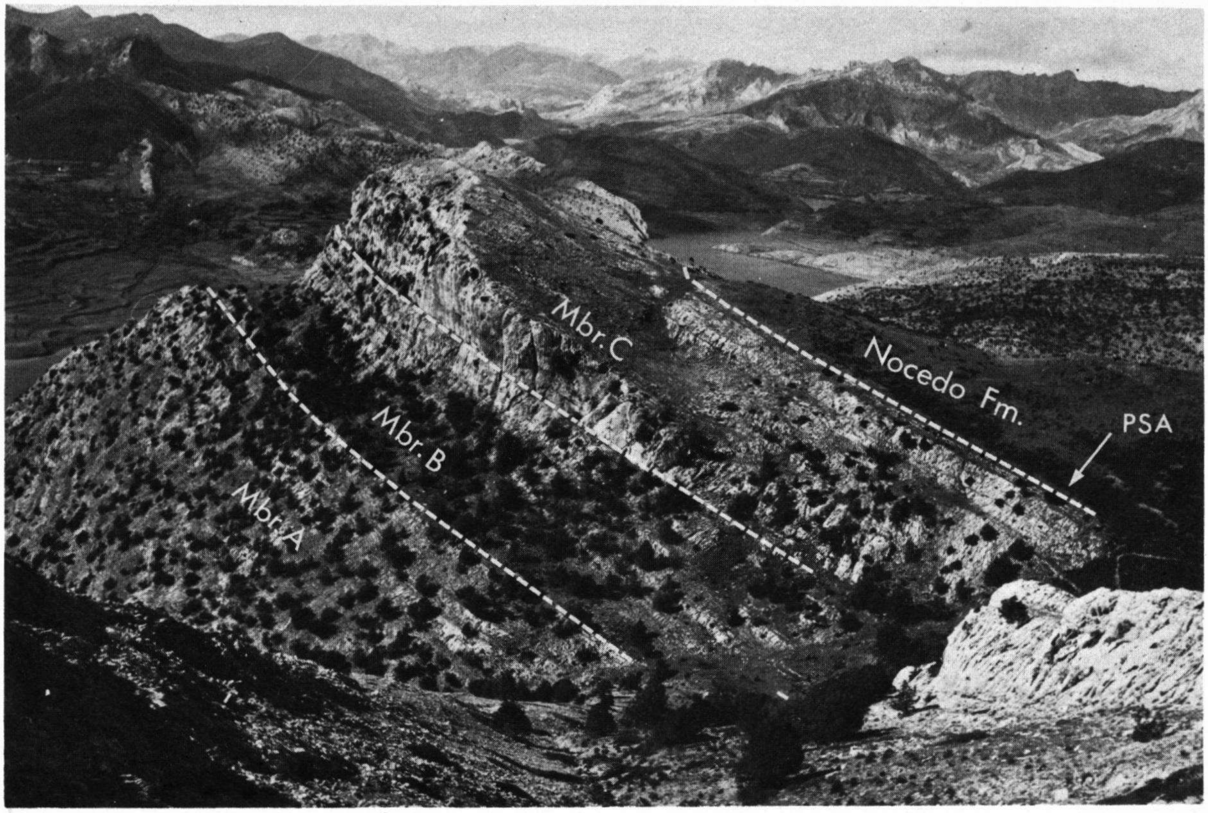


Fig. 6. Portilla Formation showing three-fold stratigraphic division at reference section PSA. View looking northwest.

part and the transition to the carbonate beds of the Portilla Formation takes place through an interval of varying thickness of calcareous shales and argillaceous limestones. Member A reaches its greatest thickness at about the reference section PSA where it measures ca. 147 m. Gradually the thickness diminishes on either side. At section PSF in the southeasterly tip of the Portilla outcrop, member A measures ca. 24 m. Close to this section internal contortion of beds have been observed in member A. Further southeasterly, the Portilla Formation wedges out. Laterally in this southeasterly direction there appears dominantly siliciclastic deposits consisting of shales, some sandstones (occasionally burrowed) and locally some isolated limestone lenses. These siliciclastic deposits contain a few spiriferids, pelecypods, and crinoid stems.

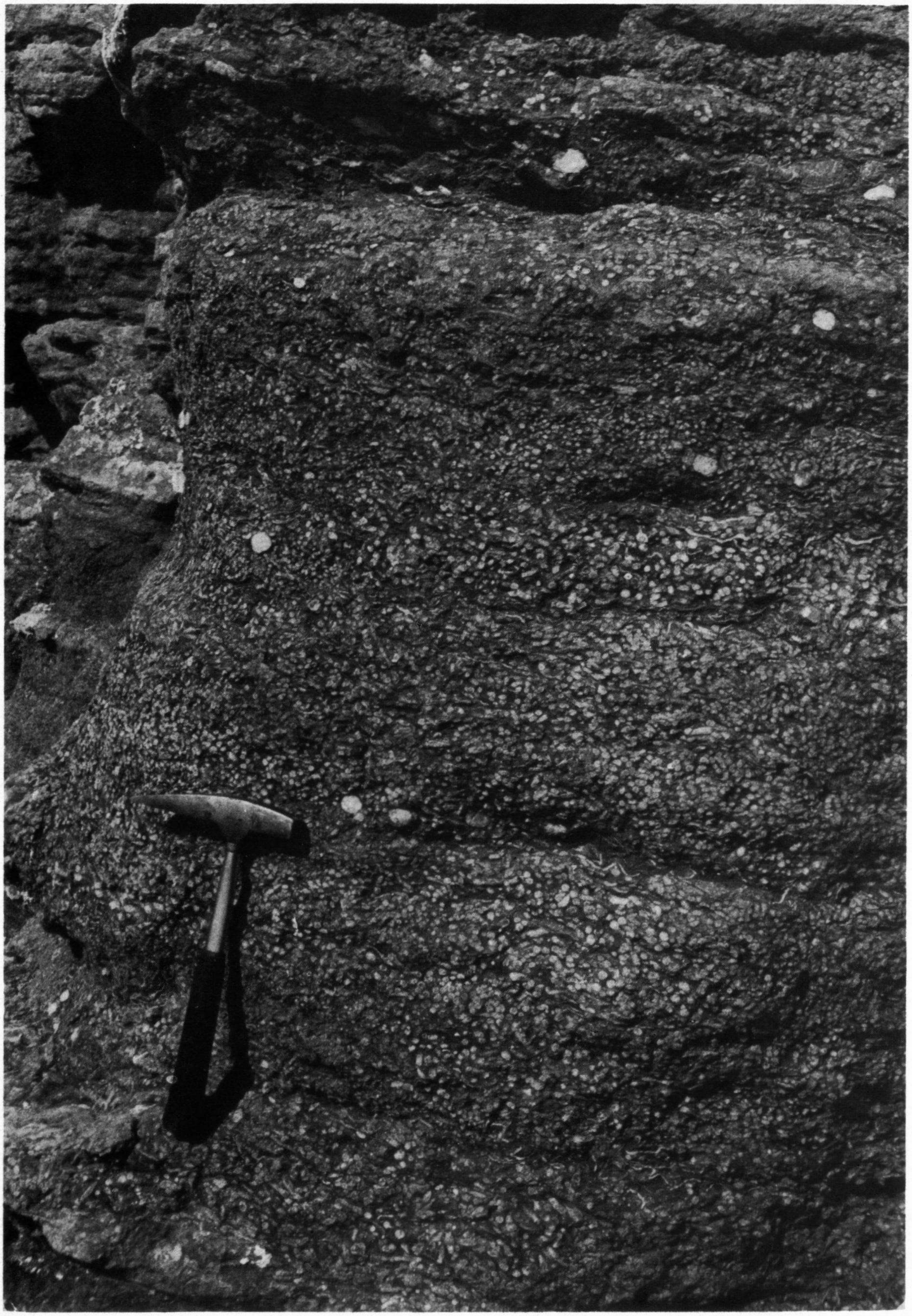
Lithology, fauna, and sedimentary features

Member A is mostly constituted of irregularly bedded (largely thin-bedded)* to massive-bedded (medium to thick-bedded) limestones. The basal part is more argillaceous. Argillaceous limestones in thin, discontinuous bands are seen in the basal part. They contain sparsely distributed fragments of echinoderms, bryozoans, and brachiopods. Few small solitary rugose corals may also be present. More upwardly, the beds appear irregularly bedded. The beds are uneven, thicken and thin in relatively short distance. The irregularly bedded lower part could be typically seen at locality PFCL 2. These beds are intercalated with soft argillaceous material having often a light olive to moderately olive brown (10 Y 5/4–5 Y 4/4)** colour. No bottom structures or cross-bedded structures were noticed. Random dsitribution of large bioclasts may be seen on some bedding surfaces. The limestone weathers light grey to yellowish grey (N 7–5 Y 7/2) with a fresh colour varying from medium light grey to light olive grey (N 6–5 Y 6/1). Freshly broken chips commonly show a yellowish brown tinge in which a rhombic outline of dolomite could sometimes be clearly seen. Tabulate corals and solitary rugose corals occur frequently in the lower bedded part. Solitary rugose corals may locally occur in large concentrations. Platy form of tabulates *Alveolites* and *Coenites* are relatively more common in the argillaceous intercalations. Fragments of *Thamnopora* and branching *Disphyllum* are randomly distributed. Massive forms of *Favosites* are conspicuous among the coralline elements. At locality PFCL 2 and at section PSD, some of the colonies may be as large as 20 or 30 cm in diameter or even more. Few colonies of *Chaetetes* occur close to

---

* Terms according to Mc Kee and Weir (1953) (in Dunbar & Rodgers, 1957, p. 97).

** Colour noted after Munshell Rock-color chart, 1963 (distributed by the Geological Society of America).



Favosites. The tabulate *Heliolites* also occurs, although it is extremely rare. Stromatoporoids occur sparsely. Both massive and laminar forms are found. Some of these massive colonies appear lensoid, and more or less hemispherical. Laminar stromatoporoids may occur in complete form or in badly broken fragments. At section PSM, in the lower crudely bedded part, small globular stromatoporoids are seen. There are also abundant fragments of branching rugose corals in argillaceous layers. Complete shells or loose fragmented valves of brachiopods are also encountered. Other faunal elements include bryozoans, gastropods, and few fragments of trilobites. Echinodermal stems and ossicles are occasionally concentrated forming small pocket or lens-like accumulations. Some of these ossicles show a pinkish tinge.

Through interfingering, the irregularly bedded limestones pass into the massive-bedded limestones of the higher part of member A. These limestones are generally medium to thick-bedded and weather a medium light grey (N 6) colour. They are relatively more resistant and are slope-forming. Greenish grey to greyish yellow green (5 GY 6/1–5 GY 7/2) (there may be rarely a pale red (5 R 6/2) tinge) soft argillaceous limestones with abundant platy tabulates (e.g. *Coenites* and *Alveolites*), and some branching tabulates (e.g. *Thamopora*) are present in few levels in the succession of these thick-bedded limestones. These weakly resistant soft argillaceous levels may run fairly continuously for some distance or may locally wedge out between the thick-bedded limestones. Locally erosional truncation of beds are seen in the thick-bedded limestones. Massive stromatoporoids and massive tabulate corals (e.g. *Alveolites*) are prominent in the faunal composition of these massive-bedded limestones. These reefal organisms may be easily seen on weathered, somewhat exfoliated rock surface where they are distinguished in the surrounding bioclastic detritus. Perhaps one may gain a fair impression of the abundance of the reefal fauna from the several polished blocks lying in a creek by section PSM. Many colonies are found to be fragmented and sometimes the fragments form unsorted angular breccias on the bedding surface. Fragments of *Thamnopora*, platy tabulates, solitary rugose corals, and fragments of brachiopods are also associated.

MEMBER B

Contact, thickness, and distribution

Member B is separated from member A by a sharp surface of discontinuity. Locally the uppermost beds of member A clearly show truncations at this contact. However, pebbles, organic borings, or conspicuous karst features have not been observed at this contact. At few places between sections PSB and PSD, abrupt cut-off of stromatoporoid and coral colonies is noticed. The contact of member B with the overlying member C is rather gradational and is arbitrarily placed at the base of the massive-bedded cliff-forming limestones of member C. This corresponds to the top of the sixth *Thamnopora*-bed as marked at the reference section PSA. The thickness of member B varies from 20–51 m between sections PSD and PSN. In the northern and southern flanks a large part of member B is absent; the few meters of member B that are present vary in thickness within 9 m. At section PSS in the Bernesga valley ca. 21 m of member B is present.

Fig. 7. Argillaceous limestone with abundant branching (*Thamnopora*) and platy tabulate corals. Member B, first *Thamnopora*-bed near section PSH.

Lithology, fauna, and sedimentary features

Prominent lithologic and faunal variations occur in this member between sections PSD and PSN. The basal part of this member between sections PSD and PSI is constituted of dusky to moderate greenish yellow (5 Y 6/4–10 Y 7/4) fossiliferous calcareous silty shales with lenses of bioclastic limestones. Although the contact of the shales with member A is largely covered, good exposures of the shales could be seen slightly higher up in the section, as at section PSH and locality PFCL 1. These calcareous silty shales also occur at locality PFCL 3 and at section PSO. At sections PSE and PSP the lithology is more of an argillaceous limestone of a yellowish grey to medium light grey (5 Y 7/2–N 6) weathering colour. The fauna of the calcareous silty shales include small and large solitary rugose corals, compound rugose corals, small, flattish cake-like massive form of tabulate corals, platy tabulate corals (locally abundant as at section PSH), few branching tabulate corals, brachiopods, bryozoans, gastropods, trilobites, and a large amount of echinodermal stems and ossicles. The relative abundance of the faunal groups may vary from place to place. The shales at places contain numerous specimens of a few species of brachiopods like atrypids, gypidulinids, and dalmanellids as at section PSO and locality PFCL 3.

The shales vertically pass into the first *Thamnopora*-bed. The first bed is the thickest (measuring ca. 16 m) out of six such beds marked out at the reference section PSA. Between sections PSD and PSI, this bed is distinguished by its marked recessive aspect. Branching tabulate coral *Thamnopora* and platy ones like *Coenites* and *Alveolites* are most plentiful in this bed constituting more than 50 % of the total volume (Fig. 7). They occur in dense argillaceous limestone which commonly shows a pale red to moderate red (5 R 6/2–5 R 5/4) colour. Some parts have, however, a greenish grey to pale olive (5 GY 6/1–10 Y 6/2) colour. Broken fragments of *Thamnopora*, lying prostrate, often show preferred alignments nearly perpendicular to each other. So do some solitary rugose corals and echinodermal stems. At few places over the outcrop, fragments of *Thamnopora* occur being differentiated into layers of coarser and finer sizes. These well differentiated layers laterally continue for about 2–3 m before merging into the adjacent relatively

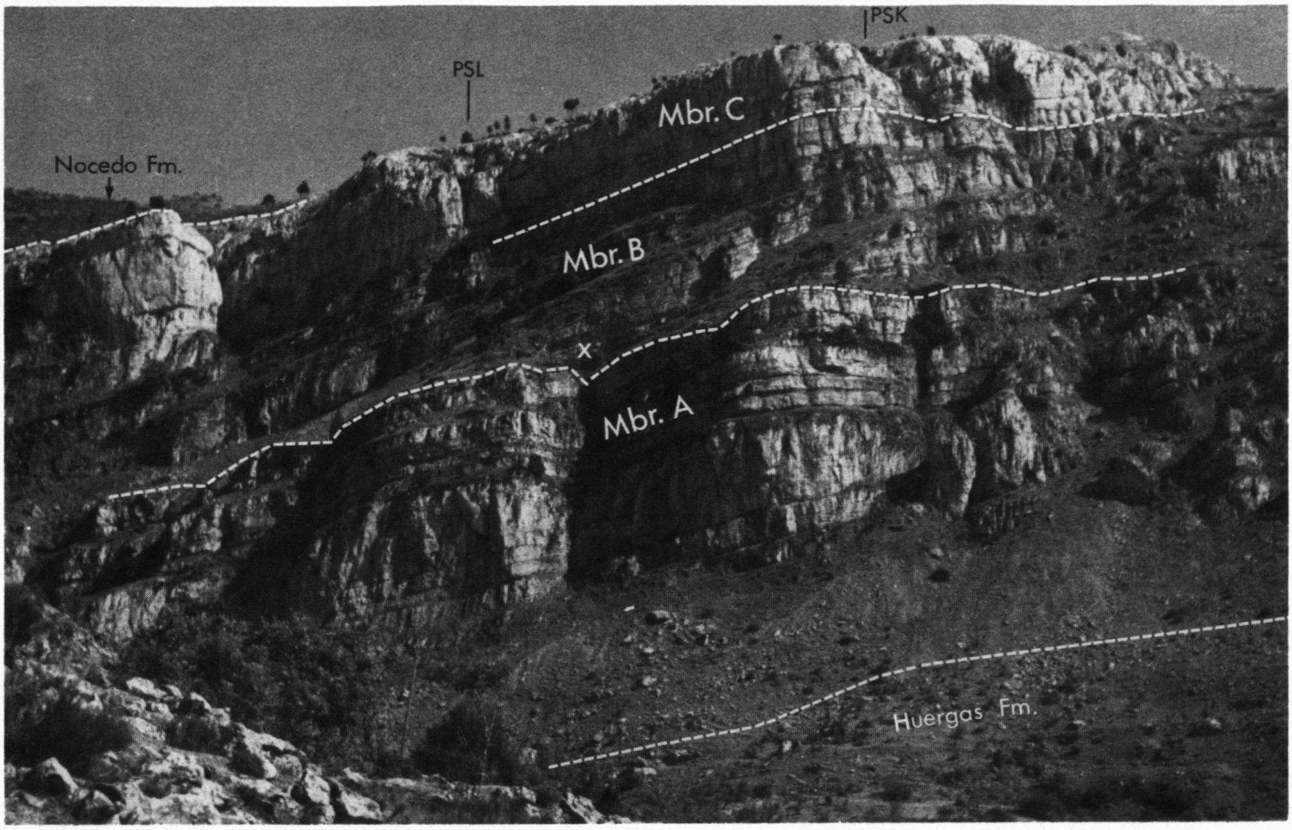


Fig. 8. 'Large-scale-cross bedding' appearance of member B of the Portilla Formation. View from the road by the side of Pantano de Luna. Right side of photo–SW.

Fig. 9. Detail of a part of the wedge marked with X (Fig. 8) showing a massive ball-shaped stromatoporoid colony (marked by hammer) likely in growth position.

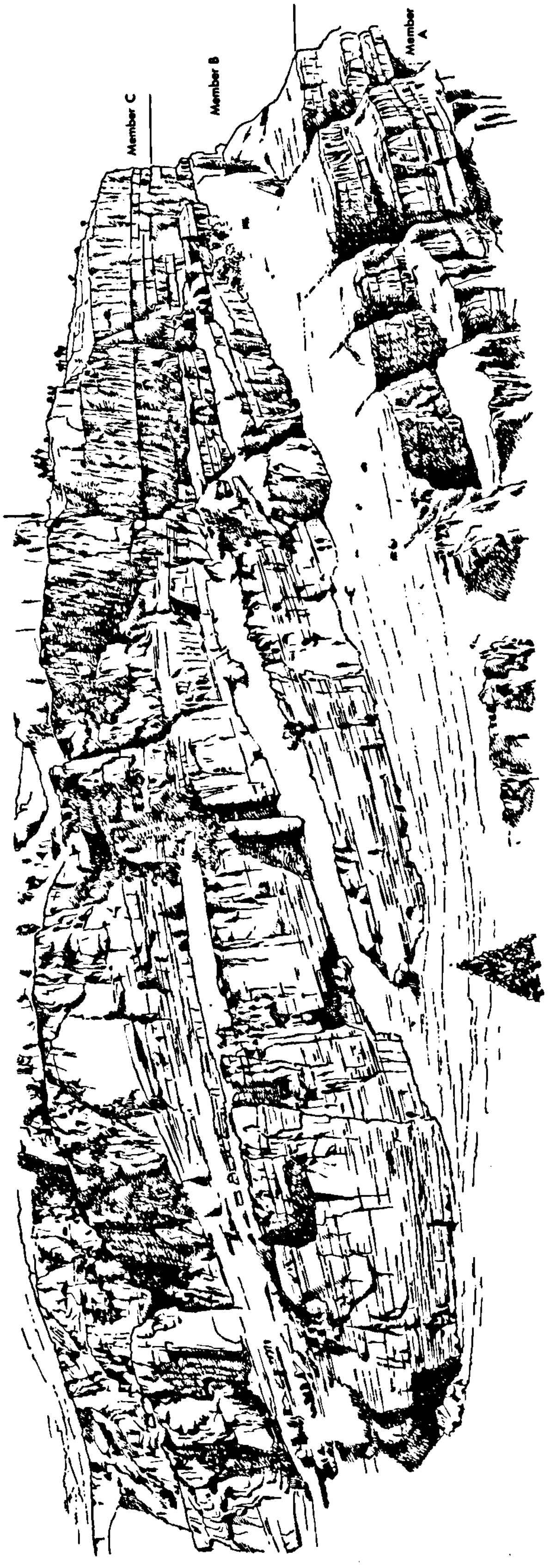


Fig. 10. 'Large-scale cross-bedding' appearance of member B of the Portilla Formation. View looking from the base of member B between sections PSM and PSN. Tracing from a photograph.

uniformly packed *Thamnopora* fragments. No channelling or cross-bedding is noticed. Solitary rugose corals like *Plasmophyllum* and *Stringophyllum* may be fairly common. Massive form of tabulate *Alveolites* is occasionally seen. The largest one observed measures as large as 2 m in length and about 40 cm in height. The few stromatoporoids that occur are found both in massive and laminar forms. They may be seen occurring close to the colonies of *Alveolites*. There are also brachiopods, bryozoans, and a large amount of echinodermal fragments. Concentrations of relatively clean bioclastic detritus occur in form of irregular bands, lenses, dyke, and more or less mound-like bodies. The first *Thamnopora*-bed pinches out at section PSD, and at section PSI it interfingers with the bedded limestones. The vertical transition into the light grey limestone is gradual. One of the conspicuous features of member B between sections PSD and PSK is a 'rhythmic' development of the previous type of *Thamnopora*-bed alternating with medium to thick-bedded limestones containing corals and stromatoporoids. These *Thamnopora*-beds of the higher part of member B also form recessive relief and as such are easy to distinguish in the relatively more resistant light grey limestone succession between sections PSD and PSK. These are, however, thinner than the first *Thamnopora*-bed; their thickness averages about 4 m. The contact of these beds with the underlying limestone is generally sharp with occasional presence of karst-like features. The upward transition into the light grey limestone is generally gradual. The contact may however, be undulating or locally sharply zig-zag probably due to differential compaction. The argillaceous matrix shows the same reddish and/or greenish colours as in the first *Thamnopora*-bed. The gross palaeontological features are the same although the taxa and their relative abundance may vary. There are also lenses of relatively clean bioclastic limestones in these beds. In the higher part of member B, near section PSB, the limestone surfaces show prominent karst-like caving. In this part, *Thamnopora* colonies in growth position are seen. Stromatoporoid colonies may be seen standing out conspicuously on the somewhat rugged limestone surface. The *Thamnopora*-beds all wedge out in the direction of section PSK. No *Thamnopora*-beds occur southeasterly of section PSD.

Broadly, the vertical cliff face between sections PSK and PSM appears as a 'large-scale cross-bedding' (Figs. 8, 10). I consider the several wedge-shaped units of bedded limestones as primary sedimentary features (see chapter V for interpretation). There is no direct evidence of tectonic disturbances, e. g., slickensliding, or tectonic brecciation. In the up-slope direction (in the direction of section PSK) the limestones are generally poorly or massive-bedded whereas in the down-slope direction bedding is very well developed. In the poorly bedded part in the up-slope direction, reefal organisms like corals and stromatoporoids occur. Some of these colonies appear fragmented and overturned. In a wedge marked with a x sign (Fig. 8) stromatoporoids occur in irregularly massive, ball-shaped (Fig. 9), and laminar forms. The ball-shaped colonies may measure as large as 30 cm in diameter. On a bedding surface, stromatoporoids look irregularly hummocky protuberances exhibiting a certain degree of similarity in their weathering features.

In the cliff face between sections PSM and PSN there is a distinct change in lithology and fauna from the bottom to the top of member B. The basal unit is a very thin-bedded, slightly argillaceous, biostromal coralline limestone unit that contains dominantly platy tabulate corals, sparse amount of branching and massive tabulate corals, compound and solitary rugose corals, few stromatoporoids, brachiopods, bryozoans, trilobites, and echinodermal fragments.

This biostromal unit passes upwardly to a more siliceous unit constituted of calcareous sandy mudstones and sandy calcilutitic limestones. The muddy siliceous areas weather yellowish grey (5 Y 7/2) and the limy areas medium dark grey (N 4). The sediments are intensely bioturbated. Horizontally lineated burrow mottling is common. Thin streaks of greyish black, bituminous material occur sporadically. Near section PSN, prominent nodular appearance is seen in the calcilutitic limestones. The faunal content is markedly reduced in comparison to the underlying biostromal unit. There are only few single valves or whole shells of brachiopods, few cephalic fragments of trilobites, small solitary rugose corals, and a few thamnoporid and echinodermal fragments.

These muddy sediments gradually pass upwards into a sequence of very well-bedded (thin-bedded) light grey limestones. Locally, however, a sharp contact is present with the uppermost few meters of the well-bedded limestones as near section PSN. Individual bed thickens and thins and may wedge out in a distance of 5–7 m or even less. Thin argillaceous intercalations between the limestone beds are more prominent in the lower 5–6 m of this sequence, gradually they die out towards the upper part and the beds become somewhat thicker. Inorganic sedimentary structures like cross-bedding, channelling, rippling etc. are not noticed. Compound rugose corals, massive tabulate corals, and stromatoporoids are commonly found through the whole sequence. In the lower part, these colonies apparently appear to be 'sitting' on the bedding. Other faunal elements that occur are few solitary rugose corals, stoutly branched *Thamnopora* fragments, and few brachiopods.

MEMBER C

Contact, thickness, and distribution

The contact between member B and member C is rather transitional. The upper contact with the Nocedo Formation is rather sharp and locally erosive between sections PSD and PSN. At section PSO, and elsewhere the contact is rather gradational. It may, however, be obscured by loose scree material. The thickness of member C between sections PSD and PSN varies from 20–40 m. Member C is present only between those sections; elsewhere it is absent.

Lithology, fauna, and sedimentary features

Member C is rather a monotonous unit. It is constituted of massive-bedded light grey limestones. Occasionally stylolitic indentations are seen that follow the bedding. Massive tabulate and compound rugose corals and stromatoporoids are the conspicuous faunal elements. There are a few argillaceous limestone levels that contain abundant branching and platy tabulate corals, and branching rugose corals. These are however, not as persistent as in member B and wedge out into the massive-bedded limestones in fairly short distance.

MAJOR FACIES AND THEIR SPATIAL DISTRIBUTION

The field observations in the area allow to introduce the following major facies.

Facies I Limestones with corals and stromatoporoids

Facies I (a) Prominent coralline fauna and sparse stromatoporoids. – Generally irregularly bedded (largely thin-bedded) limestones, locally muddy and argillaceous. Argillaceous intercalations frequent. Coralline fauna dominates. Solitary rugose corals rather conspicuous. No compound rugose corals occur. Stromatoporoids sparse. This facies characterizes the lower part of member A.

Facies I (b) Stromatoporoids more prominent. – Massive-bedded (largely medium to thick-bedded) and very well-bedded (thin-bedded) clean limestones. Massive stromatoporoids conspicuous. Massive tabulate corals and/or compound rugose corals are associated with stromatoporoids and may locally form a rigid frame. This facies characterizes higher parts of member A, parts of member B, and member C. Two divisions are made in this facies for clarity of interpretation: the massive-bedded limestones of all three members are labelled as Facies I (bi) and the very well-bedded and locally massive-bedded limestones between sections PSK and PSN in member B are grouped under Facies I (bii).

