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POLYZYGIA GUERICH (OSTRACODA) IN THE DEVONIAN OF ASTURIAS AND LEON (SPAIN)

BY

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ABSTRACT

The Devonian ostracode genus *Polyzygia* Gürich has been defined anew and its systematical position has been revaluated. It is considered as a thlipsurid (bas-relief sculpture) metacope (tripartite hinge, contact groove). Eight species (one new, one with open nomenclature) and two subspecies are described, all from the Devonian of the central part of the Cantabrian Mountains, provinces of Asturias and León, Spain. The existence of pores and of a micro-scale reticulation is established. An opinion is given concerning the calcification of the valves, and the known geographical and stratigraphical distribution is discussed.

РЕЗЮМЕ

Девонический род *Polyzygia* Gürich снова определен и его систематическая позиция переоценена. Он принадлежит к семейству Thlipsuridae (барельеф-скульптура) и к подотряду Metacopa (трехчастный замок, контактная борозда). Описываются восемь видов (в том числе один новый и один с открытой номенклатурой) и два подвида. Они все урождены из Девона Кантабрских Гор, провинции Астурия и Леон, Испания. Определено существование пор и микро-размерной сетчатости. Выражается мнение о превращении в известь створок и наконец обсуждается известное географическое и стратиграфическое распространение.

SAMENVATTING

Het devonische genus *Polyzygia* Gürich is opnieuw gedefinieerd en zijn systematische positie herwaardeerd. Het hoort thuis in de Familia Thlipsuridae (bas-reliëf sculptuur) en de Subordo Metacopa (driedelig slot, contact groeve). Acht species worden beschreven (waarvan één nieuw en één met open nomenclatuur) en twee subspecies, alle uit het Devoon van het centrale gedeelte van het Cantabrisch Gebergte, provincies Asturië en León, Spanje. Het bestaan van poriën en een reticulatie van micro-afmeting is vastgesteld. De schrijver brengt een mening naar voren over de verkalking van de kleppen en tot slot wordt de tot nu toe bekende geografische en stratigrafische verspreiding besproken.

CONTENTS

CHAPTER I

INTRODUCTION

PRELIMINARY REMARKS

The present paper records part of a larger project which investigates the biostratigraphy of the Palaeozoic of the Cantabrian Mountains (northwestern Spain) under the general direction of Prof. Dr. A. Brouwer. Some aspects of this project have already been published: van Adrichem Boogaert (1967), Bless (1968), Brouwer (1964a, 1964b, 1967, 1968), Brouwer & van Ginkel (1964), Cramer (1964), van Ginkel (1965), de Groot (1963), Krans (1965), Rácz (1964), Sleumer (1969), Westbroek (1967) and Winkler Prins (1968). Work is still in progress on some other aspects: Devonian brachiopods, Bryozoa, conodonts, ostracodes and trilobites; and Carboniferous Algae and conodonts.

Up to now, apart from a short publication by Bless & Michel (1965), nothing has been published on ostracodes from the Devonian of the Cantabrian Mountains. The present paper only deals with *Polyzygia*.

The material concerning *Polyzygia* was selected

Author	Genus	Subfamily	Family	Superfamily	Suborder	Order
Gürich, 1896 p. 387	*Polyzygia*		LEPERDITIDAE			
Gürich, 1900 p. 331–338	*Beyrichia*		LEPERDITIDAE			
Sobolev, 1909 p. 394	*Polyzygia*		LEPERDITIDAE			
Sobolev, 1909 p. 394	*Beyrichia*		LEPERDITIDAE			
Matern, 1929 p. 40–41	*Tetrasulcata*		KLOEDENELLIDAE			
Matern, 1929 p. 42	*Dizygopleura*		KLOEDENELLIDAE			
Bassler & Kellett, 1934 p. 37, 435	*Polyzygia*	DREPANELLINAE	ZYGOBOLBIDAE	BEYRICHIACEA		
Bassler & Kellett, 1934 p. 208	*Beyrichia (? Octonaria)*		BEYRICHIIDAE	BEYRICHIACEA		
Swartz, 1936 p. 553	*Polyzygia*		? DREPANELLIDAE	BEYRICHIACEA		
Schmidt, 1941 p. 50	*Polyzygia*	BASSLERATIINAE	DREPANELLIDAE	BEYRICHIACEA		
Polenova, 1952 p. 76	*Polyzygia*		? DREPANELLIDAE			
Henningsmoen, 1953 p. 274	*Polyzygia*		Incertae sedis	BEYRICHIACEA	PALEOCOPA	
Přibyl, 1953 p. 240	*Polyzygia*	BASSLERATIINAE	DREPANELLIDAE	BEYRICHIACEA		
Krömmelbein, 1953 p. 54	*Polyzygia*	BASSLERATIINAE	DREPANELLIDAE	BEYRICHIACEA		
Adamczak, 1956 p. 36	*Polyzygia*	BASSLERATINAE	DREPANELLIDAE	BEYRICHIACEA		
Jaanusson, 1957 p. 336	*Polyzygia*	BASSLERATIINAE	BASSLERATIIDAE	EURYCHILINACEA	PALAEOCOPA	
Pokorný, 1958 p. 191, 195	*Polyzygia*		KLOEDENELLIDAE		? PLATYCOPA	? PODOCOPIDA
Zanina, Zaspelova & Polenova, 1960 p. 317	*Polyzygia*	NODELLINAE	DREPANELLIDAE	BEYRICHIACEA	BEYRICHIIDA	PALAEOCOPIDA
Hessland, 1961 p. Q196	*Polyzygia*		Incertae sedis		Incertae sedis	PALAEOCOPIDA
Le Fèvre, 1963 p. 148	*Polyzygia*		Incertae sedis		Incertae sedis	PALAEOCOPIDA
Becker, 1964 p. 51	*Polyzygia*	BASSLERATIINAE	BASSLERATIIDAE	EURYCHILINACEA	PALAEOCOPINA	PALAEOCOPIDA
Weyant, 1966 p. 121	*Polyzygia*	BASSLERATIINAE	BASSLERATIIDAE			
Zagora, 1968 p. 34	*Polyzygia*		Incertae sedis	Incertae sedis		PALAEOCOPIDA
Groos, 1969 p. 21	*Polyzygia*		BASSLERATIIDAE?			PALAEOCOPIDA
Lethiers, 1970 p. 71	*Polyzygia*		Incertae familiae		BEYRICHICOPINA	PALAEOCOPIDA
Adamczak, 1971a p. 794	*Polyzygia*		THLIPSURIDAE	THLIPSURACEA	METACOPA	PODOCOPIDA
Adamczak, 1971b p. 138–139	*Polyzygia*		THLIPSURIDAE	THLIPSURIDACEA	METACOPA	PODOCOPIDA
This paper	*Polyzygia*		THLIPSURIDAE	THLIPSURACEA	METACOPA	PODOCOPIDA

Fig. 1. Taxonomic place of *Polyzygia* Gürich in the course of time.

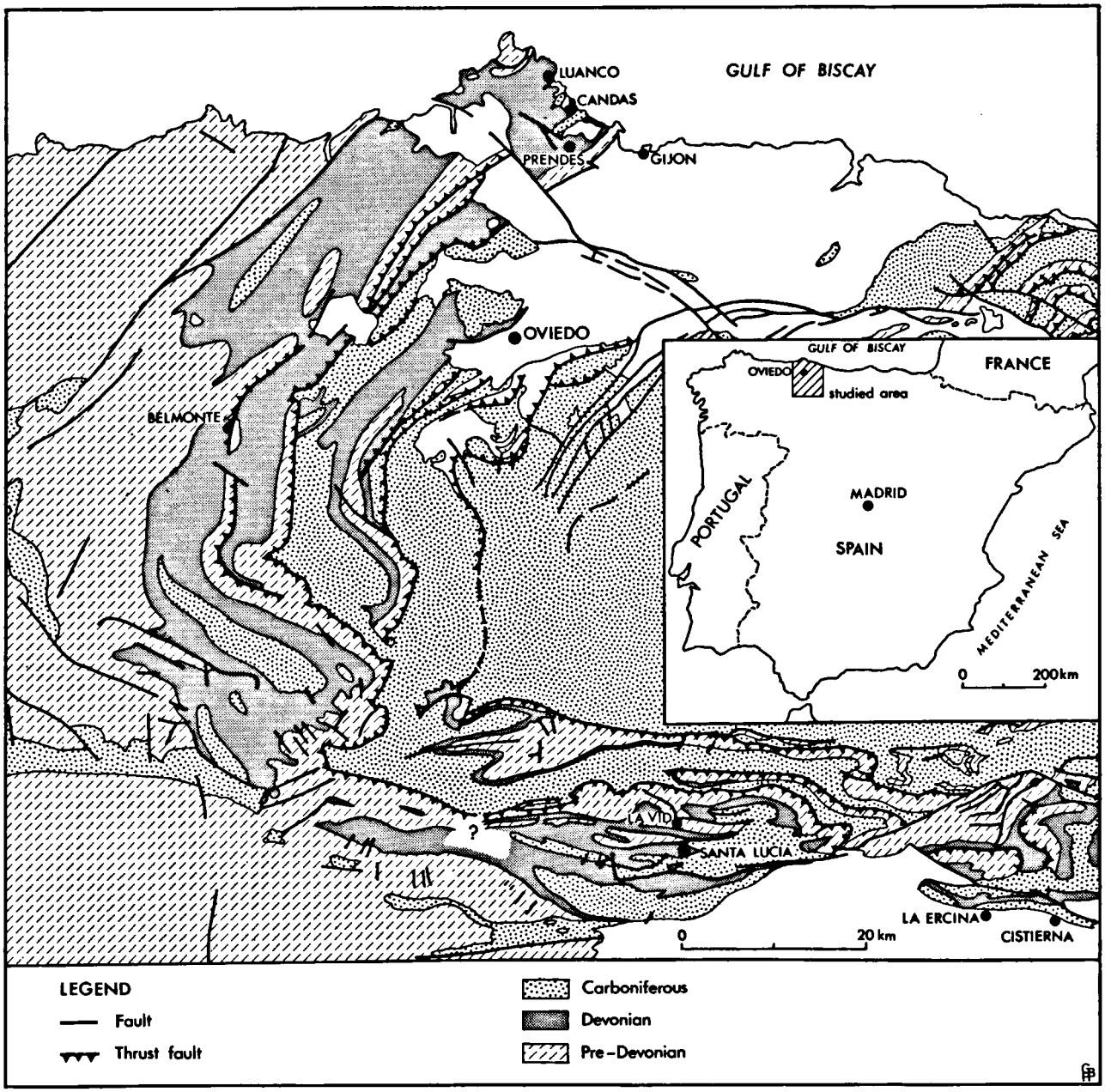


Fig. 2. Approximate distribution of Devonian sediments in the central part of the Cantabrian Mountains (after Parga-Pondal, 1967).

because at first sight this genus seemed promising for the study of regional correlations. It combined a short life-time and many species with a distribution all over Europe. To investigate the utility of *Polyzygia* for biostratigraphic purposes, its species were studied and their range was investigated. The studied specimens were deposited in the collections of the Department of Stratigraphy and Palaeontology, Geological and Mineralogical Institute, Leiden.

EARLIER RESEARCH ON *POLYZYGIA*

In the course of its 75 years of existence this genus has travelled a lot within the taxonomic ranks of the Ostracoda (Fig. 1).

Recent morphological investigations have contributed to a better knowledge of some important characteristics of the genus, especially the presence of a contact groove and the bas-relief sculpture. We propose the following systematics:

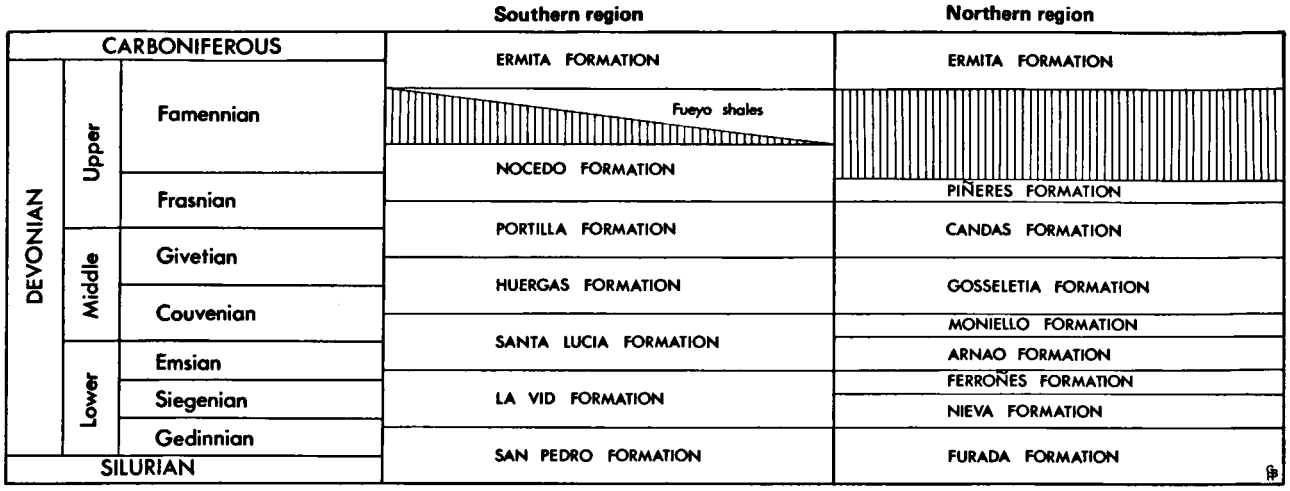


Fig. 3. Devonian stratigraphy in the central part of the Cantabrian Mountains.

Order : PODOCOPIDA Müller, 1894
Suborder : METACOPA Sylvester-Bradley, 1961
Family : THLIPSURIDAE Ulrich, 1894
Genus : *Polyzygia* Gürich, 1896

The following species and subspecies can be assigned to this genus:

symmetrica Gürich, 1896
trigonata (Gürich, 1900)
neodevonica (Matern, 1929)
beckmanni Krömmelbein, 1954
insculpta insculpta Becker, 1964
normannica Weyant, 1966
kroemmelbeini Le Fèvre & Weyant, 1966
insculpta beckeri Zagora, 1968
mirabilis Zagora, 1968
modesta Adamczak, 1971
vinea Michel, 1972

With exception of *P.mirabilis* and *P.modesta* all have been found in Devonian deposits of Asturias and León.

OUTLINE OF STRATIGRAPHY

The northern part of the Iberian peninsula consists of a long cordillera, the rocks of which vary in age, origin and composition. The Palaeozoic core of this mountain range is bounded on the East and South by Mesozoic and Cainozoic deposits; on the west side we find a gradual transition to the Cryptozoic and Variscan igneous and metamorphic rocks of Galicia (Parga-Pondal, 1967). An uplift during the Cainozoic produced the present topography (de Sitter & Boschma, 1966). A synopsis of the Variscan orogene and of its subunit, the Cantabrian Mountains, and their development has been presented by Matte (1968).

In the central region of the Cantabrian Mountains the Devonian deposits are exposed in the so-called Asturo-Leonese arch (Fig. 2). Barrois (1882) was the first to study the stratigraphy of the Palaeozoic of the northern part of the Cantabrian Mountains and his division into 'zônes' marked the starting point for the revised and more detailed stratigraphy in Asturias such as presented by Radig (1961), Llopis Lladó (1962) and Poll (1963).

In the southern region the stratigraphical division has been made by Comte (1959), who had already published preliminary notes between 1934 and 1938.

Stratigraphical data about the northern and southern borders of the Cantabrian Mountains and stratigraphical correlations of both regions can be found in van Adrichem Boogaert (1967), Brouwer (1968) and Llopis Lladó e.a. (1968). Fig. 3 is a generalized diagram which does not take into account that the boundaries of some formations may run diachronously.

LOCALITIES

The specimens of *Polyzygia* described in this paper have been obtained from seven localities, which are sketched briefly below. Most of these are shown graphically with

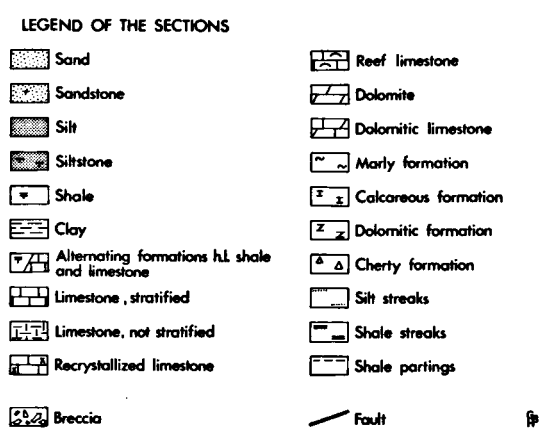


Fig. 4. Legend of the sections.

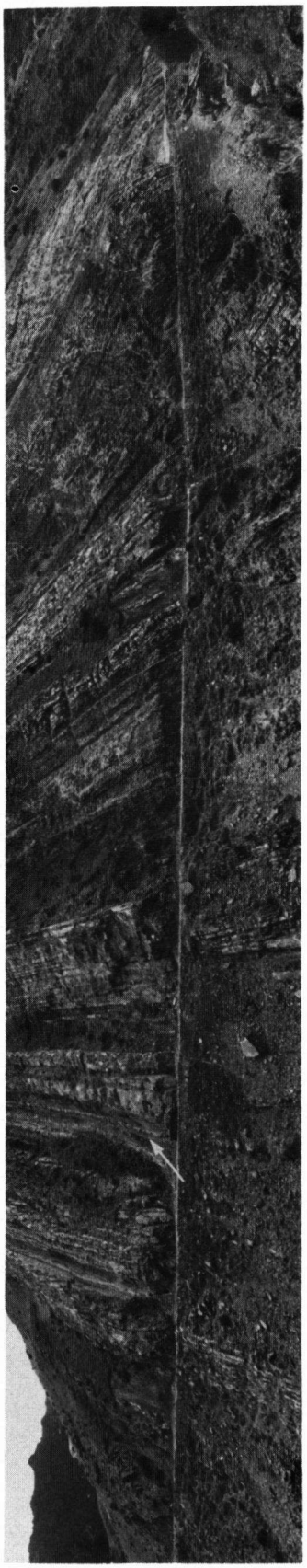


Fig. 5. Photograph of the locality La Vid, showing the lower part of the La Vid Formation. The arrow indicates the type location of *P. vinea.*

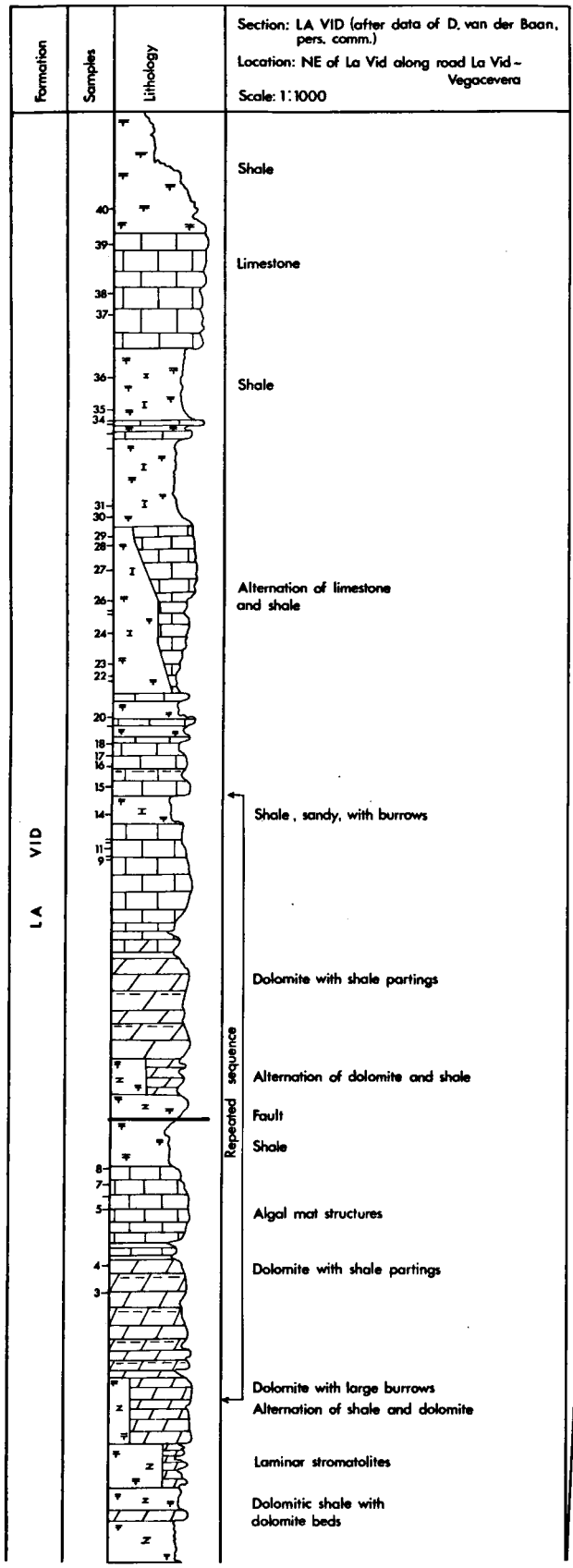
a stratigraphic colum and a topographic map, but in order to make the exact sampling level easily recognizable the locality La Vid is also shown by a photo which indicates the exact horizon.

Locality La Vid, La Vid Formation (Figs. 5–7). – This is the reference locality of the La Vid Formation used by the Geological Institute of Leiden. The type section itself is west of La Vid in the valley of the river Bernesga. Section circa 1 km east of the village of La Vid (province of León) in a road-cut along the La Vid to Vegacervera road. Brachiopods, Chitinozoa and conodonts indicate an Upper Siegenian age for the interval from which samples 11/16 and 11/17 are derived. Sample LV/6, kindly put at my disposal by Dr. H. A. van Adrichem Boogaert, also comes from the La Vid Formation. The occurrence in this sample of *Icriodus huddlei* indicates a Siegenian or Emsian age according to Carls & Gandl (1969), but unfortunately the exact sampling horizon and locality are unknown. The *Polyzygia* species encountered in the la Vid Formation (samples 11/16, 11/17) are *P. normannica, P. vinea, P.* sp. *A* and *P. beckmanni.*

Locality Llamoso, Ferroñes Formation (Fig. 9). – This exposure of limestones and marls of circa 12 m is situated in a road cut 500 m before reaching the village of Llamoso. This road to Llamoso is a crossroad that, between km 6 and 7, branches eastwards off the main road from Belmonte to Puerto de Somiedo (province of Asturias). Sample B–22 from the marls contains *P. kroemmelbeini*. Because he found no fossils, Poll (1963, p. 247) considered this exposure to be an equivalent of the lower member (sensu Radig, 1961) of the Candás Formation (Givetian). The presence of *Euryspirifer* aff. *arduennensis,* however, favours the supposition of an Upper Siegenian or Lower Emsian age.

Locality Santa Lucĭa, Santa Lucĭa Formation (Figs. 7, 10). – This section is situated 1 km west of the village of Santa Lucĭa (province of León), north of the main road from León to the Puerto de Pajares. Though not the type locality proper, which was defined by Comte (1959) (situated circa 250 m east of this section, immediately along the road), this section is better exposed. The top of the overturned sequence consists of a chamosite oolite, with abundant silicified ostracodes in places. According to de Coo (1969), who described the Santa Lucĭa Formation petrographically, this oolite must be included in the Santa Lucĭa Formation on petrographical grounds. The overlying Huergas Formation, however, also contains chamosite ooids in its basal part, though much less frequently and almost devoid of ostracodes. Samples from this oolite contain *P. symmetrica, P. insculpta beckeri, P. kroemmelbeini* and *P. beckmanni.*

Locality Prendes, Arnao Formation (Figs. 8, 14). – Along the main road Gijon to Aviles between km 79 and



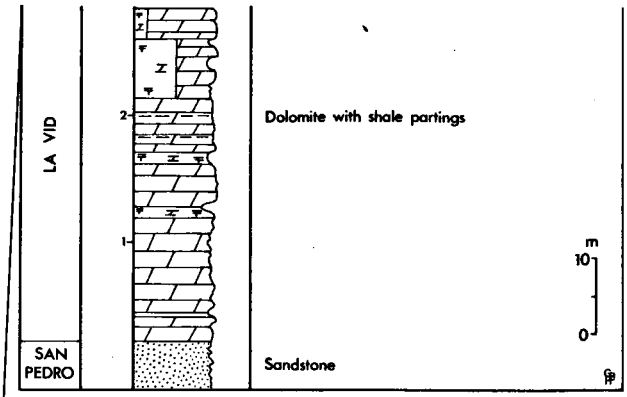


Fig. 6. Section La Vid.

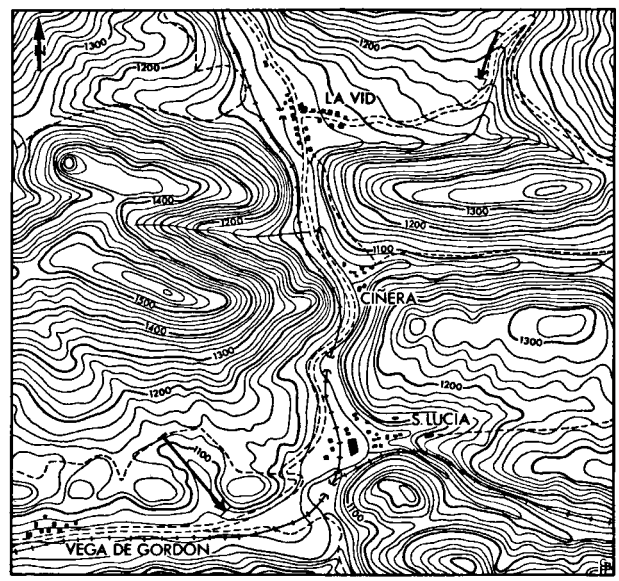


Fig. 7. Localities La Vid and Santa Lucía. Arrows indicate the youngest part of the section. 1:25,000.

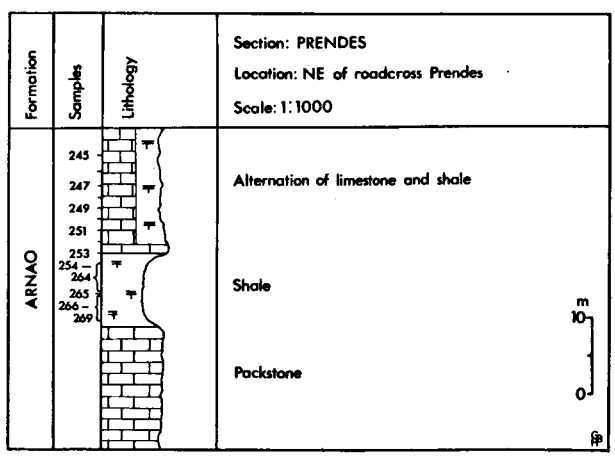


Fig. 8. Section Prendes.

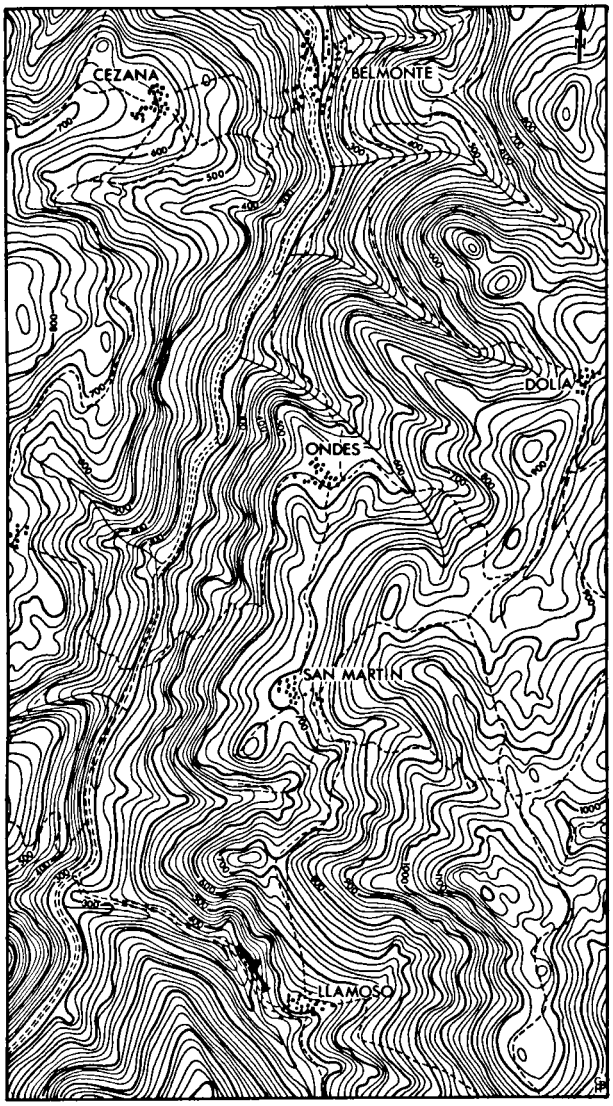
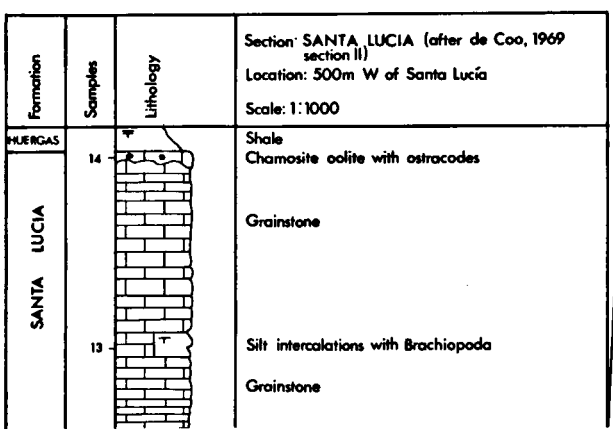


Fig. 9. Locality Llamoso. Arrow indicates the youngest part of the section. 1:25,000.



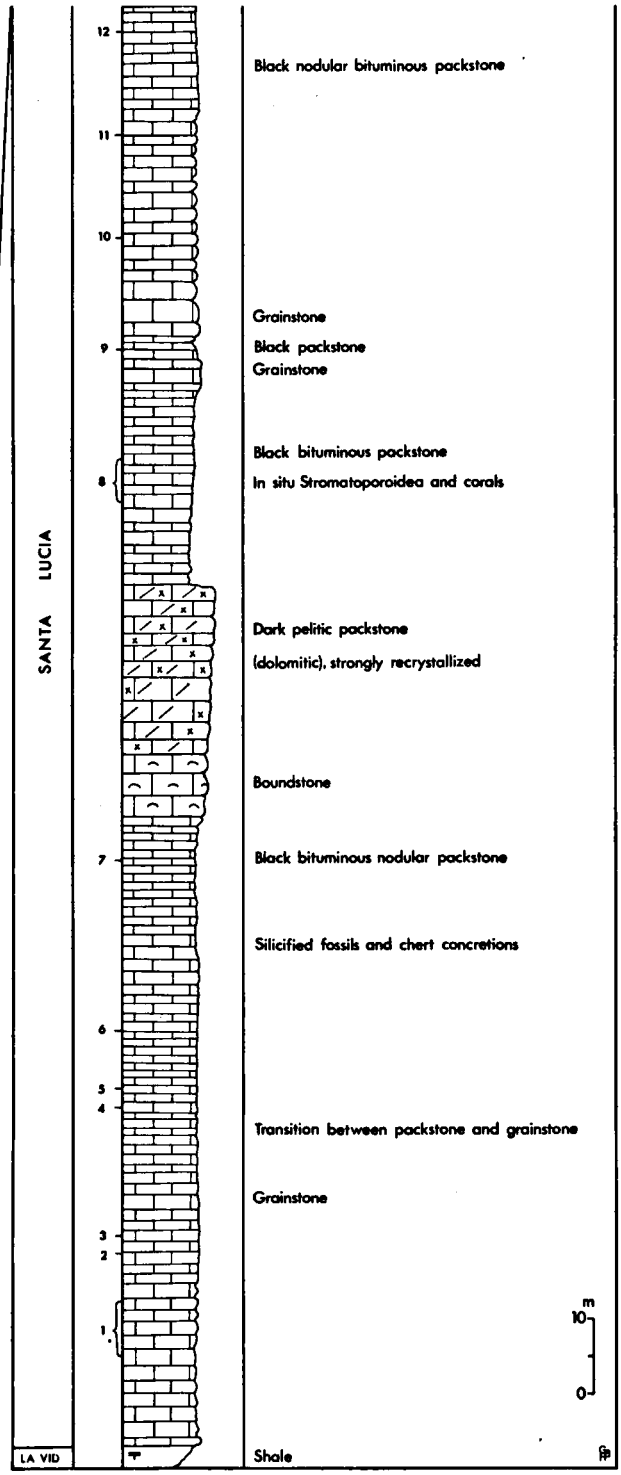


Fig. 10. Section Santa Lucía.

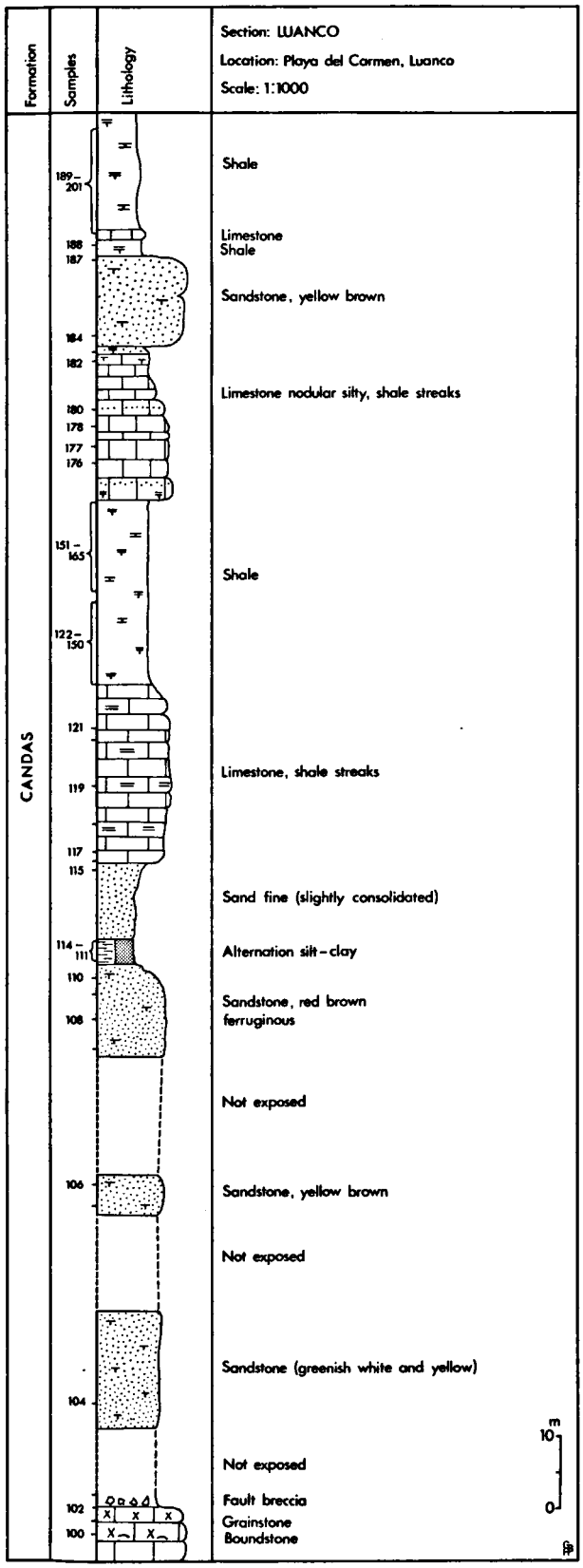


Fig. 11. Section Luanco.

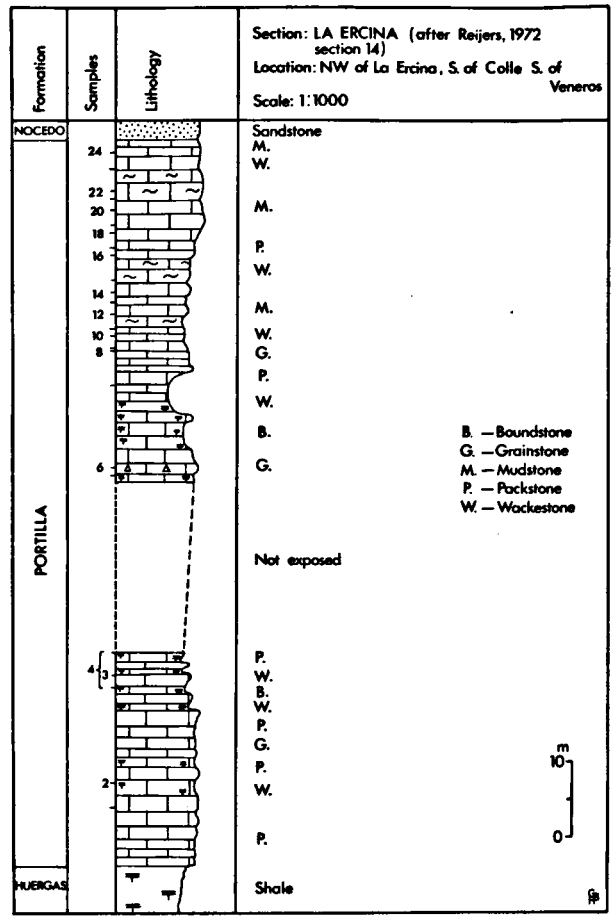


Fig. 12. Section La Ercina.

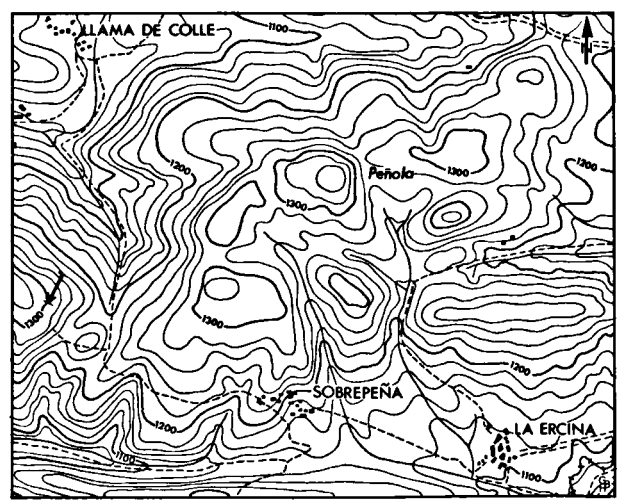


Fig. 13. Locality La Ercina. The arrow indicates the youngest part of the section. 1:25,000.

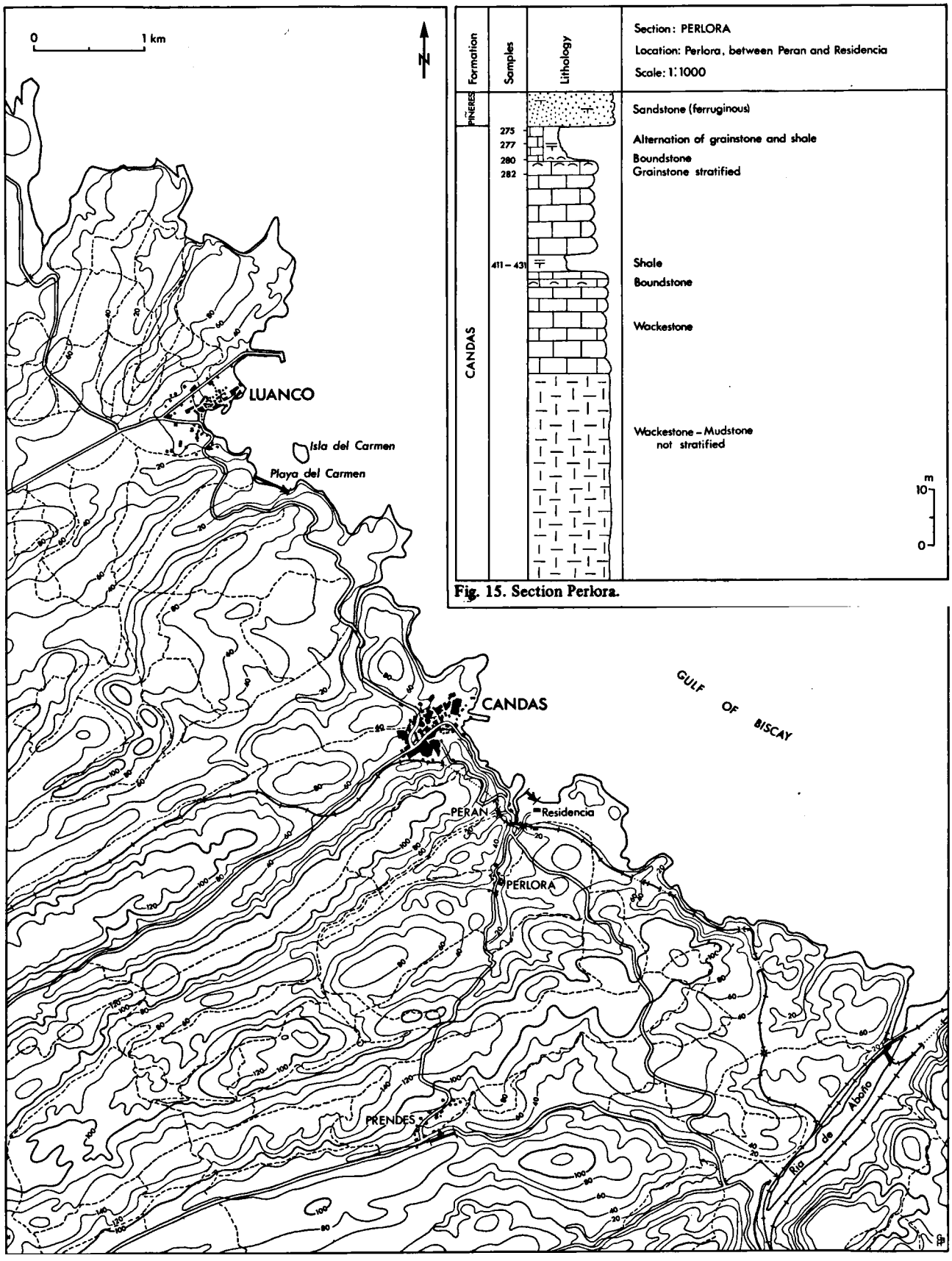


Fig. 15. Section Perlora.

Fig. 14. Localities Prendes, Luanco and Perlora. Arrows indicate the youngest part of the section. 1:25,000.

km 80, circa 100 m east of the crossroads in Prendes (province of Asturias), the road slope offers a sequence of shales and limestones. A complete stratigraphical description is being prepared by Julivert & Truyols (1972). The occurrence of *Spinella* cf. *incerta, Euryspirifer paradoxus, Adolfia cabedana* and *Euryspirifer intermedius* makes it probable that the sequence dates from the transition Emsian – Couvinian. Samples 264–265 contain *P. kroemmelbeini* (abundantly) and *P. insculpta beckeri* (rare).

Locality Luanco, Candás Formation (Figs. 11, 14). – The whole Candás Formation, though tectonically disturbed, is exposed on both sides of Luanco (province of Asturias). The section shown represents the interval exposed at the Playa del Carmen. A detailed description of this section can be found in Lopis Lladó & Valdés (1961). A revision of Llopis Lladó (1962) and of Llopis Lladó & Valdés (1961) can be found in Julivert & Truyols (1972). Samples 122–165 contain abundantly *P. neodevonica,* sometimes constituting up to 65 % of the total ostracode assemblage, *P. trigonata* (rare), *P. symmetrica* and *P. insculpta insculpta.* Sample 188 contains reworked conodonts (*Icriodus alternatus, Icriodus* sp., *Polygnathus foliata, Icriodus eslaensis*) which indicate an Upper Givetian or Lower Frasnian age. Haas (1970) attributed a Frasnian age to some trilobites from the upper part in this section.

Locality La Ercina, Portilla Formation (Figs. 12, 13). – This exposure is situated 4 km west north west of La Ercina (province of León). Though it is nearer to Colle and Veneros as the crow flies, we prefer to call this locality La Ercina, stressing the fact that it is much more easily accessible via La Ercina than via Colle or Veneros. The village of La Ercina is situated on a crossroad which branches southwards off the main road from La Robla to Cistierna. Passing westwards through Sobrepeña one comes onto a cart-track that takes one further west. Brachiopods, trilobites and conodonts indicate a Givetian – Frasnian age for the Portilla Formation exposed here. Struve & Mohanti (1970), basing their opinion on atrypids, advocate the view that the Portilla Formation, found in the Alba syncline some 50 km to the West, is of Eifelian – Givetian age, but records of other fossil groups from that region, such as conodonts and brachiopods, have not yet substantiated their opinion. Especially concerning sedimentology and environment more details can be found in Reijers (1972). Sample 16/22 contains *P. neodevonica* and *P. insculpta beckeri.*

Locality Perlora, Candás Formation (Figs. 14, 15). – Southeast of Candás (province of Asturias), at the sea side between Perán and Perlora, we find the type section of the Candás Formation, defined by Barrois (1882, zône de Calcaire de Candás avec *Spirifer verneuili*) and redescribed by Radig (1961). The stratigraphical column shown in the figure only represents the upper part of the section exposed between the entrance of the harbour of Perán and the Residencia of the Ciudad Residencial at Perlora. A detailed revision of the geology and stratigraphy of the Cabo Peñas area, such as published by Barrois (1882), Llopis Lladó (1962), Llopis Lladó e. a. (1968) and Radig (1961), can be found in Julivert & Truyols (1972). The samples 275–282 contain *P. neodevonica, P. trigonata* (rare) and *P. symmetrica. Cyrtospirifer* sp. and *Mucrospirifer bouchardi* indicate a Middle Frasnian age. Altevogt (1963) and Haas (1970) concluded to a Frasnian age for this part of the section.

PROCEDURES, TECHNIQUES AND TERMINOLOGY

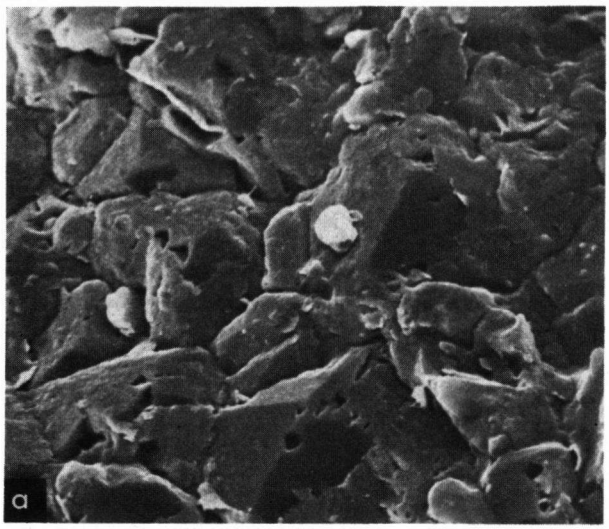
Samples. – The samples containing *Polyzygia* have been selected from samples collected during field work in the summers of 1969 and 1970 and are treated here out of their context.

Sample preparation. – Samples were soaked in a 15 % solution of hydrogen peroxide, sieved and dried; then the ostracodes were picked out. A few samples were treated with 50 % hydrofluoric acid, a treatment described by Sohn (1956). Hydrofluoric acid gives excellent results with samples that contain mostly ostracodes with thin and fragile valves. On the other hand, hydrofluoric acid has two disadvantages. In the first place it alters the micro-structure and ultra-structure of the valves. Secondly the treatment with hydrofluoric acid makes the ostracodes more brittle and fragile, so that it becomes impossible to clean them manually with a needle or mechanically with an ultrasonic vibrator.

Cleaning of the specimens. – This was done with an ultrasonic vibrator. Besides, some attempts were made to use the method described by Bassiouni (1969), but experiments of the author showed that this technique does serious damage to the specimens, especially if they are already, be it slightly, corroded.

Recently Sylvester-Bradley (1971) showed that ultrasonic cleaning may permanently and seriously damage the ultra-structure, even after only two (!) seconds. However, experiments on other ostracodes from the same samples only partly confirm the views expressed by Sylvester-Bradley. The recrystallization he postulated (p. 96) we consider highly improbable, since that would imply strong shearing forces. In our opinion this damage is due to an eroding effect (cf. Fig. 16a with Fig. 16b).