Facies II Fossiliferous calcareous silty shales and argillaceous limestones with brachiopods

Calcareous silty shales and locally argillaceous limestones. Brachiopods may locally form sizeable concentrations. Platy tabulate corals may be locally abundant. This facies is present in the very basal part of member B between sections PSF and PSI and at section PSO.

Facies III Slightly argillaceous limestones with coralline fauna

Crudely very thin-bedded, slightly argillaceous biostromal coralline limestones. Platy tabulate corals common. Also occur sparse amounts of other coral types. Compound rugose corals present. Stromatoporoids are very rare. This facies characterizes the very basal part of member B between sections PSM and PSN.

Facies IV Argillaceous limestones with abundant branching and/or platy tabulate corals
Argillaceous limestones with a dense, massive aspect. Branching tabulate coral *Thamnopora* and/or platy tabulates *Coenites* and *Alveolites* are most abundant. Locally branching rugose corals also may be abundant. This facies is present in members A, B, and C.

Facies V Calcareous sandy mudstones and sandy calcilutitic limestones
Yellowish grey to dark grey calcareous sandy mudstones and sandy calcilutitic limestones. Few fossils present. Strongly bioturbated. Nodular structure in the muddy limestones is present. This facies is present in member B between sections PSM and PSN.

CHAPTER III

MICROSCOPIC DESCRIPTIONS

TERMINOLOGY

In this thesis, carbonate terminologies of Folk (1959, 1962) and that of Dunham (1962) are followed. Grabau's (1904) terms 'calcilutite', 'calcarenite', and 'calcirudite' are used in describing the grain size of the carbonates. As regards the grain-size scale, Folk's boundary (1959, p. 16, table II) between coarse calcarenite and fine calcirudite is slightly altered here and fixed at 2 mm which is the conventional boundary between 'rudite' and 'arenite' of Grabau. All particles below 1/16 mm are grouped under 'calcilutite' or carbonate mud. Terms for dolomite fabric are used after Friedman (1965).

MINERALOGY AND TEXTURE

Polished and thin sections, insoluble residues, and x-ray analysis reveal the gross mineralogical and textural characters of the carbonates of the Portilla Formation.

Carbonate fraction

Calcite. – Calcite is the dominant carbonate mineral and texturally occurs as allochems (grains of Dunham, 1962), lime mud, and sparry calcite infillings.

Allochems are mostly bioclasts. They include corals, stromatoporoids, brachiopods, bryozoans, gastropods, echinoderms, trilobites, ostracods, foraminifers, tentaculitids, and sponges. Locally pellets occur.

Sparry calcite occurs as syntaxial pore-filling cement rim around echinodermal plates and ossicles each of which forms a single crystal (Bathurst, 1958; Murray, 1960). Staining of thin sections with a mixture of Alizarine Red- S and potassium ferricyanide revealed the presence of both non-ferroan and ferroan calcite. Around the echinodermal debris both non-ferroan and ferroan calcite are commonly present in zonal form.

Sparry calcite occurs also as intrafossil void fillings in which a geopetal fabric is sometimes distinctive as especially in some of the whole brachiopod shells. In the muddy carbonates of Facies IV, it is as well present as irregular mass (Pl. I–8) or as linear to roundish blebs in the muddy matrix. Their size normally varies from about 0.1 to 4 mm. Some of these features apparently resemble 'birds-eyes'. Most of these 'birds-eyes' are identical or broadly equivalent to 'fenestrae' of Tebutt et al. (1965). They could have been formed early in the diagenesis of sediments due to shrinkage of water-saturated mud, generation of gas or water droplets. The presence of similar sparry calcite is generally considered to be indicators of very shallow-marine environment perhaps intermittently exposed to the atmosphere (Perkins, 1963; Wolf, 1965; Dooge, 1966; Shinn, 1968). Sparry calcite apparently has been precipitated also beneath large skeletal fragments like platy and branching tabulate corals which seemingly formed 'umbrella-like' structures (Harbaugh, 1961) sheltering open voids underneath (Pl. II–1). Locally, where large bioclasts are loosely packed, they have prevented infilling of the void space between them by fine sediments and this void has been filled with sparry calcite (Pl. II–2). Widely elongate, blady calcite crystals (cf. rod or wedge shaped crystals, Friedman, 1968) occur as interparticle void fillings between debris of branching tabulate corals (samples collected from section PSC, member C) (Pl. II–4, 5). The blady calcite 'laths' measure 1–4 mm in length and are normal to the surface of coral debris. A bladed or fibrous crust of void-filling calcite is assumed to indicate a very shallow-marine environment and probable subaerial exposure of sediments (Wolf, 1965; van der Meer Mohr, 1969; de Meijer, 1971).

Patchy recrystallization of argillaceous lime mud to pseudospar (Folk, 1965) is observed in a few thin sections of Facies IV carbonates.

Dolomite. – Dolomite occurs from traces of a few rhombs to locally as much as 2–3 % in the Portilla carbonates. A discontinuous band of dolostone with a coarsely crystalline xenotopic fabric is observed between sections PSQ and PSR (member A). The dolomite rhombs in the Portilla carbonates are generally medium to coarsely crystalline. They are irregularly distributed or patchily concentrated in the carbonate beds. They are often coated with yellowish brown 'limonite'. Zoning of iron-containing minerals in the dolomite rhombs is common. Echinodermal fragments are often replaced by externally impinging (Lucia, 1962) dolomite crystals. The rhombs often follow the stylolitic contact between the bioclasts. In several thin sections, relics of bioclasts may be seen surrounded by a mosaic of hypidiotopic dolomite crystals suggesting replacement by dolomite. Hypidiotopic aggregates of dolomite also occur in the void spaces of coral skeletons replacing sparry calcite. Very rarely dolomite crystals show partial replacement by calcite commonly referred to as 'dedolomitization'. The dolomites of the Portilla Formation are considered mostly to be of a diagenetic replacement type (Friedman & Sanders, 1967).

Non-carbonate fraction

Non-carbonate fraction of the samples studied consists of detrital quartz, authigenic quartz, chert, plagioclase feldspars, kaolinite, illite, muscovite, anatase, septachlorite, chlorite(?), 'limonite', hematite, and pyrite.

CARBONATE TYPES OF THE FACIES

Facies I (a)

The carbonates are coarse biocalcarenites and fine biocalcirudites. They are grain-supported and are bioclastic packstones to grainstones. Some bands are argillaceous wackestones. The bioclasts are mostly echinodermal plates and ossicles. Fragments of corals, stromatoporoids, brachiopods, and ostracods are also encountered. Authigenic idomorphic quartz crystals occur in few thin sections.

Facies I (bi) & I (bii)

Coarse biocalcarenites and fine biocalcirudites mostly constitute this facies. The carbonates are clean and are grain-supported (Pl. I–1–3). These are bioclastic grainstones. Echinodermal fragments are dominant. Other bioclasts associated are corals, stromatoporoids, brachiopods, and sometimes a few single valves of ostracods. There are also coral-stromatoporoidal boundstones. Insoluble residue does not exceed 3 ! by weight.

Facies II

Fossiliferous calcareous silty shales with lenses of biocalcarenites and some argillaceous biocalcarenites and calcirudites are present. These are bioclastic wackestones and packstones (Pl. I–4). Insoluble residue of a shaly sample amounts to about 45 % by weight. X-ray analysis (identification by R. O. Felius, University of Leiden) of silt fraction of the insoluble residue shows the presence of quartz, plagioclase feldspars, kaolinite, muscovite, and septachlorite. The clay fraction contains quartz, trace plagioclase, trace anatase, and illite. Detrital quartz (silt) amounts to about 15 %.

Facies III

Coarse biocalcarenites dominant. These are locally argillaceous and are classified as packstones (Pl. I–5). Insoluble residue in a sample amounts to about 7 % by weight. There are a few locally occurring sparry calcitic fenestrae which probably have been formed due to burrowing organisms.

Facies IV

The carbonates are argillaceous (argillaceous material pale red to greenish grey colour) calcilutites, biocalcarenites and calcirudites. These are both mud-supported and grain-supported carbonates and are classified as argillaceous bioclastic wackestones and packstones (Pl. I–6, 7). The bioclasts include abundant platy and branching tabulate corals, solitary rugose corals, few stromatoporoids, brachiopods, bryozoans, gastropods, echinoderms, ostracods (whole carapaces and single valves), and tentaculitids (?). Solution stringers and stylolites are common in the carbonates. The bioclasts as well show stylolitic interpenetration along the contact and are occasionally fractured. This suggests compaction and pressure solution in the carbonates in a late diagenetic stage. Insoluble residue in a sample amounted to about 22 % by weight. X-ray analysis of the pale red non-carbonate silt fraction shows the presence of quartz, muscovite, hematite and in the clay fraction quartz, illite, and trace anatase. The greenish grey non-carbonate silt fraction shows quartz, muscovite, little muscovite in mixed layers, kaolinite, little chlorite (?) and in the clay fraction quartz, illite, and trace anatase. Total iron concentration in the red samples is surprisingly low with a lowest and highest concentration total iron of 0.12% Fe_2O_3 and 3.18 % Fe_2O_3 respectively.

Facies V

Calcareous sandy mudstones to sandy calcilulites (wackestones) mainly constitute this facies (Pl. II–7, 8). The allochems include bioclasts and pellets. The bioclasts are fragments of brachiopods, thin-shelled whole or single valves of ostracods, few tentaculitids, planispiral multi-champerd foraminifers, sponge spicules, echinoderm, and coralline fragments. The pellets often merge with each other or streak out into the finer matrix loosing their shape. The occurrence of pellets in these bioturbated sediments suggests that the pellets are very likely fecal pellets produced by the burrowing organisms. Insoluble residue amounts to about 60 % by weight. Angular to subangular fine detrital quartz (sand) constitutes about 30 % of the insoluble residue. The quartz (silt and sand) often shows a 'swirly' arrangement (cf. Swinchatt, 1965) as a result of the activity of burrowers. Few isolated cubes of pyrite are present.

CHAPTER IV

FAUNAL ASSOCIATIONS

It is apparent that reef-building organisms dominate the biotic constituents of the Portilla Formation. They are associated with other marine invertebrates such as brachiopods, bryozoans, gastropods, echinoderms, trilobites, ostracods, foraminifers, tentaculitids, and sponges. In this chapter, the faunal groups will be briefly described and finally a few basic assemblages will be established. These assemblages will be compared with other well-known Devonian reef fauna assemblages from Germany, Belgium, and England.

FAUNAL GROUPS

Corals

Rugose and tabulate corals are present throughout the Portilla Formation. Small and large solitary rugose corals are relatively more common in shaly or muddy carbonate layers. They seem to have preferred a low-energy environment. Branching rugose corals also have thrived in muddy, low-energy environment. Compound rugose corals are prominent in member B and member C of the Portilla Formation. Large colonies of *Phillipsastrea* are found in calcareous shales, argillaceous limestones, and pure limestones thus indicating a wide range of tolerance for substrate changes. Colonies of *Hexagonaria* and *Endophyllum* measuring as large as 20 cm in diameter occur both in argillaceous and in pure limestones. Compound rugose corals have thrived both in low-energy and high-energy environments. The tabulate coral *Favosites* always occurs in argillaceous limestones and is found in roundish massive, hemispherical, globular, and in small stubby form. It is, however, typical in Facies I (a). The most commonly occurring tabulate coral is *Alveolites*. Large irregularly massive colonies of *Alveolites* commonly occur together with massive stromatoporoids in Facies I (bi) & I (bii). The associated clean carbonates suggest that they thrived in high-energy environments. Small, isolated flattish cake-like colonies are found occasionally in shaly sediments of Facies II. A platy form of *Alveolites* and *Coenites* have been prolific in low-energy environments. They are associated with abundant fragments of branching tabulate *Thamnopora* in the muddy carbonates of Facies IV. The branching *Thamnopora* probably formed 'meadows' or 'thickets' in shallow, protected locations in a way analogous to the recent 'staghorn coral' *Acropora cervicornis*. In recent reef environment, *Acropora cervicornis* generally thrives best in quiet environment in deeper level in fore-reef zone in the windward as well as in the open shore in lagoonal and leeward parts (P. H. de Buisonjé, Geological Institute, University of Amsterdam, pers. comm., 1968). Locally occurring (few pockets between sections PSB and PSC in member B) calcite-cemented debris of *Thamnopora* might suggest that the colonies were broken and thrown off the living environment subaerially during storms (cf. 'beach rock' of *Acropora cervicornis*, Pl. II–6). Fragments of *Thamnopora* are occasionally encrusted by bryozoans and also laminar stromatoporoids (Pl. II–3). The encrustation may be confined to one side of the thamnoporid or may surround it evenly. The encrustation is perhaps analogous to that of coralline algae encrusting dead *Acropora* sticks in extremely shallow back-reef environments. In some recent shallow reef environment, fragments of *Acropora cervicornis* are encrusted by coralline algae on all sides when there is some current rolling the fragments, but when broken off a reef and deposited in deeper water (50 or 100 m) they are not encrusted at all (P. H. de Buisonjé, pers. comm., 1968). It is probable that the thamnoporid coral was dead and rolling perhaps gently to facilitate a uniform encrustation or was not rolling at all so that encrustation occurred on one side only (face towards sediment/water interface). Braithwaite (1967) records encrusting growth of *Alveolites* on *Thamnopora* fragments from the carbonate rocks of South Devon, England. The tabulate coral *Aulopora* commonly occurs as an epifaunal encrustation on platy *Coenites*, *Alveolites* and solitary rugose corals.

Stromatoporoids

Sleumer (1969) reported three species of stromatoporoids from the Portilla Formation: *Actinostroma stellulatum*, *Stromatopora concentrica*, and *Stromatoporella ? granulata*. These species are found in massive and in laminar forms. The massive forms may be hemispherical, globular, lensoid, irregular massive, and large spherical or ball-shaped. Stromatoporoids are rare or very sparsely distributed in facies with shaly or muddy carbonate layers. Stromatoporoids rarely occur in facies abounding in platy and branching tabulate corals (Facies IV). Only few laminar and lensoid colonies are seen. The laminar forms may encrust fragments of *Thamnopora* (Pl. II–3). Stromatoporoids are conspicuous in clean carbonates of Facies I (bi) & I (bii). Irregularly massive and ball-shaped colonies commonly occur together with massive tabulates and/or compound rugose corals. Stromatoporoids encrust among themselves as well as the tabulate corals. The massive stromatoporoids in Facies I (bi) & I (bii) have thrived in high-energy environment (Lecompte, 1958, 1961, 1970; Edie, 1961; Klovan, 1964; Murray, 1966; Jenik & Lerbekmo, 1968). Probably stromatoporoid abundance in the Portilla carbonate facies has been controlled primarily by the degree of muddiness of water and not primarily by any significant differences in water depth.

Brachiopods
The several groups of brachiopods occurring in the Portilla Formation belong to atrypids, athyrids, dalmanellids, davidsoniids, leptaenids, gypidulinids, spiriferids, retziids, and rhynchonellids. Locally, in Facies II (e. g. section PSO, locality PFCL 3), large numbers of specimens of a few species of atrypids, dalmanellids, and gypidulinids occur suggesting probably ecologically restricted conditions (formation of 'reef' barrier). Coarse-ribbed specimens of *Spinatrypa* (*Spinatrypa*) sp. and *Spinatrypa* (*Isospinatrypa*) sp. cf. *wotanica* are associated with branching tabulate *Thamnopora* and platy *Coenites* and *Alveolites* in Facies IV. This compares with that of the 'Biotope of attached thicket reef atrypids' of Copper (1966a, p. 258). Locally, numerous whole specimens both adult and juvenile of *Spinatrypa* (*Isospinatrypa*) sp. cf. *wotanica* occur in the same locality suggesting quiet environmental conditions. Spines in *Spinatrypa* were probably used as anchoring or stabilizing devices (Copper, 1967). The species *Davidsonia verneuili* commonly occurs attached to platy tabulate corals like *Coenites* and *Alveolites*.

Bryozoans
Fenestellate, ramose or stick-like, encrusting, and mat-like forms of bryozoans have been observed in the Portilla Formation. Bryozoans most commonly occur in shaly and muddy sediments. Bryozoa encrust the tabulate coral *Thamnopora* and *Coenites* in Facies IV. Stromatoporoids may also be encrusted by Bryozoa (Sleumer, 1969, p. 14, pl. 2, fig. 2).

Gastropods
Gastropods are very rare in the Portilla Formation.

Echinoderms
Echinodermal fragments are very common throughout the Portilla sequence. These are dominantly of crinoid columnals and plates. Few complete calyces have been observed in basal biostromal part of member B at section PSS. In Facies IV, unabraded crinoid stems as large as 8–10 cm occur together with *Thamnopora* fragments. Basal attachment discs also occur on platy tabulate corals. This suggests crinoids perhaps lived together or in the vicinity of tabulate corals forming the so-called 'crinoidal gardens'. Apparently crinoids have lived in muddy environments (Ager, 1963, p. 132). Both a rheophile and rheophobe mode of life might well have been adopted by the crinoids living in the high-energy and low-energy environments respectively (Breimer, 1969).

Trilobites
Isolated cephalic, thoracic, and pygidial fragments of trilobites occur in the Portilla, commonly in the shaly layers.

Ostracods
Complete carapaces as well as single valves of ostracods commonly occur in argillaceous carbonates. The ostracods are smooth and are both thin and thick-shelled. Ostracods probably lived in quiet environments as the associated fine sediments suggest. The presence of disarticulated and abraded valves in some clean bioclastic calcarenites and calcirudites suggest transportation probably from nearby quiet environments.

Foraminifers
Few planispiral multi-chambered foraminifers occur in Facies V.

Tentaculitids
Tentaculitids rarely occur in lenses of biocalcarenites in calcareous silty shales of Facies II. They are also present in Facies V and probably in Facies IV.

Sponges
Few calcareous sponge spicules are noted in Facies V.

Trace fossils
Biogenic activity is conspicuous in Facies V. This is characterized by 'swirly' or horizontally lineated burrow mottling, that probably has resulted out of the activity of deposit-feeders. Activity of deposit-feeders might indicate slightly deeper and quieter energy regime where food particles would easily settle so as to be used by the infaunal organisms (Seilacher, 1967). Surface spreites of the trace fossil *Zoophycos* has been observed on the bedding surface of calcareous sandstone band in the higher part of member B at section PSS. The structures are shallowly conical with curved ridges or flutings. They may measure about 10–30 cm in diameter. The origin of *Zoophycos* traces is still a matter of controversy. Their presence could indicate relatively quiet environment at shallow to intermediate depth (Seilacher, 1967; Ellenor, 1969).

FAUNAL ASSEMBLAGES

The reefal fauna of the Portilla Formation are viewed in three broad assemblages.

Assemblage of corals with few stromatoporoids
An assemblage is recognized in which corals are the dominant faunal elements and stromatoporoids are sparse. Among the corals solitary rugose corals are often

conspicuous. Branching rugose corals occur rarely. Tabulate corals like *Alveolites, Favosites, Heliolites*, and *Chaetetes* also occur. No compound rugose coral is seen.

The stromatoporoids are represented by loosely distributed hemispherical or globular colonies. This assemblage mainly corresponds to Facies I (a). An assemblage of this type with certain conspicuousness of solitary rugose corals, may be compared with the 'Rüben-Riff' association of Struve (1963) in the Middle Devonian biostromal 'reefs' in Germany.

The present assemblage may perhaps also be compared to 'zone corallienne' (sousturbulent environment) of Lecompte (1958, 1961) in the Middle to Upper Devonian biostromal 'reefs' in Belgium. The 'Combe Martin biotope' of Webby (1966) in North Devon and West Somerset, England may as well be compared with this assemblage. It is constituted of small solitary rugose corals, a few tabulates but lacks in stromatoporoids.

Assemblage of massive stromatoporoids, massive tabulates and/or compound rugose corals

This assemblage is characterized chiefly by massive stromatoporoids, massive tabulates (mainly *Alveolites*) and/or compound Rugosa (mainly phillipsastraeds). This assemblage corresponds to Facies I (bi) & I (bii). It is comparable to the 'Knollen-Block-Riff' association of Struve (1963) that is characterized by large compact, globular to cake-like colonies of stromatoporoids and colonies of rugose and tabulate corals. Struve (1963, p. 253) suggests an extremely shallow turbulent environment to this association. Jux (1960) also thought that 'Stromatoporen-Blockriff' thrived in the zone of continuous turbulence. This assemblage may be compared to 'zone des stromatopores, massif, dominants' of Lecompte (1958, 1961) (subturbulent to turbulent environment). The 'Quantock biotope' has also been considered by Webby (1966) a very shallow, turbulent environment with abundant stromatoporoid and tabulate coral fauna.

Assemblage of branching and/or platy tabulates (Thamnopora, Coenites, and Alveolites)

This assemblage is characterized by branching *Thamnopora* and/or platy *Coenites* and *Alveolites*. Solitary and branching rugose corals, rare laminar stromatoporoids, and atrypid brachiopods (*Spinatrypa* (*Spinatrypa*)sp., *Spinatrypa* (*Isosponatrypa*)sp. cf. *wotanica*, *Spinatrypina* sp., *Desquamatia* sp.) may also be associated. This assemblage corresponds to Facies IV. It reminds of the 'Rasen-Reef' association in the Middle Devonian in Germany that is characterized by branching tabulate corals and branching rugose corals. Platy form and few massive form of *Alveolites* are also associated. This association is named 'Rasen-Riff und Crinoiden-Wälder' and compared by Struve (1963, p. 252, abb. 9) to Lecompte's 'zone subturbulente'. Webby (1966) has compared the 'Brendon biotope' to the 'Rasen-Riff' association. The faunal composition of Brendon biotope is somewhat different; there are rare stromatoporoids, few tabulates (mainly *Thamnopora*) and abundant and varied compound and solitary rugose corals. Association of *Thamnopora, Alveolites*, and *Coenites* with varying amounts of horn corals are known from the 'Coral beds' in Middle Devonian reefs in Spanish Sahara (Dumestre & Illing, 1967).

CHAPTER V

ENVIRONMENT AND DEPOSITIONAL HISTORY

The areally delineated carbonate facies of the Portilla Formation reflect variations in the environmental conditions during sedimentation. The carbonate depositional texture and associated fauna enable to present the following interpretation of the environmental conditions of the various facies. Fig. 11 shows the main features of the Portilla carbonate facies.

DEPOSITIONAL ENVIRONMENT

Facies I (a)

A depositional environment with frequently fluctuating energy conditions is assigned to this facies as evidenced from the alternations of relatively well-washed packstones and grainstones with intervals of calcareous shales and argillaceous limestones. Argillaceous admixture or intercalations suggest frequent influx of siliciclastics to the depositional site. Around coral colonies e. g. *Favosites* and stromatoporoids muddy sediments occur indicating very weak or sluggish currents in the depositional milieu. Concentrations of solitary and branching rugose corals in muddy layers also point to rather quiet conditions.

Facies I (bi)

This facies was deposited in a high-energy environment. The occurrence of well-washed grainstones, eroded and overturned coral and stromatoporoid colonies, brecciated boundstones indicate turbulent conditions. The insoluble residue content is negligible and this suggests that generally little siliciclastics were supplied to the environment and a clear-water (Irwin, 1963) sedimentation prevailed.

Facies I (bii)

This facies is interpreted as a biogenetic barrier facies. From the 'large-scale cross-bedding' aspect, a gentle depositional slope (in direction of section PSM) is apparent. Stromatoporoid and coral (massive tabulates and compound rugosans) growth of a biostromal nature formed this facies. This 'reef' barrier thrived in a shallow (in order of 15 m), open marine, high-energy environment with little siliciclastic influx. The water was well-lighted, oxygenated, and warm water of normal salinity in which an abundant food supply insured proliferation of reef-building organisms. The boundstone aspect as well as the poorly developed bedding in the up-slope part of the wedges (towards section PSK) suggest relatively strong wave activity. The abundance of stromatoporoids might have been caused by the shallowness of the up-slope part. Waves and currents in this environment continuously winnowed fine sediments, produced local rounding and sorting of bioclasts, and caused short lateral transportation of bioclastic sands so that these probably spread as sheets between the colonial organisms. As Ginsburg et al. (1963) have pointed out, there is relatively little net lateral transportation of sand-sized and coarser skeletal particles within shallow-water carbonate environments. These accumulate in the same local area of sedimentary basin where they are produced. In shallow-water carbonate areas, the presence of reefs, banks, or shoals produce local relief and this impedes thorough-going water movements that could transport sediments over long distances. Prolific growth of benthic organisms also stabilizes carbonate particles at sediment/water interface and as such they inhibit the movement of particles by current traction.

The directional alignment of the wedges is striking. Prevailing wave and current direction certainly have favoured reef growth in the area, although their precise effect can not easily be shown. It is likely that slow subsidence of the bottom was another important factor in controlling the alignment of the wedges.

Facies II

A protected, back-reef environment of deposition is assigned to this facies. The calcareous silty shales, argillaceous wackstones and packstones with local concentrations of whole shells of brachiopods and in-situ colonies of compound rugose corals principally suggest a quiet environment of deposition. Siliciclastic influx was conspicuous in this environment.

Facies III

This facies was deposited in a relatively low-energy environment (in front of the 'reef' barrier) as evidenced from wackestone-packstone carbonates containing a large proportion of coralline elements nearly in-situ. The abundance of benthic organisms suggests a well-aerated milieu. Siliciclastic influx was low.

Facies IV

The abundant occurrence of platy form of tabulates (e. g. *Alveolites* and *Coenites*) and branching tabulate (e. g. *Thamnopora*) in muddy wackestone-packstone carbonates indicate generally a quiet environment of deposition. The stratigraphic framework enables to interpret the depositional environment in shallow, sheltered areas within reefal biostromes (in member A and member C) and a protected back-reef 'lagoonal' environment (in member B). In the study of the Upper Devonian reef limestones of Germany, Krebs (1966) places abundant occurrences of branching tabulate corals in a back-reef facies whereas in his central and fore-reef facies complex he finds characteristic massive and tabular stromatoporoids and massive and globular tabulate corals. In the back-reef environment of the Portilla Formation, amongst the platy and dominantly broken branching tabulate corals, there are a few occurrences of branching *Thamnopora* colonies in life position suggesting thereby that the fragments encountered in large quantity have not been washed into the environment of deposition but that the colonies flourished in the same environment where their fragments occur today. The preferred alignments of fragments of *Thamnopora* suggest rather strong water movements in the back-reef area. It resembles that of orientations of recent *Acropora* sticks in south coast (Costa Coral) of Isla Perez of the Alacran Reef area, Yucatan (Folk & Robles, 1964, pl. 2, fig. C) and in Nymph Islet, Great Barrier Reef (Maxwell, 1968, p. 123, figs. A, C). P. H. de Buisonjé (pers. comm., 1968) observed orientations of *Acropora* sticks in recent reef environment around Curaçao island and found that the sticks are oriented parallel to the current when the current is strong in one direction, but when the currents are slow or in alternating directions, the sticks roll perpendicular to the current. Currents might have been similar in causing the alignment of *Thamnopora* fragments. These fragments sometimes occur in alternating layers of coarse and fine sizes. This suggests periodic increase and decrease in energy of the environment which might well be due to passing storms. Summarily, it may be stated that this back-reef environment was generally a very shallow, quiet environment being protected by a 'reef' barrier from the open sea. However, the area was periodically swept by strong currents. The branching and platy tabulates probably baffled currents and stabilized the sediments much in the same way as marine grass *Thalassia* in shallow Florida Keys (Lowenstam & Ginsburg, 1957). Protected muddy skeletal deposits are also seen in the present back-shelf of the Florida Bay that is bordered by marginal reefs absorbing most of the oceanic turbulence (Ginsburg, 1956; Baars, 1963).

The pale red colour of the argillaceous carbonates of this facies is due to the presence of finely dispersed hematite. The red colouration is not necessarily indication of any special type of climate (Walker, 1967).

Facies V

The bioturbated muddy siliciclastics and carbonates of this facies suggest a quiet environment of deposition. Accumulation of sediments occurred below effective wave base where waves and currents were not effective to winnow away the fine sediments. The environment was shallow marine and was slightly deeper (Wilson, 1969) in front of the 'reef' barrier. The high quantity of siliciclastics in this facies (in comparison to facies III) might be due to changes in the rates of supply or due to current diversions associated with reef growth in the vicinity.

The notable reduction in benthic faunal content and relatively high organic material indicate prevalence of toxic bottom conditions inhospitable to benthic life. Purdy (1964) discusses relationship between substrates and benthic faunas and states that low current velocities generally result in non-shifting substrates containing considerable proportion of mud and organic matter. The ecological result here is usually a bottom fauna dominated by burrowing deposit feeders, and possibly few suspension feeders. The general paucity of other benthic life might be attributed to poor interstitial circulation resulting in the accumulation of toxic decomposition products and/or depletion of available oxygen. Purdy's remarks are largely in agreement with my observations on the lithology and fauna of this facies. Nodular limestones and shales similar to the present facies have been reported in front of reefs from other Devonian reef sequences (see Dooge, 1966).

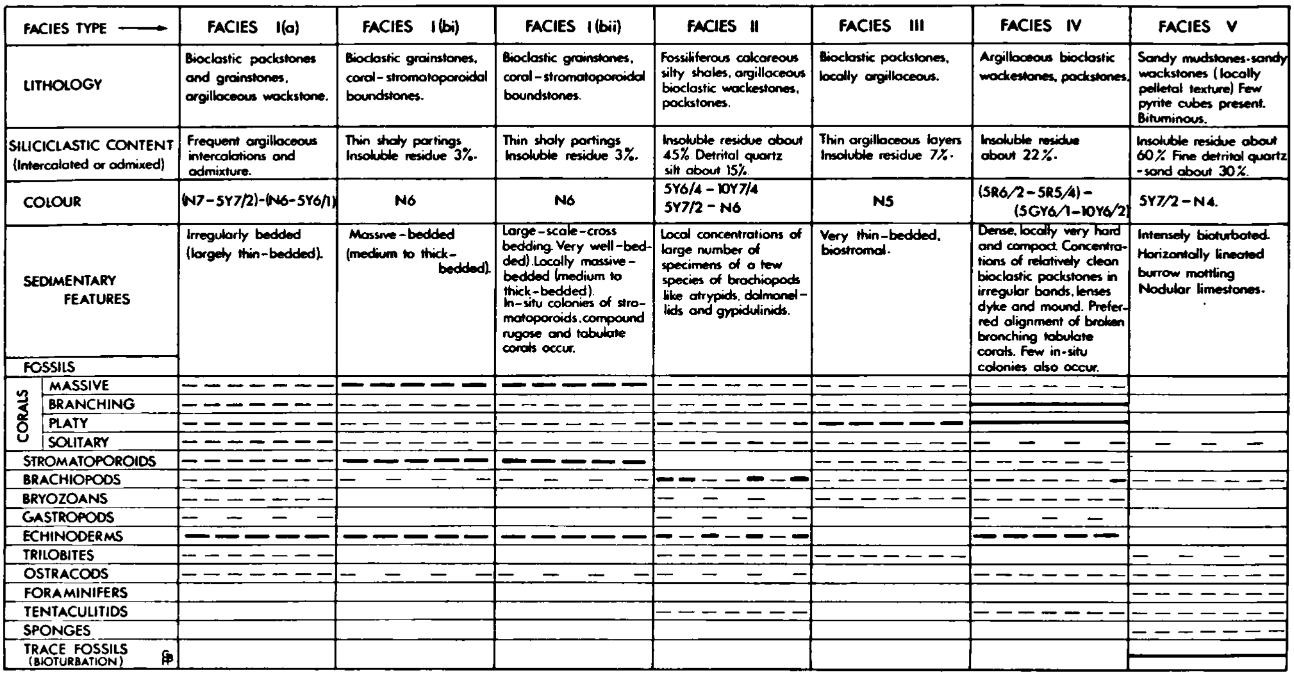
ENVIRONMENTAL SYNTHESIS

The carbonate facies types of the Portilla Formation broadly belong to a biostromal 'reef' complex. They have been deposited in a shallow-marine environment on a shelf or in an epicontinental sea. The presence of abundant reef-building organisms indicates a warm, shallow water of normal marine salinity. The variations in the siliciclastic content in the various facies probably reflects variations in amount and/or direction of supply of siliciclastics into a dominantly carbonate depositional basin (Sanders & Friedman, 1967). In member B, a biostromal 'reef' barrier protected a back-reef facies from the open marine side. The lateral environmental relationship of the facies in member B is shown in Fig. 12. In member B, the lateral facies changes substantiated from the lithology and fauna reflect changes in the contemporaneous depositional environments. The Portilla environmental picture is closely comparable to those of Copper (1966a) and Geissler (1969) for some Devonian reef areas in Germany, and of Wallace (1969) for northern France. Towards the southeastern side (section PSF), the Portilla carbonates wedge out into dominantly siliciclastic deposits. The internal contortions as noted in member A are certainly indications of slumping and suggest instability during deposition. They were probably formed as a result of bottom movements before the carbonates were completely lithified. The slumps towards the siliciclastics might indicate a slope in this direction. The absence of the Portilla carbonates southeasterly of section PSF is interpreted as a change in facies from the carbonates to the siliciclastics. Supply of siliciclastics and other unfavourable conditions hindered biogenetic carbonate sedimentation in this side. The siliciclastics are marine deposits as evidenced from the presence of few marine fossils. The relative abruptness of carbonate–siliciclastic contact might mean that the carbonates originally formed at a somewhat higher topographic level than the siliciclastics. In the recent Great Barrier Reef Province, the differences between carbonate and siliciclastic facies pattern are principally ascribed to contrasting physiographic and hydrographic settings (Maxwell & Swinchatt, 1970).

DEPOSITIONAL HISTORY

The Portilla carbonates are underlain and overlain by siliciclastic deposits of the Huergas and the Nocedo Formation respectively and constitute an interval of dominantly autochthonous carbonate sedimentation. Sedimentation of the carbonates began in Eifelian time when supply of the siliciclastics was reduced and a favourable environment prevailed for the flourishing of a rich variety of benthic life in a shallow sea. Deposition of member A started under rather fluctuating conditions with a fauna in which coralline elements were prominent. Carbonate sedimentation kept pace with subsidence of the sea bottom and the water remained shallow. Gradually more or less uniform conditions of deposition prevailed and in a shallow turbulent environment stromatoporoidal carbonates accumulated. This accumulation was interrupted few times by influx of fine siliciclastics and a rather sheltered condition was prevailing supporting platy and branching tabulate corals. The prominent stromatoporoidal content of the higher part of member A suggests extremely shallow turbulent conditions towards the end of deposition of member A.

Sharp changes in the depositional facies occurred by the end of deposition of member A in the late Eifelian, probably partly as a result of synsedimentary bottom movements. This break in sedimentation of member A was soon followed by a notable influx of siliciclastics perhaps due to emergence of the marginal areas of the carbonate depositional basin. The depositional facies pattern in member B was distinctly different from that of member A and member C. A barrier 'reef' pattern emerged at the beginning of deposition of member B approximately at the Eifelian/Givetian transition. Prolific stromatoporoid-coral growth of a biostromal nature was established on areas of slightly higher relief on a gently sloping surface of member A. This reef growth protected an area behind from strong wave activity of the open sea. The sheltered back-reef facies was initially (Phase I) characterized by calcareous silty shales and argillaceous wackestones and packstones containing platy tabulates, few compound rugose corals, and localized concentration of brachiopod shells (Facies II) (Fig. 12A). This was subsequently followed (Phase II) by a facies of argillaceous wackestones and packstones in which platy tabulates and especially branching tabulates (*Thamnopora*) abounded (Facies IV) (Fig. 12B). This



FACIES TYPE ⟶	FACIES I(a)	FACIES I(bi)	FACIES I(bii)	FACIES II	FACIES III	FACIES IV	FACIES V
LITHOLOGY	Bioclastic packstones and grainstones, argillaceous wackstone.	Bioclastic grainstones, coral-stromatoporoidal boundstones.	Bioclastic grainstones, coral-stromatoporoidal boundstones.	Fossiliferous calcareous silty shales, argillaceous bioclastic wackestones, packstones.	Bioclastic packstones, locally argillaceous.	Argillaceous bioclastic wackestones, packstones.	Sandy mudstones-sandy wackstones (locally pelletal texture) Few pyrite cubes present. Bituminous.
SILICICLASTIC CONTENT (Intercalated or admixed)	Frequent argillaceous intercalations and admixture.	Thin shaly partings Insoluble residue 3%.	Thin shaly partings Insoluble residue 3%.	Insoluble residue about 45% Detrital quartz silt about 15%.	Thin argillaceous layers Insoluble residue 7%.	Insoluble residue about 22%.	Insoluble residue about 60% Fine detrital quartz -sand about 30%.
COLOUR	(N7-5Y7/2)-(N6-5Y6/1)	N6	N6	5Y6/4 - 10Y7/4 5Y7/2 - N6	N5	(5R6/2-5R5/4) - (5GY6/1-10Y6/2)	5Y7/2 - N4.
SEDIMENTARY FEATURES	Irregularly bedded (largely thin-bedded).	Massive-bedded (medium to thick-bedded).	Large-scale-cross bedding. Very well-bedded). Locally massive-bedded (medium to thick-bedded). In-situ colonies of stromatoporoids, compound rugose and tabulate corals occur.	Local concentrations of large number of specimens of a few species of brachiopods like atrypids, dalmanellids and gypidulinids.	Very thin-bedded, biostromal.	Dense, locally very hard and compact. Concentrations of relatively clean bioclastic packstones in irregular bands, lenses dyke and mound. Preferred alignment of broken branching tabulate corals. Few in-situ colonies also occur.	Intensely bioturbated. Horizontally lineated burrow mottling Nodular limestones.
FOSSILS							
CORALS MASSIVE	– – – – – – –	▬ ▬ ▬ ▬ ▬	▬ ▬ ▬ ▬ ▬	– – – – – – –	– – – – – – –	– – – – – – –	
CORALS BRANCHING	– – – – – – –	– – – – – – –	– – – – – – –	– – – – – – –	– – – – – – –	━━━━━━━	
CORALS PLATY	– – – – – – –	– – – – – – –	– – – – – – –	– – – – – – –	▬ ▬ ▬ ▬ ▬	━━━━━━━	
CORALS SOLITARY	– – – – – – –	– – – – – – –	– – – – – – –	– – – – – – –	– – – – – – –	– – – –	– – –
STROMATOPOROIDS	– – – – – – –	▬ ▬ ▬ ▬ ▬	▬ ▬ ▬ ▬ ▬		– – – – – – –	– – – – – – –	
BRACHIOPODS	– – – – – – –	– – – –	– – – –	▬ ▬ – – ▬ – ▬	– – – – – – –	– – – – – – –	– – – – – – –
BRYOZOANS	– – – – – – –			– – –	– – – – – – –	– – – – – – –	
GASTROPODS	– – – –			– – – –		– – –	
ECHINODERMS	▬ ▬ ▬ ▬ ▬	▬ ▬ ▬ ▬ ▬	▬ ▬ ▬ ▬ ▬	▬ – ▬ – ▬ – ▬		▬ ▬ ▬ ▬ ▬	
TRILOBITES	– – – – – – –			– – – – – – –	– – – – – – –		– – – –
OSTRACODS	– – – – – – –	– – – –	– – – –	– – – –		– – – – – – –	– – – – – – –
FORAMINIFERS							– – – – – – –
TENTACULITIDS				– – – – – – –		– – – – – – –	– – – – – – –
SPONGES							– – – – – – –
TRACE FOSSILS (BIOTURBATION)							━━━━━━━

Fig. 11. Main features of the carbonate facies of the Portilla Formation.

back-reef area was separated from the area of siliciclastic deposition farther southeast of section PSF (near Sagüera village) by an extremely shallow marine or shoal area which might have been emergent. In slightly deeper open marine side of the reef growth, a coralline biostromal facies (Facies III) developed and this was followed by a bioturbated muddy carbonate facies (Facies V). The pattern of sedimentation in member B was one of rhythmic alternations of muddy *Thamnopora*-carbonates (Facies IV) with the clean reefal carbonates continuous with the 'reef' barrier (Facies I (bii)). These oscillatory environmental conditions reflect probably minor changes in sea level likely due to epeirogenetic movements of the bottom. The deposition of the carbonates was generally in shallow water and perhaps the depositional surface occasionally emerging subaerially as the solution surfaces between the clean reefal carbonates and *Thamnopora*-carbonates might indicate. During the deposition of the *Thamnopora*-carbonates siliciclastic influx, however, was notable. Epeirogenetic movements in the entire Devonian of the Cantabrian Mts. have been mentioned by some previous workers (Rupke, 1965, p. 38, 39; Evers, 1967, p. 102). Since the Sabero-Gordón line, a fundamental tectonic line, is close to the present area of study, its activity might be considered important during sedimentation of the Portilla carbonates. Rupke (1965, p. 38, 39) and Evers (1967, p. 102) presented evidences to show that this line acted from the Upper Devonian through Tertiary times. Reijers (1971) argued for earlier activity of this fundamental line during deposition of the Portilla Formation. In the Esla area, mainly in view of the differences in thickness and lithofacies in the northern autochthone of Valdoré and the southern Peña Corada unit (as part of autochthone according to Reijers, 1971), presence of biogenetic growth structures, and alteration of screes of bioherms, Reijers has argued that the Sabero-Gordón line acted as a facies boundary and perhaps as a fault during deposition of the Portilla carbonates.

The biostromal 'reef' barrier persisted throughout the deposition of member B due to favourable ecologic conditions and slow subsidence of the bottom, and a shallow-water condition was maintained throughout. In time, organic growth and associated carbonate sedimentation exceeded the rate of subsidence and as a result the 'reefs' laterally shifted seawards (in a northerly direction) thus implying a depositional regression. The back-reef facies of platy and branching tabulates also advanced in a seaward direction. A regressive 'reef' barrier development is apparent in member B of the Portilla Formation perhaps reflecting an increasingly emergent tendency of the marginal part of the carbonate basin. The upward transition from the muddy carbonates (Facies V) to the clean carbonates (Facies I (bii)) between sections PSM and PSN also reflects this regressive shoaling condition due to bottom movements. The barrier 'reef' pattern of member B probably terminated due to changes in relative subsidence during deposition of member C. The deposition of member C was more of the type of member A. A strong supply of siliciclastics during the deposition of the Nocedo brought an end to the Portilla carbonate sedimentation.

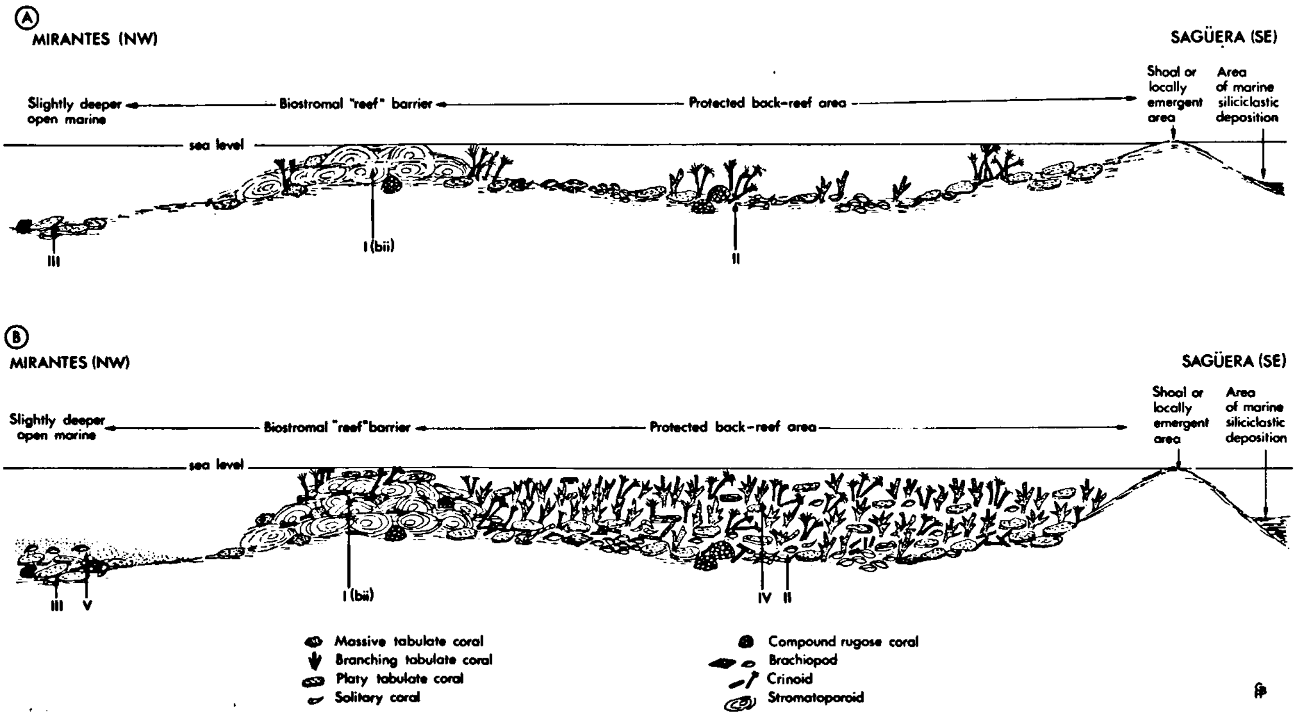


Fig. 12. Generalized lateral environmental relationships during member B deposition based on the sections between Sagüera (SE) and Mirantes (NW). A- Phase I; B- Phase II.
Facies types are indicated as I (bii), II, etc.

The variation in thickness in the Portilla Formation has been probably mainly due to a slow and prolonged differential subsidence of the carbonate depositional basin: the westerly part continuously subsiding relatively faster than the easterly or southeasterly part. The absence of a large part of member B and member C in the easterly and southeasterly directions is probably largely due to non-deposition of sediments in those parts.

CHAPTER VI

SYSTEMATIC DESCRIPTION OF THE RHYNCHONELLIDA

Among the brachiopod fauna of the Portilla Formation the rhynchonellids constitute a particularly interesting part, because of their striking similarity with the Middle Devonian material from Germany, and it was mainly therefore, that this material was selected for a detailed investigation in the framework of this thesis. The exact identification of the Spanish material was sometimes hindered by the fact that the stratigraphic position and the internal structure of the relevant German species were not always precisely known. By courtesy of Dr. Herta Schmidt (Senckenberg Museum, Frankfurt/Main) I was able to section some critical specimens for comparison and the results are figured here. The techniques used in this thesis are described in Chapter I. The morphological terminology has been adopted from Williams et al. (1965), Krans (1965), and Westbroek (1967).

The collected material and the peels are stored in the Department of Stratigraphy and Palaeontology, Geologisch en Mineralogisch Instituut der Rijksuniversiteit, Garenmarkt, Leiden.

Biostratigraphical implications of this work are presented in Chapter VII.

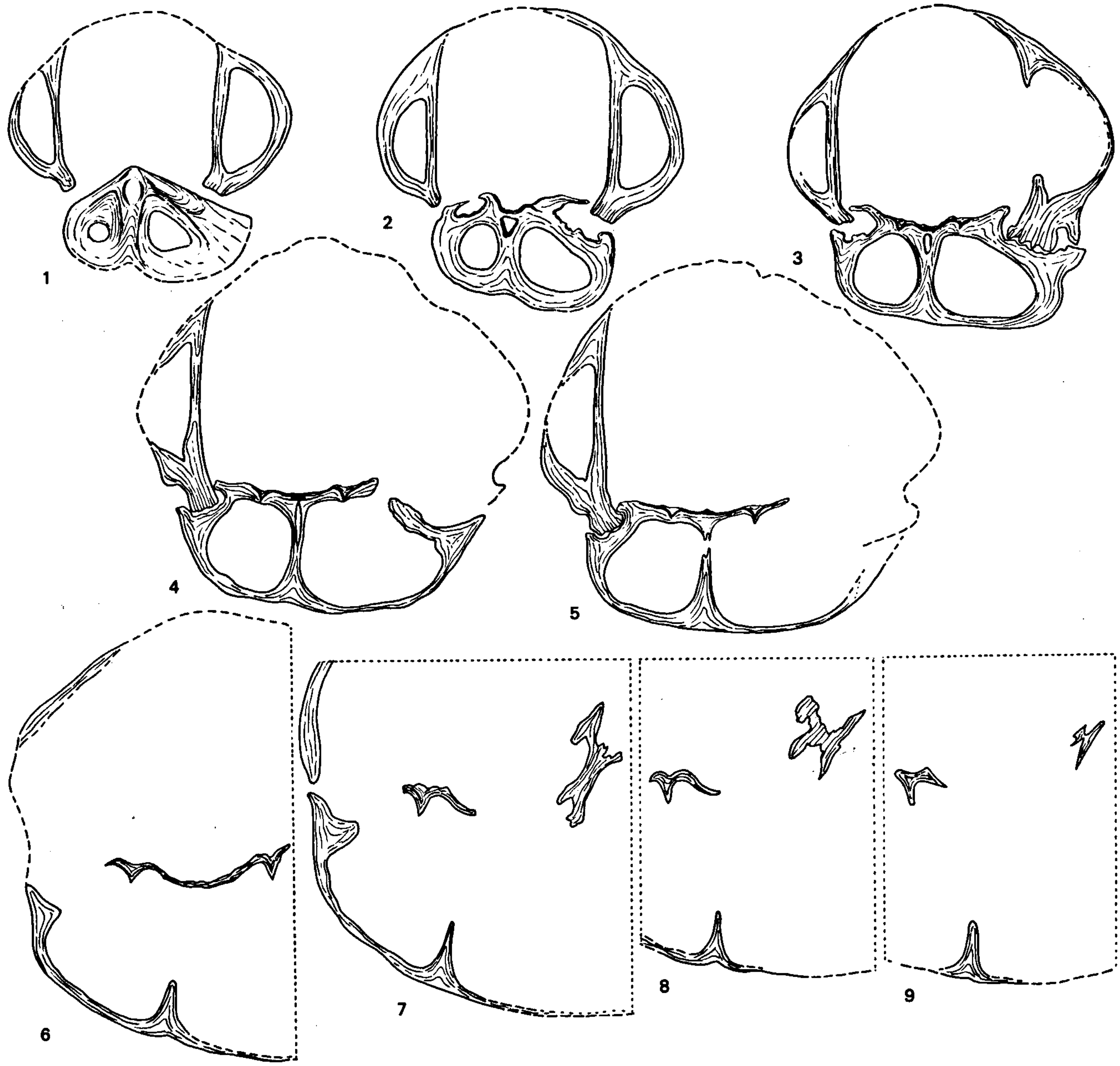
Family TRIGONIRHYNCHIIDAE McLaren, 1965

Genus CUPULAROSTRUM Sartenaer, 1961

Type species (by original designation). – *Cupularostrum recticostatum* Sartenaer, 1961.

Diagnosis. – See Sartenaer, 1961, p. 2.

Discussion. – Since the genus *Cupularostrum* has been erected by Sartenaer in 1961, it has been 'found' at a great many stratigraphic levels of the Palaeozoic and seems to follow the same fate as the now clearly defined genus *Camarotoechia* Hall & Clarke, 1893. As far as correctly ascertained, this genus is restricted to the Lower Givetian (Sartenaer, pers. comm., 1968). Our species *C. sartenaeri* is either of Upper Eifelian or Lower


1
2
3
4
5
6
7
8
9

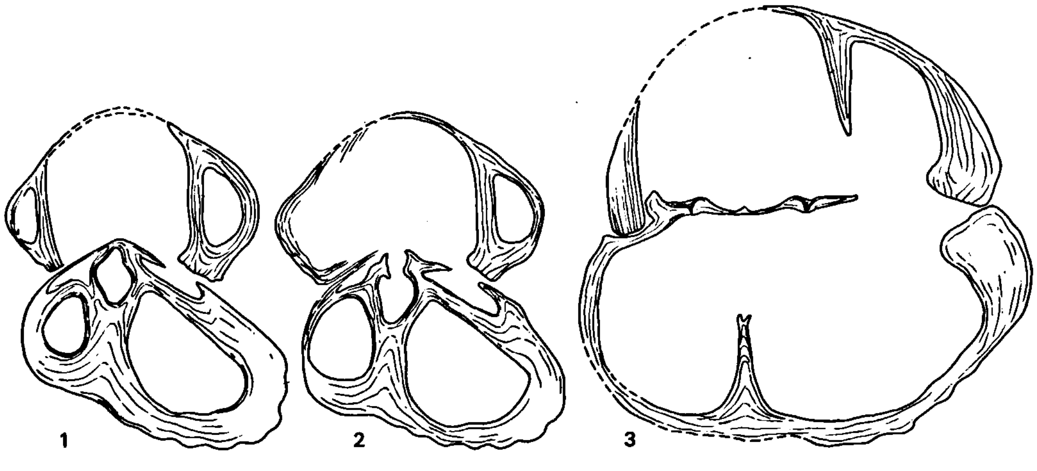

1
2
3

Fig. 13. Transverse serial sections of *Cupularostrum sartenaeri*. Specimen from section PSQ, X 14.5. sp. nov.

Givetian age but this latter age is favoured on account of the age of the well studied species (*C. recticostatum*) of the genus.

Cupularostrum sartenaeri sp. nov.

(Pl. III–1–4; Figs. 13, 14)

Holotype. – Specimen St. P. 6802003.

Locus typicus. – Section PSQ.

Stratum typicum. – Eifelian – Givetian transitional layers. Basal argillaceous limestone of Member B.

Derivatio nominis. – This species is named in honour of Dr. P. J. M. J. Sartenaer (Institut royal des Sciences naturelles de Belgique, Bruxelles).

Material & occurrence. – 37 specimens – Section PSD–St. P. 6802007 & St. P. 6802009; Section PSE–St. P. 6802010; Section PSM–St. P. 6802011; Section PSQ–St. P. 6802003–St. P. 6802006 & St. P. 6802012; Section PSS–St. P. 6802008. All specimens from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802003 Holotype (figured)	11.0	12.0	8.1	101°
2. St. P. 6802004 (figured)	14.0	14.5	8.5	100°
3. St. P. 6802005 (figured)	7.1	7.2	3.7	95°
4. St. P. 6802006	6.6	6.7	6.3	80°
5. St. P. 6802007	10.6	10.1	8.4	100°
6. St. P. 6802008	8.5	10.0	5.5	108°

Description

External characters. – Shell non-strophic; small to medium-sized, trigonal to subtrigonal in outline. Juvenile specimens are flattish; adults are more globular. Width exceeds length. Greatest width anterior to midlength. Greatest thickness posterior to midlength. Ventral beak small, pointed; beak suberect in adult specimens. Dorsal beak tucked into the delthyrium. Palintrope very narrow and depressed. Shoulder angle varies from about 80° in juvenile specimens to about 108° in adult specimens. Juvenile specimens do not show any trace of the development of sulcus and fold and the commissure is rectimarginate apart from the zig-zag deflection. Commissure uniplicate.

Fig. 14. Transverse serial sections of *Cupularostrum sartenaeri*. Specimen from section PSQ, X 14.5. sp. nov.

Pedicle valve shallow, convex umbonally, flattening laterally, longitudinal curvature gentle. Foramen and deltidial plates are covered with sediment and therefore cannot be observed. Nevertheless, deltidial plates or a deltidium may be there since some distance exists between the pedicle beak and the dorsal valve. Sulcus extremely shallow, originates in adult specimens at about midlength or anterior to midlength and is clearly delimited anteriorly in most specimens. Tongue trapezoidal, often curved at the margin.