Photographs. – The scanning electron micrographs were made with an Exa camera with a Domiplan 2,8/50 mm lens (diaphragm set at 5,6), attached to the Cambridge Stereoscan scanning electron microscope (SEM). The photographs were taken with a Summar 24 mm lens with 37 cm bellows, attached to a Nikon camera body. The type of film used in the SEM was Kodak Panatomic-X (16 DIN/32 ASA), which combines an extremely fine grain with a moderate contrast. For normal photo-



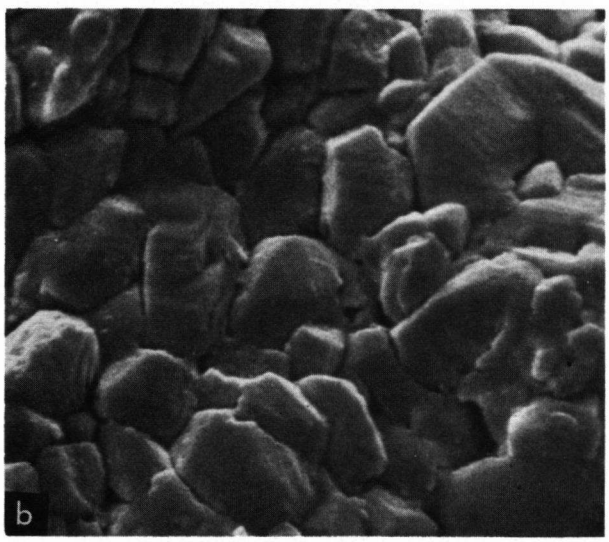


Fig. 16. The ultrastructure of the ventral region of a thlipsuride.
16a. Aspect after 2½ minutes of ultrasonic cleaning.
16b. Aspect after 10 minutes of ultrasonic cleaning.

graphy: Kodak Tri-X (27 DIN/400 ASA); otherwise the time of exposure would be too long.

Specimen preparation. – For normal photography the specimens were dyed with green washable ink and very thinly coated with ammonium-chloride. For use in the SEM the objects were mounted on specimen-stubs with double-sided adhesive tape or with a solution of collodium in amylacetate. Next they were twice coated while being rotated in a vacuum evaporator, first with carbon and then with gold. Both these coatings can be applied in only one coating cycle. Carbon evaporation gives optimal results with a vacuum of 10^{-2} to 10^{-3} torr, whereas the evaporation of the gold gives the best results in a high vacuum, 10^{-5} to 10^{-6} torr. By virtue of this procedure of double coating, the risk of a high electric charge developing in the specimen is considerably mitigated. We may also avoid the undesirable charging of the specimen (which could result in loss of detail in the scanning electron micrographs and serious damage to the specimens) by using a low acceleration voltage for the electron beam, e. g. 2 or 5 KV. With a low voltage, though, the maximum magnification is limited and the resolving power is smaller. One serious disadvantage of the gold coating is its fast deterioration under normal atmospheric conditions. Sylvester-Bradley (1971, p. 99) prefers aluminium. Its advantage, however, of being easily removable with alkali is partly cancelled by the danger of the specimen being etched while it is being immersed.

Magnification. – Of the magnification factors of the SEM in the Geological Institute in Leiden no verified standard curve exists. To test in a few cases the reliability of the indicated magnification numbers a copper grid such as used in transmission electron microscopy was mounted on a specimen stub and observed in the SEM.

Because the distance between the slits of the grid is known, the magnification could easily be calculated on the display screen; the result was compared with the magnification factor indicated by the SEM. Between both numbers differences existed from 3 to 20 %. A larger relief of the observed object combined with a tilt of the specimen stage also results in a deviation which should not be neglected (Boyde, 1970). For these two reasons we have omitted the often used scales and magnification ellipses on the scanning electron micrographs.

Cross sections. – Cross sections for observation in the scanning electron microscope were prepared as follows: Embedded in Araldite, ground to the desired level with frosted glass plates under a Wild M-5 microscope, etched with a saturated aqueous solution of EDTA for 10 to 30 seconds, and finally washed in water with a pH of 8 or 9; aqua destillata should not be used but after a check on the pH, because usually it has a pH of about 6, so it still has etching activity, be it small.

S-formula. – The sculpture of *Polyzygia* consists of a bas-relief pattern of five vertical elements and one horizontal element. These elements or sulci are numbered S_1, S_2, S_3, S_4 and S_5, symbols which refer to the sulci in such an order that S_1 stands for the one nearest to the front and S_5 stands for the one nearest to the rear; S_v refers to the horizontal furrow in the ventral part (S_{va} = anterior part of the S_v; S_{vp} = posterior part of the S_v).

These sulci are connected in a way that is characteristic for each species. Their location, outline and obliquity (defined as the degree of angular deflection from the height axis for the S_1 to S_5 and from the length axis for the S_v) may vary widely.

By means of dashes the S-formula indicates in a concise way how the sulci are connected. These dashes represent dorsal connections (S¯S) or ventral connections (S_S); moreover through this notation we can indicate whether the connection is deeply cut out (_), present(-) or but vaguely indicated(..).

Reticulation. – In this paper reticulation is defined as a net-like pattern on a surface. The meshes of this network are described as fossae and the intermediate vertical crests as muri (Sylvester-Bradley & Benson, 1971).

The present material displays two sizes of reticula. The larger reticulation has fossae which are visible with a normal light-microscope at low magnification (circa 50x). This reticulation is denominated the first-order reticulation. The other reticulation is evidently more tiny. The latter reticulation, the second-order reticulation, is usually not visible with the conventional light-microscope because of the small resolving power of that instrument.

For the meaning of other descriptive terms, the reader is referred to Kesling (1951), Moore (1961) and Sylvester-Bradley & Benson (1971).

ACKNOWLEDGEMENTS

To all those who have contributed to the completion of this publication I wish to express my gratitude. Only a few of them can be acknowledged here.

I am greatly indebted to Mr. N. O. Jørgensen, Geological and Mineralogical Institute at Copenhagen, who guided the author's first steps handling the scanning electron microscope. Most obliged I am to Dr. F. J. Adamczak, Geological Institute in Stockholm. Many of his suggestions had a deciding influence on my work.

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CHAPTER II

SYSTEMATIC DESCRIPTIONS

Subordo METACOPA Sylvester-Bradley, 1961

Diagnosis (after Adamczak, 1967). – Medium-sized ostracodes without a calcified inner lamella. The inner free margin is provided with stop ridges or with a contact groove. The hinge structure is tripartite or simplified. The muscle field consists of many scars.

Familia THLIPSURIDAE Ulrich, 1894

Diagnosis (modified after Krandiyevskij, 1968). – Metacopa with a carapace which has an elongated to subelliptical outline in lateral view; in dorsal and ventral view the outline is ovoid to subrectangular. The valves are of unequal size; the larger left valve overlaps the right valve along the free margin. The dorsal border is convex to straight; the ventral border is straight or possibly slightly convex or concave. The anterior and posterior borders are usually rounded more or less in the same way. In the posterior half the carapace is often thickened. The lateral surface is sculptured with lobi and sulci. Sometimes there are spines on the posterior half. The surface may be smooth, tuberculate or reticulated.

Genus *POLYZYGIA* Gürich, 1896

Diagnosis. – A medium-sized member of the Thlipsuridae characterized by the presence of a bas-relief pattern of five vertical elements and one horizontal element (whose interconnections are indicated by the S-formula*) and by its ornamentation with a first-order reticulation*.

Description. – In lateral view the outline is ovoid to elongatedly subrectangular; the outline in dorsal and ventral view is elliptical to trapezoid. The dorsal border is straight; the ventral border is either straight or to a slight extent convex or concave. The anterior border is generally well-rounded, sometimes slightly pointed. The posterior border is obtuse, roughly perpendicular to the ventral border. The anterior cardinal angle is usually less well defined than the posterior cardinal angle. The greatest height is situated in front of the centre of the valve (preplete). The contact margin at the inside of the left valve is provided with a groove, which centro-

* For the meaning of these terms see p. 217, 218.

ventrally displays a more or less discernable discontinuity. The contact margin of the right valve is provided with a contact ridge. Along the free margin there is usually a marginal ridge, which broadens along the anterior border and sometimes also along the posterior border. Generally a vertical posterior ledge is to be seen, roughly perpendicular to the ventral border.

The bas-relief pattern consists of five roughly vertical sulci and one horizontal sulcus; of the various connections between these, some occur much more frequently than others. Clearest of all is the never-lacking W- or U-shaped outer sulcus consisting of S_1_ S_v_ S_5. Nearly always there is a horseshoe-shaped sulcus consisting of S_2 $^-S_3$. The pattern of interconnection combined with the presence or absence of a first-order reticulation as ornamentation has specific significance. The sculpture displayed on the carapace of an adult specimen may or may not be manifest on the inside of the valves. Generally this manifestation is less clear, if it is there at all, in adult specimens than in juvenile specimens.

The hinge is tripartite. The left valve has a straight bar with distally an anterior and a posterior socket. The right valve has a straight groove which at the anterior and posterior ends has a tooth. The area where the adductor muscle was originally attached is not yet known of all species. Where observed the muscle scar is kidney-shaped or oval. Sometimes it is composed of many small scars. The muscle scar is always situated between S_2 and S_3, at their base. The surface of the species studied is smooth or ornamented with a characteristic second-order reticulation. In some species, besides this ornamentation, a first-order reticulation is to be found. The surface of the sulci, however, in all specimens studied, appeared to be lacking the second-order reticulation.

Ontogeny. – Unfortunately the Spanish material, with a few exceptions, does not contribute anything to this matter, since it is too poor to permit a thorough examination with regard to ontogenetic stages.

Variation. – Especially in outline the variation is enormous, from rectangular to triangular and ellipsoid. There are great differences in orientation, width, depth and obliquity of the sulci.

Dimorphism. – Unfortunately the Spanish material does not allow any contribution in this respect. For details see Adamczak (1956, 1971b).

Discussion. – Adamczak (1971a, p. 794) suggested that *Polyzygia* should be assigned to the Thlipsuridae, a view which the present author shares. The systematic position adopted is based on:

the typical outline, both in lateral and ventral/dorsal view,
the posterior thickening of the carapace,
the sculpture characteristically consisting of a bas-relief pattern,
the ontogenetic development of the sculpture,
the hinge,
and on the presence of a contact groove in the left valve with ventral (semi)discontinuity.

Remarks. – The second-order reticulation has also been observed on topotypic specimens of *P. symmetrica* (Pl. XII, 3a, 3b) from the Upper Eifelian of the Holy Cross Mountains (Poland), which were kindly put at my disposal by Dr. F. J. Adamczak.

My supposition that the sculpture consists of sulci and not of lobi, which is of some significance, is supported by observations on adult specimens of *P. insculpta insculpta* and juvenile specimens of other species. When seen in dorsal and ventral view the sculpture is evidently cut out in the surface.

Occurrence. – *Polyzygia* is limited to the Devonian. Geographically its occurrence has been reported previously from Algeria, France, Belgium, West Germany, East Germany, Poland and the Soviet Union, with a stratigraphical range of Siegenian to Frasnian.

Herewith its occurrence in Spain is also recorded from Siegenian to Frasnian.

Polyzygia kroemmelbeini Le Fèvre & Weyant, 1966
(Figs. 17–19; Pl. I, 1–5, Pl. II, 1–4, Pl. III, 1–6)

1966 *Polyzygia kroemmelbeini* Le Fèvre & Weyant sp. n. pro parte. – Weyant, p. 124–126, pl. III, fig. 4, 6 (non fig. 5=*P. normannica*), pl. V, fig. 3
1967 *Polyzygia kroemmelbeini* Le Fèvre & Weyant. – Gayet, p. 353
1967 *Polyzygia kroemmelbeini* Le Fèvre & Weyant. – Le Fèvre, p. 382–384
1971 *Polyzygia kroemmelbeini* Le Fèvre & Weyant. – Le Fèvre, p. 822, 825, 831
1971 *Polyzygia kroemmelbeini* Le Fèvre & Weyant. – Adamczak, p. 141–143, fig. 1e, 5, 12, pl. II, fig. 1–7.

Diagnosis. – A species of *Polyzygia* characterized by the shape of its bas-relief pattern (Fig. 17), which consists of one sulcus. S-formula: S_1_S_v_$S_5$$^-$$S_4$_$S_3$$^-$$S_2$.

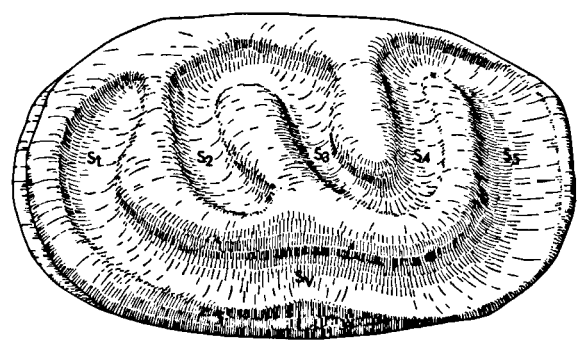


Fig. 17. *Polyzygia kroemmelbeini.* Left valve. The same specimen is shown on Pl. I, 1.

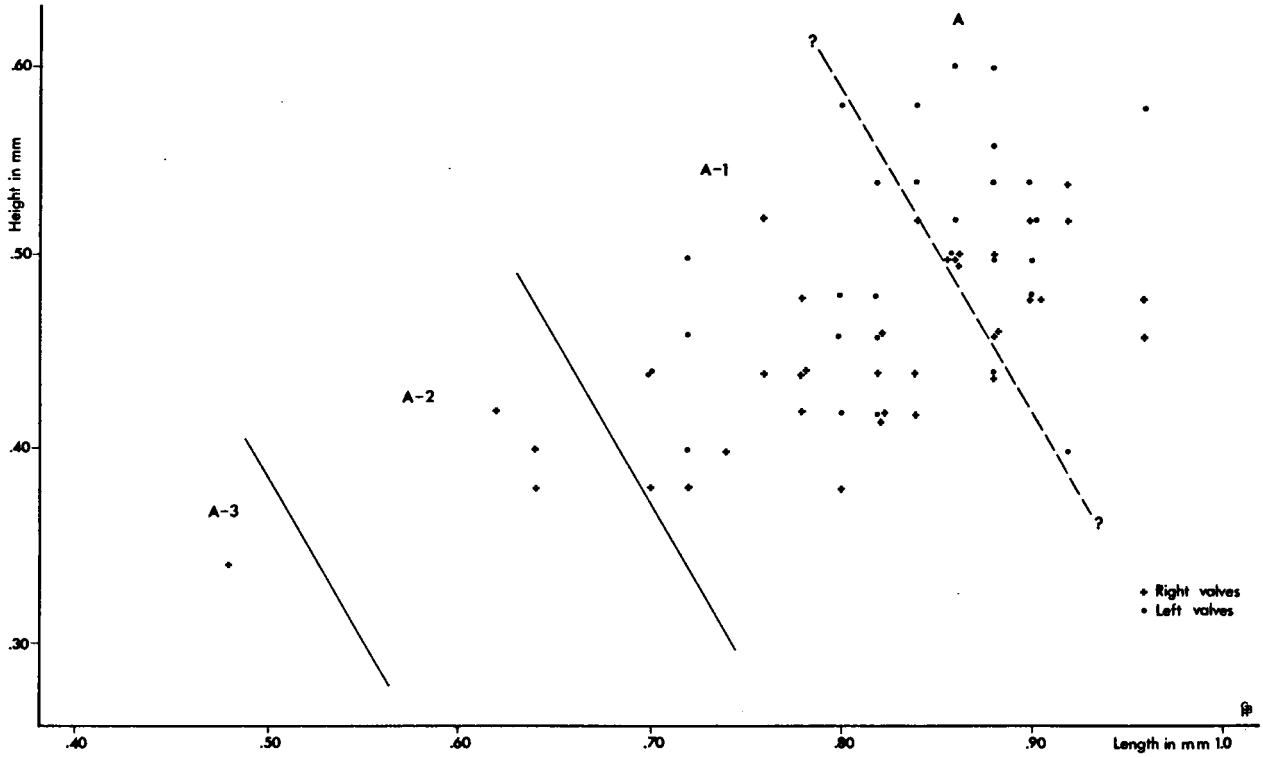


Fig. 18. *Polyzygia kroemmelbeini.* Length and height plots of 65 specimens from locality Prendes.

Material. – Over a hundred carapaces and valves.

Dimensions. – See length and height plots, Fig. 18.

Description. – The outline is subrounded and elongated in lateral view; in dorsal and ventral view the outline is almost trapezoid.

The dorsal border is slightly convex, the ventral border is straight to slightly concave. The anterior border is evenly rounded to slightly pointed, the posterior border is more blunt than the anterior border and roughly perpendicular to the ventral border.

The posterior cardinal angle is clearly visible as a distinct bend that marks the end of the hinge. The anterior cardinal angle is less well defined.

The anterior corner is situated at mid-height, the posterior corner above mid-height or occasionally, but rarely, at mid-height.

The contact groove in the left valve is not well developed; the right valve does have a clear contact ridge, which centroventrally is slightly concave. There is also a narrow marginal ridge bordering the free margin, which clearly broadens along the anterior border and rarely does so along the posterior border. This small marginal ridge may be straight or undulating.

In dorsal and ventral view the posterior border has the appearance of a slightly projecting ledge which may be sharp-edged.

In anterior and posterior view it is easily perceivable that there is a gap at both corners between the margins of the valves.

The sculpture consists of one sulcus with the S-formula $S_1\_S_v\_S_5{}^{-}S_4\_S_3{}^{-}S_2$. This sulcus is of varying smoothness; it may range all the way from being a distinctly cut out trench (in cross section U-shaped) to being a smoothly curved depression (in cross section shaped like a wide V). The sculpture pattern on the left valve is the mirror image of that on the right valve. The presence of the sulcus may manifest itself on the inside of the valve in the form of projections, but comparing Pl. I, 2 and Pl. III, 3, 6 one notes that this manifestation is not always equally clear; somestimes it is only vaguely indicated. Generally juvenile specimens show more relief on the inside than adult ones.

The hinge is straight. It occupies 5/9 of the maximum length of the valve. It is tripartite with an additional complication. On the right valve there is a wide groove with a narrow list in the middle; at both ends one tooth is present. The hinge elements of the left valve consist of a broad bar with in the middle a close groove and distally of this bar on its ventral side we make out elongated sockets, the exact delineation of which, unfortunately, cannot be ascertained through lack of well-preserved material. Looking at the outside one sees that the hinge of the right valve slightly overlaps the left valve. The hinge axis makes a conspicuous angle of approximately 15 degrees with the horizontal axis.

The muscle scar area is oval to kidney-shaped. The scar

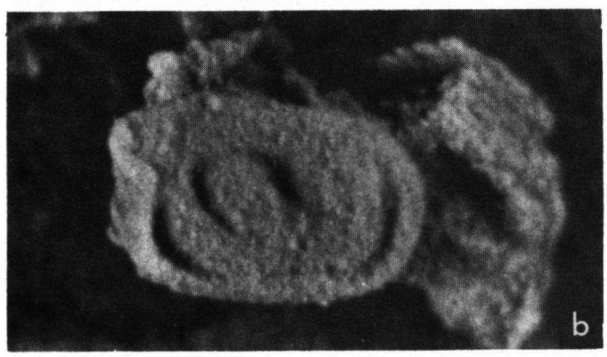


Fig. 19. *Polyzygia kroemmelbeini.* Locality Prendes.
19a. Left lateral view of A–1 specimen. STP/Mi. 72–33.
19b. Left lateral view of A–2 specimen. STP/Mi. 72–34.
19c. Right lateral view of A–3 specimen. STP/Mi. 72–35

is situated in the central area of the valve at the base of the S_2–S_3 part of the sculpture. It may often interfere in the pattern of ornamentation, its presence being manifest on the outside of the valve (Pl. II, 2).

The surface of the valve either is smooth or may display a second-order reticulation consisting of elongated laterally compressed fossae. The anterior and posterior corners may show the same elongated fossae, but these fossae in some instances are polygonal or even hexagonal.

Pores have been observed only once, on the surface of the marginal ridge (Pl. II, 4b, 4c).

Ontogeny. – Fig. 18 shows that there are several instars in the populations studied. The author believes that four instars are represented. In addition to the normal changes in size during the ontogenetic development, some morphological changes were observed to have occurred (Fig. 19).

In the A-1 instar the valves are essentially like those of the adult specimens. The S_v differs, being narrower and less deep, also the S_4, which is only superficially visible, and finally the connection between the S_3 and the S_4, which is scarcely developed at all. Furthermore the central area is slightly depressed; this is probably the result of muscle pull.

In the A-2 instar we find a more 'thickset' outline than in an adult specimen. The S_4 is only vaguely indicated or not present at all. Of the S_v only the anterior and posterior parts are developed; in the centre we see but a faint vestige of it. The connection between the S_2 and the S_3 is narrow and superficial. A very slight depression indicates the muscle attachment area.

In the A-3 instar we have an approximately ovoid outline which is truncated on the posterior side. The sculpture is not essentially different from that on the A-2, only less distinctly chiselled out. The place where the muscle was attached is indicated, just as in the other instars, by a slight depression, but in this instar it is situated in the postero-central area.

Variation. – For size variation see Fig. 18. The profile and the obliquity of the sulci may vary notably, especially in the S_5 and the location of the S_v. The anterior and posterior borders show variation in outline.

Discussion. – *P. kroemmelbeini* is easily distinguishable by its typical sculpture of one sulcus. *P. vinea* has a roughly similar shaped sulcus, though less prominently chiselled, but *P. vinea* displays a characteristic first-order reticulation which *P. kroemmelbeini* lacks.

Remarks. – The specimen shown by Weyant (1966) on Pl. III, fig. 5 is identified as *P. normannica*. No ventral connection is present between S_3 and S_4; the lobe which remains between S_4, S_5 and S_{vp} is well-rounded, instead of narrow and elongated. The lack of a reticulation on the latter area may be due to preservation.

Occurrence. – Dḳhissa Formation (Siegenian) and Teferguenit Formation (Lower Emsian), Beni Abbès, Saoura, Algeria; schistes à *Athyris undata* (Middle Siegenian), Sable, Laval, France; schistes à *Athyris undata* (Upper Siegenian), Baubigny, Normandy, France; basal part of the Ferroñes Formation (Lower Emsian), Llamoso, near Belmonte, Asturias, Spain; Arnao Formation (transition Emsian – Couvinian), Prendes, Asturias, Spain; top of the Santa Lucía Formation (Lower Couvinian), Santa Lucía, León, Spain; Grzegorzowice beds (Lower Eifelian), Holy Cross Mountains, Poland.

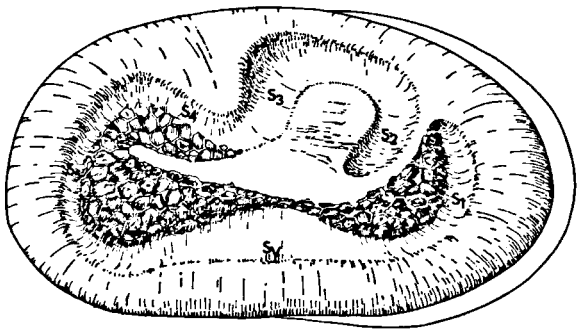


Fig. 20. *Polyzygia vinea.* Right valve. The same specimen is shown on Pl. IV, 3.

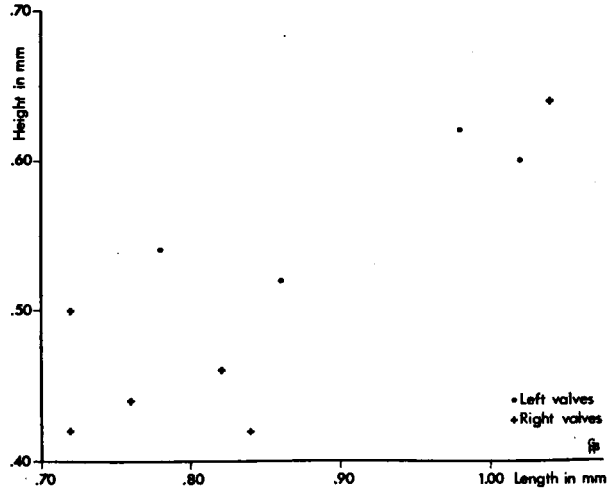


Fig. 21. *Polyzygia vinea.* Length and height plots of 10 specimens from locality La Vid.

Polyzygia vinea Michel sp. n.
(Figs. 20, 21; Pl. IV, 1–3, Pl. V, 1, 2)

1966 *Polyzygia* sp. *B* sp. n. Weyant. – Weyant, p. 127–128, pl. III, fig. 9, 10; pl. V, fig. 4.

Derivatio nominis. – Provenance from La Vid (Spain). La Vid is probably derived from Latin 'vitis', which means vine and thence also vineyard. The adjective 'vineus' has been formed from Latin 'vinea', vineyard.

Holotype. – A carapace STP/Mi. 72–10; its right valve is represented on Pl. IV, 3a–3e and on Pl. V, 1; the left valve is too encrusted with sediment to be cleaned.

Paratype. – A broken left valve STP/Mi. 72–8, represented on Pl. IV, 1 and Pl. V, 2.

Locus typicus. – La Vid, province of León, Spain. See Fig. 5 and 7.

Stratum typicum. – La Vid Formation, limestone member, Upper Siegenian, (Fig. 5).

Material. – Twelve valves and one carapace.

Diagnosis. – A species of *Polyzygia* characterized by its bas-relief pattern (Fig. 20), which consists of one sulcus. S-formula: $S_1\_S_v\_S_5{}^-S_4\_S_3{}^-S_2$. There is an ornamentation, which consists of a first-order reticulation, in the area enclosed by S_2, S_1, S_v, S_5 and S_4.