Brachial valve more convex at the beak than the pedicle valve and flattens anteriorly and laterally. In more globular specimens, the curvature in longitudinal direction is uniformly convex. Fold low, inconspicuous and rather poorly differentiated from the lateral slopes of the shell. Surface of the shell covered with prominent costae. Costae simple; angular in transverse section.

The generalized costal formula for these specimens is:

$$\frac{3-5}{2-4}\text{; or }\quad \frac{0-1}{0-1}\text{ or }\quad \frac{1-0}{1-0}\text{ or }\quad \frac{1-1}{1-1}\text{; }\quad \frac{6-10}{5-9}$$

Number of costae varies from 5–8 per 2 mm anteromedially at a distance of 4 mm from the beak.

Internal characters. – Dental plates are well-developed. In transverse serial sections the dental plates are nearly parallel. Central apical cavity is much wider than the lateral apical cavities. Teeth stout and short; their dorsal face is slightly crenulated. The dorsal median septum is well developed. It carries a distinct septalium. In one specimen (Fig. 13) the septalium is rather peculiar; it widens posteriorly and narrows anteriorly. This may be an important indication for the function of this element. In two other specimens serially sectioned (Fig. 14), the septalium is normal and broadens anteriorly. A solid connectivum is developed on the anterior part of the septalium leaving a perforation posteriorly through which the diductor muscles might have passed. The walls of the septalium and the top surface of the connectivum (Pl. III–4) have finely fibrous calcitic layers probably indicating attachment of muscles (probably accessory diductors and primary diductors respectively). Crural bases triangular in transverse serial sections. Crura long, strongly curved ventrally and ridged at their distal ends.

Remarks. – *Cupularostrum recticostatum* Sartenaer may be distinguished from the Spanish species in having

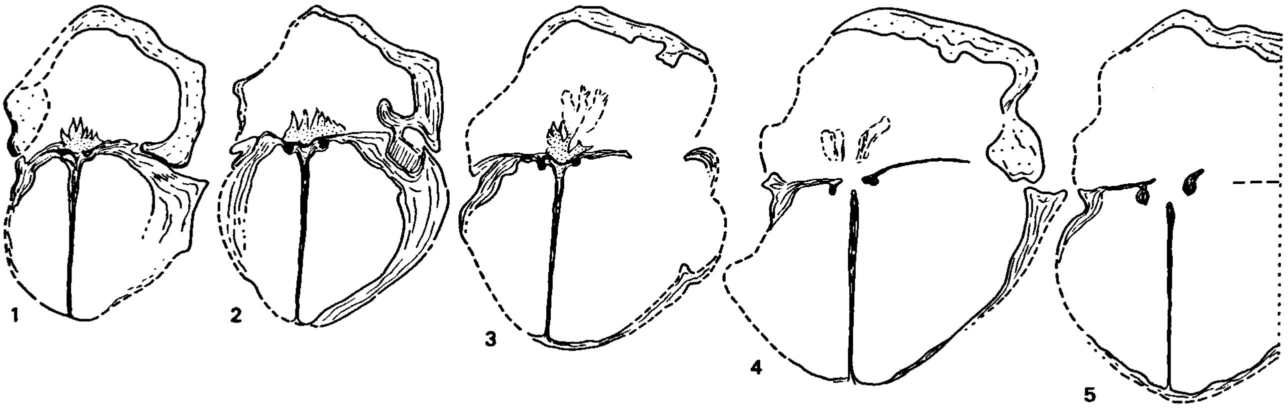


Fig. 15. Transverse serial sections of *'Cassidirostrum'* sp. Specimen from section PSC, X 7.5.

shallower and narrower sulcus and tongue and a greater number of ribs.

'Cassidirostrum' sp.

(Pl. III–5; Fig. 15)

Material & occurrence. – 2 specimens – Section PSC–St. P. 6802013 & St. P. 6802014. Specimens from higher part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802013 (figured)	19.2	21.5	15	110°

Description

External characters. – Shells large-sized, roundish subpentagonal in outline. Greatest width at or anterior to midlength. Ventral beak small, suberect, pointed. Sulcus and fold poorly developed. Tongue short, wide, almost vertical. Commissure uniplicate with very weak zig-zag deflections. Pedicle valve shallowly convex, elevated at the umbonal region. Brachial valve more convex than the pedicls valve.

Costae subangular; they reach the beak, anteriorly they widen. No bifurcations of costae observed. There are about 9 costae in the sulcus and about 10 on each lateral flank. Average width of a costa in the sulcus about 1 mm.

Internal characters. – In the pedicle valve dental plates are poorly developed. In the brachial valve there is a well-developed, rather thin median septum that supports a shallow, reduced septalium. Cardinal process is present, anteriorly apparently bilobate.

Remarks. – The Spanish specimens are provisionally placed under *Cassidirostrum* McLaren, 1961 (see also McLaren, 1962) and retained in the family Trigonirhynchiidae as per the suggestion of Johnson (1970). I have examined plaster casts of type specimens of the type species *C. pedderi* McLaren, 1961, from the collection of Dr. P. J. M. J. Sartenaer. Our specimens are distinguished in having a wider outline, a less globose shape and a wider sulcus and tongue. *C. eurekaensis* Johnson, 1966 (see Johnson, 1970) from the Eifelian to the Lower Givetian of Central Neveda is a much smaller species with a somewhat pyriform outline and a strongly convex brachial valve.

Family UNCINULIDAE Rzhonsnitskaya, 1956
Subfamily HEBETOECHIINAE Havlíček, 1960

'Hebetoechia' sp.

(Pl. V–6; Fig. 16)

Material & Occurrence. – 3 specimens well preserved apart from the beak – Section PSS–St. P. 6802015, St. P. 6802016a & St. P. 6802016b. All specimens are from basal part of member B.

Dimensions (in mm). –

	lenght	width	thickness	shoulder angle
1. St.P. 6802015 (figured)	10.1(?)	13.9	11.4	110°
2. St. P. 6802016a	8.5	11.6	8.4	120°

Description

External characters. – Shell transversely elliptical in ventral and dorsal views. Commissure situated near the margin of the very high paries geniculatus. Consequently the tongue is very well-developed. It is rectangular in outline and on either side laterally delimited by one single costa and groove. Sulcus and fold are low and only

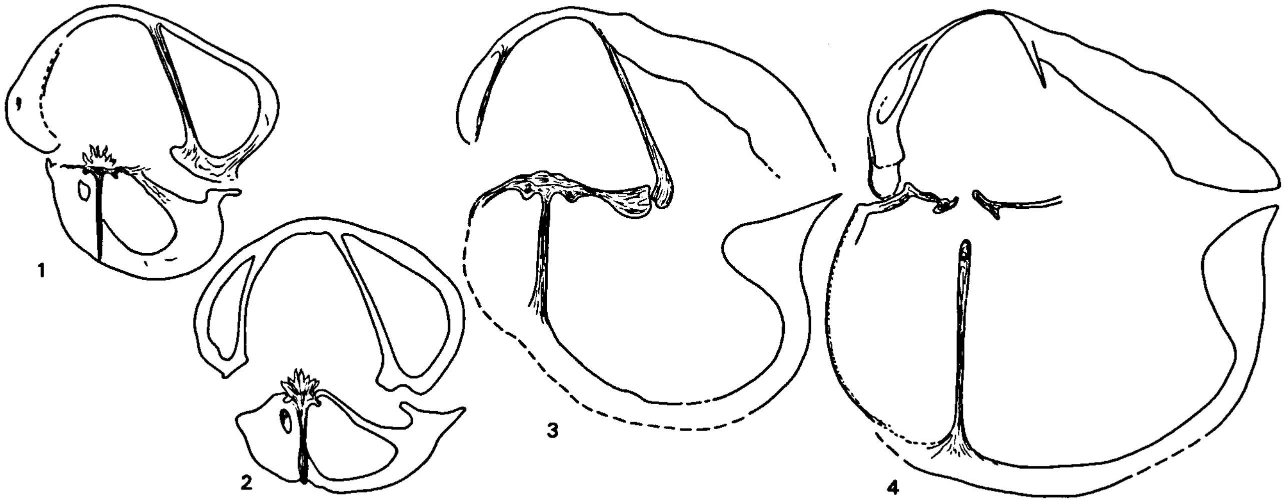


Fig. 16. Transverse serial sections of *'Hebetoechia'* sp. Specimen from section PSS, X 10.

developed in the anterior part of the concha plana. Five or six crenulate costae are present in the sulcus and six to seven in the fold. Number of lateral costae variable (12 have been counted in one well-preserved specimen). The costae originate not far away from the paries geniculatus. No bifurcation or intercalation of costae have been observed. Zig-zag deflection is well-developed. Secondary grooves are pronounced. Marginal spines are short: the primary layer has been found to extend medially along the external face. They correspond with type A as described by Westbroek (1967, p. 40, fig. 43; p. 55, fig. 60). As a result of poor preservation, the umbonal part of the shell could not be observed.

Internal characters. – Dental plates well developed, thin. Central apical cavity is wide as compared to lateral cavities. In the brachial valve a well-developed median septum supports the hinge plate. Septalium very much reduced or absent. Cardinal process stout. Shell mosaic very coarse.

Remarks. – On superficial inspection, the present material suggests a close affinity with *Hypothyridina* Buckman, 1906; the paries geniculatus is very high, the commissure is situated near the margin of the paries geniculatus and the tongue is elongated and rectangular. All this gives the shell a typical 'cuboidal' aspect. However, the very characteristic marginal spines of *Hypothyridina* (see Westbroek, 1967, p. 61, fig. 68; p. 62, fig. 69) do not occur in the Spanish specimens. Another important distinction with *Hypothyridina* is the presence in the present species of a well-developed median septum. From the Givetian genus *Hydrorhynchia* McLaren, 1961, the Spanish material is distinguished in having a well-developed paries geniculatus with secondary grooves and marginal spines and also in having a stout cardinal process. The morphology of the present species suggests a very close relationship with the Upper Silurian and Lower Devonian genus *Hebetoechia* Havlĭcek, 1961. This is especially evident from the very coarse shell mosaic and the primitive aspect of the marginal spines (see Westbroek, 1967, p. 40, fig. 43). Unfortunately, due to bad preservation the deltidium could not be studied. The only character which distinguishes this material from *Hebetoechia* is the absence of a well-developed septalium and concomittantly the formation of an undivided cardinal process. However, it is of interest to note the presence of such primitive uncinulids in the Spanish Middle Devonian. Apparently, the material under consideration is phylogenetically derived from *Hebetoechia*, but it has not undergone the same important morphological modifications as *Kransia* during its evolution. It might represent on the contrary a very conservative line of descent, contemporary with the *Kransia* lineage.

Genus KRANSIA Westbroek, 1967

Type species (by original designation). – *Terebratula parallelepipeda* Bronn, 1837.

Diagnosis. – See Westbroek, 1967, p. 81.

Discussion. – Westbroek (1967), in his morphological work on the uncinulids erected the genus *Kransia* with *Terebratula parallelepipeda* Bronn, 1837 as the type species. The erection of *Kransia* merits attention in so far as it points now to a pressing need for the redescription of the genus *Uncinulus* Bayle, 1878 and revision of the several species (ranging from the Lower to the Upper Devonian: see Havlĭcek, 1961, p. 140) assigned to this genus. However, it is unfortunate that *Terebratula parallelepipeda* Bronn is chosen as the type species of *Kransia* since this species is ill-defined and no types exist. Redescription of the German material and the election of types are now urgently needed. Westbroek (1967, p. 81) states that the septum supports the hinge plate in

Fig. 17. Transverse serial sections of *Kransia* aff. *parallelepipeda* (Bronn, 1837). Specimen from section PSS, X 14.5.

Kransia parallelepipeda. This, however, can be maintained for one of the two specimens he has sectioned (specimen from the 'Ahrdorfer Schichten', Eifel, collection Westbroek, Dept. Strat. & Pal., Leiden, serial sections No. 1035–1050). By personal inspection of the peels I found that a connection only exists in the very posterior part of the shell, and that the mediotest of the septum never touches the hinge plate. The other specimen sectioned by him (specimen from the 'Rommersheimer Schichten', Eifel, collection Westbroek, Dept. Strat. & Pal., Leiden, serial sections No. 1051a–1051l) as well as a specimen from the Upper Eifelian of the Prümer Mulde, Eifel (kindly provided by Dr. Herta Schmidt) sectioned by me (Fig. 19) and sections figured by Biernat (1966, p. 91, fig. 30) show that the median septum does not support the hinge plate. Therefore, I tentatively conclude that Westbroek's statement in the diagnosis of the genus that the septum directly supports the hinge plate must be altered into: 'The septum and the hinge plate only touch in the very posterior part of the shell, or they do not touch at all'. I regard *Kransia* as a valid genus but I think that species other than *parallelepipeda* provisionally assigned to this genus by Westbroek (e. g. '*Uncinulus*'*signatus* (Schnur, 1853) and '*Uncinulus*' *minor* (Schnur, 1853) may be better included in other genera.

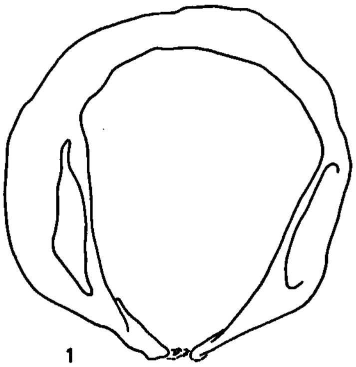
Kransia aff. *parallelepipeda* (Bronn, 1837)
(Pl. III–6; Pl. IV–1, 2; Figs. 17, 18)

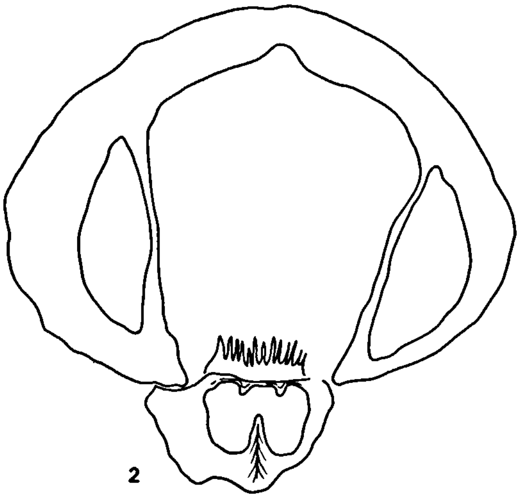
1941a *Uncinulus parallelepipedus* (Bronn 1837). – Schmidt, p. 18, pl. 1, figs. 17–18; pl. 4, figs. 63–67; pl. 6, figs. 14–16.

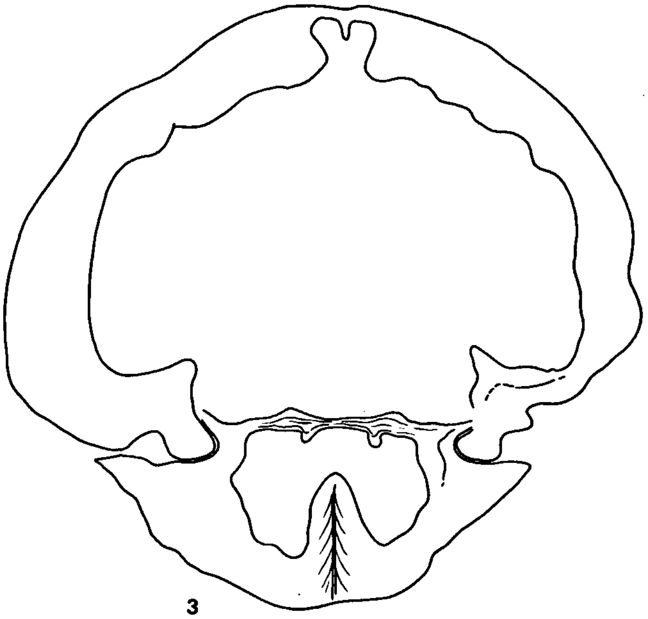
1964 *Uncinulus parallelepipedus* (Bronn, 1837). – Drot, p. 151, pl. 17, fig. 2.

1966 *Uncinulus parallelepipedus* (Bronn, 1837). – Biernat, p. 90, pl. 17, figs. 8–11, text-fig. 30.

Material & occurrence. – 51 specimens; all are adult and thus geniculated – Section PSE–St. P. 6802023; Section PSH–St. P. 6802020; Section PSM–St. P. 6802021 & 6802024; Section PSN–St. P. 6802022 & St. P. 6802025; Section PSS–St. P. 6802017–St. P. 6802019 & 6802026. All specimens are from basal part of member B.







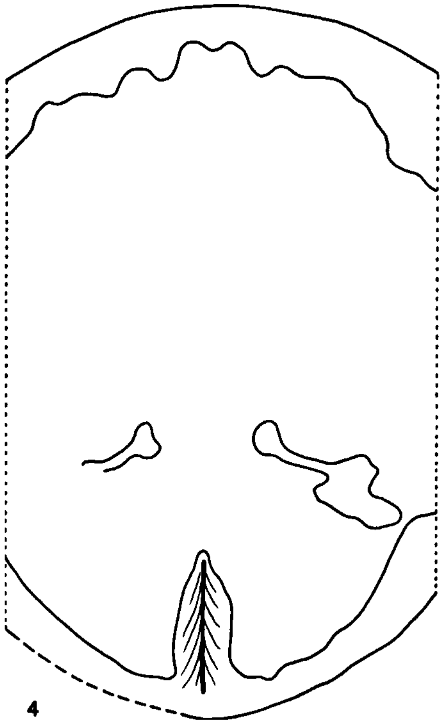


Fig. 18. Transverse serial sections of *Kransia* aff. *parallelepipeda* (Bronn, 1837). Specimen from section PSE, X 14.5.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802017 (figured)	10.0	10.5	7.1	126°
2. St. P. 6802018 (figured)	10.0	9.7	8.4	108°
3. St. P. 6802019	10.2	10.5	8.0	125°
4. St. P. 6802020	10.0	10.0	8.4	98°
5. St. P. 6802021	6.8	6.8	5.0	92°
6. St. P. 6802022	9.1	9.7	7.3	107°

Description

External characters. – Shell medium-sized to small, pentagonal in outline. Some specimens relatively more narrow and globular. Others comparatively flattish and wide. Greatest width nearly at midlength. Hinge very short. Hinge pattern probably strophic. Ventral beak rather short, suberect. Commissure completely straight apart from the usual broad median deflection. No serial zig-zag deflection present. Sulcus and fold poorly developed. Paries geniculatus of moderate height. Marginal spines long, rather stout at their bases and tapering gradually. Primary layer in marginal spines probably extending towards the tip of the spines. Squama and glotta well-developed and slanting. Pedicle valve shallow with moderately convex umbo. Foramen and deltidium well-developed. Sulcus very shallow,

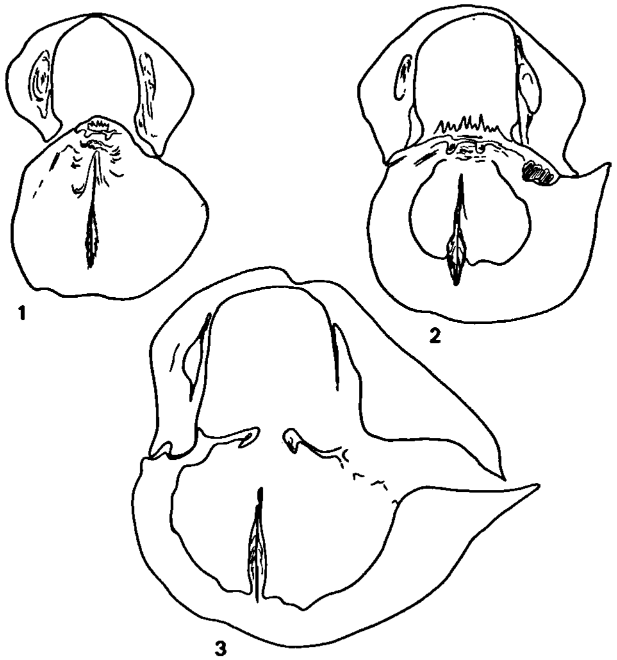


Fig. 19. Transverse serial sections of *Kransia parallelepipeda* (Bronn, 1837). Specimen from Upper Eifelian, Prümer Mulde, Eifel, Germany, X 7.

nearly with a flat floor in more globular specimens and slightly deeper with a concave floor in wider specimens. Sulcus begins anterior to midlength and is bordered laterally by two elevated ridges. Sulcus passes into a low and short tongue. The part of the commissure delimiting the tongue is smoothly rounded and not influenced by the costation. Longitudinal curvature of brachial valve more convex than of pedicle valve. Fold low, more marked at the anterior end. Anterior part of the surface of concha plana marked by smooth costae of moderate coarseness. Average width of a costa at the paries geniculatus measures 0.4 mm. Costation crenulate; the costae are rounded and grooves sharp. Costae somple. They are more pronounced anteriorly. Median costae relatively more prominent than the lateral costae. Paries geniculatus bears only the primary grooves; no secondary grooves are developed. Number of costae varies from 6–9 in the sulcus and 7–10 in the fold. There are at least 14–17 costae on a lateral slope.

Internal characters. – Dental plates well-developed, convergent dorsally in serial transverse sections, slightly arched towards the central apical cavity. Central apical cavity wider than the lateral apical cavities. Low myophragm divides deeply situated adductor muscle scars. Hinge plate continuous. Cardinal process well-developed. Median septum present, thickened by secondary shell material. It does not support the hinge plate. Mediotest present. Fibres moderately divergent away from the mediotest. Posterior brachial cavity clogged with secondary shell material.

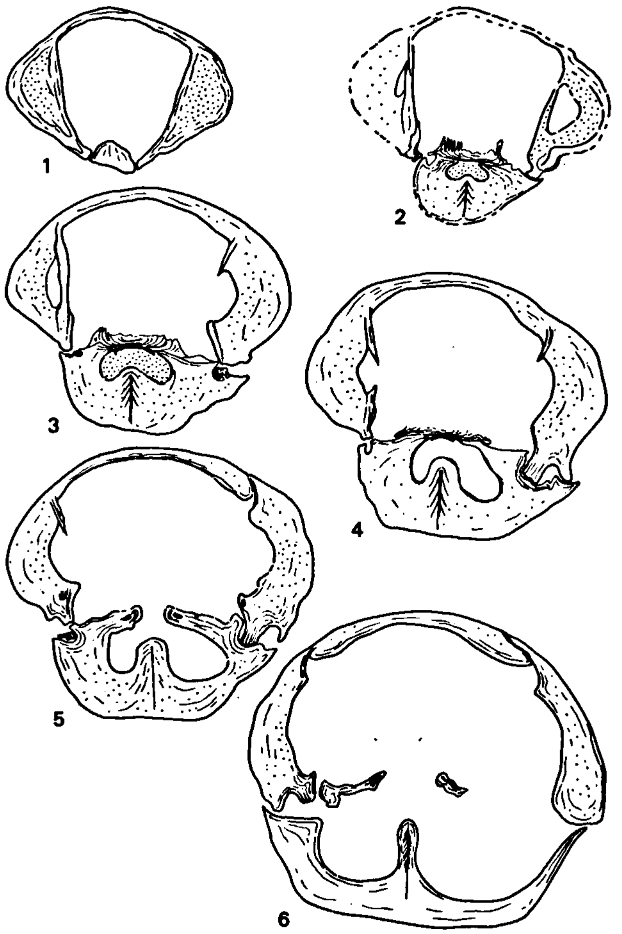


Fig. 20. Transverse serial sections of *Kransia subcordiformis* (Schnur, 1853). Specimen from section PSS, X 7.

Remarks. – In Germany, the species *Kransia parallelepipeda* extends from Eifelian to Givetian. According to Schmidt (1941a, p. 18) this species is very variable, and she is not able to provide any further clear-cut subdivision. A statistical treatment of the material is certainly needed, since this will lead to a better specific and generic definition. Comparison of our forms with typical Eifelian specimens from Germany suggests that they differ in some respects: in the Spanish material the shells are generally smaller, the ribs are finer and the sulcus and fold are shallower. Therefore, the present form is referred to here as *Kransia* aff. *parallelepipeda*.

Kransia subcordiformis (Schnur, 1853)
(Pl. IV–3, 4; Figs. 20, 21)

1941a *Uncinulus subcordiformis* (Schnur 1853). – Schmidt, p. 19, pl. 2, fig. 20; pl. 4, fig. 71.

1966 *Uncinulus subcordiformis* (Schnur, 1854). – Biernat, p. 88, pl. 20, figs. 5–21; text-fig. 29.

Material & Occurrence. – 47 specimens. All are adult and geniculated. Many specimens are compressed – Section PSM–St. P. 6802034; Section PSN–St. P. 6802033;

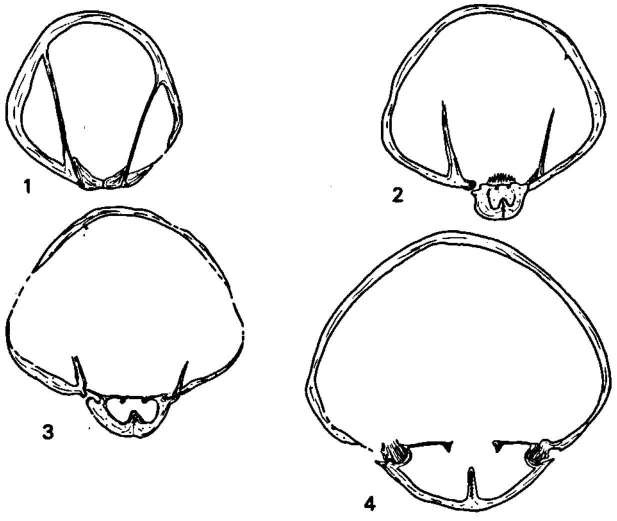


Fig. 21. Transverse serial sections of *Kransia subcordiformis* (Schnur, 1853). Specimen from section PSS, X 7.

Section PSQ–St. P. 6802035; Section PSS–St. P. 6802027–St. P. 6802032 & St. P. 6802036. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802027 (figured)	15.2	16.9	9.0	105°
2. St. P. 6802028 (figured)	12.5	13.0	8.0	98°
3. St. P. 6802029	13.1	14.7	9.6	101°
4. St. P. 6802030	15.5	18.9	8.1 (?)	105°
5. St. P. 6802031	12.0	11.3	7.0	90°
6. St. P. 6802032	9.4	9.8	4.9	88°
7. St. P. 6802033	16.5	19.0	12.8	104°

Description

External characters. – Large shells, rounded subpentagonal in outline. Greatest width at about midlength. Hinge very short and reduced. Hinge growth probably strophic. Ventral beak rather short, nearly straight to slightly incurved. Commissure straight apart from median plication. Paries geniculatus rather low. Marginal spines elongated, stout at their bases and gradually tapering. Primary layer extending not far beyond the bases of the spines. Squama and glotta developed and slanting. Pedicle valve shallow, moderately convex at the beak, medially depressed and gently sloping laterally. Deltidium well-developed. Foramen submesothyrid. Sulcus well-developed, starting about 1/4 the distance of the length from the beak. Flanks of the sulcus bordered by slightly elevated walls. Floor shallowly concave. Sulcus passes into a wide and short tongue characteristic of this species. Tongue vertical with gently rounded flanks. Brachial valve convex umbonally, gently sloping anteriorly. Longitudinal curvature gently convex. Fold weakly expressed, broad. Ornamentation in concha plana consists of smooth rather coarse costae. Crenulated. Costae begin very close to the beak and are anteromedially better developed than laterally. The number of costae slightly increases during growth of the concha plana by occasional intercalations and bifurcations. There are 10–12 costae in the sulcus and 9–10 in the fold. There are 14–17 lateral costae on each lateral slope. No secondary grooves observed. Number of costae about 8–10 per 2 mm at a distance of about 4 mm from the beak.

Internal characters. – Fibres very coarse in pedicle valve. Dental plates well-developed, dorsally convergent in transverse serial sections and slightly arched towards the central apical cavity. Central apical cavity wider than lateral apical cavities. Median septum well-developed, does not touch the hinge plate, rather thickened with secondary shell. Mediotest present. Fibres diverging away from mediotest. Cardinal process well-developed. Hinge plate continuous. No septalium.

Remarks. – The present species as studied from the Spanish collection corresponds in all respects to the generic diagnosis of *Kransia* as given by Westbroek (1967, p. 81) and altered in the present discussion of the

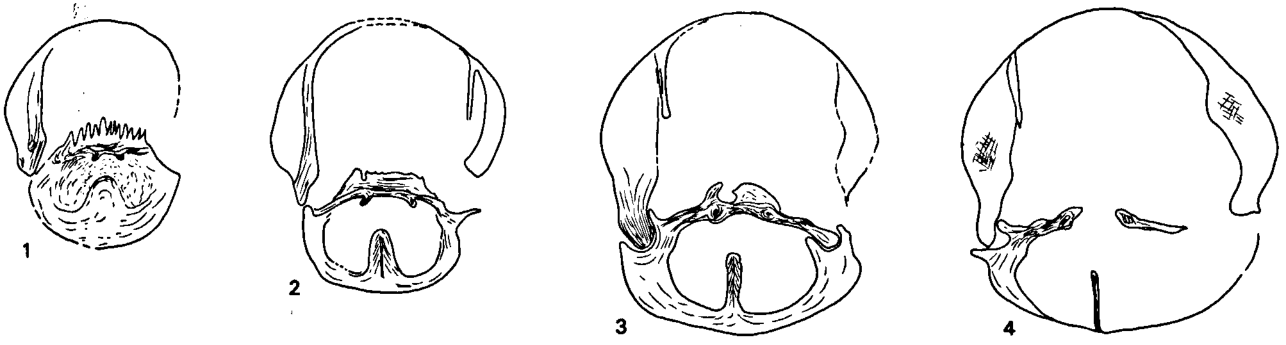


Fig. 22. Transverse serial sections of *Kransia subcordiformis* (Schnur, 1853). Specimen from Lower Givetian, Eifel, Germany, X 7.

genus. Therefore, I do not hesitate to allocate this species to *Kransia*. One specimen from the Eifel (Germany), of Lower Givetian age, has been obtained for comparison from Dr. Herta Schmidt, and sectioned (Fig. 22). The internal characters were essentially similar.

'Kransia' cf. *pentagonus* (Kayser, 1871)

One poorly preserved specimen comparable to *'Uncinulus' pentagonus*. Section PSH–St. P. 6802037. Basal part of member B.

Nalivkinaria aff. *lacunata* forma *tenuicostata* Rzhonsnitskaya, 1968

(Pl. IV–5, 6; Pl. V–1, 2; Fig. 23)

Material & Occurrence. – 23 specimens. All are adult and well geniculated. Some specimens are damaged – Section PSE–St. P. 6802044; Section PSM–St. P. 6802041–St. P. 6802043 & St. P. 6802045; Section PSN–St. P. 6802046; Section PSS–St. P. 6802038–St. P. 6802040 & St. P. 6802047. All specimens are from basal part of member B.

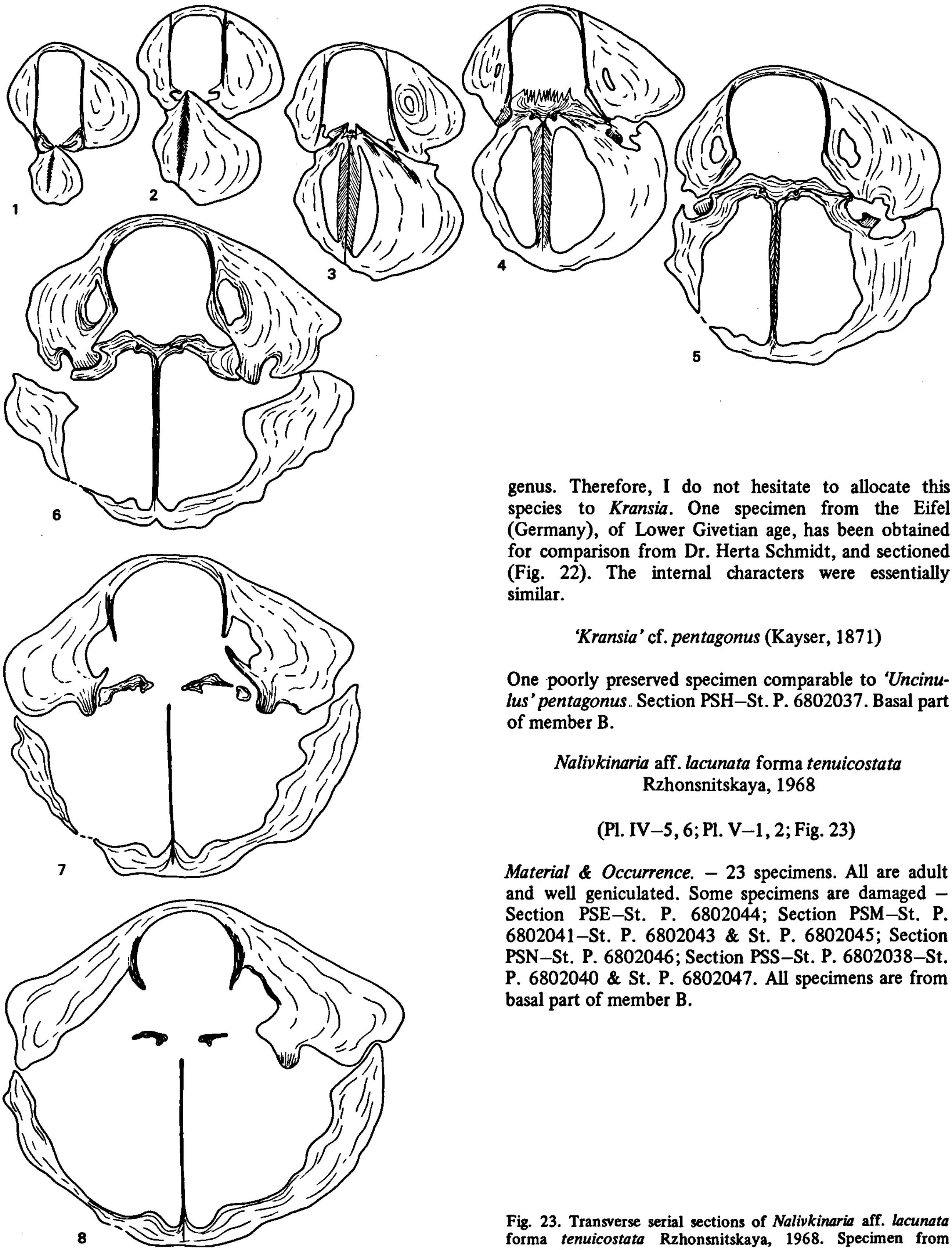


Fig. 23. Transverse serial sections of *Nalivkinaria* aff. *lacunata* forma *tenuicostata* Rzhonsnitskaya, 1968. Specimen from section PSS, X 6.

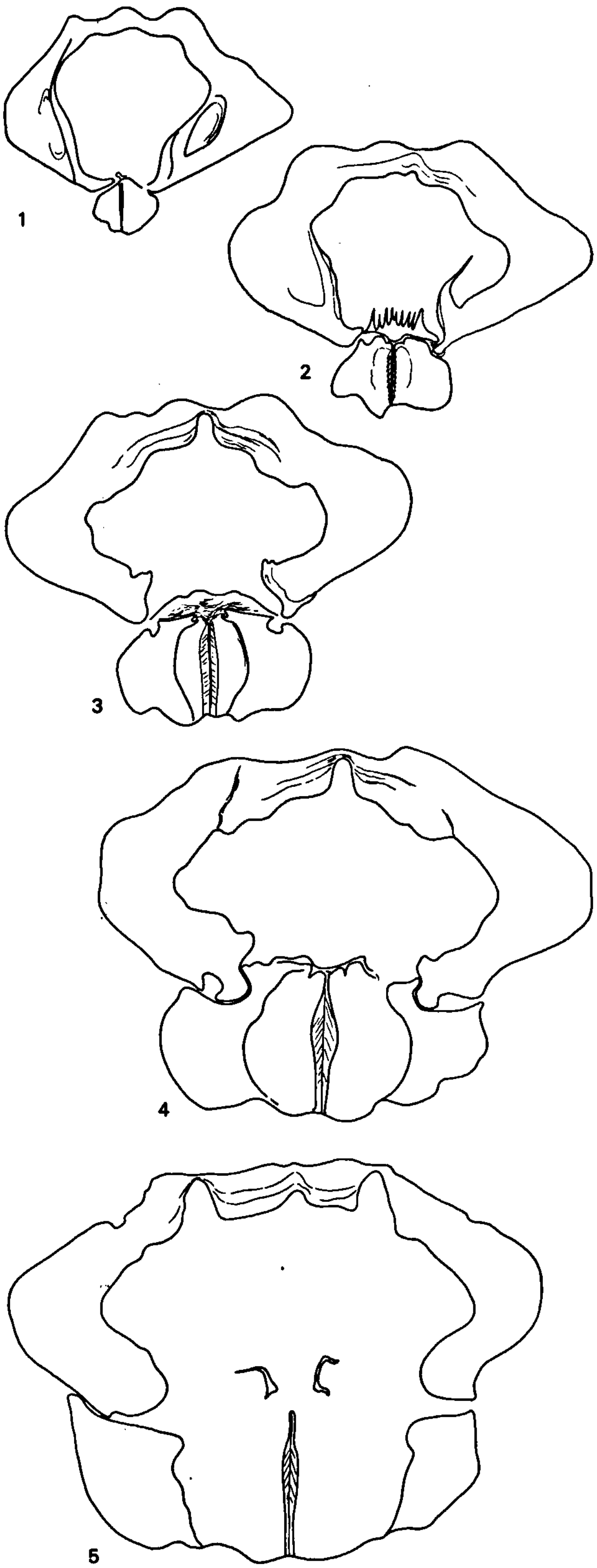


Fig. 24. Transverse serial sections of *Nalivkinaria signata* (Schnur, 1853). Specimen from Eifelian, Prümer Mulde, Eifel, Germany, X 8.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802038 (figured)	16.5	19.1	13.4	115°
2. St. P. 6802039 (figured)	18.8	20.4	16.2	122°
3. St. P. 6802040 (figured)	12.8	15.4	9.6	118°
4. St. P. 6802041	15.6	18.8	12.0	125°
5. St. P. 6802042 ?	16.7	21.0	15.4	127°
6. St. P. 6802043	13.3	14.9	10.0	119°

Description

External characters. – Shells large-sized; widely subpentagonal in outline, transversely eliptical. Width is greater than length. Greatest width at or anterior to midlength. Greatest thickness anterior to midlength. Ventral beak small, suberect to erect. Hinge pattern probably strophic. Cardinal areas very small. Commissure straight; apart from broad median deflection very reduced zig-zag deflections may occur. Sulcus and fold well-developed. Paries geniculatus of moderate height. Marginal spines elongated, bases stout, gradually tapering towards the tip. Primary layer extending only for a short distance along the marginal spines. Apart from paries geniculatus the pedicle valve is shallow, flattish. Posteriorly the median umbonal region is slightly elevated. Foramen and deltidial plates observed. Sulcus is delimited by flat rooflike flanking slopes. It begins anterior to midlength and is more prominent at the anterior end. Floor of the sulcus moderately concave to flat. Sulcus passes smoothly to an extended tongue. Dorsal commissure of the tongue straight to very gently convex in anterior view. The straight flanks of the tongue are delimited each by one single costa and make clear-cut angles with the median and lateral parts of the anterior commissure. Brachial valve more prominently convex than pedicle valve. Fold begins about halfway the shell length. The ornamentation on the anterior part of the concha plana is marked by smooth and coarse costae. Average width of a costa at the paries geniculatus measures 1.0 mm. Costation crenulate. Costae simple, few intercalations and divisions. Posterior part of shell is smooth. Paries geniculatus bears well-developed primary and secondary grooves. There are 4–5 costae in the sulcus and 5–6 in the fold. On the lateral flanks there are at least 7–10 costae. Parietal costae rudimentary or absent.

Internal characters. – Dental plates with mediotest arching towards the central apical cavity. Central apical cavity wide and large. Lateral cavities poorly developed. Teeth without crenulations.

Median septum well-developed. The fibres strongly diverge away from mediotest. Cardinal process well-developed with about 15 lamellae on the posterior surface. Septalium small. Septalial complex enclosed in a thick pad of secondary shell.

Remarks. – I hesitate to assign the Spanish species to *Kransia* Westbroek, 1967 since internally it is conspicuously different from *parallelepipeda*, the type species of *Kransia*. In *parallelepipeda* the hinge plate is continuous and usually is not supported by the septum (see also p. 160). But in the present species a well-developed median septum is continuous with the hinge plate forming a strong septalial complex. This seems to me a distinction of generic importance. There are, of course, also differences such as the external shape and the flanks of the tongue. On the basis of comparison of the figures given by Rzhonsnitskaya (1968b, pl. 37, figs. 5–7; text–fig. 11, p. 119) as well as of my own observations of two casts of the holotype of *Nalivkinaria lacunata* forma *typica*, I am inclined to assign the present species to the genus *Nalivkinaria* Rzhonsnitskaya, 1968, described from the Eifelian of the southern margin of Kuznetsk Basin, U.S.S.R. The casts were kindly shown to me by Dr. P. J. M. J. Sartenaer. The only difference could be the alleged presence of a spondylium in *Nalivkinaria lacunata*. However, the text–fig. 11 of Rzhonsnitskaya is not decisive on this point: the dark structure which she presumably considered as the spondylial median septum is most probably a myotest.

The Spanish forms exhibit a striking similarity to *N.lacunata* forma *tenuicostata* figured by Rzhonsnitskaya (1968b, pl. 37, fig. 6). Unfortunately, no precise information about the internal structure of this form is provided, so that the identification is not fully warranted. But there can hardly be any doubt about a close relationship between the Spanish and the Russian material. The German species *'Uncinulus' signatus* (Schnur, 1853) (see also Schmidt, 1941a) and the Burmese species *'Uncinulus' subsignatus* (Reed, 1908) (see also Anderson et al., 1969) both of Eifelian age are considered here as belonging to *Nalivkinaria*. Dr. Herta Schmidt has kindly provided a specimen of *'U.' signatus* from the Eifelian of the Prümer Mulde Eifel for serial sectioning (Fig. 24). It is clear that the species mentioned form a strongly coherent group. The present species is distinguished from *'Uncinulus' signatus* in the following characters: it has a flatter pedicle valve, costae originate halfway between the beak and the paries geniculatus, ribs and grooves are more closely spaced and shallow, no distinct ridges laterally delimit the sulcus and fold; the latter are more confined to the anterior part of the shell; they do not originate at the beak.

As stated above, the genus *Nalivkinaria* is very closely related to *Kransia*. They both are best included in the subfamily Hebetoechiinae Havlĭcek, 1961 (see Westbroek, 1967, p. 81) and not in the family Septalariidae Havlĭcek, 1961, as proposed by Rzhonsnitskaya, (1968b, p. 117). Anderson et al. (1969) include *Nalivkinaria subsignata* in the genus *Uncinulus*. Westbroek (1967) has found that phylogenetically *Uncinulus* is rather remote from *Kransia* and thus also from *Nalivkinaria*, although they are very similar on superficial inspection. Brice (1970) questionably assigns specimens of *'Uncinulus' subsignatus* (Reed, 1908) from Afghanistan to the genus *Kransia*. The specimens after her statement are questionably from the Eifelian horizon.

Genus BECKMANNIA gen. nov.

Type species. – *Uncinulus minor beckmanni* Schmidt, 1951 (Schmidt, 1951, pl. 1, figs. 1a–d, 2a–c, 3).

Derivatio nominis. – Genus name is derived from the name of the subspecies.

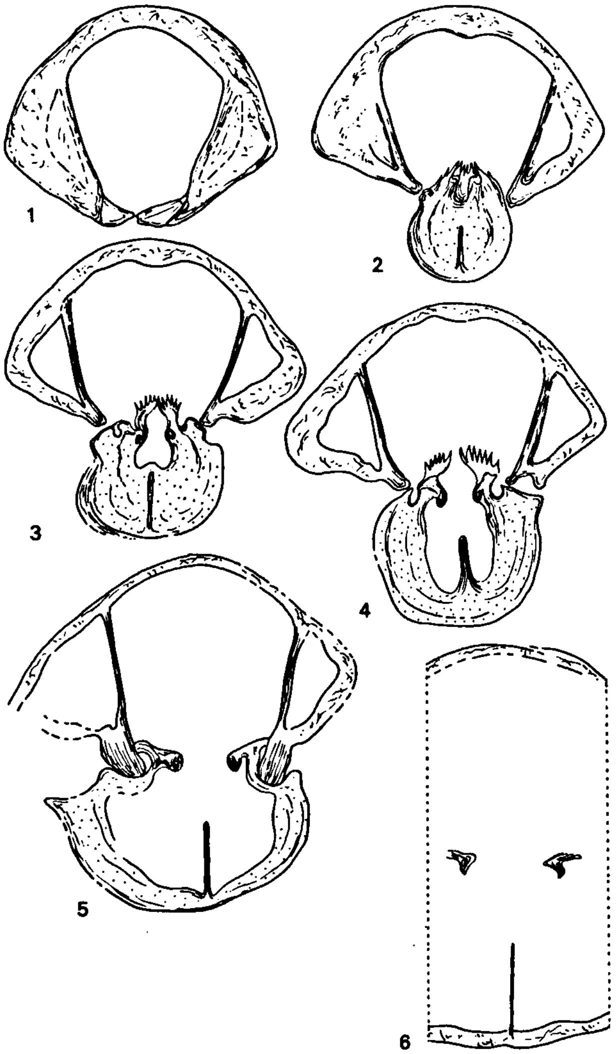


Fig. 25. Transverse serial sections of *Beckmannia minor beckmanni* (Schmidt, 1951). Specimen from section PSS, X 14.5.

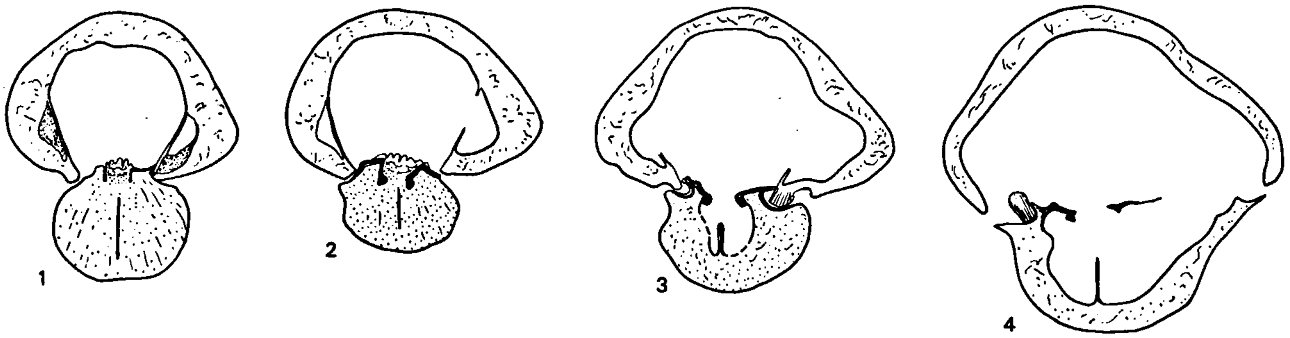


Fig. 26. Transverse serial sections of *Beckmannia minor beckmanni* (Schmidt, 1951). Topotype specimen, Germany, X 14.5.

Species assigned to this genus. – *Beckmannia minor beckmanni* (Schmidt, 1951). The internal structure of the Eifelian subspecies *'Uncinulus' minor minor* (Schnur, 1853) from Germany has not yet been studied. Therefore, the inclusion of this subspecies in *Beckmannia* is not completely warranted.

Diagnosis (see also Figs. 26, 27). – Very small uncinulid brachiopod. Sulcus, fold, and tongue very much reduced. Paries geniculatus low. Zig-zag deflection absent in adult specimens. Ventral beak suberect. Deltidium present. Dental plates developed, relatively thin, leaving narrow lateral apical cavities. Median septum thin, fragile, without mediotest and diverging fibres. It does not support the hinge plate. Hinge plate divided. Cardinal process present. No septalium. Fibres of secondary shell very coarse.

Comparison. – The genus *Pseudouncinulus* Rzhonsnitskaya, 1968 (Rzhonsnitskaya, 1968a, pl. 36, figs. 7–9) from the Eifelian of southwest margin of Kuznetsk Basin, U.S.S.R., bears some external resemblance to *Beckmannia*. But it is distinguished in having a well delimited sulcus, fold, and tongue and internally in the absence of a median septum and in the weak development of dental plates. Externally *Beckmannia* closely resembles *Kransia* Westbroek, 1967; the main differences, however, are the small size of *Beckmannia* and the very poor development of sulcus, fold, and tongue. Internally they differ in that in *Beckmannia* the hinge plate is divided, the septum is thin, fragile and lacks a mediotest with diverging fibres.

Beckmannia minor beckmanni (Schmidt, 1951)
(Pl. V–3–5; Fig. 25; Figs. 26, 27
from topotypical material, Germany)

Material & Occurrence. – 36 specimens – Section PSP–St. P. 6802054; Section PSQ–St. P. 6802053 & St. P. 6802055; Section PSS–St. P. 6802048–St. P. 6802052 & St. P. 6802056. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802048 (figured)	7.1	6.8	5.0	99°
2. St. P. 6802049 (figured)	6.4	6.4	4.6	100°
3. St. P. 6802050	6.9	6.9	5.0	100°
4. St. P. 6802051	5.9	5.6	4.3	85°
5. St. P. 6802052	5.0	4.9	3.0	90°
6. St. P. 6802053	8.0	8.0	5.5	100°

Description

External characters. – Shells small; roundish pentagonal in outline. Length is nearly equal or slightly greater than width. Greatest thickness anterior to midlength. Ventral beak small, suberect. Hinge extremely short. Paries geniculatus low. Sulcus and fold not well developed, only slightly marked anteriorly. Commissure straight, apart from a very mild median deflection. Marginal spines short. Primary layer probably does not reach upto the tip of the spines. Pedicle valve more convex posteromedially than brachial valve. Tongue very short, its flanks are not influenced by costation. Brachial valve gently convex throughout. Ornamentation consists of 23 costae or more on each valve; there are about 3 costae in the sulcus and 4 in the fold. Crenulate, undivided costae originate close to the beak. They are slightly more distinct laterally than medially. Average width of a costa in paries geniculatus measures 0.9 mm.

Internal characters. – Thin dental plates with mediotest, dorsally convergent. Central apical cavity wide, lateral apical cavities narrow. Outer hinge plate narrow and robust. Median septum present, does not support hinge

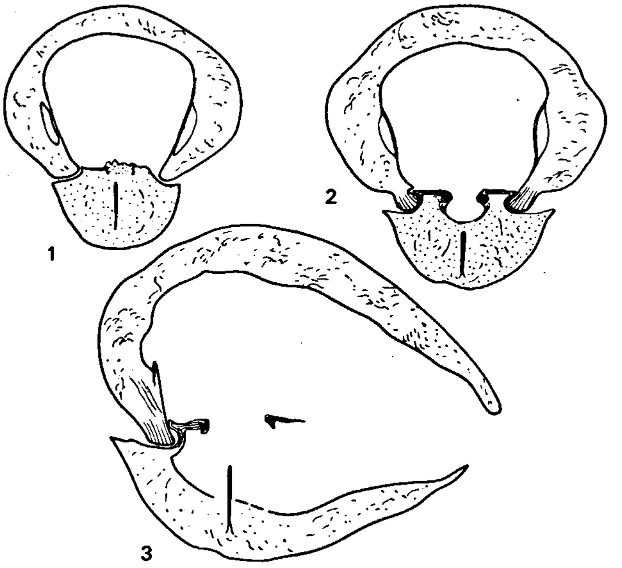


Fig. 27. Transverse serial sections of *Beckmannia minor beckmanni* (Schmidt, 1951). Topotype specimen, Germany, X 14.5.

plate, rather slender, no mediotest from which fibres diverge away. Posterior part of the cardinal region filled with secondary shell material.

Remarks. – The Spanish specimens agree closely with the external and internal characters of the genotype. Internally an elevated and bilobate cardinal process appears to be present in the Spanish material (Fig. 25). This has not been found in the German material (Figs. 26, 27). However, this difference can at least partly be explained away as due to a difference in the direction of the sections. Therefore, I do not accept this as a valid criterion for systematic differentiation.

Subfamily HYPOTHYRIDININAE

'Hypothyridina' sp. indet.

One poorly preserved specimen (St. P. 6802057–Section PSO) has been found which externally is very much like *Hypothyridina*. This material did not allow any further specification. Basal part of member B.

Family PUGNACIDAE Rzhonsnitskaya, 1956

'Pugnax' sp.

(Pl. VI–1; Fig. 28)

Material & occurrence. – 3 specimens (2 are damaged in the umbonal region) – Section PSS–St. P. 6802058 & St. P. 6802059. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802058 (figured)	20.0	24.4	18.7	105°

Description

External characters. – Shells large, strongly inequivalve, wider than long, greatest width anterior to midlength. Greatest height also anterior to midlength. Ventral beak small, sharp, suberect. Dorsal beak tightly pressed into the pedicle valve. Postero-lateral flanks depressed. Commissure uniplicate, strongly zig-zag deflected. Sulcus and fold well-marked at the frontal side. Tongue well-developed. Shells not geniculated. 4–5 costae on the sulcus, 5–6 on the fold, 4 costae on the lateral side of the dorsal valve. The costae are rounded, stout, and are only developed anteriorly and antero-laterally.

Internal characters. – Dental plates present, central apical cavity wide, lateral apical cavities narrow. Hinge plate divided, crural plates concave towards the middle of the shell in cross section. No median septum.