Dimensions. – See length and height plots in Fig. 21.

Description. – The outline is ovoid in lateral view; in dorsal and ventral view the outline is rectangular with rounded corners.

The dorsal border is straight to slightly convex, the ventral border is slightly concave. The anterior border is evenly rounded to slightly asymmetrically pointed, the posterior border is more blunt than the anterior border and roughly perpendicular to the ventral border.

The posterior cardinal angle is better defined than the anterior cardinal angle.

The anterior corner is situated at mid-height, the posterior corner either at mid-height or slightly above mid-height.

The contact margin was unobservable because of a sediment layer. A marginal ridge has been established along the anterior border.

The posterior part of the valve, in ventral view, may have a sharp to very sharp ledge, especially in immature specimens.

The sculpture consists of one sulcus with an S-formula: $S_1\_S_v\_S_5{}^-S_4\_S_3{}^-S_2$. The S_v may display a strong up-and-down curve in its central part.

Observations on the hinge were only possible with one damaged right valve. There seemed to be a groove in the hinge area.

A muscle scar was not observable.

The ornamentation of *P. vinea* is twofold. A first-order reticulation of polygonal fossae is to be found in the area enclosed by S_2, S_1, S_v, S_5 and S_4. This reticulation may sometimes cover the whole sulcus; in some instances it may be discontinuous in the centre, thus forming two separate triangular areas. Also there is a second-order reticulation which at first sight seems to be a striation covering the whole carapace but which at closer examination turns out to be a real reticulation consisting of extremely elongated fossae. These fossae become better discernible near the ends, where they also lose their extremely elongated appearance; on the posterior border they are polygonal.

Pores were observed in the fossae of the first-order reticulation and between these fossae on the muri.

Ontogeny. – The lack of well-preserved immature specimens precluded the possibility of ontogenetic observations.

Variation. – The area of the first-order reticulation may

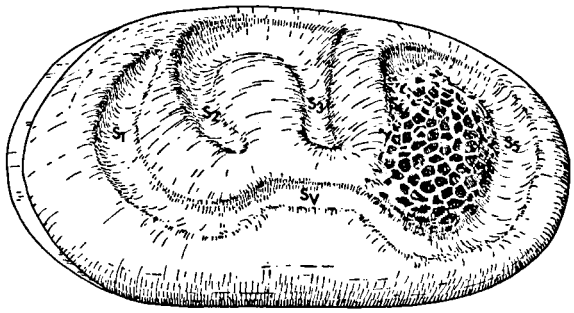


Fig. 22. *Polyzygia normannica.* Left valve. The same specimen is shown on Pl. VI, 4.

vary in its extension and in its tendency to be narrower or even interrupted in the centre. There is also variation in the outline and in the location of the sulcus.

Discussion. – Though as yet the hinge, the muscle scar and the contact margin are not known, the characteristic sculpture and accompanying first-order reticulation justify the assignment of this species to *Polyzygia*. Moreover, these diagnostic characteristics are of such a nature that they clearly distinguish it from other species. *P. kroemmelbeini* does have the same S-formula, but it does not have the first-order reticulation.

Remarks. – Weyant (1966) mentions the presence of a postero-dorsal 'ear' as a diagnostic characteristic. However, we seldom find this feature in the material offered here, moreover it is not restricted to *P. vinea*; it may occur in other species of *Polyzygia* particularly in immature instars.

Occurrence. – La Vid Formation (Upper Siegenian), La Vid, province of León, Spain; schistes à *Athyris undata* (Upper Siegenian), Baubigny, Normandy, France.

Polyzygia normannica Weyant, 1966
(Figs. 22–24, Pl. VI, 1–4)

1966 *Polyzygia normannica* sp. n. Weyant. – Weyant, p. 122–124, pl. III, fig. 1–3, 7, pl. V, fig. 1,2
1966 *Polyzygia kroemmelbeini* Le Fèvre & Weyant pro parte. – Weyant, pl. III, fig. 5a, b (non pl. III, fig. 4, 6, pl. V, fig. 3 = *P. kroemmelbeini*). Syn. nov.
1971 *Polyzygia normannica* Weyant. – Adamczak, fig. 11 pro parte (non specimens from Thuringia).

Diagnosis. – A species of *Polyzygia* characterized by the shape of its bas-relief pattern (Fig. 22), which consists of two sulci, a horseshoe-shaped one in the centre with an S-formula $S_2{}^{-}S_3$, which is surrounded by the other one, a sulcus shaped like a wide W with at the posterior end a curl that loops down inward. S-formula of the latter sulcus: $S_1\_S_v\_S_5{}^{-}S_4$. The area between S_{vp}, S_5 and S_4 is ornamented with a first-order reticulation.

Material. – Eleven right valves and six left valves.

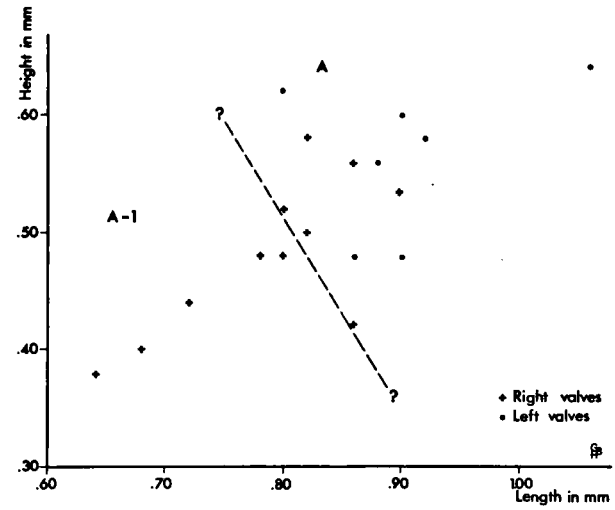


Fig. 23. *Polyzygia normannica.* Length and height plots of 17 specimens from locality La Vid.

Dimensions. – See length and height plots, Fig. 23.

Description. – The outline is ellipsoid to ovoid in lateral view, in dorsal and ventral view the outline is rectangular with rounded ends.

The dorsal border is straight to slightly convex, the ventral border is straight to slightly concave. The anterior border is evenly rounded, the posterior border is more blunt.

The posterior cardinal angle is usually hardly discernable. The anterior cardinal angle, which is not always clearly defined, marks the anterior limit of the hinge.

The greatest height is situated before mid-length.

The anterior corner is situated at mid-height, the posterior corner below mid-height in some specimens and above it in other ones.

The contact margin was not observable in the material at hand. Probably there is a narrow marginal ridge along the whole free margin, its presence was established along the anterior border, where it clearly broadens.

The posterior border has the appearance of a slightly projecting ledge, which may have a sharp edge.

The sculpture consists of two sulci, one inside the other. The central horseshoe-shaped sulcus consists of S_2 dorsally connected with S_3 and is surrounded by the outer W-shaped one that has the S-formula: $S_1\_S_v\_S_5{}^{-}S_4$. The S_4 fades out in the ventral direction. In the centroventral area the S_v shows a typical up-and-down curve.

The muscle scar and the hinge were not observable in the available material.

One always finds a first-order reticulation of polygonal to hexagonal fossae in the area between S_4, S_5 and S_{vp}; in one immature specimen it was also observed in the triangular area between S_2, S_1 and S_{va}, but only at the ventral side. The whole surface except that of the sulci is covered with a second-order reticulation of elongated fossae.

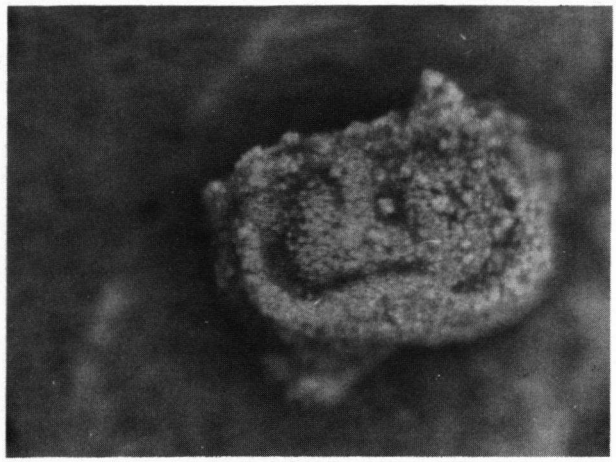


Fig. 24. *Polyzygia normannica.* Locality La Vid. Right lateral view of immature specimen. STP/Mi. 72–36.

Ontogeny. – In Fig. 23 one sees that two instars were found in the samples studied. The poor preservation of the material entails that only minor comments can be given on the ontogenetic development.

The features of the A-1 (Fig. 24) are essentially the same as in the adult specimens. It is smaller, the S_v is narrower and less deep and tends to be interrupted in the antero-ventral part, the S_4 is shorter and less deep.

Variation. – The outline of the carapace may vary, as well as the location, obliquity and the shape of the sculpture, particularly the S_4 and the distribution of the first-order reticulation.

Discussion. – Though the typical contact groove, the hinge and the muscle scar are still unknown, there is no doubt as to the assignment of this species to *Polyzygia*; the sculpture, the first-order and the second-order reticulation are too typical to be neglected. Though Weyant (1966), as a diagnostic feature, stated that the first-order reticulation also occurs on other parts of the valve (in casu on the 'L_1' and 'L_2'), this was not supported by observations on adult specimens from Spain.

Remarks. – It is notable that the juvenile specimens of *P.normannica* in Weyant's material show a relief which is much more pronounced than that of the adult specimens (see Weyant, 1966, p. 123). The specimen identified by Weyant (op. cit., pl. III, fig. 5) as *P. kroemmelbeini* in reality is *P. normannica*. There is no ventral connection between S_3 and S_4 and the area between S_4, S_5 and S_{VD} is not narrow and elongated as in *P. kroemmelbeini*, but well-rounded.

Occurrence. – Schistes à *Athyris undata* (Upper Siegenian), Baubigny, Normandy, France; La Vid Formation (Upper Siegenian), La Vid, province of León, Spain.

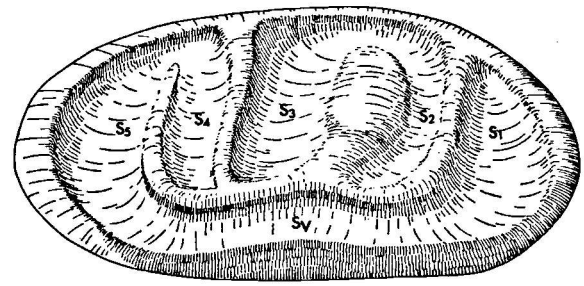


Fig. 25. *Polyzygia* sp. *A*. Right valve. The same specimen is shown on Pl. V, 4.

Polyzygia sp. *A* Weyant, 1966
(Fig. 25; Pl. V, 3, 4)

1966 *Polyzygia* sp. *A* sp. n. Weyant. – Weyant, p. 126–127, pl. III, fig. 8, pl. V, fig. 5
1966 *Polyzygia* sp. *A* Weyant. – Groos, p. 22, pl. 18, fig. 19.

Diagnosis. – A species of *Polyzygia* characterized by its bas-relief pattern of two sulci (Fig. 25). S-formulas: $S_2{-}S_3$ and $S_1\_S_v\_S_5{-}S_4$.

Material. – Two right valves, one left valve and one half external mould of a left valve.

Dimensions. – RV L: .69 mm; H: .38 mm
RV L: 1.04 mm; H: .71 mm
LV L: .90 mm; H: .63 mm

Description. – The outline is elongated ellipsoid in lateral view. The dorsal border is straight to slightly convex, the ventral border is straight to slightly concave. The anterior border is well-rounded, slightly asymmetrical; the posterior border is more blunt than the anterior border.

The anterior cardinal angle is better defined than the posterior cardinal angle.

The anterior corner is situated below mid-height, the posterior corner above mid-height.

The contact area was not observed. There is a narrow marginal ridge along the whole free margin, which broadens along the anterior border.

The posterior border has the appearance of a ledge with a sharp edge.

The sculpture consists of two sulci, one inside the other. The outer W-shaped sulcus has the S-formula: $S_1\_S_v\_S_5{-}S_4$. Only narrow ridges remain between the sulci. The inner horseshoe-shaped sulcus consists of $S_2{-}S_3$; the enclosed node has a roughly straight posterior side and a strongly curved anterior side. The posterior limit of the S_3 is straight.

Hinge, pores and muscle scar were not observed.

The surface does not seem to be ornamented.

Ontogeny. – No well-preserved juvenile specimens were found.

Variation. – Variable are the prominence and obliquity of the sulci and the shape of the remaining lobus between S_2 and S_3.

Discussion. – The sculpture pattern resembles that of *P. normannica*, but there are significant differences. Firstly, *P. normannica* has an unmistakable first-order reticulation, secondly, the S_4 of *P. normannica* fades out when approaching the ventral sulcus, and thirdly and lastly, the remaining lobus between S_{vp}, S_5 and S_4 is clearly rounded in *P. normannica* and it is a narrow ridge in *P.* sp. *A*. A close resemblance also exists with *P. trigonata*. In the latter the outline is more triangular; the ventral connection between S_2 and S_3 is better developed and the remaining ridge between S_4, S_5 and S_{vp} is triangular instead of narrow.

Remarks. – The material now available does not justify a formal name.

Occurrence. – Schistes à *Athyris undata* (Upper Siegenian), Baubigny, Normandy, France; La Vid Formation (Upper Siegenian), La Vid, province of León, Spain; La Vid Formation (Siegenian – Emsian?), locality unknown, province of León, Spain; Hobräcker Schichten (Lower Eifelian), Rhenish Slate Mountains, W. Germany.

Polyzygia beckmanni Krömmelbein, 1954
(Fig. 26; Pl. VII, 1–6, Pl. VIII, 1–4, Pl. IX, 1, 2, Pl. XV, 1)

1954 *Polyzygia beckmanni* sp. n. Krömmelbein. – Krömmelbein, p. 253–255, pl. 2, fig. 7a–b, 8a–c, 9
1962 *Polyzygia beckmanni* Krömmelbein. – Arbeitskreis Deutscher Mikropaläont., pl. 3 (top)
1964 *Polyzygia beckmanni* Krömmelbein. – Le Maître & Magne, p. 130
1968 *Polyzygia beckmanni* Krömmelbein. – Lecompte, p. 43, t. XVII
1968 *Polyzygia beckmanni antecedens* ssp. n. Zagora. – Zagora, p. 34–35, pl. 7, fig. 6, 9–13
1968 *Polyzygia beckmanni antecedens* Zagora. – Zagora & Zagora, t. 1
1969 *Polyzygia beckmanni antecedens* Zagora. – Groos, p. 23, pl. 4, fig. 8
1970 *Polyzygia beckmanni* Krömmelbein. – Lethiers, p. 71, pl. VI, fig. 5, 6
1970 *Polyzygia beckmanni antecedens* Zagora. – Jordan, p. 20, fig. 5, p. 22, 23, tab. 2, fig. 7
1971 *Polyzygia beckmanni* Krömmelbein. – Adamczak, fig. 10, 11, p. 139.

Diagnosis. – A species of *Polyzygia* characterized by its bas-relief pattern and the accompanying first-order reticulation (Fig. 26). S-formula:
$S_3 \overline{\overline{\ }} S_2(\overline{\ }\overline{\ })S_1\_S_v\_S_5\overline{\ }S_4$.
The first-order reticulation is restricted to the areas enclosed by S_2, S_1 and S_{va} and by S_{vp}, S_5 and S_4, which areas may be connected to each other.

Material. – Two left valves (damaged) and eight external moulds of left valves (five) and right valves (three).

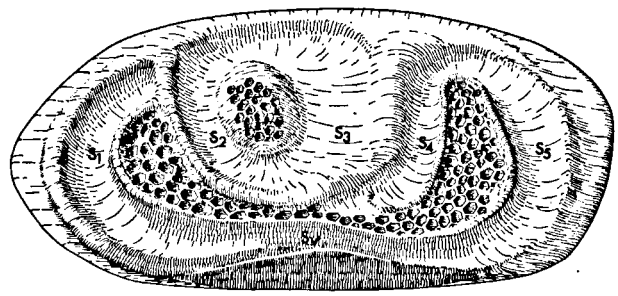


Fig. 26. *Polyzygia beckmanni.* Left valve. Reconstruction of the specimen shown on Pl. IX, 2.

Dimensions. – LV L: 1.04 mm; H: .38 mm
LV L: 1.06 mm.

Description. – The outline is elongated ellipsoid in lateral view, in dorsal and ventral view the outline is ovoid to elongated.

The dorsal border is straight and long, the ventral border slightly concave, but occasionally may be straight or even convex. The anterior and posterior borders are asymmetrically rounded; the posterior border is more blunt than the anterior border.

The cardinal angles may or may not be defined.

The anterior corner is situated below mid-height, the posterior corner above mid-height.

The contact region in the Spanish material was unobservable. There is a marginal ridge bordering the free margin, which clearly broadens along the anterior border. It may be smooth or undulating.

On the posterior part of the valve a roughly vertical ledge is developed.

The sculpture consists of a bas-relief pattern with an S-formula: $S_3 \overline{\overline{\ }} S_2(\overline{\ }\overline{\ })S_1\_S_v\_S_5\overline{\ }S_4$. The S_1 in cross section is shaped like a wide and asymmetrical V; its dorsal connection with the S_2 is sometimes altogether absent; when present it may be almost invisibly interrupted by a narrow and very faint ridge. The S_v often shows a well-rounded up-and-down curve in its central part. The ventral terminal point of the S_4 fades out but often is defined rather distinctly. The ventral connection between S_2 and S_3 is less deep and less pronounced than the dorsal connection, moreover it is traversed by a faint connecting ridge that runs between the central node and the reticulated area below the sulcus (Pl. IX, 1a).

Hinge, muscle scar and pores were not observed.

The ornamentation is twofold. There is a first-order reticulation of polygonal fossae on the central node and in the two areas enclosed by S_2, S_1 and S_{va} and by S_4, S_5 and S_{vp} respectively, which two areas are ventrally more or less evidently connected. A second-order reticulation of very elongated fossae has been observed in the centro-ventral area. The fossae of the first-order reticulation are hexagonal, polygonal or even subrounded.

Ontogeny. – Through lack of juvenile specimens there are no ontogenetic data available.

Variation. – The number and outline of the first-order fossae may vary, as well as the shape of the areas with a first-order reticulation. From one of the figures of Groos (1969, pl. 4, fig. 8) we may deduce that the very existence of the first-order reticulation may be subject to variation. Moreover there is a considerable variation in depth, distinctness, obliquity and shape of the sculpture.

Discussion. – To justify the denomination of *P. beckmanni antecedens* Zagora (1968) enumerated five criteria (op. cit., p. 34), all of which, judging from the material of the type locality of *P. beckmanni* at my disposition, are covered by the existing variation within *P. beckmanni.*

Remarks. – In order to ascertain the assignment of this species to *Polyzygia,* topotypic material was studied, especially the hinge and contact region because these were not mentioned by Krömmelbein (1954).

The hinge is long and tripartite. The right valve has a straight groove in the middle which distally peters out to be replaced by two terminal teeth. Correspondingly, we see two elongated sockets at the ends of the straight hinge bar the left valve has. It is as if these sockets change gradually into the bar, they seem to become the bar (Pl. XV, 1).

The muscle scar area is not at all distinctly delineated and contains many small scars. It is situated between the S_2 and S_3 at their base.

In the left valve there is a clearly visible contact groove with mid-ventrally a discontinuity that is not visible from all angles of vision. The right valve has a contact ridge, the centre of which is perfectly adapted to fit into the discontinuity of the left valve.

Occurrence. – La Vid Formation (Upper Siegenian), La Vid, province of León, Spain; La Vid Formation (Siegenian – Emsian?), locality unknown, province of León, top of the Santa Lucía Formation (Lower Couvinian), Santa Lucía, province of León, Spain; Tentaculitenschiefer (Lower Eifelian), Creunitz near Gräfenthal, E. Germany; Wissenbacher Schichten (Lower Eifelian), Meggen, W. Germany; Wiehler Schichten (Lower Eifelian), Fahrenberg, W. Germany; Schmallenberger Schichten (Lower Eifelian), Werpe, W. Germany; Refrather Schichten (Givetian), Paffrather Mulde, W. Germany; schistes de Beaulieu (Lower Frasnian), Bas-Boulonnais, France; assise de Frasnes (Middle Frasnian), Frasnes, Belgium.

Polyzygia insculpta Becker, 1964
(Figs. 27–30; Pl. X, 1, 2, Pl. XI, 1)

Synonymy. – See below under *P.insculpta insculpta.*

Diagnosis. – An ovoid species of *Polyzygia* characterized by its bas-relief pattern, which consists of three sulci, two roughly vertical ones, which sometimes are connected dorsally, enclosed by a sulcus shaped like a wide U. S-formulas: $S_1\_S_v\_S_5\bar{}S_4$ and $S_2(\bar{})S_3$.

Remarks. – At present a distinction between two subspecies is possible, based on the shape, depth and distinctness of their sculptural elements. Becker (1969, p. 259) proposes a third subspecies of *P.insculpta*, viz. *P. insculpta deinceps*. However, the specimen shown and its description do not conform to the diagnosis originally given for *P. insculpta*: 'Velarstruktur entlang dem Hinterrande zugeschärft und von der Carina getrennt durch eine schmale U-förmige Furche, die sich posterodorsal mit einem Bogen in den S_3 fortsetzt'. For further details the reader is referred to the discussion of *P. neodevonica* in this paper.

Polyzygia insculpta insculpta Becker, 1964
(Figs. 27, 28; Pl. X, 1, 2)

1964 *Polyzygia* ? *insculpta* sp. n. Becker. – Becker, p. 53–54, pl. 7, fig. 5, 6
1965 *Polyzygia* ? *insculpta* Becker. – Fuchs, p. 381
1968 *Polyzygia* ? *insculpta* Becker. – Bultynck, p. 429, tab. III
1968 *Polyzygia insculpta insculpta* Becker. – Zagora, p. 35
1969 *Polyzygia* ? *insculpta* Becker. – Winter, p. 346
1969 *Polyzygia insculpta* Becker. – Groos, p. 21, pl. 4, fig. 6
1969 *Polyzygia* ? *insculpta insculpta* Becker. – Becker, p. 259
1971 *Polyzygia* ? *insculpta insculpta* Becker. – Becker, p. 806, fig. 4, p. 806, 807
1971 *Polyzygia insculpta insculpta* Becker. – Adamczak, p. 144, 145, fig. 1A, 4, 6, 7, pl. I, fig. 1, pl. IV, fig. 1–10.

Diagnosis. – A subspecies of *P.insculpta* in which the S_2 and the S_3 dorsally never are connected. S-formula: $S_1\_S_v\_S_5\bar{}S_4$, S_2 and S_3; the S_1 is short (Fig. 27).

Material. – Two carapaces and two right valves (one of them juvenile).

Dimensions. – RV L: .62 mm; H: .34 mm
RV L: .94 mm; H: .52 mm
LV L: .84 mm; H: .56 mm
LV L: .94 mm; H: .54 mm
LV L: .86 mm; H: .48 mm

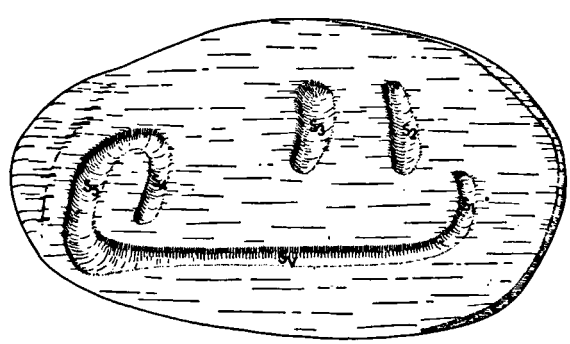


Fig. 27. *Polyzygia insculpta insculpta.* Right valve. The same specimen is shown on Pl. X, 1.

Description. – The outline is ovoid and quite 'thickset' in lateral view, in dorsal and ventral view the outline is elongated rhomboidal.

The dorsal border is slightly convex, the ventral border is straight. The anterior border is evenly rounded, slightly asymmetrical. The posterior border is pointed.

The cardinal angles are not well or not at all defined. The anterior corner is situated at mid-height, the posterior corner above mid-height.

The contact margin was unobservable in the available material.

There is a posterior ledge, roughly perpendicular to the ventral border.

In anterior and posterior view a gap may be visible between the margins of the valves.

The sculpture consists of three sulci, two short comma-shaped ones, surrounded by a larger one that is shaped like a wide U and has a rounded posterior curl that loops back inwards. The S-formula of the outer sulcus is $S_1\_S_v\_S_5\ ^-S_4$. The S_1 is short. It is clearly visible that the S_v makes an angle with the ventral border and then ascends to the front. The other two, the comma-shaped S_2 and S_3, are situated in the dorso-central half of the valve. The S_2 is a strongly curved thin comma; the S_3 tends to be vaguely elliptical, with a convex posterior side and an anterior side that tends to be also convex.