Remarks. – Our specimens could be compared with

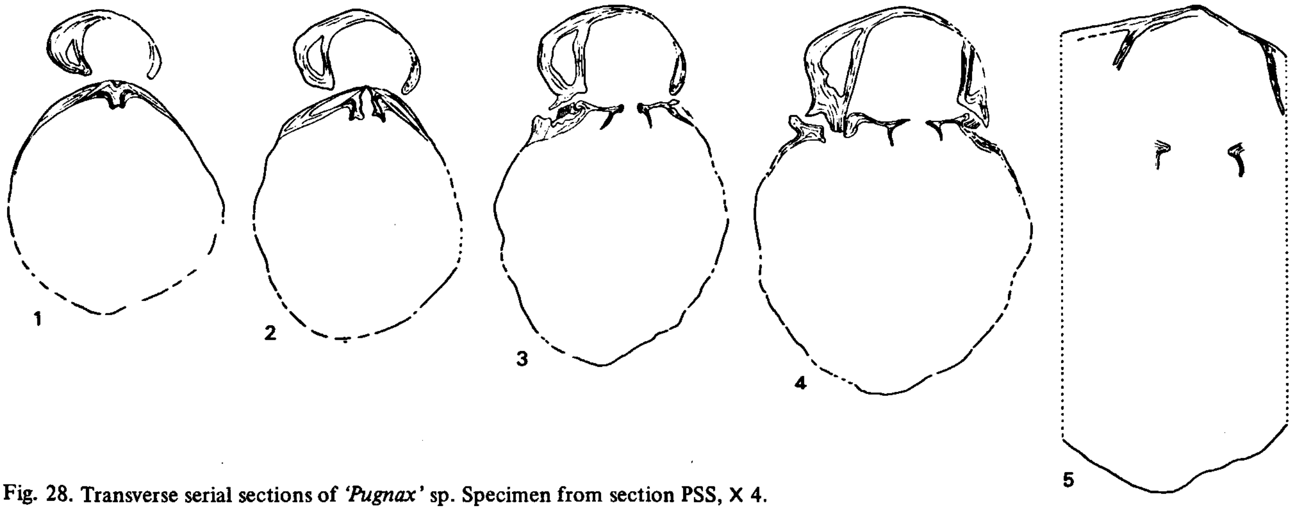
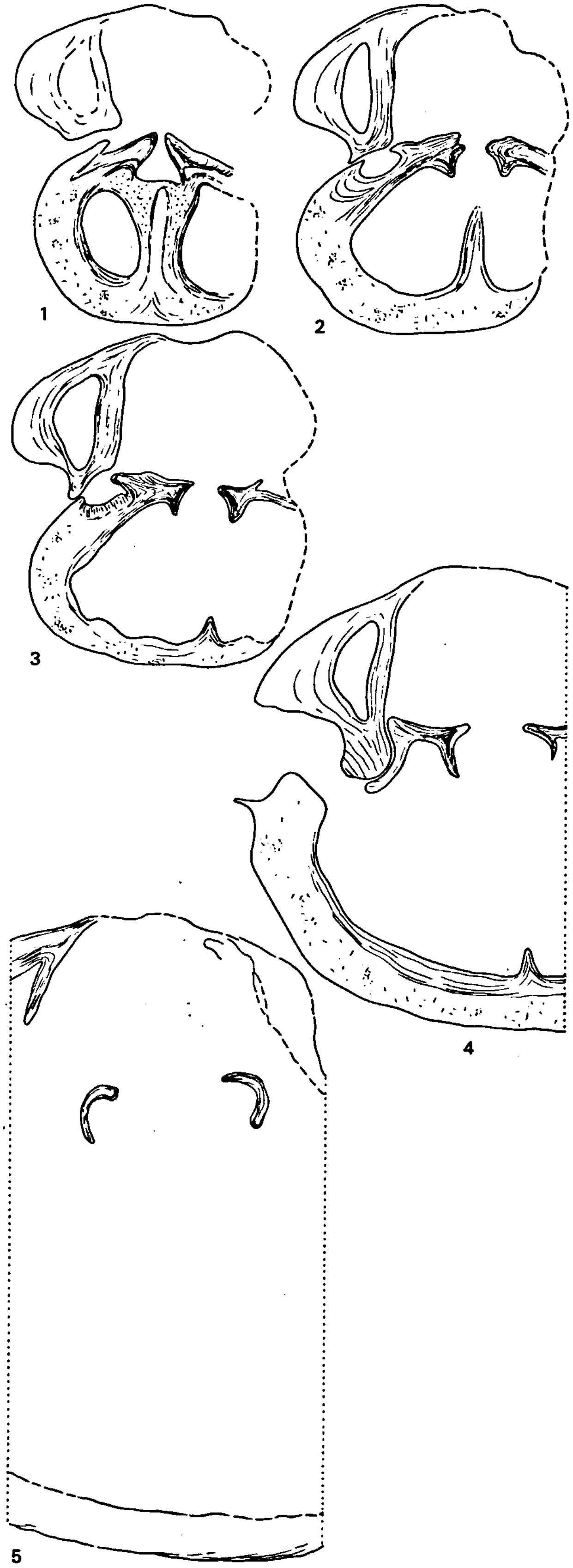


Fig. 28. Transverse serial sections of *'Pugnax'* sp. Specimen from section PSS, X 4.



'Pugnax' pugnoides latus (Schmidt, 1941a, pl. 2, figs. 30A, B) from Upper Eifelian of Germany. But there are some differences: the pedicle valve is more sharply curved towards the umbo in our species. Moreover, the tongue is narrower and more sharply delimited laterally and the shoulder angle appears to be larger. Our material looks very similar to *Pugnax pugnus pugnus* (Martin) (Schmidt, 1941b, pl. 1, fig. 5) from Lower Carboniferous of England. But it does not have the very distinctive longitudinal curvature of this species (see Schmidt, 1941b, pl. 1, fig. 5c; p. 285 abb., 10b) and has a more distinctive 'bulging' fold anteriorly and a relatively narrow tongue bordered by sharp ridges. The internal characters of *Pugnax pugnus pugnus* are not known. Hence no comparison can be made.

'Pugnax' bernesgae sp. nov.
(Pl. VI–2, 3; Fig. 29)

Holotype. – Specimen St. P. 6802060.

Locus typicus. – Section PSS.

Stratum typicum. – Basal biostromal argillaceous limestone of member B; Eifelian – Givetian transitional beds.

Derivatio nominis. – The species is named after the river Bernesga near by the section PSS.

Material & occurrence. – 7 specimens – Section PSS–St. P. 6802060–St. P. 6802062 & St. P 6802063. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802060 Holotype (figured)	8.7	11.1	6.1	111°
2. St. P. 6802061 (figured)	7.4(?)	11.3	6.3	111°
3. St. P. 6802062	7.2(?)	12.5	6.2	112°

Description

External characters. – Shells small to medium-sized, very transverse in outline; width much greater than length. Brachial valve more convex than pedicle valve. Flanks of pedicle valve slightly concave. Ventral beak small, inconspicuous, suberect (?). Umbonal region difficult to observe due to bad preservation. Wide sulcus and fold confined to anterior part of the shell. Shells are

Fig. 29. Transverse serial sections of *'Pugnax' bernesgae* sp. nov. Specimen from section PSS, X 14.5.

all geniculated. Paries geniculatus rather low. Commissure uniplicate, strongly zig-zag deflected. The costae are confined to the anterior part of the shell. Three to four costae in the sulcus and four to five in the fold. About four lateral costae. Costae are very pronounced, especially in the fold and laterally in the pedicle valve. Average width of a costa on the sulcus is 1.3 mm. The pronounced and sharp zig-zag gives rise only to a very reduced costation pattern on the paries geniculatus. On damaged shells short marginal spines have been observed but these structures have not been studied in sections.

Internal characters. – Shell mosaic generally coarse with square mosaic elements. In the pedicle valve dental plates thick, slightly diverging towards the dorsal valve in transverse serial sections. Central apical cavity wide, lateral apical cavities well-developed. In the dorsal valve median septum present. It is connected to the hinge plate, thereby producing a poorly developed septalium which is confined only to the very posterior part of the dorsal beak. Crura characteristically concave towards the middle of the shell in cross section.

Remarks. – The present species apparently belongs to the *Pugnax*-group. But unfortunately it cannot be assigned to any of the known genera. At present the *Pugnax*-group is under revision (see Sartenaer, 1966, 1968; Sartenaer & Rozman, 1968). I therefore, refrain from erecting a new genus at this stage. Our species could be compared with *'Pugnax' pugnus praevius* Schmidt, 1941 (Schmidt, 1941a, pl. 2, figs. 34–36; 1941b. p. 285, abb. 13) from the Upper Eifelian – Lower Givetian beds of Eifel, Germany, in general size and shape. But it is distinguished from the German species by its wider outline, more raised lateral flanks, the development of a paries geniculatus and marginal spines. To the best of my knowledge the species has never been described before.

Genus ISOPOMA Torley, 1934

Type species (by original designation). – *Terebratula brachyptycta* Schnur, 1853.

Discussion. – Torley (1934) established the genus *Isopoma* with *Terebratula brachyptycta* Schnur, 1853 as the type species. He, then, assigned the Upper Givetian 'Massenkalk' specimens from Bilveringsen to this species. Later, Schmidt (1941a) selected a lectotype for *Isopoma brachyptyctum* from Schnur's original collection (in Geol.-Paläontol. Inst., Bonn: Schmidt, 1941a, pl. 4., fig. 88), while describing specimens of her own collection from the Eifel area.

Schnur (1853) had only mentioned the occurrence of *Terebratula brachyptycta* in the 'Kalk zu Blankenheim' (p. 178). Schmidt, while selecting the lectotype of *Isopoma brachyptyctum*, did neither indicate any type horizon. However, externally the lectotype closely resembles the Middle Eifelian specimen of *Isopoma brachyptyctum* (Schmidt, 1941a, pl. 3, fig. 53) collected by her from the 'Gondelsheimer Schichten (Geeser Horizont)' (presently Ahrdorf Schichten) from the Eifel area. Therefore, it is probable that the type material of *I. brachyptyctum* comes from the Middle Eifelian, approximately from the Ahrdorf horizon.

Since the genus *Isopoma* is customarily bound to the type species *Terebratula brachyptycta* Schnur, 1853, the diagnosis of the genus is naturally incumbent upon a modern study of specimens which originate approximately from the Ahrdorf horizon of the Eifel area. It appears that this has not been done uptil now. Internal structures of the Middle or Upper Eifelian specimens of *Isopoma brachyptyctum* have not been investigated by modern techniques. In 1965 Schmidt, however, illustrated serial and single transverse sections of the Lower Eifelian species *Isopoma gryps* from the 'Greifensteiner Kalk' (p. 14, abb. 18–19) and the Upper Givetian *'Isopoma brachyptyctum'* from Bergisches Land (Schneppruthe) and Sauerland (Bilveringsen) (p. 14, abb. 15–17). She stated that there is no difference as regards internal structures in those species (p. 16). After studying the sketches provided by her, I doubt if it is the case. As far as I see the Upper Givetian *'Isopoma brachyptyctum'* shows something like elongated crural plates (especially fig. 15) whereas I wonder whether the same feature is present in the Lower Eifelian *Isopoma gryps*. In my study of the serial sections of the Upper Eifelian Spanish from (which I presently assign to the genus *Isopoma*), I do not see any 'crural plates', but a secondary filling of shell material in the brachial cavity in the posterior part of the cardinal region leaving roughly a U-shaped trough open ventrally (Fig. 31, Pl. VII–4, 5). In the material described by Biernat (1966) as *I.brachyptyctum* from the Upper Eifelian of Poland no crural plates are present either (her fig. 35, p. 107). This observation may be important in so far it may question the importance of crural plates in the generic diagnosis of *Isopoma*. A modern study of the interior of Middle to Upper Eifelian specimens of *I.brachyptyctum* from Eifel area in Germany would be necessary before this doubt is definitely removed.

In the collection at Senckenberg, I have examined a number of specimens of *'Isopoma brachyptyctum'* from the Upper Givetian 'Massenkalk' of Germany. There are external differences between the Eifelian specimens of *I.brachyptyctum* and the Upper Givetian specimens in shell outline, shoulder angle, nature of the sulcus, and the ribs. More study would be necessary to delimit the range of variability of the Eifelian and the Givetian forms.

Isopoma hertae sp. nov.
(Pl. VI–4; Pl. VII–1–5; Figs. 30, 31)

Holotype. – Specimen St. P. 6802064.

Locus typicus. – Section PSP.

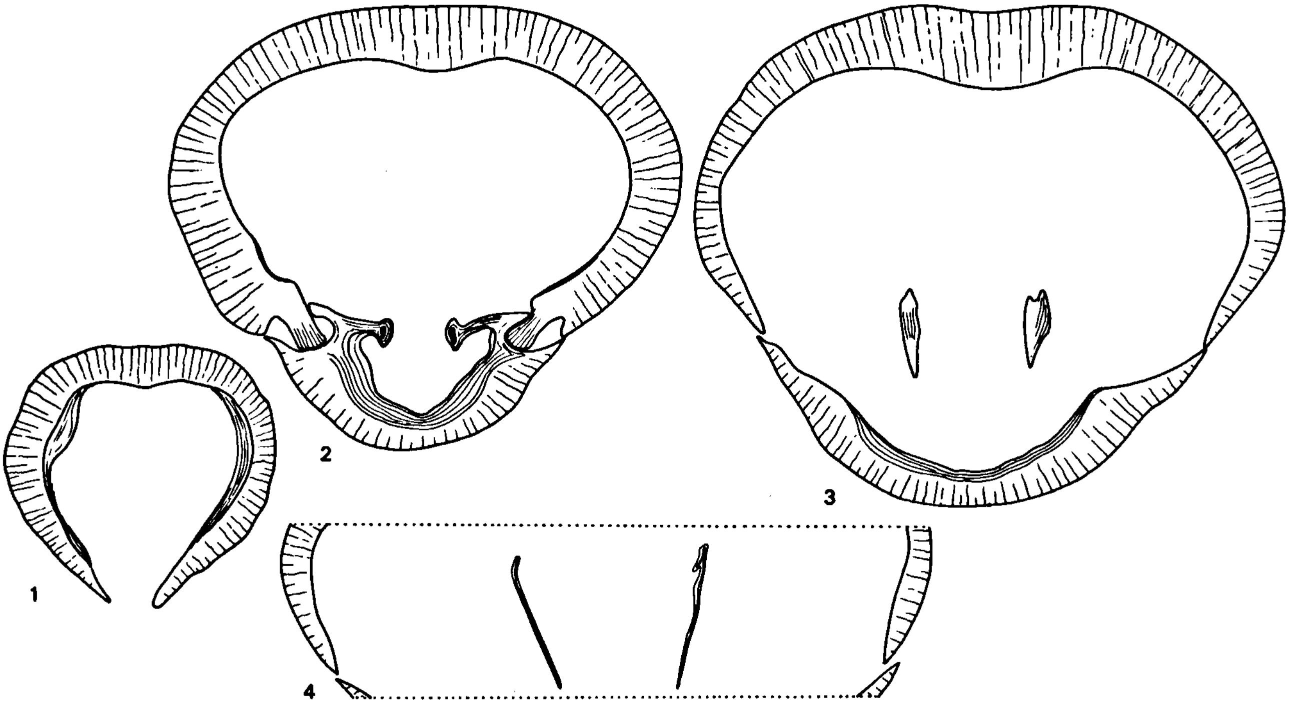


Fig. 30. Transverse serial sections of *Isopoma hertae* sp. nov. Specimen from section PSP, X 14.5

Stratum typicum. – Eifelian – Givetian transitional layers; basal coralline argillaceous limestone of Member B.

Derivatio nominis. – This species is named after Dr. Herta Schmidt (formerly at Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt/Main).

Material & Occurrence. – 73 specimens – Section PSP–St. P. 6802064–St. P. 6802068 & St. P. 6802069; Section PSQ–St. P. 6802070; Section PSS–St. P. 6802071. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802064 (Holotype, figured)	7.5	8.7	5.4	95°
2. St. P. 6802065 (figured)	8.5	8.5	6.4	90°
3. St. P. 6802066	8.7	8.7	5.8	91°
4. St. P. 6802067	8.5	9.1	6.1	90°
5. St. P. 6802068	8.4	9.0	5.5	90°

Description

External characters. – Shells small roundish subpentagonal in outline. Nearly equally biconvex. Greatest width anterior to midlength. Greatest thickness nearly at midlength. Beak short, inconspicuous; ventral beak suberect. Commissure shallowly uniplicate with strong serial zig-zag deflections. Sulcus and fold are weakly developed. Pedicle valve gently convex posteriorly, weakly depressed anteriorly. Deltidium not observed. Sulcus extremely shallow and only well marked at the anterior end. Tongue short, rather wide, trapezoidal. Longitudinal curvature of the brachial valve uniformly convex. Fold very vague. Ornamentation consists of 2 short costae in the sulcus and 3 in the fold and 2–3 on each lateral flank. The anterolateral costae are shorter and less conspicuous. Width of a costa at the anterior commissure measures about 1.5 mm. In transverse view the costae develop from rounded at their posterior end to angular anteriorly. The very medially situated groove in the pedicle valve is most prominent as regards its depth and continuity. The corresponding fold in the brachial valve does not show this prominence.

Internal characters. – From transverse sections through the shell it can be inferred that the majority of the fibres of the secondary shell are radially arranged at their origin, at sharp angle with the primary layer; they then bend so that their course becomes perpendicular to the shell surface, and finally they resume their radial course (Pl. VII–2, 3). Most fibres are extremely thick and this will correspond with a very coarse mosaic pattern.

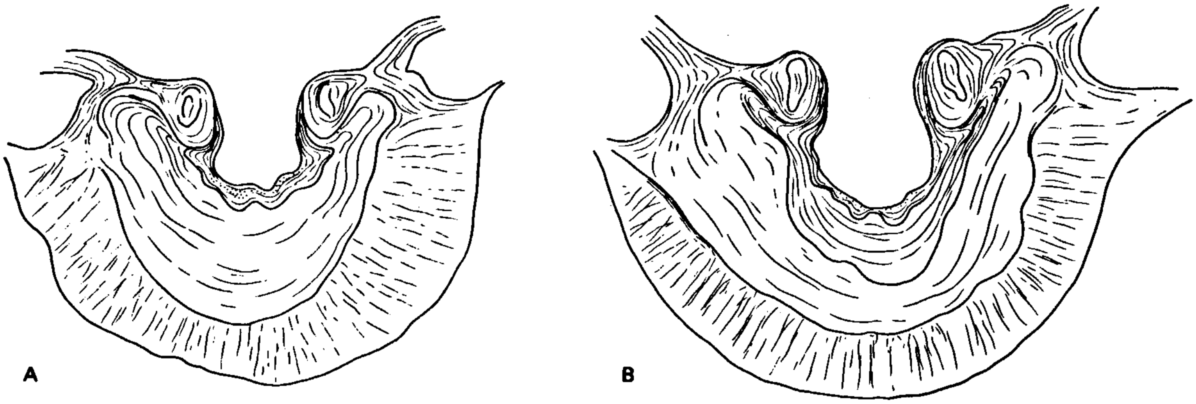


Fig. 31. A & B. Reconstruction of the growth pattern in the brachial valve of *Isopoma hertae* sp. nov. A differentiation of shell material in the central cavity parallel to the growth lines is to be seen (see also Pl. VII–4, 5). Figure A is from a peel posterior to that of Figure B, X 46.

Dental plates missing in the pedicle valve. A low and broad median ridge is present. Dorsal faces of the teeth may show very weak crenulation. Ventral apical cavity twice or slightly more as wide as the dorsal cavity. In the brachial valve outer hinge plates well developed. Ventral face of the two outer hinge plates nearly straight and may be slightly sloping dorsomedially. Posteriorly the dorsal cavity is filled with secondary shell material which leaves roughly a U-shaped trough open at the posterior end in transverse sections (Figs. 31; Pl. VII–4, 5). Crural bases are roundish, posteriorly deeply embedded in secondary shell filling. In more anterior sections the crura appear elongated, subparallel to dorso-laterally directed. Septum, crural plates, septalium, and cardinal process are absent.

Remarks. – I place the Spanish form in the genus *Isopoma* Torley, on the basis of strong external similarities with the lectotype (Schmidt, 1941a, pl. 4, fig. 88) and also with the specimen from the 'Gondelsheimer Schichten' figured by Schmidt (1941a, pl. 3, fig. 53), although I am fully aware that the internal structure of the German type is yet to be investigated. I also compared the Spanish specimens with specimen XVII 342 K from the 'Gondelsheimer Schichten (Geeser Horizont)' and specimen XVII 342 j from 'Steinmanni-Kalk' from the Blankenheim syncline (for further notes see Schmidt, 1941a, p. 45) and found appreciable external similarities. However, the Spanish form is distinguished from *Isopoma brachyptyctum* Torley in having a marked median groove in the pedicle valve which continues towards the umbo. Biernat (1966, p. 106–108, pl. 22, figs. 1–9, text–fig. 35) described *Isopoma brachyptyctum* from the Upper Eifelian Skaly Beds from the Bodzentyn Syncline, Holy Cross Mts., Poland, and mentioned that the Polish form has a marked deep medial furrow which distinguished it from the German form. Probably the Polish form is not conspecific with the German form. The Polish form grossly resembles *Isopoma hertae* externaly and internally. But it is distinguished in being wider and in having a medial furrow that apparently does not extend as prominently towards the umbo as it does in *I.hertae.*

Family CAMAROTOECHIIDAE Schuchert & Le Vene, 1929
Subfamily SEPTALARIINAE Havlíček, 1960
Genus SAGUERESIA gen. nov.

Type species. – *Sagueresia saguerana* sp. nov.

Derivatio nominis. – Genus name derived from the name of the village Sagüera where the type species has been collected.

Species assigned to this genus. – *Sagueresia saguerana* and *Pseudocamarophoria undulataeformis* Biernat, 1966 (Biernat, 1966, p. 102, 103, pl. 19, figs. 1–22, text–fig. 34)

Diagnosis. – A small septalariid genus, subpentagonal to roundish in outline. Thick globular aspect. Equally biconvex. In the sulcus there is one median costa not reaching the umbo, corresponding with a median depression in the fold of the brachial valve. On each flank one to two low, rounded costae. No dental plates. Hinge plate undivided. A well-developed, high median septum. Median septum does not support the hinge plate. May be only connected at the posterior extremity. No cardinal process.

Comparison. – The internal characters of *Sagueresia* resemble those of the other genera of the subfamily Septalariinae as for instance, *Amissopecten*, Havlíček, 1960; and *Pseudocamarophoria* Wedekind, 1925 and consequently this genus is placed in this subfamily. However, externally *Sagueresia* is very distinctive from the other genera in having a small and more globose form, fewer costae on the flanks, a median costa in the sulcus corresponding with a median depression in the fold and a short and flattish tongue. Internally it differs only from *Septalaria* in having no cardinal process and dental plates.

Sagueresia saguerana gen. et sp. nov.
(Pl. VIII–1–3; Pl. IX–1–3; Fig. 32)

Holotype. – Specimen St. P. 6802072.

Locus typicus. – Section PSE.

Stratum typicum. – Eifelian – Givetian transitional horizon. Basal argillaceous limestone of member B.

Material & occurrence. – 5 specimens – Section PSE–St. P. 6802072–St. P. 6802074 & St. P. 6802075. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802072 (Holotype, figured)	11.0	11.0	9.3	97°
2. St. P. 6802073 (figured)	10.0	10.4	7.5	95°
3. St. P. 6802074 (figured)	10.1	10.5	7.3	92°

Description

External characters. – Shells small to medium-sized; subpentagonal to roundish in outline. Thick, globular aspect, equally biconvex. Length and width nearly equal; greatest width at midlength, greatest thickness at or posterior to midlength. Cardinal areas very small; it has not been possible to ascertain whether the hinge growth is strophic or non-strophic. Beak small, inconspicuous, postero-lateral slopes near the beak very narrowly excavated. Anterior commissure uniplicate. Fold low and sulcus shallow. Costae few in number, coarse, more prominent at the antero-lateral slopes, they never reach the beak; the rest of the shell smooth. The curvature of the pedicle valve is greatest on the beak, and decreases anteriorly, laterally the valve is gently sloping. Ventral beak sharp, pointed, incurved. Foramen probably small. Deltidial plates or deltidium not clearly discernible. Sulcus wide, shallow, well delimited from the anterolateral slopes and only conspicuous at the anterior end. Floor of the sulcus flat to weakly concave, sulcus passes imperceptibly to a narrow and short trapezoidal tongue. In the brachial valve the greatest curvature is situated posteriorly. Rather inconspicuous fold joins the tongue very gradually. Ornamentation consists of a few coarse costae that are only conspicuous on the antero-lateral flanks. Costae never reach the midlength of the shell. There is one median costa in the sulcus corresponding to a median depression in the fold, on each flank two costae are present. Costae are low and broadly roundish in transverse view. The interspaces are very shallow and as wide as the costae. Faint fine concentric growth lines are present.

Internal characters. – In the pedicle valve dental plates are absent. Low ridge-like outgrowths are present on the lateral sides of the central apical cavity near the teeth. Central apical cavity wide. A deep median muscle scar is present. In the brachial valve a cardinal process is absent. Hinge plate very well developed, undivided. Median septum high. It is connected to the hinge plate at the very posterior extremity as seen in one serially sectioned specimen (Pl. IX–1; Fig. 32 (3a)). In another specimen sectioned, such connection could not be clearly seen. Median septum does not support the hinge plate anteriorly.

Remarks. – The Polish species *Pseudocamarophoria undulataeformis* Biernat, 1966 is placed in this genus since its characters are very similar to the Spanish material. The differences between *undulataeformis* and *saguerana* are that the thickness of *undulataeformis* is much greater and that the lateral costae are better developed. Possibly *Septalaria undulata* Schmidt, 1941 (Schmidt, 1941a, p. 39, pl. 3, fig. 46; pl. 4, fig. 81; pl. 7, fig. 26) belongs to this genus.

Septalaria sp.
(Pl. VIII–4; Fig. 33)

Material & occurrence. – 4 specimens – Section PSE–St. P. 6802078 & St. P. 6802079. All specimens are from basal part of member B.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802076 (figured)	9.0	8.7	5.6	90°
2. St. P. 6802077	9.3	8.2 (?)	6.8	88°
3. St. P. 6802078	9.0	8.2 (?)	5.5	90°

Description

External characters. – Medium-sized, narrow, subtriangular in outline. Maximum width anterior to midlength. Ventral beak small, pointed, suberect. Anterior commissure uniplicate. Lateral commissure ventrally deflected. Zig-zag deflection very reduced. Ornamentation usually consists of 3 costae in the sulcus and 4 in the fold. Lateral costae are very indistinct. Costae low, roundish, separated by narrow grooves. Costae are confined to the anterior part of the shell.

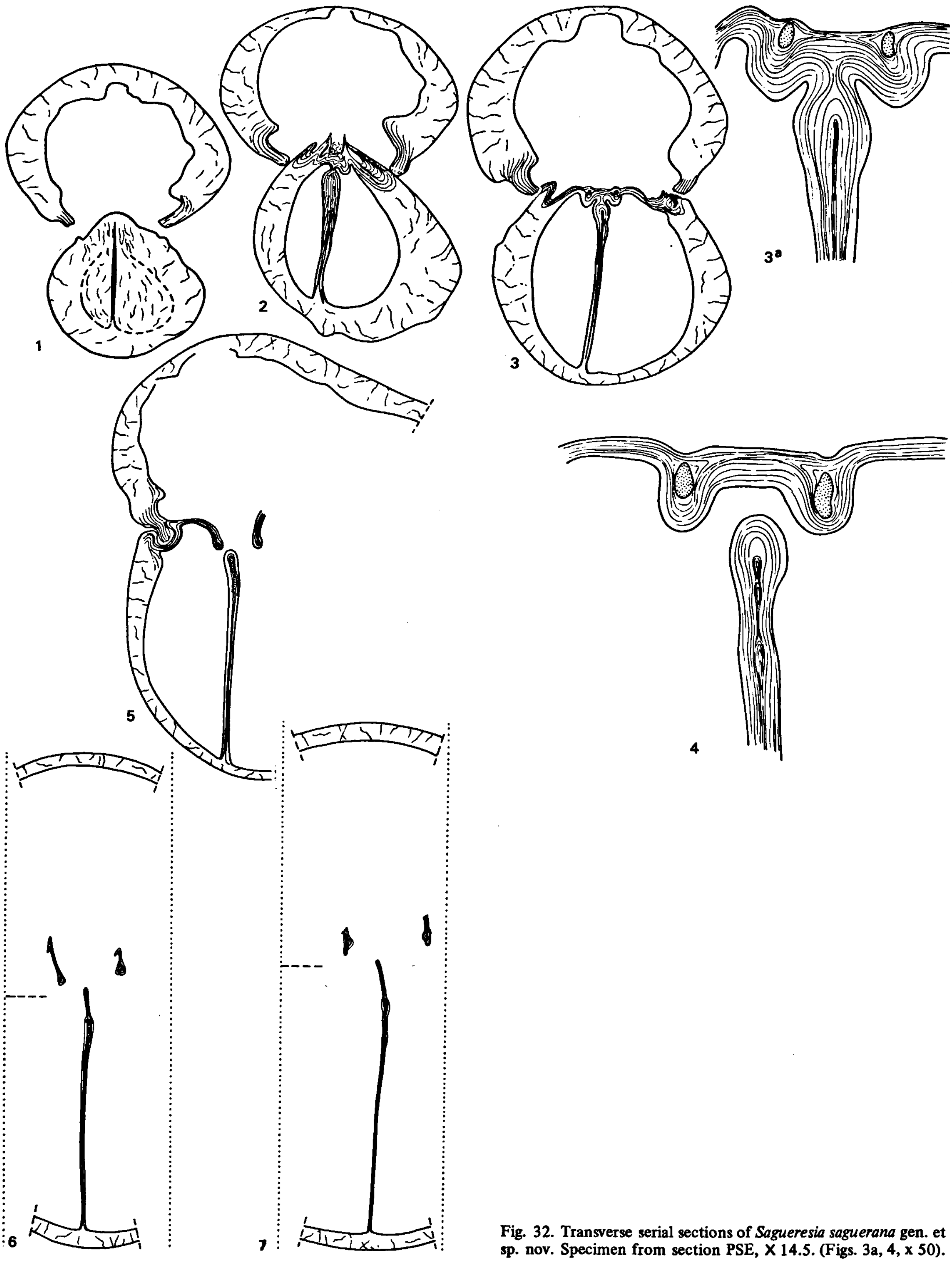


Fig. 32. Transverse serial sections of *Sagueresia saguerana* gen. et sp. nov. Specimen from section PSE, X 14.5. (Figs. 3a, 4, x 50).