Observations on the hinge were not possible in the Spanish material. According to Becker (1969, non 1964) and Adamczak (1971b) the hinge of *P. insculpta insculpta* is tripartite. The left valve has two elongated sockets with a straight bar between them; the right valve has a straight groove between two elongated teeth.

The surface is smooth, without any ornamentation.

Muscle scar and pores were not observed.

Ontogeny. – One right valve has been found of a juvenile specimen (Fig. 28). The outline of this presumably A-1 specimen is more elongated than that of the adult instar.

The posterior and anterior borders are well-rounded. The differences with the adult instar are:
(1) the $S_1^{'}$ is ventrally not connected with the S_v,
(2) the anterior part of the S_v is not developed,
(3) the S_4 is almost invisible.

Variation. – Judging only by the poor material available, one would still say there is some variation, especially in the outline of the carapace.

Discussion. – *P. insculpta insculpta* resembles *P. neodevonica*, but in the latter the S_4 is never connected to the S_5. *P. insculpta insculpta* is closely related to *P. insculpta beckeri*, but nevertheless easily distinguishable from it, since (1) the sculpture is less profoundly cut out, (2) the S_4 is shorter and more separated from the S_5, (3) the dorsal connection between the S_4 and the S_5 is well-rounded, (4) the S_v is straight even in its posterior part (whereas in *P. insculpta beckeri* the S_v swings downward in the posterior part).

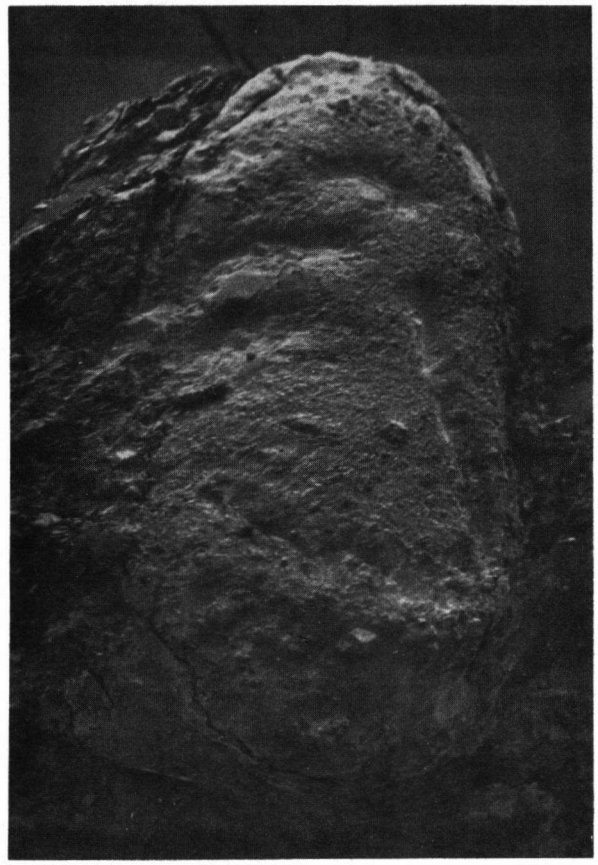


Fig. 28. *Polyzygia insculpta insculpta.* Locality Luanco. Anterior view of a tilted right valve of an A–1(?) specimen. STP/Mi. 72–46.

Remarks. – Becker (1969, p. 259) points out once more that the assignment of this subspecies to the genus *Polyzygia* should be accompanied by a question -mark, since it has a tripartite hinge. However, also other species of *Polyzygia* have been demonstrated to have a more complicated hinge (cf. Groos, 1969, p. 23). This question-mark is now superfluous because Adamczak (1971b) clearly demonstrates that the type species also has a tripartite hinge and not a bar & groove type (Adamczak, 1956).

Occurrence. – Obere Nohn – Freilingen Schichten (Eifelian), Sötenicher Mulde, W. Germany; Ahbacher Schichten (Upper Eifelian), Gerolsteiner Mulde, Hillesheimer Mulde, W. Germany; Hobräcker – untere Honseler Schichten (Eifelian – Lower Givetian), Bergisches Land, Sauerland, W. Germany; upper part of the assise de Couvin (Upper Couvinian), Couvin, Belgium; Skały beds (Upper Eifelian), Skały, Holy Cross Mountains, Poland; Lower Candás Formation (Givetian), Luanco, province of Asturias, Spain; upper part of the Portilla Formation (Frasnian), La Ercina, province of León, Spain; Upper Candás Formation (Frasnian), Perlora, province of Asturias, Spain.

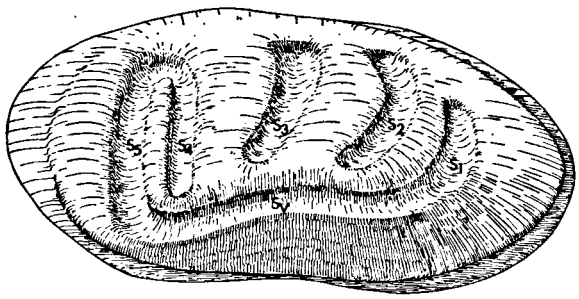


Fig. 29. *Polyzygia insculpta beckeri.* Right valve. The same specimen is shown on Pl. XI, 1.

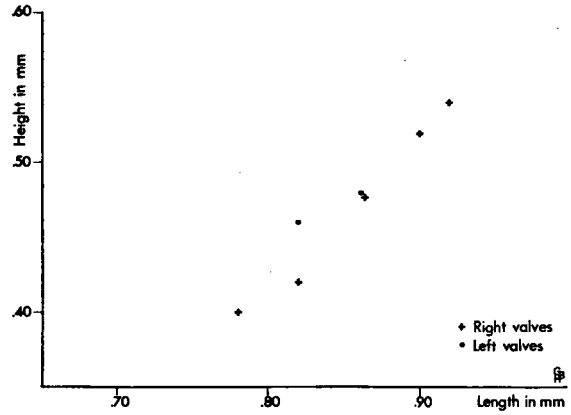


Fig. 30. *Polyzygia insculpta beckeri.* Length and height plots of 7 specimens from locality Prendes.

Polyzygia insculpta beckeri Zagora, 1968
(Figs. 29, 30; Pl. XI, 1)

1968 *Polyzygia insculpta beckeri* ssp. n. Zagora. – Zagora, p. 35, 36, pl. 7, fig. 1–5, 7
1968 *Polyzygia insculpta beckeri* Zagora. – Zagora & Zagora, table 1
1970 *Polyzygia insculpta beckeri* Zagora. – Jordan, p. 22, 23, table 2.

Diagnosis. – A subspecies of *P. insculpta* with a distinct and clear bas-relief pattern (Fig. 29). S-formula: $S_1\_S_v\_S_5\overline{\ }S_4$ and $S_2(\overline{\ })S_3$. The S_2 and the S_3 are dorsally connected in the left valve; in the right valve they are separated. The S_4 and S_5 run parallel, leaving a narrow lobe between them.

Material. – Three carapaces and three right valves.

Dimensions. – See length and height plots in Fig. 30.

Description. – The outline is ellipsoid in lateral view, in dorsal and ventral view the outline is rectangular with a pointed posterior end and a rounded anterior end.

The dorsal and ventral borders are roughly straight. Both anterior and posterior border are pointed, but the posterior border is more blunt than the anterior border.

The cardinal angles are not defined.

The anterior corner is situated below mid-height, the posterior corner above mid-height.

The right valve has a contact ridge; the contact area of the left valve was not observed. There is also a marginal ridge bordering the free margin, which broadens along the anterior border.

In the posterior part of the valve we see a clearly developed ledge, usually roughly perpendicular to the ventral border.

In ventral view the free margin of the left valve shows an evident lip; in the right valve we see that the marginal ridge is not discontinuous in that place (Pl. XI, 1h).

In anterior and posterior view a gap is visible between the marginal ridges of the valves.

The sculpture consists of two vertical sulci in the central area, which are dorsally connected to each other in the left valve but not in the right valve, and a larger one surrounding them, shaped like a wide oblique U and having a narrow posterior curl that loops back inward. The two central sulci are like commas with their outsides turned to the front. The S-formula of the outer sulcus is: $S_1\_S_v\_S_5\overline{\ }S_4$. The S_4 and the S_5 run parallel and very close to each other, thus leaving only a narrow ridge between them. The sculpture on the two valves is not identical. The sculpture on the right valve conforms to the diagnostic features of *P. insculpta beckeri*, mentioned by Zagora (1968), but the left valve shows a pattern in which the S_2 and S_3 are dorsally connected to one another.

The hinge was not accessible for observation. According to Zagora (1968, p. 36) there is a list in the left valve and a groove in the hinge of the right valve, but a tripartite nature should not be excluded. In dorsal view the right valve slightly protrudes over the left valve in the hinge area.

The muscle scar is as yet unidentified.

Pores are visible, though they are poorly preserved.

On the lateral surfaces the Spanish specimens faintly show a second-order reticulation of extremely elongated fossae.

Ontogeny. – The Spanish material did not occasion any ontogenetic observations.

Discussion. – The sculpture on the right valve, different from the one on the left valve, shows the exact characteristics of *P. insculpta beckeri* which Zagora (1968) defined as typical for the subspecies. At close inspection the specimens he showed also tend to have a connection between the S_2 and the S_3, vide Zagora op. cit., pl. 7, fig. 5 and 8. *P.insculpta beckeri* is closely related to *P. insculpta insculpta*; for differences see the discussion on *P. insculpta insculpta.*

Remarks. – This is the first time that any mention is made of the occurrence of this subspecies outside Thuringia.

Occurrence. – Arnao Formation (transition Emsian – Couvinian), Prendes, province of Asturias, Spain; Tentaculitenschiefer (Lower Eifelian), Creunitz near Gräfenthal, E. Germany; top of the Santa Lucía Formation (Lower Couvinian), Santa Lucía, province of León, Spain.

Polyzygia symmetrica Gürich, 1896
(Figs. 31–33; Pl. XII, 1–3)

1896 *Polyzygia symmetrica* sp. n. Gürich. – Gürich, p. 387–388, pl. 14, fig. 8, 9
1909 *Polyzygia symmetrica* Gürich. – Sobolev, p. 394
1934 *Polyzygia symmetrica* Gürich. – Bassler & Kellett, p. 435, fig. 10, 8
1952 *Polyzygia guerichi* sp. n. Polenova. – Polenova, p. 77, 78, pl. 2, fig. 5
1953 *Polyzygia symmetrica* Gürich. – Přibyl, p. 321, 322, pl. 2, fig. 2–11
1953 *Polyzygia gürichi* sp. n. Krömmelbein. – Krömmelbein, p. 54, 55, pl. 3, fig. 1
1953 *Polyzygia geesensis* sp. n. Krömmelbein. – Krömmelbein, p. 56, pl. 3, fig. 2
1955 *Polyzygia guerichiana* nom. nov. Krömmelbein. – Krömmelbein, p. 371
1956 *Polyzygia symmetrica* Gürich. – Adamczak, p. 40–46, pl. 2, fig. 1–8, pl. 3, fig. 1–7
1964 *Polyzygia symmetrica* Gürich. – Becker, p. 51, 52, pl. 7, fig. 7
1969 *Polyzygia symmetrica* Gürich. – Winter, p. 346
1969 *Polyzygia symmetrica* Gürich. – Groos, p. 21, pl. 4, fig. 9
1969 *Polyzygia symmetrica* Gürich. – Becker, p. 242, 246, 248, 252, 255, 256
1971 *Polyzygia symmetrica* Gürich. – Adamczak, p. 797, 798, fig. 8
1971 *Polyzygia symmetrica* Gürich. – Becker, p. 807, fig. 4
1971 *Polyzygia symmetrica* Gürich. – Le Fèvre, p. 823, 825, 829, 839, 841
1971 *Polyzygia symmetrica* Gürich. – Adamczak, p. 140, 141, fig. 1D, 2, 3, 8, pl. I, fig. 3–6, pl. II, fig. 8, 9, pl. III, fig. 1, 2.

Diagnosis. – This is a relatively large species of *Polyzygia*, which has a bas-relief pattern with the general S-formula $S_1\_S_v\_S_5(^-)S_{4(-)}S_{3(-)}(^-)S_2$ and a characteristic elongated vertical node in the area between S_2 and S_3 (Fig. 31).

Material. – Nine left valves and eleven right valves.

Dimensions. – See length and height plots, Fig. 32.

Description. – The outline is rectangular with rounded ends in lateral view; in dorsal and ventral view the outline is roughly rectangular also.

The dorsal border is straight and not parallel to the ventral border; towards the front they slightly diverge. The ventral border is slightly concave.

The anterior border is well-rounded and asymmetrical, the posterior border is more blunt than the anterior border and almost perpendicular to the ventral border.

The cardinal angles are both defined and mark the ends of the long hinge.

The anterior corner is situated below mid-height, the posterior corner above mid-height.

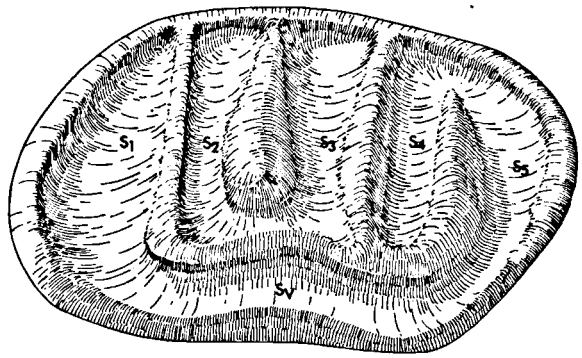


Fig. 31. *Polyzygia symmetrica.* Left valve. The same specimen is shown on Pl. XII, 1.

In the left valve there is a contact groove. There is a marginal ridge bordering the free margin, which broadens along the anterior border.

The posterior border has the appearance of a slightly projecting ledge, which may be sharp-edged.

At the anterior corner there is a clearly visible gap between the valves.

The sculpture consists of a bas-relief pattern of one or two sulci. Specimens from the type locality show a sculpture with the S-formula; $S_1\_S_v\_S_5{}^-S_4\_S_3{}^-S_2$ (Pl. XII, fig. 3a). The same pattern is found on material shown by Becker (1964, pl. 7, fig. 7) and Groos (1969, pl. 4, fig. 9a).

In the present Spanish material, especially from locality Santa Lucía, the sulci and their interconnections vary greatly (Fig. 33). S-formula as displayed by the Spanish material: $S_1\_S_v\_S_5(^-)S_{4(-)}S_{3(-)}(^-)S_2$ (compare also the variation in sculpture as visible in the specimens figured by Přibyl (1953) and Krömmelbein (1953)). Though the shape of the remaining lobi is also subject to variation, the central lobe is always elongated and generally rounded.

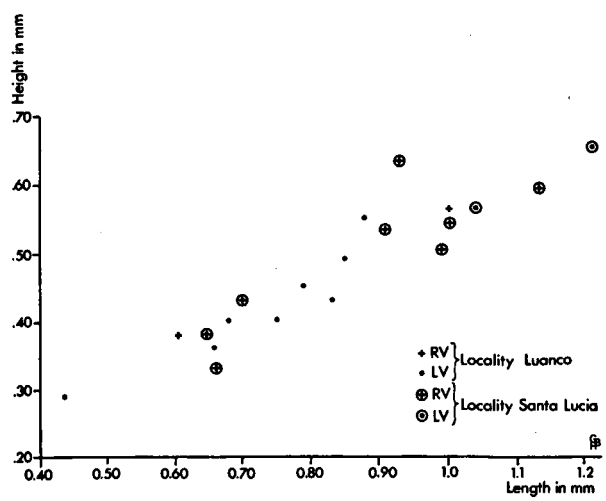
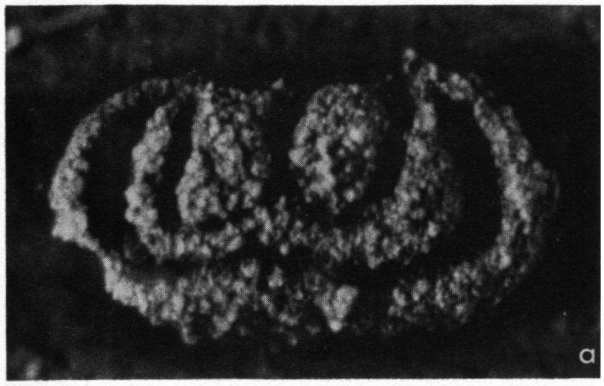
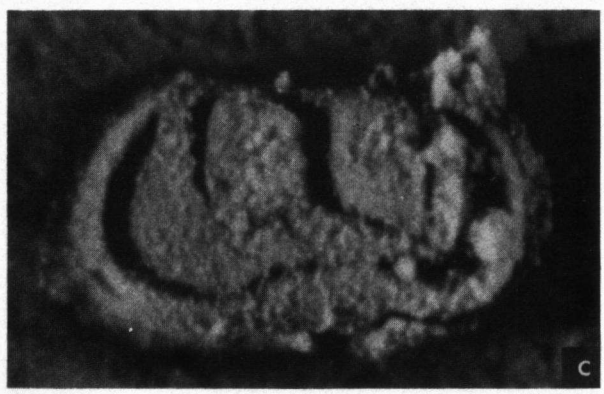
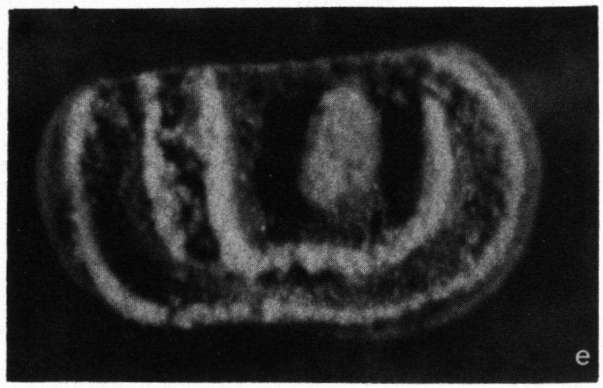


Fig. 32. *Polyzygia symmetrica.* Length and height plots of 20 specimens from localities Santa Lucía and Luanco.







The hinge is hardly distinguishable in the Spanish material; it seems to consist of a groove in the right valve and a bar in the left one. The finer details are not visible but judging from cross sections it is quite probable that a narrow groove is present in the middle of the left hinge bar and a corresponding ridge in the groove of the right valve.

According to Adamczak (1971b non 1956) the right hinge has a distinct anterior and posterior tooth at the ends of the groove; the left valve has a distinct bar with an anterior and a posterior socket.

Neither the muscle scar nor any pores have been observed yet.

Ontogeny. – For an extensive description of juvenile instars the reader should consult Adamczak (1956).

Variation. – As stated above, the connections between the sulci and the shape of the lobi may vary considerably. The outline of the valve, i. e. the L/H ratio, and the depth and distinctness of the sulci may also vary.

Discussion. – Though the bas-relief pattern shows an extensive variation, *P. symmetrica* is easily set apart from other species by the combination of outline, bas-relief sculpture and the central node.

Occurrence. – Hobräcker – lower part of the Honseler Schichten (Eifelian – Lower Givetian), Rhenish Slate Mountains, W. Germany; upper Nohn – Freilingen Schichten (Eifelian), Sötenicher Mulde, W. Germany; Geeser Schichten (Eifelian), Gerolsteiner Mulde, W. Germany; Schleddenhofer Schichten (Upper Givetian), Dorlar, Rhenish Slate Mountains, W. Germany; Teferguenit Formation (Upper Couvinian – Givetian), Beni Abbès, Saoura, Algeria; top of the Santa Lucía Formation (Lower Couvinian), Santa Lucía, province of León,

Fig. 33. *Polyzygia symmetrica.* Variation in sculpture.
33a. Right lateral view. STP/Mi. 72–36. Santa Lucía.
33b. Left lateral view. STP/Mi. 72–37. Santa Lucía.
33c. Left lateral view. STP/Mi. 72–38. Santa Lucía.
33d. Left lateral view. STP/Mi. 72–47. Santa Lucía.
33e. Right lateral view. STP/Mi. 72–39. Luanco.

Spain; Skały beds (Upper Eifelian), Skały, Holy Cross Mountains, Poland; Lower Candás Formation (Givetian), Luanco, province of Asturias, Spain; Starooskol horizon (Upper Givetian), Syzran, USSR; Upper Candás Formation (Frasnian), Perlora, province of Asturias, Spain.

Polyzygia trigonata (Gürich, 1900)
(Fig. 34; Pl. IX, 3, 4, Pl. XII, 4)

1900 *Beyrichia* ? *trigonata* sp. n. Gürich. – Gürich, p. 366, pl. 15, fig. 12
1909 *Beyrichia* ? *trigonata* Gürich. – Sobolev, 394
1934 *Beyrichia* (*Octonaria* ?) *trigonata* Gürich. – Bassler & Kellett, p. 208
1953 *Polyzygia trigonata* (Gürich). – Přibyl, p. 322–324, pl. 2, fig. 1, pl. 3, fig. 1–15.
1956 *Polyzygia trigonata* (Gürich). – Adamczak, p. 38–40, pl. 1, fig. 1–8, pl. 2, fig. 9
1964 *Polyzygia trigonata* (Gürich) ? . – Becker, p. 52, 53
1969 *Polyzygia trigonata* (Gürich). – Groos, p. 22–23, text fig. 11, pl. 4, fig. 1–5, pl. 18, fig. 7–9
1971 *Polyzygia trigonata* (Gürich). – Adamczak, p. 143, 144, fig. 1C, 13, pl. I, fig. 2, pl. III, fig. 3–7.

Diagnosis. – A species of *Polyzygia* characterized by the shape of its bas-relief pattern, which consists of two or three sulci. S-formulas: $S_1\_S_v\_S_5(^-)S_4$ and $S_2\overline{\ \ }S_3$ (Fig. 34).

Material. – Four left valves and two right valves, poorly preserved.

Dimensions. – LV L: .70 mm; H: .44 mm
LV L: .79 mm; H: .46 mm
LV L: .76 mm; H: .46 mm
LV L: .93 mm; H: .54 mm
RV L: .99 mm; H: .53 mm
RV L: .66 mm; H: .40 mm

Description. – The outline is pear-shaped or ellipsoid in lateral view; in dorsal and ventral view the outline is elongated to ellipsoid.

The dorsal border is straight, the ventral border is straight to slightly convex. The anterior border is well-rounded, the posterior border is more pointed.

The anterior cardinal angle marks the anterior end of the hinge. The posterior cardinal angle is less well defined.

The anterior corner is situated at or below mid-height, the posterior corner above mid-height.

The contact area was not observed. However, cross sections show a groove in the left valve. There is also a narrow marginal ridge bordering the free margin, which broadens along the anterior border and, though rarely, along the posterior border. This marginal ridge may be straight or undulating.

There is a roughly vertical posterior ledge.

The sculpture consists of two sulci (or occasionally three), of which the larger has the S-formula: $S_1\_S_v\_S_5\overline{\ }S_4$. The S_v may have a more or less vague up-and-down swing in its central part. In some specimens

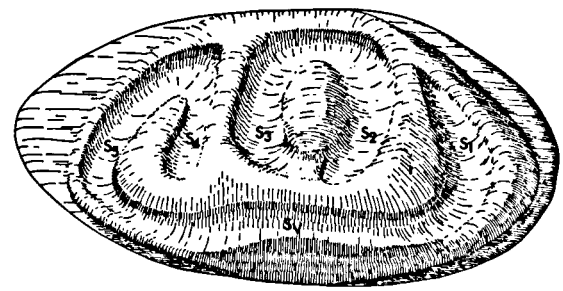


Fig. 34. *Polyzygia trigonata.* Right valve. The same specimen is shown on Pl. IX, 4.

the S_4 is not connected with the S_5, thus producing the third sulcus. The S-formula of the central sulcus is $S_2\overline{\ \ }S_3$; there is always a more or less clear node left. The ventral connection between S_2 and S_3 is less deeply cut out than the dorsal connection.

In the material at hand the hinge in the left valve consists of a central bar with an anterior and a posterior socket; the right hinge was not observable.

Pores nor muscle scar were observed. Pores were mentioned by Groos (1969); in adult specimens the whole carapace was seen to be covered with them.

The Spanish specimens have a smooth surface.

Ontogeny. – See Adamczak (1956) and Groos (1969).

Variation. – Shape, ornamentation and depth and distinctness of the sulci may vary, especially the S_4 and its connection with S_5.

Discussion. – Groos (1969, p. 22) mentions specimens with 'kleine Waben'. Judging from her pl. 18, fig. 8a, we take this to be a first-order reticulation in the area between S_{vp}, S_5 and S_4, so that in this respect there is a resemblance to *P. beckmanni.*

It is remarkable that all specimens shown by Groos have two posterior spines instead of the usual posterior ledge. Generally these spines are mentioned for juvenile specimens only (cf. Adamczak, 1956). In *P. neodevonica* also, spines occur only in juvenile instars. This fact, combined with the measurements Groos gives (op. cit., p. 23), induces one to suppose that all these specimens are juvenile instars; otherwise this would mean that a juvenile characteristic (posterior spines instead of a posterior ledge) was retained in the adult stage.

Occurrence. – Junkerberg Schichten (Lower Eifelian), Eifel Mulde, W. Germany; Schmallenberger – Schleddenhofer Schichten (Eifelian – Givetian), Rhenish Slate Mountains, W. Germany; Skały beds (Upper Eifelian), Skały, Holy Cross Mountains, Poland; Reggane basin (Givetian), Algeria; Lower Candás Formation (Givetian), Luanco, province of Asturias, Spain.

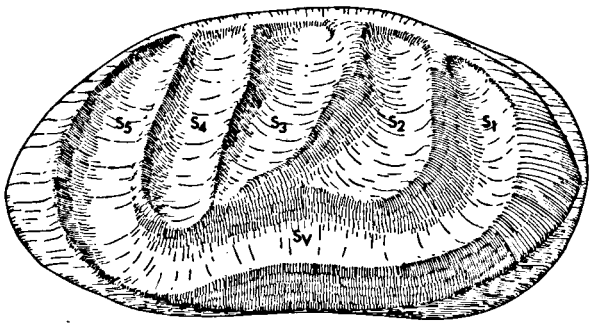


Fig. 35. *Polyzygia neodevonica.* Right valve. The same specimen is shown on Pl. XIII, 5.

Polyzygia neodevonica (Matern, 1929)
(Figs. 35–38; Pl. XIII, 1–7, Pl. XIV, 1–5, Pl. XV, 2)

1929 *Dizygopleura neodevonica* sp. n. Matern. – Matern, p. 42, pl. 3, fig. 30a-e
1929 *Tetrasulcata fluens* g. n. & sp. n. Matern. – Matern, p. 40, 41, pl. 2, fig. 26a-c. Syn. nov.
1968 *Polyzygia neodevonica* (Matern). Lecompte, p. 43
1969 *Polyzygia neodevonica* (Matern). – Groos, pl. 4, fig. 7
1972 *Polyzygia neodevonica* (Matern). – Reijers, p. 197, encl. 1, section 14.

Material. – Several hundred valves and carapaces.

Diagnosis. – A species of *Polyzygia* characterized by its bas-relief pattern, which consists of four sulci. The largest sulcus has an S-formula: $S_1\_S_v\_S_5$, the other ones are separate (Fig. 35).

Dimensions. – See length and height plots, Fig. 36.

Description. – The outline is subrounded or pear-shaped in lateral view; in dorsal and ventral view the outline is ellipsoid.

The dorsal border is straight to slightly convex – in the right valve the dorsal border is more convex than in the left valve. The ventral border is straight. The anterior and posterior borders are asymmetrically rounded and pointed.

The anterior cardinal angle is well defined, the posterior cardinal angle occasionally so.

The anterior and posterior corners are generally well defined. The anterior corner is situated either at mid-height or above mid-height, the posterior corner below mid-height.

In the interior of the left valve there is a well-developed contact groove with a mid-ventral discon-

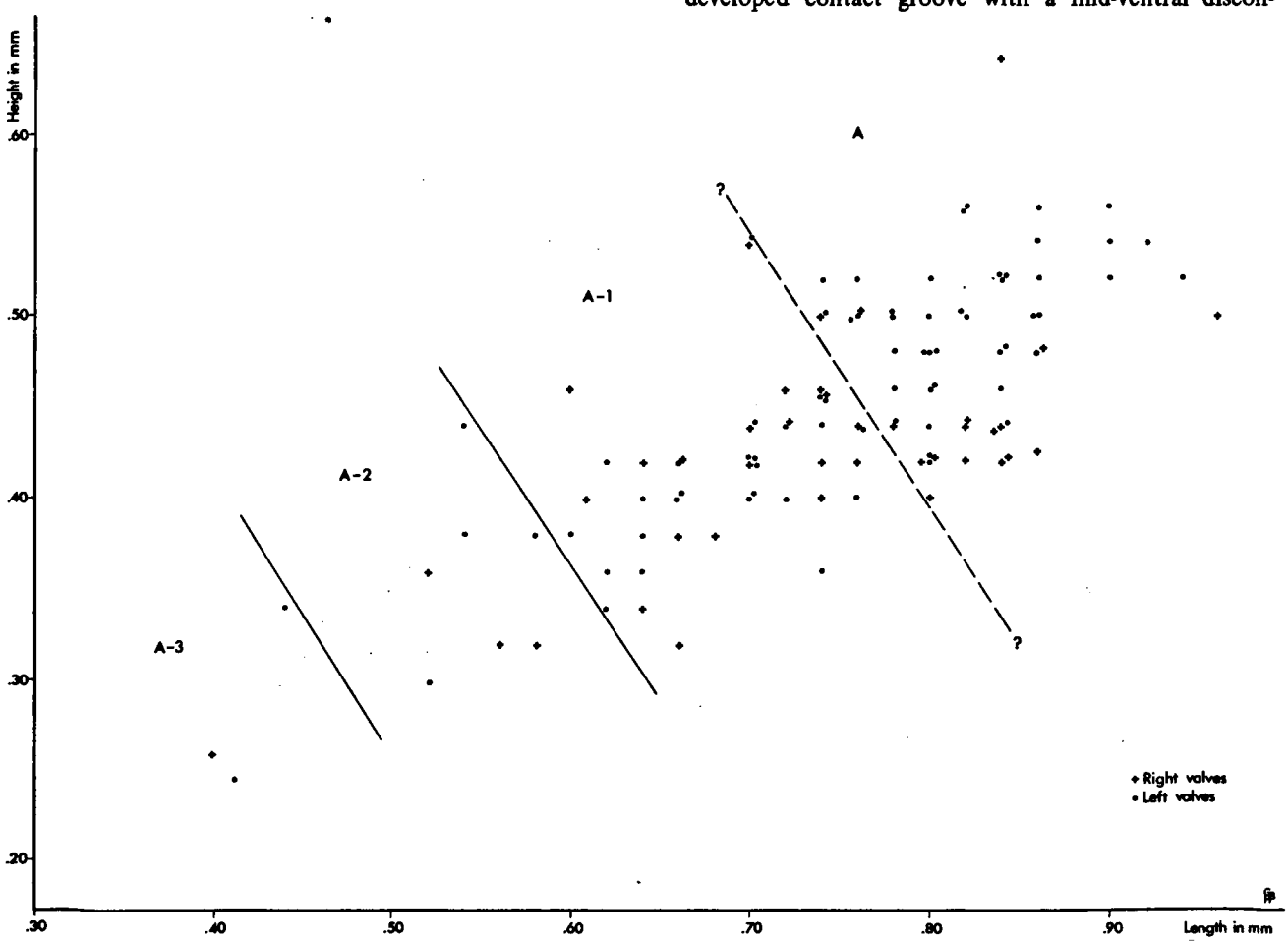


Fig. 36. *Polyzygia neodevonica.* Length and height plots of 113 specimens from locality Luanco.

tinuity; sometimes it is a semi-discontinuity. At the point of that discontinuity the ventral border of the right valve is more concave. There is a clear contact ridge in the right valve. Also there is a smooth marginal ridge bordering the free margin, which considerably broadens along the anterior border and to a lesser degree along the posterior border in the right valve; in the left valve only a wide marginal ridge exists along the anterior border.

The posterior border often looks like a ledge, which may have a sharp edge.

A gap between the valves may be visible in anterior and posterior view.

The sculpture consists of four sulci; one big sulcus shaped like a wide U encloses three separate vertical ones. The sculpture of one valve is not always the mirror image of the sculpture of the other one; sometimes it appears to have been slightly rotated with regard to the other one. On the inside of the valve the S_2 and the S_3 are generally manifest as little projecting parts – usually the other sulci are hardly or not at all manifested on the inside. The hinge is tripartite and almost half the maximum length of the valve. The right valve has a straight groove which is dorsally and ventrally bordered by strong lists. The list ventral of the groove is a direct continuation of the contact ridge of the right valve. In the groove a narrow list is faintly visible; a corresponding faint narrow groove is visible on the hinge bar of the left valve; this narrow groove is the continuation of the contact groove. The straight hinge bar has on the ventral side elongated sockets at both ends. The hinge axis makes an approximately 15-degree angle with the horizontal axis.

The muscle scar region, which is not well delineated consists of several small scars and is situated in the central area of the valve at the base between S_2 and S_3.

The surface of the valves is smooth.

Pores were observed in the surface of one juvenile specimen.

The centro-posterior part of the valve is sometimes remarkably pointed in lateral view and flattened in ventral and dorsal view. In specimens with a flattened posterior part a strongly developed ledge appears between this flattened part and the S_5. This ridge is roughly perpendicular to the ventral border.

Ontogeny. – In the Spanish material several instars were found (Figs. 36, 37).

The A-1 instar is like the adult one but for the depth and distinctness of the sulci and the interruption in the central part of the S_v. In the adult-1 specimens the sulci are smoother and the S_v is discontinuous (Fig. 37a).

In the A-2 instar we see a short S_1, S_2 and S_3. The S_4 is narrow and separated from the S_5 by a very narrow ridge. The anterior part of the S_v is not yet developed, its posterior part is short and curls upwards toward the anterior. There is a posterior ledge behind the S_5 (Fig. 37b).

The A-3 specimens are like the A-2 ones but for the posterior ledge, which is more strongly developed here and terminates at both ends in backwardly directed spines, which slightly diverge (Fig. 37c).

Variation. – Position, orientation, obliquity, depth and distinctness of the sculptural elements may vary, also the development of the posterior ridge and the degree of symmetry in the two valves. There is a wide variation in outline.

Discussion. – A close relationship exists between *P. neodevonica* and *P. insculpta*, but they remain clearly distinguishable, because in *P. neodevonica* the S_4 and S_5

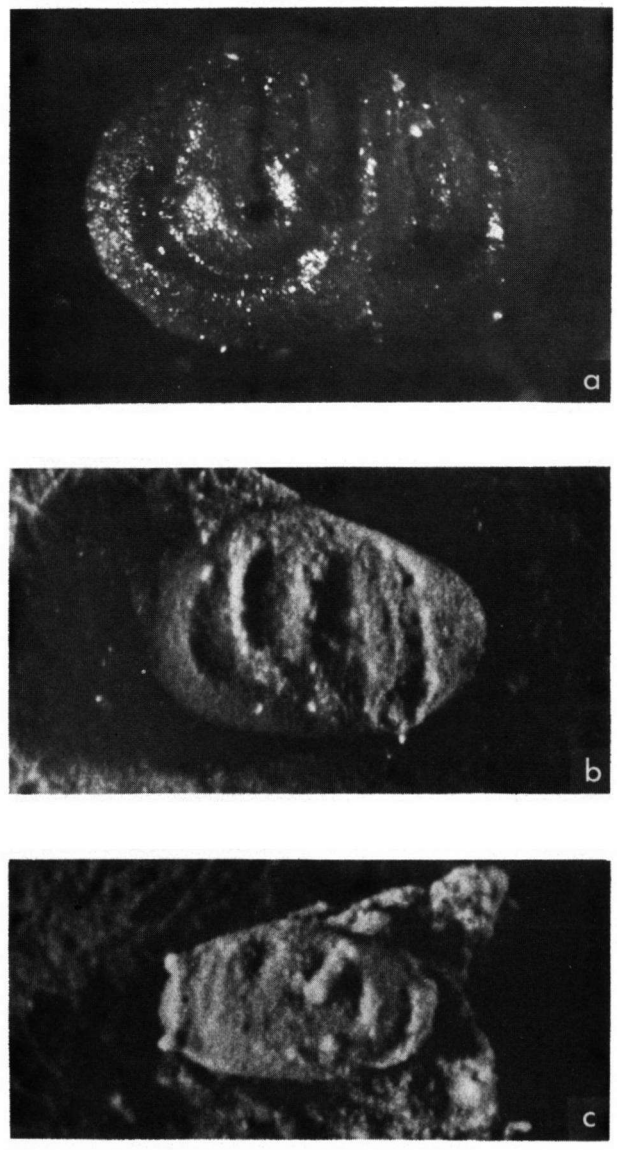
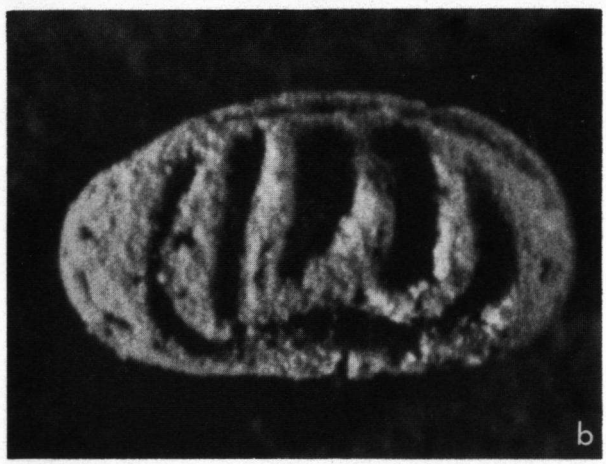


Fig. 37. Polyzygia neodevonica. Locality Luanco.
37a. Left lateral view of A–1 specimen. Specimen accidentally destroyed in the SEM; the same specimen is shown on Pl. XIV, 2.
37b. Left lateral view of A–2 specimen. STP/Mi. 72–40.
37c. Right lateral view of A–3 specimen. STP/Mi. 72–41.



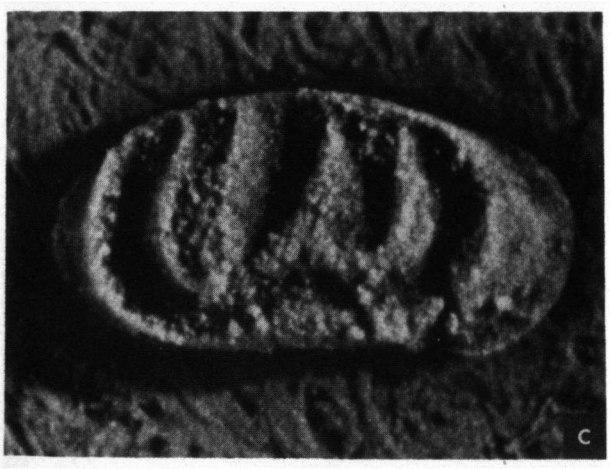


Fig. 38. *Polyzygia neodevonica.* Variation in sculpture, outline and development of the posterior ledge. Locality Perlora.
38a. Left lateral view. STP/Mi. 72–42.
38b. Right lateral view. STP/Mi. 72–43.
38c. Right lateral view. STP/Mi. 72–44.

are never dorsally connected as in *P. insculpta* and its subspecies.

According to the description published by Becker (1969), there is a closer affinity to *P. insculpta deinceps*. In the latter from the German Sötenicher Mulde there is no dorsal connection between the S_4 and S_5. Arguments which Becker (op. cit., p. 259, 260) adduces to rule out a possible synonymy with *P. neodevonica* are: firstly, the presence in *P. insculpta deinceps* of a sharp posterior ledge, secondly, the asymmetry of the posterior and anterior borders in *P. insculpta deinceps,* and thirdly, the less pronounced sculpture in *P. insculpta deinceps.*

All these arguments are disproved by material of *P. neodevonica* from the type locality and from other localities in Spain. Fig. 38 shows three specimens from locality Perlora from the same spot sample. It is evident that the expression of the sculpture is highly variable; moreover one observes the asymmetry of the anterior and posterior borders and the presence of a sharp posterior ledge. However, a definite decision about the supposed synonymy of *P. neodevonica* and *P. insculpta deinceps* cannot be justified without more material of the latter.

Tetrasulcata fluens is doutblessly an A-2 instar of *P. neodevonica*. The S_1 is present; the S_2 and S_3 are short; between the S_4 and S_5 there is a hardly discernible narrow ridge; in the posterior part one sees a sharp almost vertical ledge.

Remarks. – The orientation of the valves adopted in this paper is the reverse of that used by Matern. This is based on such characteristics as marginal rim, location of the hinge, obliquity of the sculpture, contact region and ontogeny.

Occurrence. – Lower Candás Formation (Givetian), Luanco, province of Asturias, Spain; Agaz section (Lower Frasnian), Saoura, Algeria; upper part of the Portilla Formation (Frasnian), La Ercina, province of León, Spain; Upper Candás Formation (Frasnian), Perlora, province of Asturias, Spain; assise de Frasnes (Middle – Upper Frasnian), Ardennes, Belgium; Frasnian limestone (Frasnian), Ratingen, Rhenish Slate Mountains, W. Germany; Upper Frasnian beds, Bas-Boulonnais, France.

A key to the species and subspecies of *Polyzygia* (included *P. modesta* and *P. mirabilis*) could run as follows:

1. The sculpture consists of 4 sulci . *P. neodevonica*
   The sculpture consists of 1, 2 or 3 sulci 2
2. No S_1 present *P. modesta* (see Adamczak, 1971b)
   S_1 present 3
3. The S_v shows an extremely sharp kink . . . . . *P. mirabilis* (see Zogora, 1968)
   The S_v is straight or has a more or less smooth up-and-down curve 4
4. The straight hinge-line is longer than half the maximum length . . . . . *P. symmetrica*

The hinge-line is shorter than half the maximum length 5
5. The S_1 is short to very short 6
The S_1 is normal 7
6. Both valves have 3 sulci . . *P. insculpta insculpta*
The right valve has 3 sulci, the left valve has but 2 sulci . . . . . *P. insculpta beckeri*
7. The S_2 and S_3 are ventrally connected 8
The S_2 and S_3 are ventrally not connected . . . 9
8. The whole area enclosed by S_4, S_5 and S_{vp} and S_2, S_1 and S_{va} is covered with a first-order reticulation . . . . . *P. beckmanni*
The first-order reticulation on the latter areas is less evident, partly or not all present . . . . *P. trigonata*
9. A first-order reticulation is present 10
No first-order reticulation is present 11
10. The sculpture consists of 1 sulcus . . . . *P. vinea*
The sculpture consists of 2 sulci . . . *P. normannica*
11. The sculpture consists of 1 sulcus *P. kroemmelbeini*
The sculpture consists of 2 sulci . . . . . *P.* sp. *A*

CHAPTER III

THE STRUCTURE OF THE VALVE

To investigate the structure of the valve in the scanning electron microscope, transverse, longitudinal and tangential cross sections were studied.

The outer surface of *Polyzygia* is composed of thin plate-like particles which are arranged roughly parallel (Fig. 39). The flake-like calcite particles can also be observed on the surface of the ornamented areas (Fig. 40).

Cross sections show a foliated aspect (Fig. 41). At the outer border the calcite particles are flat and small, roughly parallel (Fig. 42). Towards the interior the overall aspect changes. In some places a much more chaotic arrangement is visible (Fig. 41 and 43); in other places a lamination can be seen (Fig. 41); near the inner border the arrangement is once more less chaotic.

Sylvester-Bradley & Benson (1971) observed that the interior and exterior surfaces of the foliated layer are covered by a thin laminar layer. With the exception of one dubious case (Fig. 44) this laminar layer has never been observed in the material at hand.

Though there is no direct evidence concerning the mechanics of calcification some explanation of the structure is possible.

First, the organic matrices were secreted. Such an organic support, which is necessary to maintain the shape of the carapace during the moulting process, has been observed by Jørgensen (1970) when he had dissolved the valve in hydrochloric acid.

Immediately after the formation of such an organic network the growth of the ostracode takes place. This supposition would explain why the fossae of the second-order reticulation on the lateral surfaces are extremely elongated whereas the fossae on the anterior and posterior ends are generally polygonal (Pl. II, 4a, 4d, Pl. V, 1), a feature we have repeatedly observed. The proposed mechanism resembles that of a nylon stocking being stretched out over a darning ball.

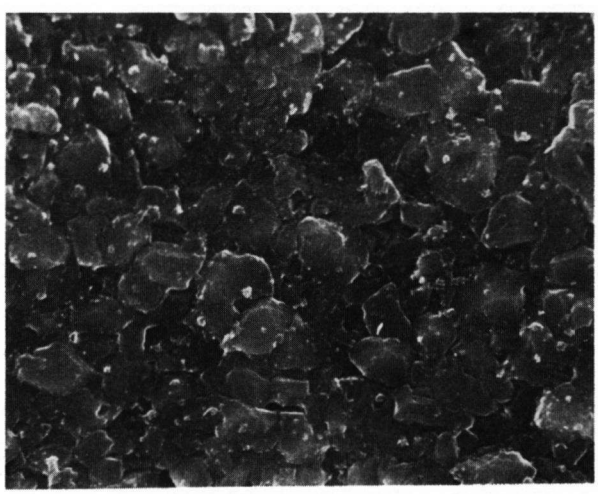


Fig. 39. Valve structure of *Polyzygia kroemmelbeini*. Detail of the area between S_1, S_2 and S_v. STP/Mi. 72–3, Prendes. Left valve. x2000.

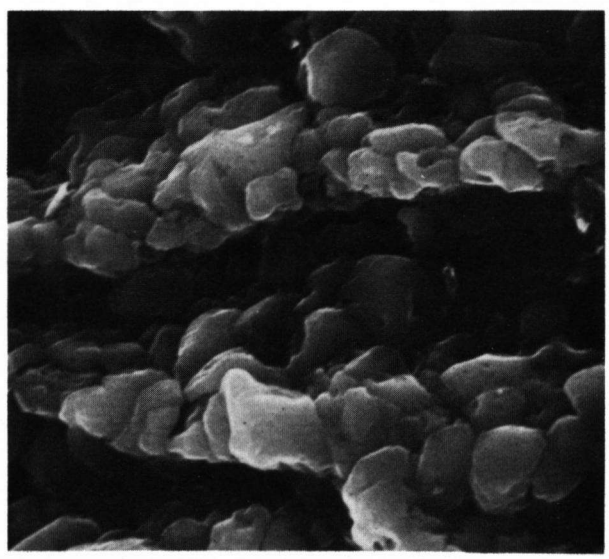


Fig. 40. Valve structure of *Polyzygia kroemmelbeini*. Detail of the anterior border of the left valve. STP/Mi. 72–3, Prendes. x4750.

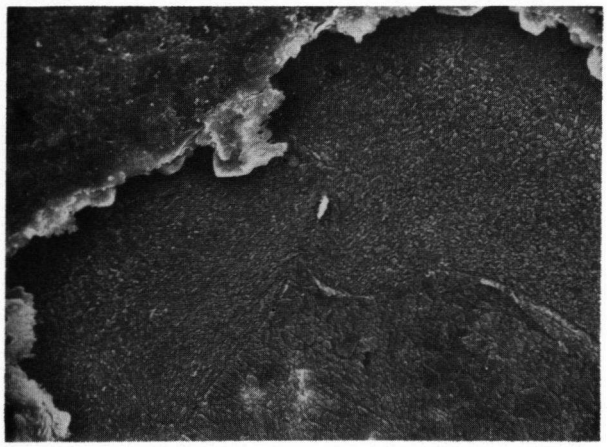


Fig. 41. Transverse cross section of *Polyzygia neodevonica*. Detail of the dorsal region. Section through the anterior hinge socket. Perlora. x390.

After the formation of the appropriate crystallizing fluid, the nucleation is initiated by external and internal physico-chemical conditions. Still the nature of the organic tissues and matrices which may calcify is largely unknown (Sylvester-Bradley & Benson, 1971).

The initiation of the nucleation process could well be triggered by a specific composition of the body fluid solutions at a given moment, combined with the stereochemical qualities of the organic compound.

It is probable that the crystal growth would begin in the area contiguous to the outer chitinous layer. It is assumed that in the beginning the crystal growth is relatively slow; the particles are thin and plate-like, they often have well-defined crystal faces and a rather conspicuous orientation (cf. the calcitostracum of molluscs).

The speed of the crystallization increased gradually. More to the interior it seems that the animal's control over crystal growth is less and less; the crystals are less orderly shaped and larger. In some areas laminations are present, which may represent growth lines.

The supposition that crystallization started from the outside and then moved inwards is supported by the observation that surface details (such as spines) extend down through the calcified layer, where they slowly fade out. Moreover it is conjectured that calcification is regulated by the layer of epidermal cells situated along the interior side of the inner chitinous layer (cf. van Morkhoven, 1962, fig. 2). If calcification had begun contiguous to the inner chitinous layer, this would have prevented the migration of ingredients necessary for calcification from epidermal cells to the calcifiable tissues and vice versa.

Definite conclusions are unwarranted because of the limited amount of material studied, but this hypothesis may serve as a model for future studies.