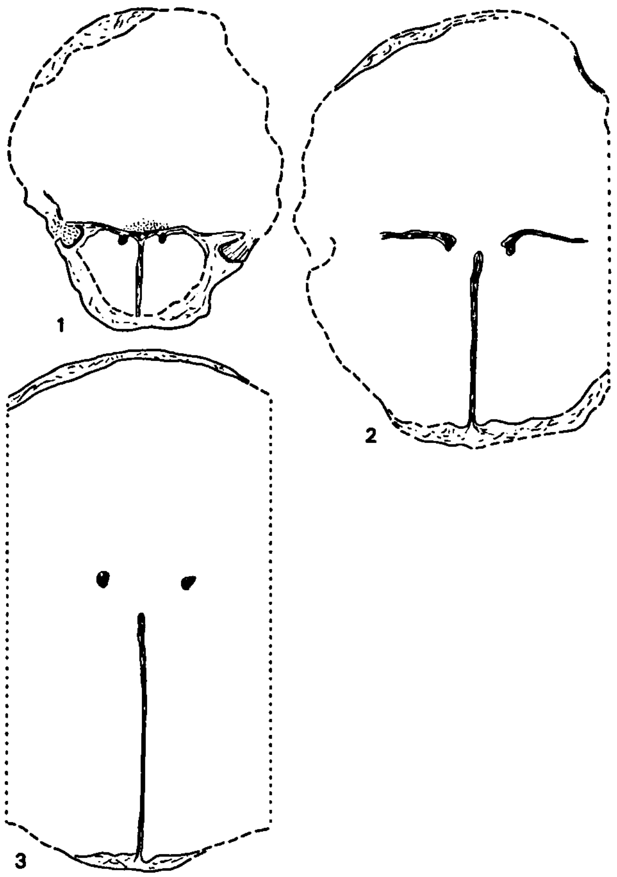


Fig. 33. Transverse serial sections of *Septalaria* sp. Specimen from section PSE, X 14.5.

Very fine concentric growth lamellae are seen in the frontal part of the tongue. Pedicle valve shallow, medially more convex near the umbo. Sulcus well-marked anteriorly, passes into a well-developed high tongue. On both sides of the tongue the flanks show a more or less ventrally directed growth, so that two distinct angular projections are formed. Brachial valve is gently convex. Fold anteriorly marked.

Internal characters. – Dental plates have been observed. Cardinal process is probably lost by recrystallization. A high median septum is present supporting the undivided hinge plate.

Remarks. – Our specimens are closer to *Septalaria ascendens* (Steininger, 1853) (see Steininger, 1853, p. 61, pl. 5, fig. 3, non fig. 2 and Schmidt, 1941a, pl. 2, fig. 40) than to *Septalaria subtetragona* (Schnur, 1853) (see Schnur, 1853, pl. 23, fig. 4 and also Schmidt, 1941a, pl. 3, fig. 43). Schmidt (written comm., 1969) considers *Septalaria ascendens* (Steininger, 1853) as a distinct species which she had formerly retained as Form A in the *subtetragona*-group (Schmidt, 1941a, p. 36, pl. 2, fig. 40). However, she is of the opinion that *Septalaria ascendens* from the Middle Eifelian of the Eifel area is not identical with *Septalaria ascendens* from the Upper Givetian from the area east of the Rhine river as mentioned by Holzapfel (1895) and Torley (1934). *Septalaria ascendens* is distinguished from our material in having a more globose shell, by its larger size (about twice that of our species) and by its rather gentle deflection of the flanks of the tongue without forming the projections as seen in our species. *Septalaria subtetragona tarfayensis* Drot, 1964 (pl. 20, figs. 1, 4, 5, & 6) from the Lower Eifelian of Morocco shows a greater external similarity with our forms than *Septalaria lehmani* Drot, 1964 (pl. 20, figs. 7–9 & 13) from the Upper Givetian of Morocco. But *subtetragona tarfayensis* has a more pinched apical part, the brachial valve is flattish in the posterior region and has a higher number of costae in the sulcus and flanks (the costae in the flanks are well marked).

Family CAMEROPHORINIDAE Rzhonsnitskaya, 1958
Camerophorina leonensis sp. nov.
(Pl. IX–4; Fig. 34)

Holotype. – St. P. 6802080.

Locus typicus. – Section PSM.

Stratum typicum. – Basal irregularly bedded biostromal limestones of member A. Eifelian.

Derivatio nominis. – The name is after the Province of León, Spain.

Material & occurrence. – 2 specimens – Section PSM-ST. P. 6802080 and St. P. 6802081. Specimens are from lower part of member A.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802080 (Holotype, figured)	16.7	18.0	14.1	100°

Description

External characters. – Shells medium-sized. Subtriangular in outline. Greatest width anterior to mid-length. Ventral beak small, suberect. Commissure uniplicate, strongly zig-zag deflected. Sulcus and fold marked on the anterior side. Ornamentation consists of 3 stout roundish and wide costae in the sulcus and 4 in the fold. There are 2–3 poorly developed lateral costae. Costae do not reach the middle of the shell. Average width of a costa in the sulcus measures 1.4 mm. There are fine concentric growth lines. Pedicle valve shallow, very gently convex. Sulcus anteriorly well-developed. The sulcus is bordered by two distinct depressions

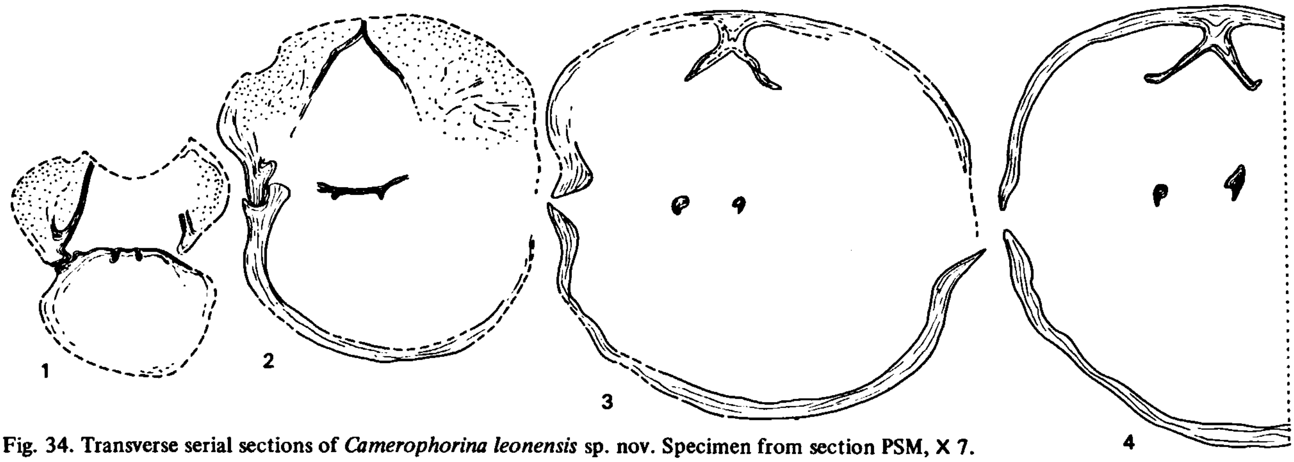


Fig. 34. Transverse serial sections of *Camerophorina leonensis* sp. nov. Specimen from section PSM, X 7.

laterally. The floor of the sulcus is slightly convex. Tongue short, wide and vertical. Brachial valve more convex than pedicle valve. The lateral flanks slope gently from the median convex portion. Fold developed anteriorly.

Internal characters. – In the pedicle valve, dental plates are present. They unite to form a spondylium that is supported by a low septum. In the brachial valve, hinge plate undivided. No septum, septalium, and cardinal process present.

Remarks. – It has been recognized by Schmidt (1941a, 1950) that there are two distinct species of *Camerophorina*, viz. *pachyderma* (Quenstedt, 1871) and *bijugata* (Schnur, 1853). The Spanish species of *Camerophorina* is distinguished from *bijugata* by its wider outline, low tongue, presence of more ribs in the tongue. From *pachyderma*, it is distinguished by its more narrow and triangular outline, its higher number of costae in the sulcus, delimitation of the sulcus by two furrows and the gently convex floor of the sulcus in frontal view.

Family YUNNANELLIDAE Rzhonsnitskaya, 1959

Schnurella ? sp.

(Pl. IX–5, 6)

Material & Occurrence. – 4 specimens (2 broken single valves, one specimen broken in the posterior and anterior part) – Section PSK–St. P. 6802082, St. P. 6802083 & St. P. 6802084. All specimens are from lower part of member A.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802082 (figured)	20	25.3	16.4	100°
2. St. P. 6802083 (figured)	22.1 (?)	27.8	19.2 (?)	90°

Description. – Shells large-sized, triangular. Lateral sides steep. Postero-lateral flanks concave. Greatest width anterior to midlength. Ventral beak small, pointed, suberect. Anterior commissure strongly zig-zag deflected. Ornamentation consists of 3 costae in sulcus, 2 in fold and 2–3 costae in the lateral flanks. These coarse costae are very anteriorly confined. Fine costellae begin from the beak and anteriorly they join the coarse costae. Pedicle valve shallow. Sulcus shallow, occupying almost the width of the pedicle valve. Tongue short, straight. Brachial valve more convex than pedicle valve. Fold low. Internal characters could not be studied.

Remarks. – In its external characters, our material compares closely with that of *Schnurella* Schmidt, 1964 (see also Schmidt, 1965). I could not make serial sections to study the internal characters as our specimens are generally fragmentary or damaged in the umbonal region. Therefore, I hesitate to definitely assign the specimens to *Schnurella*. From the Givetian type species *Schnurella schnurii* (Verneuil, 1840), the Spanish specimens are distinguished by their larger size, widely triangular outline, wide and somewhat more prominent sulcus. Sartenaer (pers. comm., 1968) (see also Sartenaer, 1971) considers the Russian Givetian species *Yunanella innae* Ivanova, 1962 (Ivanova, 1962, p. 67–69, pl. 3, figs. 3–7, text–fig. 29), *Yunanella olgae* Ivanova, 1962 (Ivanova, 1962, p. 69–70, pl. 3, figs. 1–2), and *Yunanella transversiformis* Tiajeva, 1962 (Tiajeva, 1962, p. 54–56, pl. 12, figs. 1–6, text–fig. 6) as congeneric with *Schnurella* Schmidt, 1964. Comparison of the figures given for the Russian species do not suggest complete identity with the Spanish material.

Family uncertain

Genus MIRANTESIA gen. nov.

Type species. – *Mirantesia mirantana* sp. nov.

Derivatio nominis. – Genus name derived from the name of the village Mirantes where the type species has been collected.

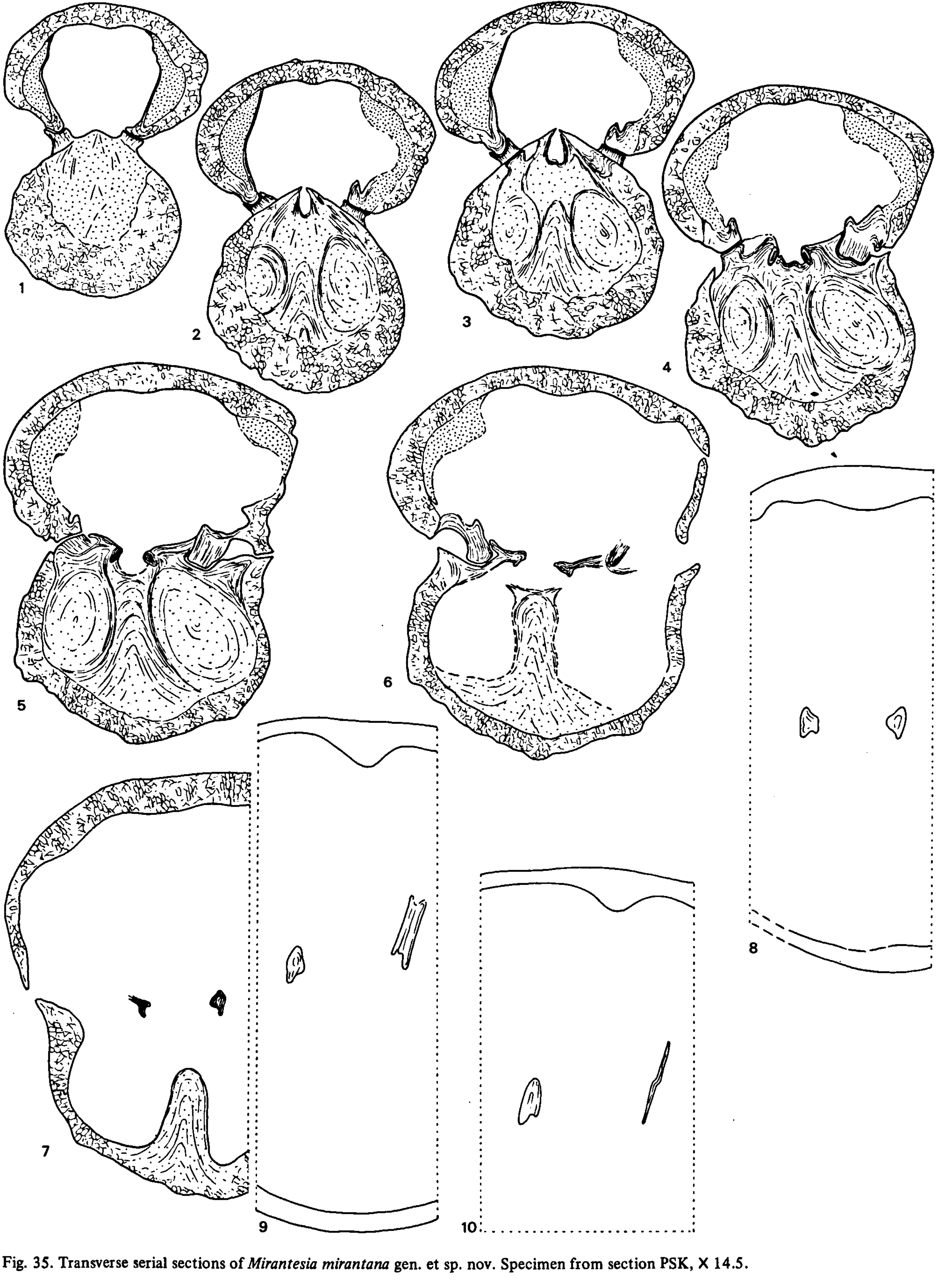


Fig. 35. Transverse serial sections of *Mirantesia mirantana* gen. et sp. nov. Specimen from section PSK, X 14.5.

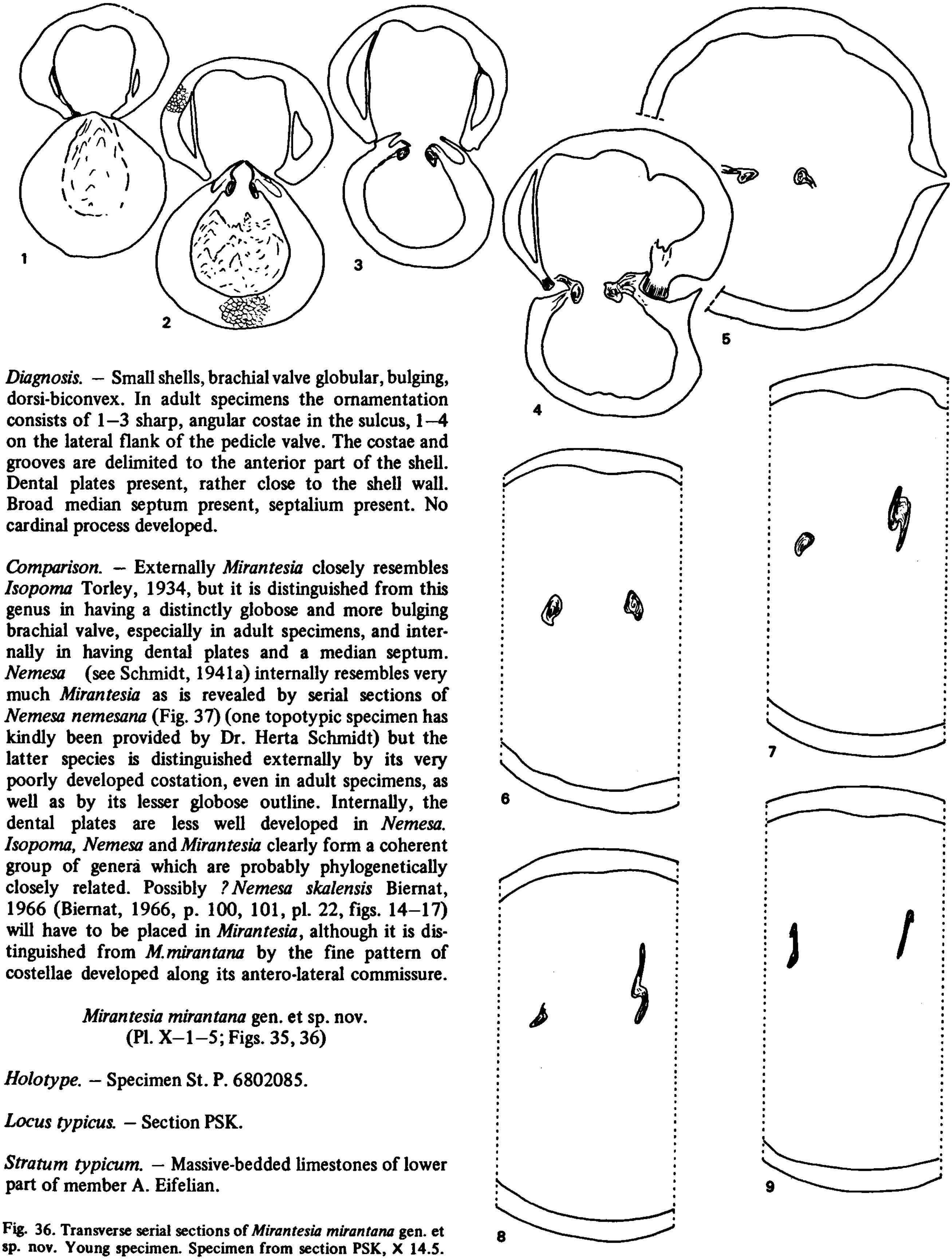


Fig. 36. Transverse serial sections of *Mirantesia mirantana* gen. et sp. nov. Young specimen. Specimen from section PSK, X 14.5.

Diagnosis. – Small shells, brachial valve globular, bulging, dorsi-biconvex. In adult specimens the ornamentation consists of 1–3 sharp, angular costae in the sulcus, 1–4 on the lateral flank of the pedicle valve. The costae and grooves are delimited to the anterior part of the shell. Dental plates present, rather close to the shell wall. Broad median septum present, septalium present. No cardinal process developed.

Comparison. – Externally *Mirantesia* closely resembles *Isopoma* Torley, 1934, but it is distinguished from this genus in having a distinctly globose and more bulging brachial valve, especially in adult specimens, and internally in having dental plates and a median septum. *Nemesa* (see Schmidt, 1941a) internally resembles very much *Mirantesia* as is revealed by serial sections of *Nemesa nemesana* (Fig. 37) (one topotypic specimen has kindly been provided by Dr. Herta Schmidt) but the latter species is distinguished externally by its very poorly developed costation, even in adult specimens, as well as by its lesser globose outline. Internally, the dental plates are less well developed in *Nemesa*. *Isopoma*, *Nemesa* and *Mirantesia* clearly form a coherent group of genera which are probably phylogenetically closely related. Possibly *?Nemesa skalensis* Biernat, 1966 (Biernat, 1966, p. 100, 101, pl. 22, figs. 14–17) will have to be placed in *Mirantesia*, although it is distinguished from *M.mirantana* by the fine pattern of costellae developed along its antero-lateral commissure.

Mirantesia mirantana gen. et sp. nov.
(Pl. X–1–5; Figs. 35, 36)

Holotype. – Specimen St. P. 6802085.

Locus typicus. – Section PSK.

Stratum typicum. – Massive-bedded limestones of lower part of member A. Eifelian.

Material & occurrence. – 44 complete shells – Section PSK–St. P. 6802085–St. P. 6802091 & St. P. 6802092. All specimens are from lower part of member A. Most of the material in fairly good state of preservation. Few specimens are broken at the edges and slightly deformed.

Dimensions (in mm). –

	length	width	thickness	shoulder angle
1. St. P. 6802085 (Holotype, figured)	9.0	9.5	8.2	105°
2. St. P. 6802086 (figured)	7.5	8.1	6.6	102°
3. St. P. 6802087 (figured)	7.2	7.8	5.8	100°
4. St. P. 6802088 (figured)	6.1	6.4	3.7	95°
5. St. P. 6802089	6.2	6.8	5.2	100°
6. St. P. 6802010	7.1	7.3	5.0	95°
7. St. P. 6802011	5.6	5.4	4.0	85°

Description

External characters. – Shells small, subpentagonal in outline, globular. Young specimens flat. Adult ones are strongly inequivalve, dorsi-biconvex. Width is greater than length. Greatest width anterior to midlength. Maximum thickness is nearly at midlength. Ventral beak small, suberect. Shell widely and shallowly uniplicate; apart from the median deflection the commissure develops from straight in young to undulate and finally angularly zig-zag deflection in adult specimens. Sulcus and fold not very pronounced. Pedicle valve shallow. Well-developed deltidium. Foramen sub-mesothyrid. Sulcus extremely shallow; it originates at a distance of about 2/3 of the length of the shell away from the umbo. It passes into a very short, wide and vertical tongue. The flanks of the tongue coincide with the flanks of the adjacent lateral costae of the pedicle valve. Brachial valve is highly convex, medially producing a 'bulging' aspect. Lateral slopes fall rather steeply from the median bulging part. Young specimens do not show such high convexity. Fold is extremely inconspicuous. Ornamentation in adult specimens consists of 1–4 very short lateral costae on either side of the pedicle valve and 1–3 median costae in the sulcus. Short antero-lateral costae originate anterior to the median costae and are less pronounced. Costae are sharply angular in trans-

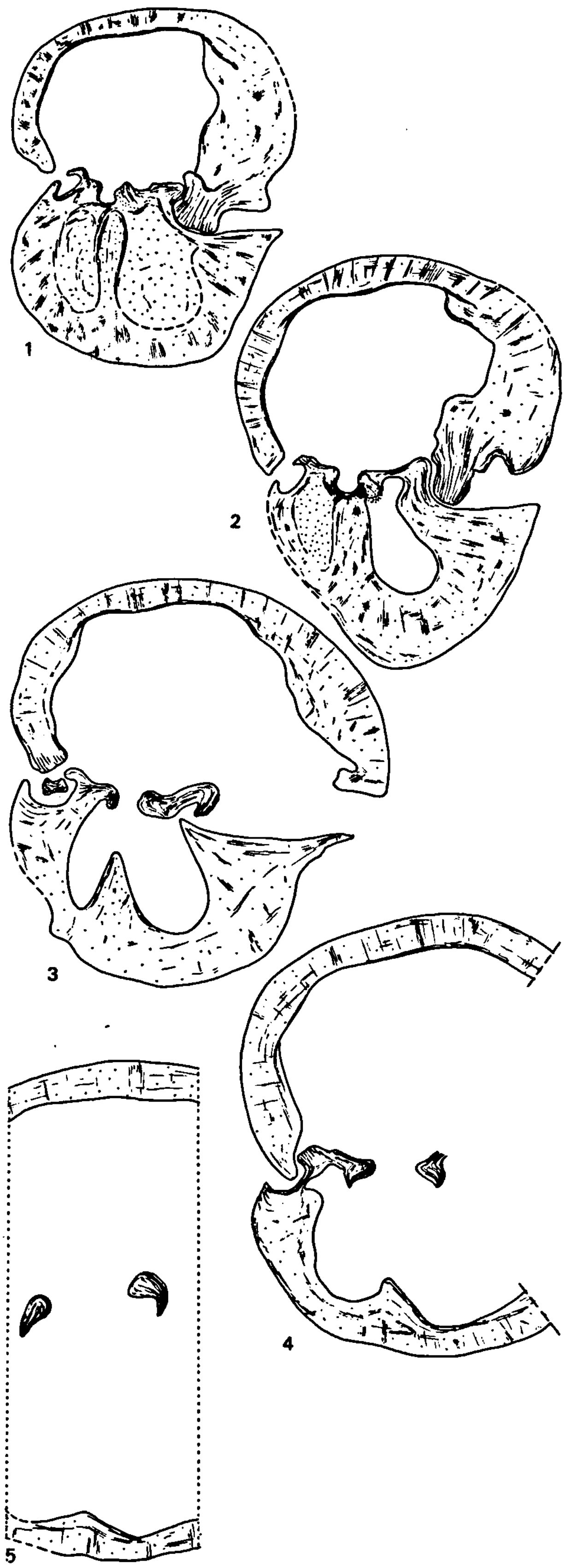


Fig. 37. Transverse serial sections of *Nemesa nemasana* Schmidt, 1941. Topotype specimen from Germany, X 14.5.

verse sections. Posterior and lateral parts of the shell are smooth and marked by faint concentric growth lines.

Internal characters. – Fibres are very coarse. Dental plates well-developed and rather close to the shell wall in the pedicle valve. The pedicle lateral cavities are largely filled up with secondary shell. In adult specimens a broad median septum is present in the brachial valve. In young specimens no septum or ridge present or may be very vague. Its anterior margin is rounded and therefore, it does not show a dense and sharply delimited and finely fibrous core in transverse sections. Posteriorly the septum fuses with the crural bases forming a shallow septalium. No inner hinge plates and no cardinal process. Secondary thickening in adult individuals and in younger forms no thickening.

CHAPTER VII

BIOSTRATIGRAPHIC CONSIDERATIONS

The age of the Portilla Formation was regarded as late Givetian to early Frasnian by Comte (1959, p. 41, 311, 317). This view has been generally maintained in publications dealing with the Devonian stratigraphy of the Cantabrian Mts. (Brouwer, 1968; Llopis llado et al., 1968). Recently, however, Struve & Mohanti (1970) after a study of the atrypid brachiopods pleaded for an Eifelian – Givetian age for the Portilla Formation in the Alba syncline between the Luna and Bernesga rivers. In this chapter, additional information from the rhynchonellid brachiopods will be provided. The collection of spiriferids which I made from this formation is being studied by Dr. Th. F. Krans (University of Leiden). In enclosures A and B, the occurrences of the rhynchonellid and atrypid species in different lithostratigraphic units have been shown.