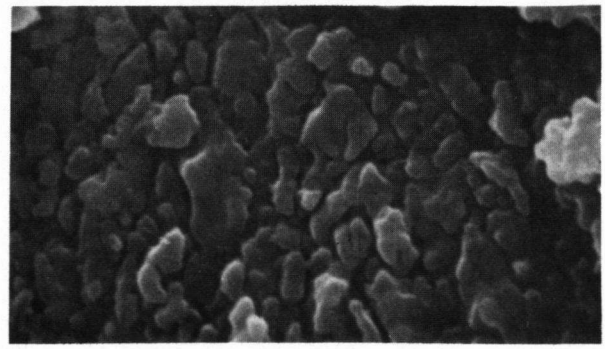


Fig. 42. Transverse cross section of *Polyzygia trigonata*. Detail of the valve structure immediately under the surface. Luanco. x5700.

Fig. 43. Transverse cross section of *Polyzygia neodevonica*. Section through the hinge area. Perlora. x950.

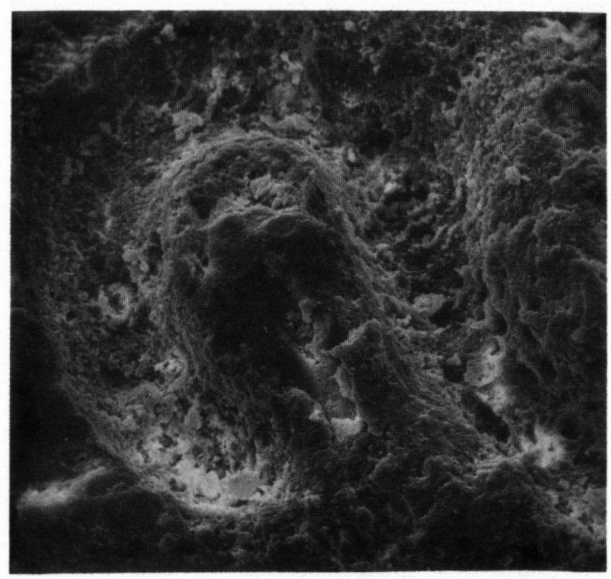


Fig. 44. Valve structure of *Polyzygia kroemmelbeini*. Detail of the region between S_2 and S_3. Note the laminar aspect of the surface. However, this may be an artefact due to the preparation of the sample with HF. STP/Mi. 72–1. Llamoso. x 300.

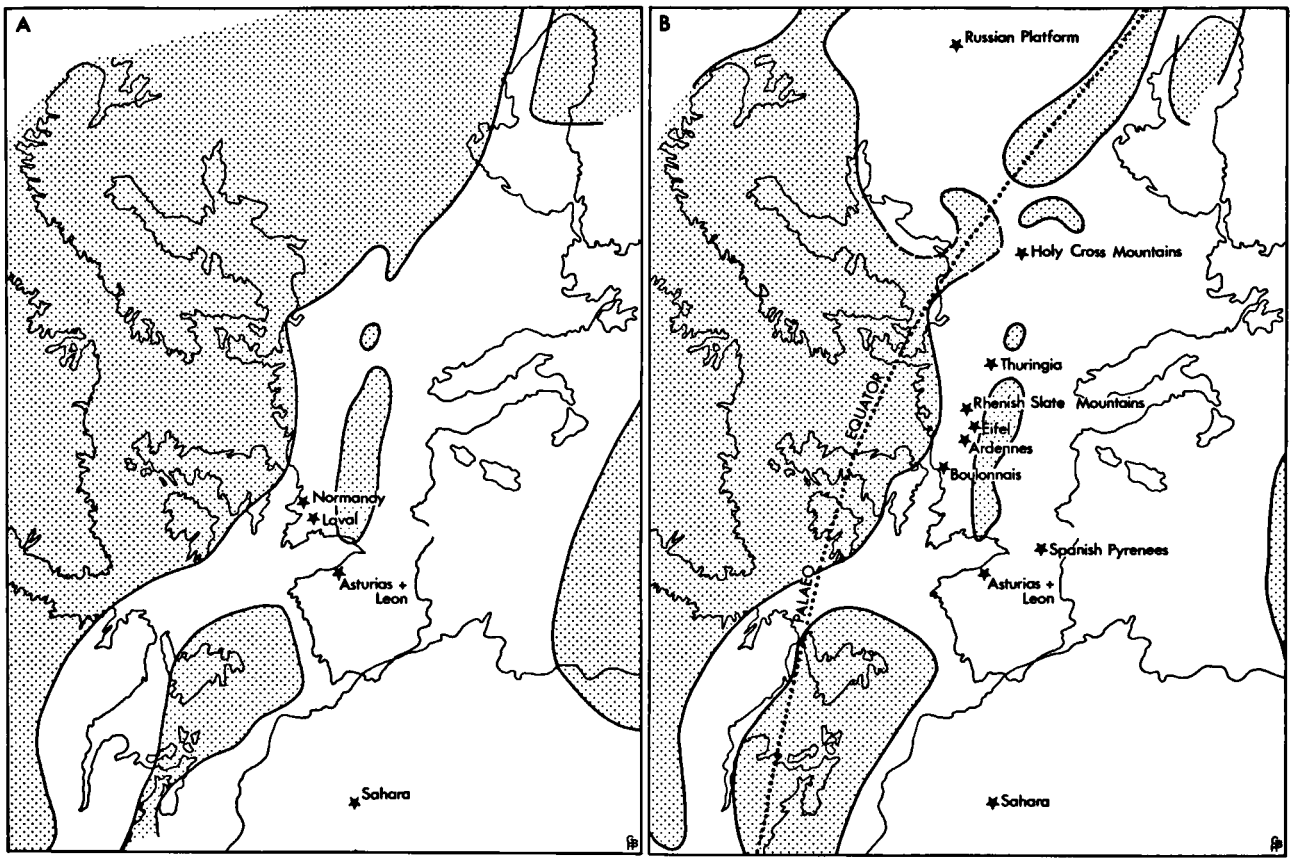


Fig. 45. Reconstructions of the shore-lines. Asteriscs indicate the occurrences of *Polyzygia*.
45a. Lower Devonian.
45b. Middle Devonian.

CHAPTER IV

DISTRIBUTION

Thus far *Polyzygia* has not been found outside North Africa, Central Europe and the Russian Platform; as yet no traces of it have been found in North America, in southeastern Europe and Asia, though it must be admitted that the regions where ostracodes were sampled and studied are not evenly distributed all over the world. Ostracode studies of the Devonian deposits in southeastern Europe, Turkey, Afghanistan, Burma, e.g., are only fragmentary if undertaken at all.

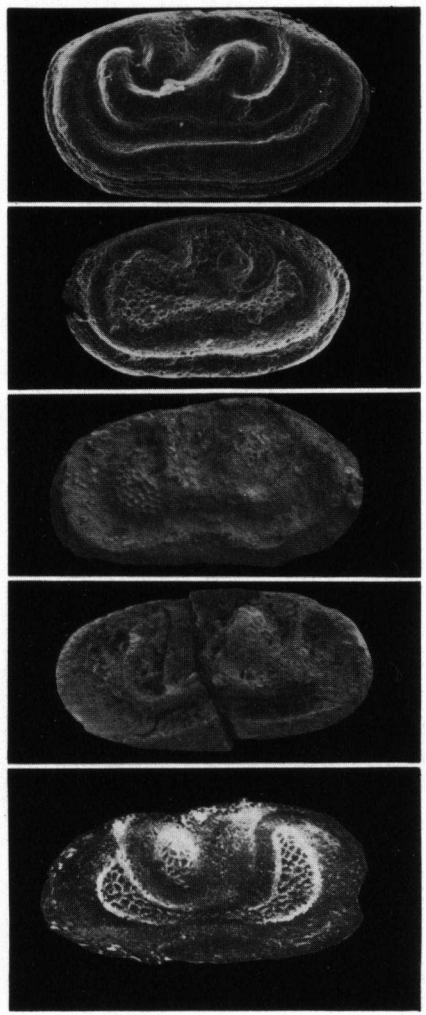
Looking at Fig. 45 a and b which represent reconstructions of the shorelines* in Lower and Middle Devonian times respectively, one can understand why in Russia no *Polyzygia* has been found in sediments older than the Givetian. It is not clear, however, why this genus does not occur in North America; common genera which accompany *Polyzygia* in Europe (e. g. *Amphissites, Ctenoloculina, Jenningsina, Hollinella* and *Ponderodictya*) do occur in North America.

All species of *Polyzygia* which are known so far have been found in full-marine, low-energy environments. The Spanish specimens seem to have felt most at ease in a shallow, protected sea; in the shales and marls of such an environment they usually constitute minor but unvarying parts of the ostracode assemblages. The normal rate is about 5 % (exceptions are *P.* sp. *A* with less than 1 % and *P. neodevonica* with up to 65 %).

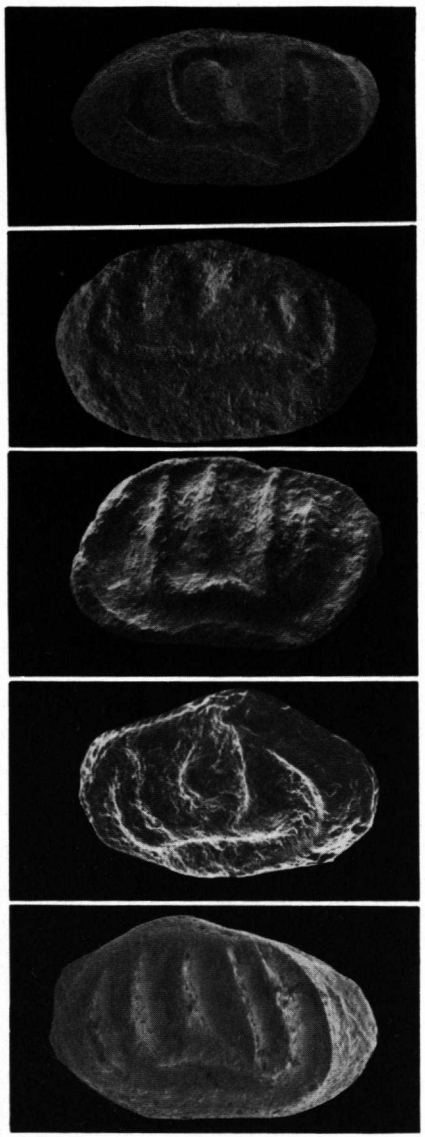
Polyzygia has a relatively strongly-calcified carapace suggesting the presence of currents and an outline which probably indicates a crawling way of life (Hartmann, 1964, fig. 2). Because of its benthonic way of living, its distribution certainly is influenced by physical factors such as vegetation, salinity, substrate and currents (Gründel, 1969).

An environment with a normal salinity, badly sorted sediments and without strong currents is pre-eminently suited for the development of rich and variegated

* Reconstruction of the shore-lines after data of Allen e. a., 1968; Boucot & Johnson, 1968; Burollet e. a., 1968; Erben & Zagora, 1968; Hollard, 1968; Lecompte, 1968; Legrand, 1968; Llopis Lladó e. a., 1968; Pajchlowa, 1968; Rzhonsnitskaya, 1968. Reconstruction of the map after Bullard e. a., 1965.



	DEVONIAN				
	LOWER		MIDDLE		UPPER
	Siegenian	Emsian	Couvinian	Givetian	Frasnian
KROEMMELBEINI	LAVAL	ALGERIA NORMANDY	SPAIN POLAND		
VINEA		SPAIN NORMANDY			
NORMANNICA		SPAIN NORMANDY			
sp. A		SPAIN NORMANDY	RHENISH SLATE MOUNTAINS		
BECKMANNI			SPAIN THURINGIA	RHENISH SLATE MOUNTAINS	BOULONNAIS ARDENNES



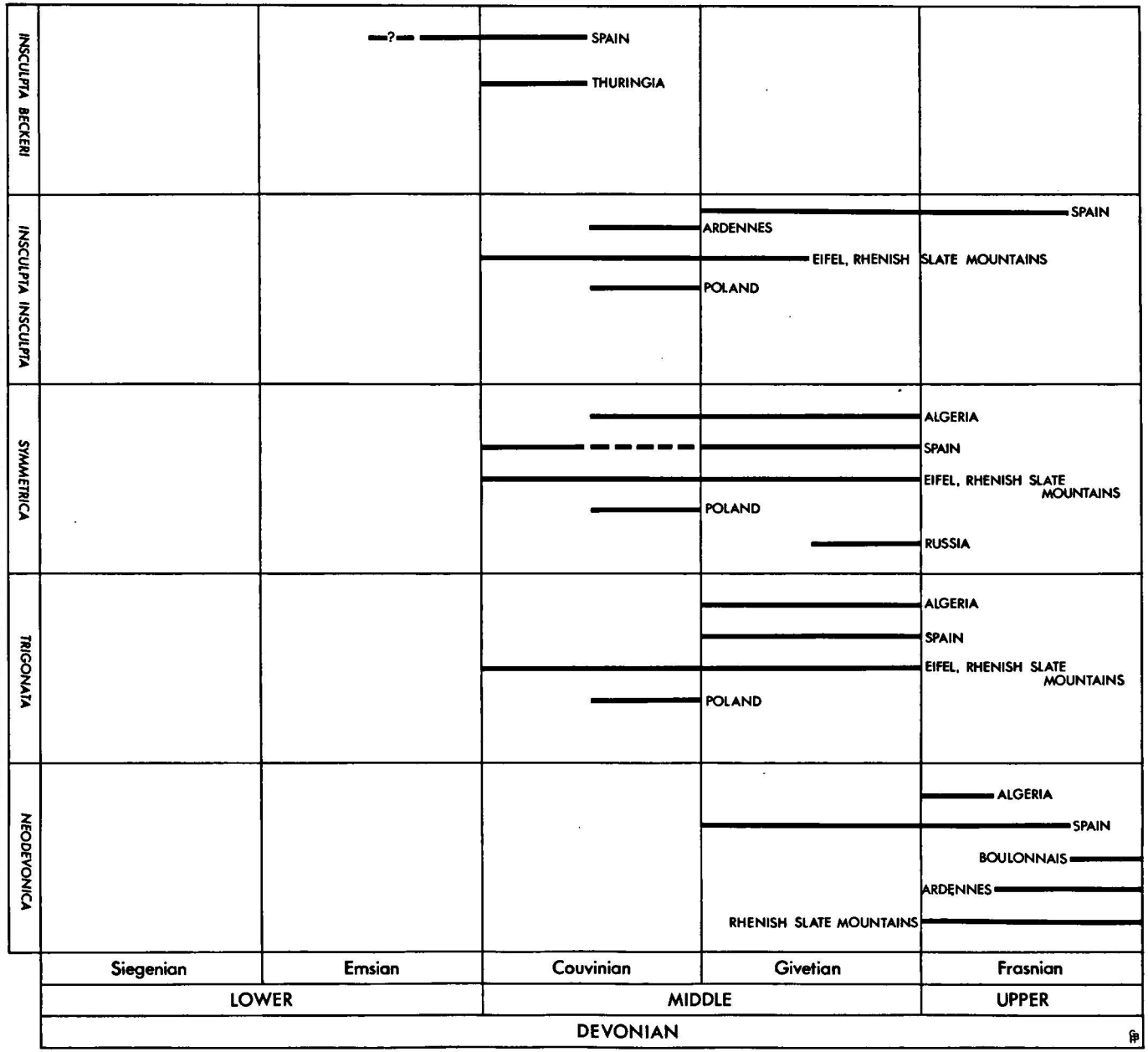


Fig. 46. Range chart of *Polyzygia*.

ostracode assemblages (see also Krebs, 1971, fig. 1). Polyzygiae are generally found in low-energy environments without strong currents which do undergo influence of winds and waves. The only exception to this general picture is offered by Becker (1969, 1971). He claims that the ostracode frequency in the Sötenicher Mulde is at a maximum in the high-energy reef environment.

It is highly probable that there were currents. Climatology teaches that the relative positons of the palaeoequator* and the continents as shown in Fig. 45 would produce winds, probably monsoon winds. During the summer in the northern hemisphere there would be a low pressure area over the heated continent and a high pressure area over the colder sea. These would generate a wind which would blow from southeast to northwest, and in this region so near the equator, almost parallel to it. During the winter in the northern hemisphere the wind would blow in the opposite direction. The influence of the winds and of the currents generated by them surely affect the distribution and therefore should not be neglected.

In Fig. 46 the stratigraphic distribution of *Polyzygia* in Spain is shown, together with the range of its species as it was reported from other regions. Some species have an apparently limited range, but in Spain the upper limit is often demonstrably due to abrupt changes in environments, sometimes this may be observed at the lower limit too. We would not be surprised to learn that in the future many ranges of *Polyzygia* species, and not only those from Spain, will be extended. Though they may be useful for local correlations, the foregoing demonstrates that the species of *Polyzygia* are unsuitable for regional correlations.

* Reconstruction of the palaeoequator after Tarlo, 1968 and Khramov, 1968.

REFERENCES

Adamczak, F., 1956. *Polyzygia* Gürich an ostracod genus from the Givetian of the Holy Cross Mountains Acta Palaeont. Polon., 1/1, p. 35–48.

–, 1967. Morphology of two Silurian metacope ostracodes from Gotland. Geol. Fören. Stockholm Förhandl., 88, p. 462–475.

–, 1971a. On some ostracod assemblages of Middle Devonian rocks. In: Colloquium on paleoecology of ostracodes Pau 1970, p. 787–800 (H. J. Oertli, ed.), Bull. Centre Rech. Pau SNPA, 5 suppl.

–, 1971b. The Devonian metacope genus *Polyzygia* (Ostracoda). Stockholm Contr. Geol., 23/5, p. 127–150.

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.

Allen, J. R. L., 1968. Old Red Sandstone basins of North America and Northwest Europe. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 69–98 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Altevogt, G., 1963. Die oberdevonischen rugosen Korallen von der Asturischen Küste (Cabo Peñas, Nordspanien). N. Jahrb. Geol. Paläont., Abh., 117, p. 9–39.

Arbeitskreis Deutscher Mikropaläontologen (ed.), 1962. Leitfossilien der Mikropaläontologie. Part 1, p. 1–432; part 2, 61 plates, 22 tables, Nicolassee, Berlin.

Barrois, Ch., 1882. Recherches sur les terrains anciens des Asturies et de la Galice. Mém. Soc. Géol. Nord, 2, I, p. 1–630.

Bassiouni, M. A., 1969. Technische Hinweise zur Säuberung von Ostracoden-Schalen. Paläont. Z., 43, p. 230–231.

Bassler, R. S. & Kellett, B., 1934. Bibliographic index of Paleozoic Ostracoda. Geol. Soc. America, Spec. Pap., 1, p. 1–500.

Becker, G., 1964. Palaeocopida (Ostracoda) aus dem Mitteldevon der Sötenicher Mulde (N-Eifel). Senckenbergiana lethaea, 45/1–4, p. 43–113.

–, 1969. Ostracoda aus dem Mitteldevon der Sötenicher Mulde (N-Eifel). Biostratigraphie, Paläökologie und taxonomische Bemerkungen. Senckenbergiana lethaea, 50, p. 239–271.

–, 1971. Paleoecology of Middle Devonian ostracodes from the Eifel region, Germany. In: Colloquium on paleoecology of ostracodes Pau 1970, p. 801–816 (H. J. Oertli, ed.), Bull. Centre Rech. Pau SNPA, 5 suppl.

Bless, M. J. M., 1968. On two hollinid ostracode genera from the Upper Carboniferous of northwestern Spain. Leidse Geol. Med., 43, p. 157–212.

– & Michel, M. Ph., 1965. An ostracode fauna from the Upper Devonian of the Gildar-Monto region (NW Spain). Leidse Geol. Med., 39, p. 269–271.

Boucot, A. J. & Johnson, J. G., 1968. Appalachian province early Devonian palaeogeography and brachiopod zonation. In: Intern. Symp. on the Devonian system Calgary 1967, vol. II, p. 1255–1268 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Boyde, A., 1970. Practical problems and methods in the three-dimensional analysis of scanning electron microscope images. In: Scanning electron microscopy, 1970. Proc. 3rd annual scanning electron microscope symposium, p. 105–112. ITT Research Inst. Chicago, Illinois.

Brouwer, A., 1964a. Devonian biostromes and bioherms of the southern Cantabrian Mountains, northwestern Spain. In: Deltaic and shallow marine deposits, p. 48–53 (L. M. J. U. van Straaten, ed.). Developments in sedimentology, 1. Elsevier, Amsterdam.

–, 1964b. Deux facies dans le Dévonien des Montagnes cantabriques meridionales. Bol. Inst. Estud. Asturianos, suppl. ciencias, 10, p. 3–10.

–, 1967. Le Dévonien inférieur des Montagnes cantabriques (Espagne du Nord-Ouest). In: Colloque Dévonien inférieur et ses limites Rennes 1964. Mém. BRGM, 33, p. 197–203.

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

– & Ginkel, A. C. van, 1964. La succession carbonifère dans la partie méridionale des Montagnes cantabriques (Espagne du Nord-Ouest). C. R. Vème Congr. Strat. Géol. Carbonifère Paris 1963, p. 307–319.

Bullard, E. e. a., 1965. The fit of the continent around the Atlantic. Phil. Trans., A, 258/1088, p. 41–51.

Burollet, P. F. & Manderscheid, G., 1968. Le Dévonien en Libye et en Tunisie. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 285–302 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Bultynck, P. L., 1968. Description revisée de la coupe-type du Couvinien à Couvin. In: Intern. Symp. on the Devonian system Calgary 1967, vol. II, p. 421–440 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Carls, P. & Gandl, J., 1969. Stratigraphie und Conodonten des Unter-Devons der östlichen Iberischen Ketten (NW-Spanien). N. Jahrb. Geol. Paläont. Abh., 132/2, p. 155–218.

Comte, P., 1959. Recherches sur les terrains anciens de la cordillère cantabrique. Mem. Inst. Geol. Miner., 60, p. 1–440.

Coo, J. C. M. de, 1969. De Santa Lucía Formatie. Internal report, Geological Institute Leiden, p. 1–26.

Cramer, F. H., 1964. Microplankton from three Palaeozoic formations in the province of León (NW-Spain). Leidse Geol. Med., 39, p. 255–361.

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

Fuchs, G., 1965. Geologie des Westteils der Hillesheimer Mulde (Mitteldevon, Eifel). Fortschr. Geol. Rheinl. Westf., 9, p. 323–448.

Gayet, J., 1967. Microfaune des Schistes et Calcaire à *Athyris undata* du Siegénien moyen dans le bassin de Laval. In: Colloque sur le Dévonien inférieur et ses limites Rennes 1964. Mém. BRGM, 33, p. 349–354.

Ginkel, A. C. van, 1965. Spanish Carboniferous fusulinids and their significance for correlation purposes. Leidse Geol. Med., 34, p. 172–225.

Groos, H., 1969. Mitteldevonische Ostracoden zwischen Ruhr und Sieg (Rechtsrheinisches Schiefergebirge). Göttinger Arb. Paläont., 1, p. 1–110.

Groot, G. E. de, 1963. Rugose corals from the Carboniferous of northern Palencia (Spain). Leidse Geol. Med., 29, p. 1–124.

Gründel, J., 1969. Ueber Beziehungen zwischen Lebensraum und Gehäusebau bei rezenten Ostracoden. N. Jahrb. Geol. Paläont. Mh., 1969-4, p. 220–231.

Gürich, G., 1896. Das Palaeozoicum im Polnischen Mittelgebirge. Russ. Kaiserl. Miner. Ges., Verh., 32, p. 1–539, St. Petersburg.

–, 1900. Nachträge zum Palaeozoicum im Polnischen Mittelgebirge. N. Jahrb. Miner. Geol. Palaeont., 13, p. 331–388.

Haas, W., 1970. Zur Phylogenie und Systematik der Asteropyginae und Beschreibung einiger neuer Arten (Phacopacea, Trilobita). Senckenbergiana lethaea, 51/2–3, p. 97–131.

Hartmann, G., 1964. The problem of polyphyletic characters in ostracods and its significance to ecology and systematics. In: Ostracods as ecological and palaeontological indicators. Pubbl. Sta. Zool. Napoli, 33 suppl., p. 32–44.

Henningsmoen, G., 1953. Classification of Paleozoic straight-hinged ostracods. Norsk Geol. Tidsskr., 31, p. 185–288.

Hessland, I., 1961. *Polyzygia*. In: Treatise on invertebrate paleontology, part Q-3, p. Q196–Q197 (R. C. Moore & Ch. W. Pitrat, eds.). Geol. Soc. America & Univ. Kansas Press.

Hollard, H., 1968. Le Dévonien du Maroc et du Sahara nord-occidental. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 203–244 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Jaanusson, V., 1957. Middle Ordovician ostracodes of central and southern Sweden. Bull. Geol. Inst. Univ. Uppsala, 37, p. 173–442.