THE RHYNCHONELLIDS

The assemblage of the rhynchonellids is suggestive of a Middle Devonian (Eifelian – Givetian) age for the Portilla Formation. However, the precise stratigraphic range of some of the species can not be ascertained until a revision of the known species and genera from the type region is accomplished. Most of the known Middle Devonian rhynchonellid species are in great need of revision. It seems evident, for example that *'Uncinulus' parallelepipedus* (Bronn, 1837) (= *Kransia parallelepideda*) and *'Uncinulus' subcordiformis (Schnur, 1853) (= Kransia subcordiformis*) encompass various forms and that for this reason their precise stratigraphic range can not be ascertained. The species *'Uncinulus' parallelepipedus* Bronn is known from Upper Emsian to Upper Givetian strata of several parts of Europe, North Africa, and Asia. It is, however, commonly reported from Eifelian. The species *'Uncinulus' subcordiformis* Schnur is reported in Europe from Upper Emsian to Upper Givetian strata. However, it seems to be a very common species in Givetian deposits. The species *'Uncinulus' pentagonus* (Kayser, 1871) is known in Europe both in Eifelian and Givetian. The genus *Nalivkinaria* Rzhonsnitskaya, 1968 is only known from Eifelian deposits of the southern margin of the Kuznetsk Basin, Russia. The species *'Uncinulus' signatus* (Schnur, 1853) and *'Uncinulus' subsignatus* (Reed, 1908) presently assigned to the genus *Nalivkinaria* are known only from Middle to Upper Eifelian of Europe (Germany (only from the Eifel region), Belgium) and Asia (Burma, Afghanistan). The presence of *Nalivkinaria* in the Portilla Formation, therefore, suggests a late Eifelian age. The genotype *Beckmannia minor beckmanni* (Schmidt, 1951) is from the Upper Givetian 'FlinzKalk' from the east of the Rhine river, Germany. The presence of this species in the Portilla Formation indicates an Upper Givetian age. However, the close association with other rhynchonellids with an Eifelian tinge does not preclude the possibility that its range extends into Lower Givetian. The *'Pugnax'* specimens in the Spanish assemblage show a great similarity with some of the *'Pugnax'* species from Eifelian in Germany. The Spanish *Isopoma hertae* has a greater similarity with the Eifelian *Isopoma brachyptyctum* than with specimens from the Upper Givetian 'Massenkalk' in Germany. The presence of the genus *Cupularostrum* is indicative of a Givetian age. The species *Cupularostrum sartenaeri* also occurs on the northern slope of the Peña Corada between the rivers Esla and Cea at the Portilla – Nocedo boundary (collection kindly shown by D. van der Baan, University of Leiden). The genus *Camerophorina* is known from Eifelian in Germany and Givetian in Moravia, Czechoslovakia. Few large specimens are questionably referred to as *Schnurella*. I have, however, seen a specimen (somewhat deformed) closely comparable to *Schnurella schnurii* (Verneuil, 1840) in the collection of D. van der Baan from middle part of the lower member of the Portilla Formation at the road section north of Cistierna, prov. León. The genus *Schnurella* is known from Givetian of Germany, Belgium, Russia, and Burma.

Most of these rhynchonellids occur in the basal part of member B within 6 m of argillaceous limestones. In the assemblage, there are genera and species having strongly an Eifelian aspect and some with a Givetian aspect. The forms that point to an Eifelian age are *Kransia* aff. *parallelepipeda, Nalivkinaria* aff. *lacunata* forma *tenuicostata, Isopoma hertae*, and the *'Pugnax'* specimens, while those pointing to a Givetian age are *Kransia subcordiformis, Beckmannia minor beckmanni*, and *Cupularostrum sartenaeri*. This 'mixed fauna' in the basal part of member B is probably a boundary phenomenon implying a transition from Eifelian to Givetian. In the present state of our knowledge, we could only give an Upper Eifelian to a Lower Givetian age to the rhynchonellid assemblage in the basal part of member B of the Portilla Formation.

THE ATRYPIDS

The problems relating to the biostratigraphic significance of the atrypids are fully discussed elsewhere (Struve & Mohanti, 1970). It is only recalled here that an age corresponding with the Eifelian – Givetian boundary for the basal part of member B seems the most likely in so far as the atrypid fauna is concerned.

OTHER BRACHIOPODS

In the Spanish collection the genus *Plectospira* Cooper, 1942 is present. *Plectospira* is reported from Emsian and Middle Devonian strata of Europe and Asia (Boucot et al., 1969). In Bohemia, Havlíček (written comm., 1969) records the first appearance of *Plectospira* from the top layers of the Lochkov limestones (probably Siegenian in age). According to Havlíček, these specimens are poorly preserved and are not suitable for study. The youngest *Plectospira* in Czechoslovakia is *P. ferita* (Buch.) occurring rarely in the Givetian limestones at Celechovice (Moravia). The species *Davidsonia verneuili* is present in the Spanish collection. This species is known in Germany from Eifelian strata.

FAUNAL AFFINITIES

The Middle Devonian brachiopod fauna from the Cantabrian Mountains, show a great affinity with the fauna from the Middle Devonian of the Eifel region in Germany. As far as Rhenish, Hercynian, and mixed facies types (see Erben, 1962; Erben & Zagora, 1968) are concerned, the brachiopod fauna from the Cantabrian Mts. could be assigned to the mixed or Eifel facies (Copper, 1966a) or close to this type. In the Eifel region, this mixed facies is constituted of muddy limestones and calcareous shales rich in rugose and tabulate corals, stromatoporoids, brachiopods, and crinoids. The brachiopods are varied, multispecific groups occur; mainly atrypids, spiriferids, rhynchonellids, athyrids, and also gypidulids, and meristellids. Everything in the Spanish atrypids seems typical of the atrypids of mixed facies despite differences in some generic and specific characters. In a larger zoogeographic sense, the mixed facies brachiopods would belong to the Rhenish subprovince of the Old World Province (of Boucot et al., 1968). The rhynchonellid fauna from the Cantabrian Mts. is not exactly identical in all its generic and specific compositions to the known rhynchonellids from Germany. The genera provisionally referred to as *'Hebetoechia'* and *'Cassidirostrum'* apparently are not known in the German Middle Devonian rhynchonellids. The genus *Mirantesia* is certainly new. Some other new species are recorded in the Spanish fauna. Several of the Spanish atrypid genera and subgenera come very close to the known Middle Devonian atrypid genera and subgenera from Germany. However, they are not identical. When arranged in a stratigraphic order, the Spanish atrypid 'species' show no distinct trend in the development of characters comparable to the trend in the central European atrypids. This might mean that development of species was endemic in Spain, or the species immigrated from some region other than central Europe. The brachiopod fauna from Spain also shows a striking similarity to the Middle Devonian fauna of the Skaly beds, of the Bodzentyn syncline, Holy Cross Mountains, Poland (Biernat, 1964, 1966). The Skaly beds with its shales, siltstones, marls, and limestones have been dated as Lower Givetian and questionably Upper Eifelian by Biernat (1964, 1966) on brachiopod evidence. Copper (1966b, p. 40) from atrypid evidence suggested an Eifelian age for the Skaly beds. Specimens of the rhynchonellid genus *Nalivkinaria* from Spain show affinity with *Nalivkinaria lacunata forma tenuicostata* from Eifelian of the Kuznetsk Basin, U.S.S.R.

CONCLUDING REMARKS

The evidence obtained from the atrypid and rhynchonellid faunas strongly suggests that the Eifelian – Givetian boundary lies in the basal part of member B. It is suggested that member A is of Eifelian age and that members B and C, apart from the basal part of member B belong to the Givetian. The Givetian sequence in the Alba syncline is probably complete or largely complete between sections PSD and PSN whereas farther on the southern and northern flanks a large part of the Givetian is probably missing, suggesting a hiatus.

REFERENCES

Adrichem Boogaert, H. A. van, 1967. Devonian and Lower Carboniferous conodonts of the Cantabrian Mountains (Spain) and their stratigraphic application. Leidse Geol. Med., 39, p. 129–192.

Ager, D. V., 1963. Principles of paleoecology. McGraw-Hill Book Comp., Inc., New York, London, 371 p.

Anderson, M. M., Boucot, A. J., & Johnson, J. G., 1969. Eifelian brachiopods from Padaukpin, Northern Shan States, Burma. Bull. Brit. Mus. (Nat. Hist.), 18/4, p. 107–163.

Baars, D. L., 1963. Petrology of carbonate rocks. In: Shelf carbonates of the Paradox Basin – A Symposium, Bass, R. O. & Sharps, S. L. (eds.), Four Corners Geol. Soc., p. 101–129.

Bathurst, R. G. C., 1958. Diagenetic fabrics in some British Dinantian limestones. Liverpool and Manchester Geol. Journ., 2, p. 11–36.

Biernat, G., 1964. Middle Devonian Atrypacea (Brachiopoda) from the Holy Cross Mountains, Poland. Acta Pal. Pol., 9/3, p. 277–356.

–, 1966. Middle Devonian Brachiopods of the Bodzentyn syncline (Holy Cross Mountains, Poland). Palaeontologia Polonica, Nr. 17, 162 p.

Boucot, A. J., Johnson, J. G., & Talent, J. A., 1969. Early Devonian brachiopod zoogeography. Geol. Soc. Amer., Spec. Paper, 119, 113 p.

Breimer, A., 1969. A contribution to the palaeoecology of Palaeozoic stalked crinoids. Proc. Kon. Ned. Akad. van Wet., serie B, 72/2, p. 139–150.

Brice. D., 1970. Etude paléontologique et stratigraphique du Dévonien de l'Afghanistan: Contribution à la connaissance des brachiopodes et des polypiers rugueux. Notes et Mém. sur le Moyen-Orient, Mus. nat. d'Hist. naturelle, Paris, Tome XI, 364 p.

Brouwer, A., 1968. Devonian of the Cantabrian Mountains, northwestern Spain. In: Intern. Symp. Dev. Syst., Calgary, 1967, Oswald, D. H. (ed.), Alberta Soc. Petrol. Geol., vol. II, p. 37–45.

Buisonjé, P. H. de, & Zonneveld, J. I. S., 1960. De Kustvormen van Curaçao, Aruba en Bonaire. Nieuwe West-Indische Gids, 40, p. 121–144.

Comte, P., 1959. Recherches sur les terrains anciens de la Cordillère Cantabrique. Mem. Inst. Geol. Minero España, 60, p. 440 p.

Copper, P., 1966a. Ecological distribution of Devonian atrypid brachiopods. Pal. geogr.- Pal. climat.- Pal. ecol., 2, p. 245–266.

–, 1966b. The *Atrypa zonata* brachiopod group in the Eifel, Germany. Senck. leth., 47, p. 1–55.

–, 1967. Adaptations and life habits of Devonian atrypid brachiopods. Pal. geogr.- Pal. climat.- Pal. ecol., 3, p. 363–379.

Cumings, E. R., 1932. Reefs or bioherms? Bull. Geol. Soc. Amer., 43, p. 331–352.

Dooge, J., 1966. The stratigraphy of an Upper Devonian carbonate-shale transition between the north and south Ram rivers of the Canadian Rocky Mountains. Leidse Geol. Med., 39, p. 1–53.

Drot, J., 1964. Rhynchonelloidea et Spiriferoidea siluro-dévoniens du Maric pré-saharien. Notes et Mém. Serv. Géol. Maroc, Nr. 178, 286 p.

Dumestre, A. & Illing, L. V., 1968. Middle Devonian reefs in Spanish Sahara. In: Intern. Symp. Dev. Syst., Calgary, 1967, Oswald, D. H. (ed.), Alberta Soc. Petrol. Geol., vol. II, p. 333–350.

Dunbar, C. O. & Rodgers, J., 1957. Principles of stratigraphy. John Wiley & Sons, Inc., New York, 356 p.

Dunham, R. J., 1962. Classification of carbonate rocks according to depositional texture. In: Classification of carbonate rocks – A Symposium, Ham, W. E. (ed.), Amer. Ass. Petr. Geol. Mem., 1., p. 108–121.

Edie, R. W., 1961. Devonian limestone reef reservoir Swan Hills Oil field, Alberta. Canadian Inst. Min. & Met. Trans., 64, p. 278–285.

Ellenor, D. W., 1969. The occurrence of the trace fossil *Zoophycos* in the Middle Devonian of northeastern New South Wales, Australia. Pal. geogr.-Pal.climat.-Pal. ecol., 7, p. 69–78.

Erben, H. K., 1962. Zur Analyse und Interpretation der rheinischen und hercynischen Magnafazies des Devons. 2. Intern. Arbeitstagung über die Silur/Devon-Grenze und die Stratigraphie von Silur und Devon, Bonn-Bruxelles, 1960, (herausgeg. von H. K. Erben), Schweizerbart., Stuttgart, p. 42–61.

– & Zagora, K., 1968. Devonian of Germany. In: Intern. Symp. Dev. Syst., Calgary, 1967, Oswald, D. H. (ed.), Alberta Soc. Petrol. Geol., vol. I, p. 53–68.

Evamy, B. D., 1963. The application of a chemical staining technique to a study of dedolomitisation. Sedimentology, 2, p. 164–170.

Evers, H. J., 1967. Geology of the Leonides between the Bernesga and Porma rivers, Cantabrian Mountains, NW Spain. Leidse Geol. Med., 41, p. 83–151.

Folk, R. L., 1959. Practical petrographic classification of limestones. Amer. Ass. Petr. Geol. Bull., 43, p. 1–38.

–, 1962. Spectral subdivision of limestone types. In: Classification of carbonate rocks – A symposium, Ham, W. E. (ed.), Amer. Ass. Petr. Geol. Mem. 1, p. 62–84.

–, 1965. Some aspects of recrystallization in ancient limestones. In: Dolomitization and limestone diagenesis – A Symposium, Pray, L. C. & Murray, R. C. (eds.), Soc. Econ. Pal. Min., Spec. Publ. Nr. 13, p. 14–48.

– & Robles, R.; 1964. Carbonate sands of Isla Perez, Alacran Reef Complex, Yucatán, Journ. Geol., 72, p. 255–292.

Friedman, G. M., 1959. Identification of carbonate minerals by staining methods. Journ. Sed. Petr., 59, p. 87–97.

–, 1965. Terminology of crystallisation textures and fabrics in sedimentary rocks. Journ. Sed. Petr., 35, p. 643–655.

–, 1968. The fabric of carbonate cement and matrix and its dependence on the salinity of water. In: Recent developments in carbonate sedimentology in central Europe, Müller, G. & Friedman, G. M. (eds.), Springer-Verlag, Berlin, 255 p.

– & Sanders, J. E., 1967. Origin and occurrence of dolostones. In: Carbonate rocks, origin, occurrence and classification, Chilingar, G. V., Bissell, H. J., & Fairbridge, R. W. (eds.), Developments in Sedim., 9A, Elsevier Publ. Co., Amsterdam, p. 169–265.

Geissler, H., 1969. Zur stratigraphie und fazies der Finnentroper Schichten sowie zur Ökologie ihrer Fauna (Mittlere Givet-Stufe, nordöstliches Sauerland, Rheinisches Schiefergebirge). Göttinger Arbeiten zur Geol. u. Pal. Nr. 4, 67 p.

Ginsburg, R. N., 1956. Environmental relationships of grain-size and constituent particles in some South Florida carbonate sediments. Amer. Ass. Petr. Geol. Bull., 40, p. 2384–2427.

– & Lowenstam, H. A., 1958. The influence of marine bottom communities on the depositional environments of sediments. Journ. Geol., 66, p. 310–318.

–, Michael Lloyd, R., & Stockman, K. W., 1963. Shallow-water carbonate sediments. In: The Sea, vol. 3, Hill. M. N. (ed.), Interscience Publishers, New York, p. 554–582.

Grabau, A. W., 1904. On the classification of sedimentary rocks. Amer. Geol., 33, p. 228–247.

Harbaugh, J. W., 1961. Relative ages of visibly crystalline calcite in Late Palaeozoic limestones. Kansas State Geol. Surv. Bull., 152, p. 93–126.

Havlícek, V., 1961. Rhynchonelloidea des böhmischen Paläozoikums (Brachiopoda). Rozpr. Ústr. Úst. Geol., 27, 211 p.

Hedberg, H. D. (ed.), 1961. Stratigraphic classification and terminology. Intern. Geol. Congr., Rept. 21st session, part 25, p. 1–38.

Holzapfel, E., 1895. Das Obere Mitteldevon (Schichten mit *Stringocephalus burtini* und *Maeneceras terebratum*) im Rheinischen Gebirge. Abh. k. Preuss. Geol. Landesanst., N.F., 16, 459 p.

Irwin, M. L., 1965. General theory of epeiric clear water sedimentation. Amer. Ass. Petr. Geol. Bull., 49, p. 445–459.

Ivanova, E. A., 1962. Ekologiia i razvitie brakhiopod siloura i devona Kouznetzkogo, Minouskogo i Touvinskogo basseinov. Akademiya Nauk S.S.S.R., Institut Paleontologii Trudy, 88, p. 1–151.

Jenik, A. J. & Lerbekmo, J. F., 1968. Facies and geometry of Swan Hills Reef Member of Beaverhill Lake Formation (Upper Devonian), Goose River Field, Alberta, Canada. Amer. Ass. Petr. Geol. Bull., 52, p. 21–56.

Johnson, J. G., 1966. Middle Devonian brachiopods from the Roberts Mts., Central Nevada. Palaeontology, 9, p. 152–181.

–, 1970. Early Middle Devonian brachiopods from Central Nevada. Journ. Pal., 44, p. 252–264.

Jux, U., 1960. Die Devonischen Riffe im Rheinischen Schiefergebirge. Neues Jahrb. Geol. Paläont. Abh., 110, p. 186–258.

Klovan, J. E., 1964. Facies analysis of Redwater reef complex, Alberta, Canada. Canadian Petr. Geol. Bull., 12, p. 1–100.

Krans, Th. F., 1965. Études morphologiques de quelques spirifères dévoniens de la Chaîne Cantabrique (Espagne). Leidse Geol. Med., 33, p. 71–148.

Krebs, W., 1966. Der Bau des oberdevonischen Langenaubach-Breitscheider Riffes und seine weitere Entwicklung im Unterkarbon (Rheinisches Schiefergebirge). Abh. Senck. Naturforsch. Ges., 511, p. 1–105.

Laporte, L. F., 1967. Carbonate deposition near mean sea-level and resultant facies mosaic: Manlius Formation (Lower Devonian) of New York State. Amer. Ass. Petr. Geol. Bull., 51, p. 73–101.

Lecompte, M., 1958. Les récifs paléozoics en Belgique. Geol. Rundschau, 47, p. 384–401.

–, 1961. Facies marines et stratigraphique dans le Dévonien de l'Ardenne. Ann. Soc. Géol. Belg., 85, p. 1–57.

–, 1970. Die Riffe im Devon der Ardennen und ihre Bildungsbedingungen. Geologica et Palaeontologica, 4, p. 25–71.

Llopis llado, N., De Villata, J. F., Cabanas, R., Pelaez Prunda, J. R., & Vilas, L., 1968. Le Dévonien de l'Espagne. In: Intern. Symp. Dev. Syst., Calgary, 1967, Oswald, D. H. (ed.), Alberta Soc. Petrol. Geol., vol. I, p. 171–187.

Lucia, F. J., 1962. Diagenesis of a crinoidal sediment. Journ. Sed. Petr., 32, p. 848–865.

Maxwell, W. G. H., 1968. Atlas of the Great Barrier Reef. Elsevier Publ. Co., Amsterdam, 258 p.

– & Swinchatt, J. P., 1970. Great Barrier Reef: regional variation in a terrigenous-carbonate province. Geol. Soc. Amer. Bull., 81, p. 691–724.

McLaren, D. J., 1961. Three new genera of Givetian and Frasnian (Devonian) rhynchonellid brachiopods. Bull. Inst. roy. Sc. Nat. Belg., Tome XXXVII, Nr. 23, p. 1–7.

–, 1962. Middle and early Upper Devonian rhynchonellid brachiopods from western Canada. Geol. Surv. Canada, Bull., 85, 122 p.

Meer Mohr, C. G. van der, 1969. The stratigraphy of the Cambrian Lancara Formation between the Luna river and the Esla river in the Cantabrian Mountains, Spain. Leidse Geol. Med., 43, p. 233–316.

Meijer, J. J. de, 1971. Carbonate petrology of algal limestones (Lois-Ciguera Formation, Upper Carboniferous, León, Spain). Leidse Geol. Med., 47 p. 1–53.

Murray, J. W., 1966. An oil producing reef-fringed carbonate bank in the Upper Devonian Swan Hills Member, Judy Creek, Alberta. Canadian Petr. Geol. Bull., 14, p. 1–103.

Murray, R. C., 1960. Origin of porosity in carbonate rocks. Journ. Sed. Petr., 30, p. 59–84.

Perkins, R. D., 1963. Petrology of the Jeffersonville Limestone (Middle Devonian) of southeastern Indiana. Geol. Soc. Amer. Bull., 74, p. 1335–1354.

Reed, F. R. C., 1908. The Devonian faunas of the Northern Shan States. Mem. Geol. Surv. India, Paleontologica Indica, New Series, 2, p. 1–183.

Reijers, T., 1972. Facies and diagenesis of the Devonian Portilla Limestone Formation between the river Esla and the Embalse de la Luna, Cantabrian Mountains, Spain. Leidse Geol. Med., 47, p. 163–217.

Rupke, J., 1965. The Esla nappe, Cantabrian Mountains, Spain. Leidse Geol. Med., 32, p. 1–74.

Rzhonsnitskaya, M. A., 1968a. Novyie vidy sredniedevonskikh uncinulid okrainy kuznietzkovo bassiena. In: Novyie vidy drevnikh rastienij i bezpozvonochuykh U.S.S.R., Markovskij, B. P. (ed.), vol. 2, part 2, p. 109–115.

–, 1968b. Novyie vidy sredniedevonskikh septalariid i hypothyridinid okrainy Kuznietzkovo bassiena. In: Novyie vidy drevnikh rastienij i bezpozvonochuykh U.S.S.R., Markovskij, B. P. (ed.), vol. 2, part 2, p. 117–122.

Sanders, J. E. & Friedman, G. M., 1967. Origin and occurrence of limestones. In: Carbonate rocks, origin, occurrence and classification, Chilinger, G. V., Bissell, H. J. & Fairbridge, R. W. (eds.), Developments in Sedim., 9A. Elsevier Publ. Co., Amsterdam, p. 169–265.

Sartenaer, P., 1961. Étude nouvelle, en deux parties, du genre *Camarotoechia*, Hall et Clarke, 1893. Deuxième partie: *Cupularostrum recticostatum*. n. gen., n. sp. (1). Bull. Inst. roy. Sc. Nat. Belg., Tome XXXVII, Nr. 25, p. 1–15.

–, 1966. Frasnian Rhynchonellida from the Ozbak-Kuh and Tabas regions (East Iran). Geol. Surv. Iran, Report Nr. 6, p. 25–53.

– & Rozman, Kh. S., 1968. *Physetorhyncha*, new genus of late Famennian rhynchonellids. Paleont. Journ., 2, p. 275–276.

–, 1968. *Eurycolporhynchus*, nouveau genre de brachiopode rhynchonellide du Givetien supérieur. Senck. leth., 49, p. 565–574.

–, 1971. Redescription of the brachiopod genus *Yunnanella* Grabau, 1923 (Rhynchonellida). In: Palaeozoic perspectives: A palaeontological tribute to G. Arthur Cooper- Dutro, J. T. (ed.), Smithsonian Contributions to Palaeobiology, Nr. 3, Smithsonian Institute Press, City of Washington, p. 203–218.

Schieferdecker, A. A. G. (ed.), 1959. Geological Nomenclature. J. Noorduijn & Zn., Gorinchem, 521 p.

Schmidt, Herta, 1941a. Die mitteldevonischen Rhynchonelliden der Eifel. Abh. Senck. Naturforsch. Ges., 459, 79 p.

–, 1941b. Rhynchonellidae aus rechtsrheinischem Devon. Senckenbergiana, 23, p. 277–290.

–, 1950. Zur Fauna und Stratigraphie der Gondelsheimer Schichten. Senckenbergiana, 31, p. 79–87.

–, 1951. Zur Brachiopoden-Fauna des Mitteldevonischen Flinzkalkes von Iserlohn-Letmathe. Senckenbergiana, 32, p. 87–94.

–, 1964. Neue Gattungen paläozoischer Rhynchonellacea (Brachiopoda). Senck. leth., 45, p. 505–506.

–, 1965. Neue Befunde an paläozoischen Rhynchonellacea (Brachiopoda). Senck. leth., 46, p. 1–25.

Schnur, J., 1853. Zusammenstellung und Beschreibung sämmtlicher im Uebergangsgebirge der Eifel vorkommenden Brachiopoden nebst Abbildungen derselben. Palaeontographica, 3, p. 169–247, Cassel.

Seilacher, A., 1967. Bathymetry of trace fossils. Marine Geology, 5, p. 413–428.

Shinn, E. A., 1968. Practical significance of birdseye structures in carbonate rocks. Journ. Sed. Petr., 38, p. 215–223.

Sitter, L. U. de, 1962. The structure of the southern slope of the Cantabrian Mountains. Leidse Geol. Med., 26, p. 255–264.

Sleumer, B. H. G., 1969. Devonian Stromatoporoids of the Cantabrian Mountains (Spain). Leidse Geol. Med., 44, p. 1–52.

Staalduinen, C. J. van, (in prep.). Geology of the area between the rivers Luna and Torio (southern Cantabrian Mountains, NW Spain). Leidse Geol. Med.

Steininger, J., 1853. Geognostische Beschreibung der Eifel. 143 p., Trier.

Struve, W., 1963. Das Korallen-Meer der Eifel vor 300 Millionen Jahren. Funde, Deutungen, Probleme. Natur u. Museum, 93/6, p. 237–276.

– & Mohanti, M., 1970. A Middle Devonian atrypid brachiopod fauna from the Cantabrian Mountains, northwestern Spain, and its stratigraphic significance. Leidse Geol. Med., 45, p. 155–166.

Swinchatt, J. P., 1967. Formation of large-scale cross-bedding in a carbonate unit. Sedimentology, 8, p. 93–120.

Tebutt, G. E., Conley, C. D., & Boyd, D. W., 1965. Lithogenesis of a distinctive carbonate rock fabric. Contrib. to Geol. Univ. of Wyoming, 4/1, p. 1–13.

Tiajeva, A. P., 1962. Brakhiopody srednedevonskikh otlojenii zapadnykh i tzentralnykh raionov zapadnogo sklona ioujnogo Ourala. In: Brakhiopody, ostrakody i spory srednego i verkhnego devona Bachkirii, Tiajeva, A. P., Rojdestvenskaia, A. A. & Tchbrikova, E. V. (eds.), Akademiya Nauk U.S.S.R., Bashkirskii Filial, Institut Gornago-Geologii, p. 5–165.

Walker, T. R., 1967. Formation of red beds in modern and ancient deserts. Geol. Soc. Amer. Bull., 78, p. 353–368.

Wallace, P., 1969. The sedimentology and palaeoecology of the Devonian of the Ferques inlier, northern France. Quart. Journ. Geol. Soc. London, 125, p. 83–124.

Webby, B. D., 1966. Middle-Upper Devonian palaeogeography of North Devon and West Somerset, England. Pal. geogr.- Pal. climat.–Pal. ecol., 2, p. 27–46.

Westbroek, P., 1967. Morphological observations with systematic implications on some Palaeozoic Rhynchonellida from Europe, with special emphasis on the Uncinulidae. Leidse Geol. Med., 41, p. 1–82.

Williams, A., Rowell, A. J., Ager, D. V., Elliot, G. F., Grant, R. E., Muir-Wood, H. M., & Stehli, F. G., 1965. Morphological terms applied to brachiopods. In: Treatise Invertebrate Palaeont., Moore, R. C. (ed.), Pt. H, vol. 2, Univ. Kansas Press, p. 139–155.

Wilson, J. L., 1969. Microfacies and sedimentary structures in 'deeper water' lime mudstones. In: Depositional environments in carbonate rocks – A symposium, Friedman, G. M. (ed.), Soc. Econ. Pal. Min., Spec. Publ. Nr. 14, p. 4–19.

Wolf, K. H., 1965. Littoral environment indicated by open-space structures in algal limestones. Pal. geogr.–Pal. climat.–Pal. ecol., 1, p. 183–225.