Jordan, H., 1970. Die Ostracoden im Paläozoikum des zentralen Mitteleuropas. Freiberg. Forsch. H., C-265, Paläont., p. 7–40.

Jørgensen, N. O., 1970. Ultrastructure of some ostracods. Bull. Geol. Soc. Denmark, 20, p. 79–92.

Julivert, M. & Truyols, J., 1972. Geologia y estratigrafia de la region de Cabo Peñas (in prep.).

Kesling, R. V., 1951. Terminology of ostracod carapaces. Contr. Mus. Paleont. Univ. Michigan, 9, p. 93–171.

Khramov, A. N., 1968. Importance of palaeomagnetic data for Devonian stratigraphy and palaeography in the USSR. In: Intern. Symp. on the Devonian system Calgary 1967, vol. II, p. 1363–1370 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Krandiyevskij, V. S., 1968. Revisiya syemyejstva Thlipsuridae Ulrich, 1894. In: Paleontologiya i stratigrafiya inzhnego paleozoya Volyno-Podoliyi, p. 63–78 (V. S. Krandiyevskij, T. A. Ishenko & V. V. Kir'yanov, eds.). Akad. Nauk Ukraine, Kiev.

Krans, Th. F., 1965. Etudes morphologiques de quelques spirifères dévoniens de la Chaîne cantabrique (Espagne). Leidse Geol. Med., 33, p. 74–148.

Krebs, W., 1971. Devonian reef limestones in the eastern Rhenish Schiefergebirge. In: Sedimentology of parts of central Europe. Guidebook VIII, intern. sedimentological congress Heidelberg 1971, p. 45–81 (G. Müller, ed.). Waldemar Kramer Verlag, Frankfurt am Main.

Krömmelbein, K., 1953. Nachweis der polnischen Gattungen *Polyzygia* und *Poloniella* im Mittel-Devon der Eifel. Senckenbergiana, 34/1–3, p. 53–59.

–, 1954. Eine Ostrakoden-Fauna aus der Riff-Einlagerung im Plattenkalk der Paffrather Mulde (Givetium, Bergisches Land). Senckenbergiana, 34, p. 247–258.

–, 1955. *Polyzygia gürichiana* n. n. pro *Polyzygia gürichi* Krömmelbein 1953 (Ostracoda). Senckenbergiana lethaea, 35, p. 371.

Lecompte, M., 1968. Le Dévonien de la Belgique et le Nord de la France. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 15–52 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Le Fèvre, J., 1963. Microfaunes de l'Emsien et du Dévonien moyen de la région Ougarta–Saoura (Sahara). Rapp. internes SNPA, Dir. Explor. Prod., Centre Rech. Pau, 3 parts.

–, 1967. Succession d'associations d'ostracodes et de conodontes dans le Silurien, le Dévonien inférieur et l'Eifélien de quelques coupes de France et du Sahara. In: Colloque sur le Dévonien inférieur et ses limites Rennes 1964. Mém. BRGM, 33, p. 372–389.

–, 1971. Paleoecological observations on Devonian ostracodes from the Ougarta Hills (Algeria). In: Colloquium on paleoecology of ostracodes Pau 1970, p. 817–841 (H. J. Oertli, ed.). Bull. Centre Rech. Pau SNPA, 5 suppl.

Legrand, Ph., 1968. Le Dévonien du Sahara algérien. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 245–284 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Le Maître, D. & Magne, F., 1964. Le Dévonien des carrières du 'Banc Noir' et du 'Griset' (Boulonnais). Ann. Soc. Géol. Nord, 84, p. 129–131.

Lethiers, F., 1970. Quelques ostracodes frasniens du Bas-Boulonnais (France). Ann. Soc. Géol. Nord, 90/2, p. 69–75.

Llopis Lladó, N., 1962. Mapa geologico de Asturias. Hojas 1 & 2 Cabo Peñas. Inst. Estud. Asturianos, Diputacion prov., Oviedo, p. 1–116, 2 maps.

– e. a., 1968. Le Dévonien de l'Espagne. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 171–187 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

– & Valdés, J., 1961. Sobre la extension de la biozona de stringocefalidos en Asturias. Breviora Geol. Asturica, V/1–2, p. 17–34. Inst. Geol. aplicada, Oviedo.

Magne, F., 1964. Données micropaléontologiques et stratigraphiques dans le Dévonien du Boulonnais (France) et du Bassin de Namur (Belgique). Thèse 3me cycle, Paris. 2 parts.

Matern, H., 1929. Die Ostracoden des Oberdevons. 1. Teil Aparchitidae, Primitiidae, Zygobolbidae, Beyrichidae, Kloedenellidae, Entomidae. Preuss. Geol. Landesanstalt, N. F., 118, p. 1–100.

Matte, Ph., 1968. La structure de la virgation hercynienne de Galice (Espagne). Géol. Alpine, 44, p. 157–280, Grenoble.

Moore, R. C., 1961. Glossary of morphological terms applied to Ostracoda. In: Treatise on invertebrate paleontology, part Q-3, p. Q47–Q56 (R. C. Moore & Ch. W. Pitrat, eds.). Geol. Soc. America & Univ. Kansas Press.

Morkhoven, F. P. C. M. van, 1962. Post-Palaeozoic Ostracoda. Vol. I, p. 1–204. Elsevier, Amsterdam-London-New York.

Müller, G. W., 1894. Die Ostracoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Zool. Stat. Neapel, p. 1–404.

Pajchlowa, M., 1968. Le Dévonien de la Pologne. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 311–330 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Parga-Pondal, I., (ed.), 1967. Carte géologique du nord-ouest de la péninsule ibérique (hercynien et ante-hercynien) suivant accord de la première réunion sur la géologie de la Galice et du nord du Portugal 1965.

Pokorný, V., 1958. Grundzüge der zoologischen Mikropaläontologie, vol. II, p. 1–453, VEB Deutscher Verlag Wissenschaften, Berlin.

Polenova, E. N., 1952. Ostrakody verchnej casti zhivetskogo jarusa Russkoj platformy. In: Microfauna SSR, Trudy VNIGRI, 60/5, p. 65–176, Leningrad.

Poll, K., 1963. Zur Stratigraphie des Altpaläozoikums von Belmonte (Asturien, Nordspanien). N. Jahrb. Geol. Paläont., Abh., 117, p. 235–250.

Přibyl, A., 1953. Skořepatci polského středního devonu (givetu) z profilu Grzegorzewice – Skały v horách Svatokřížských. Sbornik, Ústředního ústavo geologického, XX, p. 233–344.

Rácz, L., 1964. Carboniferous calcareous Algae and their associations in the San Emiliano and Lois–Ciguera Formations (prov. León, NW-Spain). Leidse Geol. Med., 31, p. 1–112.

Radig, F., 1961. Zur Stratigraphie des Devons im Asturien. Geol. Rundschau, 51, p. 249–267.

Reijers, T. J. A., 1972. Facies and diagenesis of the Devonian Portilla Limestone Formation between the river Esla and the Embalse de la Luna, Cantabrian Mountains. Leidse Geol. Med., 47/2, p. 163–249.

Rzhonsnitskaya, M. A., 1968. Devonian of the USSR. In: Intern. Symp. on the Devonian system Calgary 1967, vol. I, p. 331–348 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Schmidt, E. A., 1941. Studien im Böhmischen Caradoc (Zahoran-Stufe). 1. Ostrakoden aus den Bohdalecschichten und über die Taxonomie der Beyrichiacea. Senckenb. Naturf. Gesell., Abh., 454, p. 1–96.

Sitter, L. U. de & Boschma, D., 1966. Explanation geological map of the Palaeozoic of the Southern Cantabrian Mountains 1:50 000, sheet 1 Pisuerga. Leidse Geol. Med., 31, p. 191–238.

Sleumer, B. H. G., 1969. Devonian stromatoporoids of the Cantabrian Mountains (Spain). Leidse Geol. Med., 44, p. 1–136.

Sobolev, D., 1909. Srednij devon Kielecko-Sandomirskogo krjasha. Materialien Geologie Russlands. Russ. Kaiserl. Miner. Ges., Verh., 24, p. 1–536, St. Petersburg.

Sohn, I. G., 1956. The transformation of opaque calcium carbonate to translucent calcium fluoride in fossil Ostracoda. Jour. Paleont., 30, p. 113–114.

Struve, W. & 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.

Swartz, F. M., 1936. Revision of the Primitiidae and Beyrichiidae with new Ostracoda from the Lower Devonian, Pennsylvania. Jour. Paleont., 10/7, p. 541–586.

Sylvester-Bradley, P. C., 1961. Subordo Metacopa. In: Treatise on invertebrate paleontology, part Q-3, p. Q358–Q359 (R. C. Moore & Ch. W. Pitrat, eds.). Geol. Soc. America & Univ. Kansas Press.

–, 1971. The reaction of systematics to the revolution in micropalaeontology. In: Scanning electron microscopy, p. 95–112. (V. H. Heywood, ed.). Systematics Association, Spec. Vol. 4. Academic Press, London-New York.

– & Benson, R. H., 1971. Terminology for surface features in ornate ostracodes. Lethaia, 4/3, p. 249–286.

Tarlo, Halstead L. B., 1968. Major faunal provinces in the Old Red Sandstone of the northern hemisphere. In: Intern. Symp. on the Devonian system Calgary 1967, vol. II, p. 1231–1238 (D. H. Oswald, ed.). Alberta Soc. Petrol. Geol., Calgary.

Ulrich, E. O., 1894. The Lower Silurian Ostracoda of Minnesota. Minnesota Geol. Nat. Hist. Surv., Rep., vol. 3/2, p. 629–693.

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.

Weyant, M., 1966. Représentants de quelques familles d'ostracodes du Dévonien inférieur de la Normandie (Leperditiidae, Bolliidae, Arcyzonidae, Bassleratiidae, Kloedenellidae, Thlipsuridae, incertae familiae). Bull. Soc. Linn. Normandie, 10/7, p. 117–141.

Winkler Prins, C. F., 1968. Carboniferous Productidina and Chonetidina of the Cantabrian Mountains (NW Spain): Systematics, stratigraphy and palaeoecology. Leidse Geol. Med., 43, p. 41–126.

Winter, J., 1969. Zur Alterstellung des Mühlwäldchen-Mergels der Gerolsteiner Mulde – ein Vorkommen von Stringocephalus im Ober-Eifelium der Eifel. N. Jahrb. Geol. Paläont., Abh., 132/3, p. 333–354.

Zagora, K., 1968. Ostracoden aus dem Grenzbereich Unter-/Mitteldevon von Ostthüringen. Geologie, 17, Beih., 62, p. 1–91.

Zagora, I. & Zagora, K., 1968. Die Ostracodengemeinschaften des Unter- und Mitteldevons von Ostthüringen. Ber. deutsch. Ges. Geol. Wiss., Reihe A, Geol. Paläont., 13/2, p. 185–190.

Zanina, I. E., Zaspelova, V. S. & Polenova, E. N., 1960. Nadsyemyejstva Drepanellacea. In: Tschlenistonogye trilobitobrasnye i rakoobrasnye, Osnovy Palaeontologii, p. 314–320 (E. N. Chernysheva, ed.). Akad. Nauk SSSR, Moscow.

PLATES

PLATE I

I–1a, b and c. *Polyzygia kroemmelbeini*. Left valve. STP/Mi. 72–1. Llamoso, Asturias, Spain.

I–1a. Lateral view. x95.

I–1b. Ventral view. Note the sharp posterior ledge and second-order reticulation. x85.

I–1c. Dorsal view. x85.

I–2. *Polyzygia kroemmelbeini*. Left valve. STP/Mi. 72–2. Llamoso, Asturias, Spain. Interior view. M= muscle scar. x95.

I–3a and b. *Polyzygia kroemmelbeini*. Carapace. STP/Mi. 72–3. Prendes, Asturias, Spain.

I–3a. Dorsal view. Note the overlap of the right valve over the left valve in the hinge area. x100.

I–3b. Ventral view. Note the second-order reticulation and marginal ridges. x105.

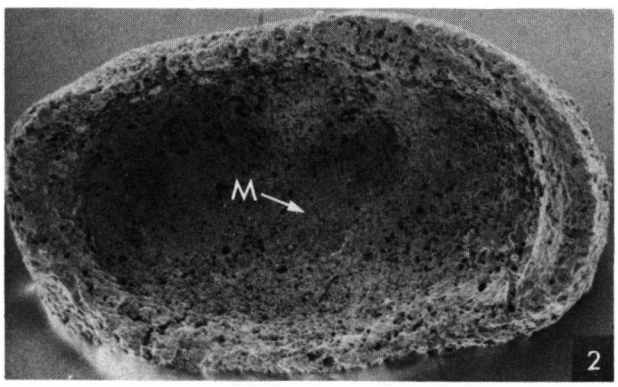
I–4. *Polyzygia kroemmelbeini*. Carapace. STP/Mi. 72–4. Prendes, Asturias, Spain. Right lateral view. x95.

I–5a and b. *Polyzygia kroemmelbeini*. Right valve. STP/Mi. 72–5. Llamoso, Asturias, Spain.

I–5a. Interior view. CR= contact ridge. x110.

I–5b. Dorsal view. AT= anterior hinge tooth; PT= posterior hinge tooth. x105.


1a



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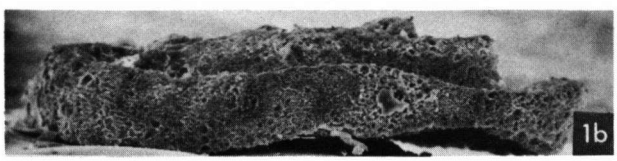
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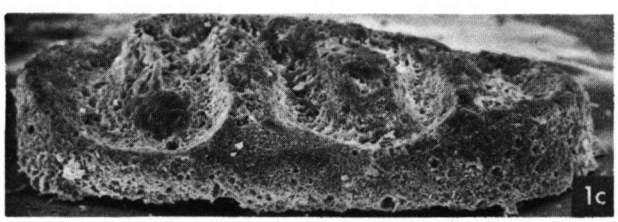
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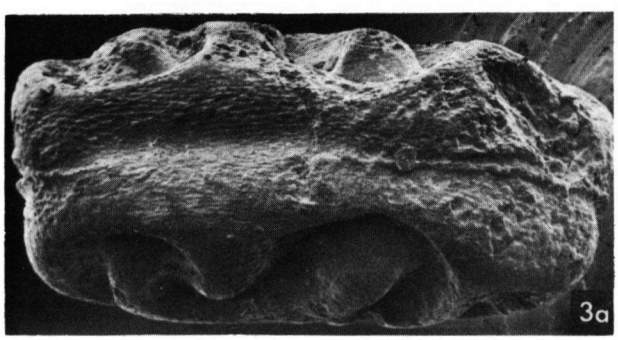
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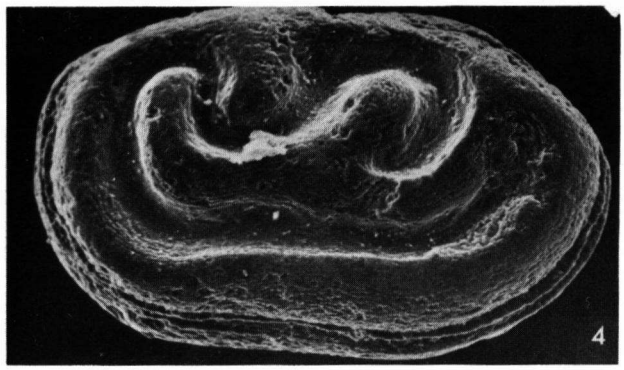
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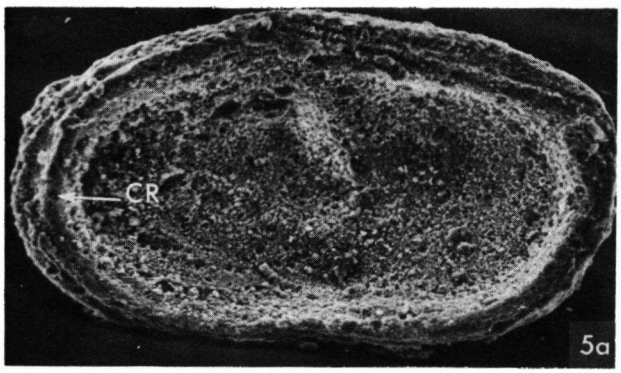

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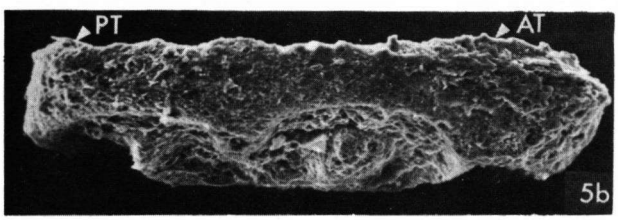

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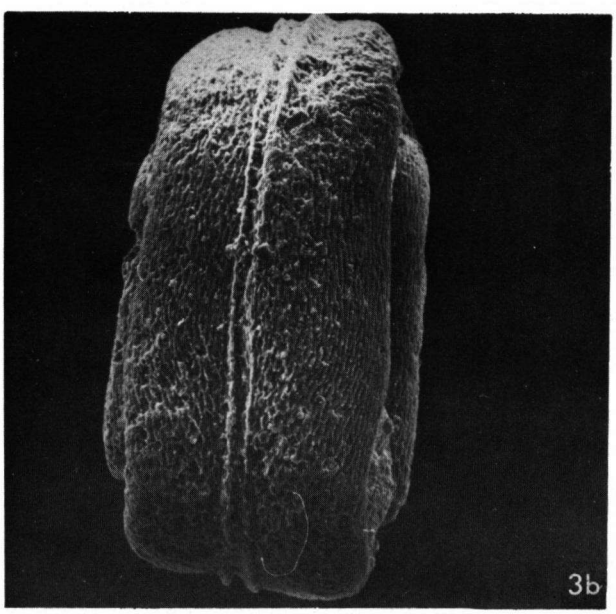
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PLATE II

II–1. *Polyzygia kroemmelbeini.* Carapace. STP/Mi. 72–4. Prendes, Asturias, Spain. Dorsal view, hinge area. Note the overlap of right valve over left valve. x190.

II–2. *Polyzygia kroemmelbeini.* Carapace. STP/Mi. 72–3. Prendes, Asturias, Spain. Detail of the area between S_2, S_3 and S_v of the left valve. The muscle scar pattern can be seen interfering with the pattern of reticulation. x320.

II–3. *Polyzygia kroemmelbeini.* Right valve. STP/Mi. 72–5. Llamoso, Asturias, Spain. Interior view. Note the concavity of the contact ridge in the mid-ventral area. AT= anterior hinge tooth; HL= central hinge list; PT= posterior hinge tooth. x160.

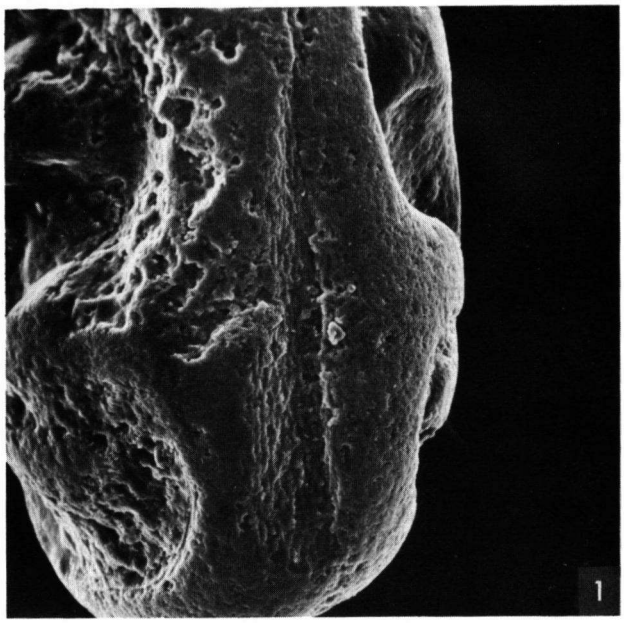
II–4a, b, c and d. *Polyzygia kroemmelbeini.* Carapace. STP/Mi. 72–6. Prendes, Asturias, Spain.

II–4a. Right ventro-lateral view. Note the smoothness of the sculpture and undulating marginal ridge. x90.

II–4b. Detail of the central-anterior area of the marginal ridge of the right valve. Note pores. x800.

II–4c. Detail of II–4b, showing a pore. x3600.

II–4d. Detail of the antero-ventral region. Note second-order reticulation with elongated and polygonal fossae. x185.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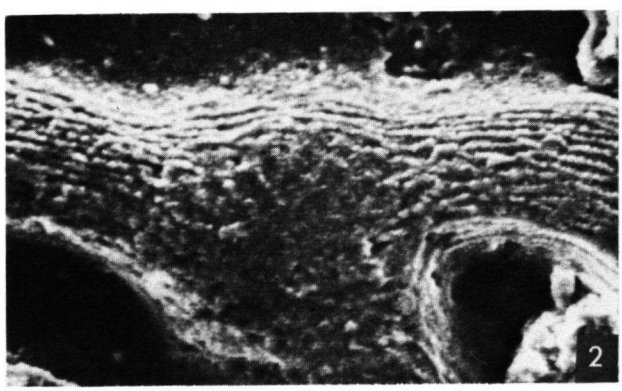
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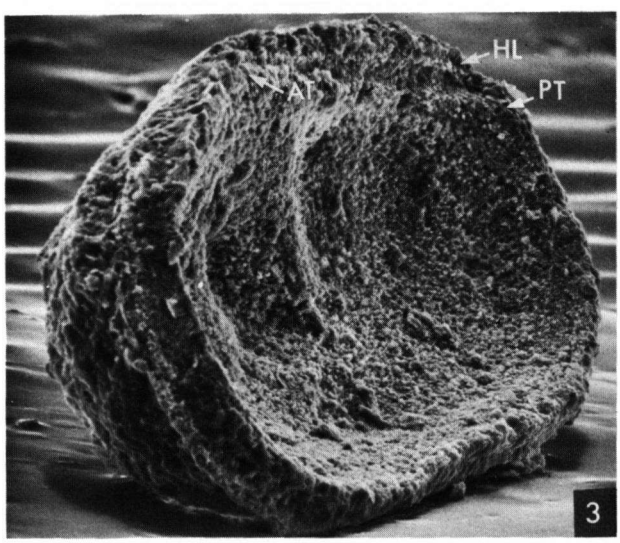

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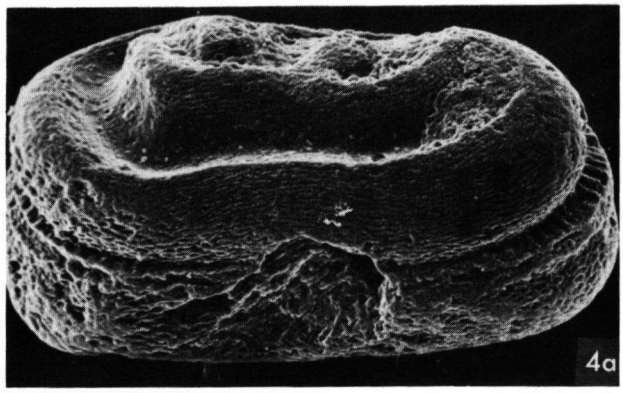
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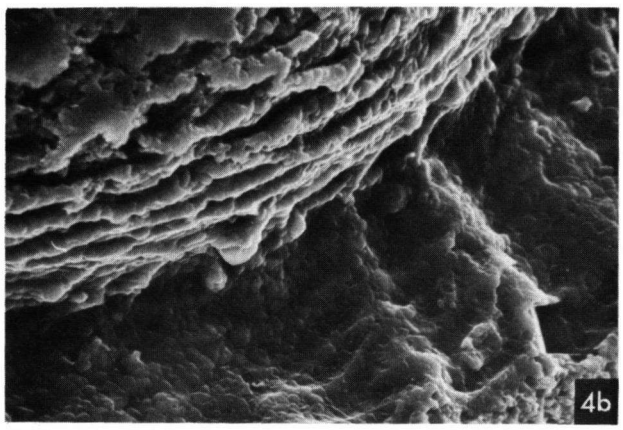
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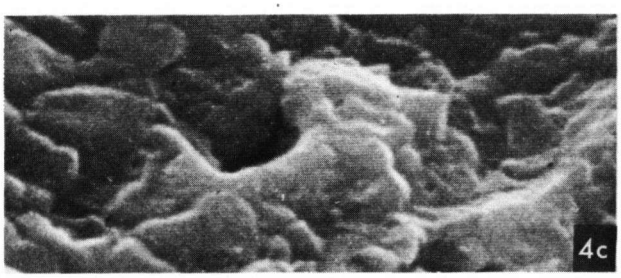
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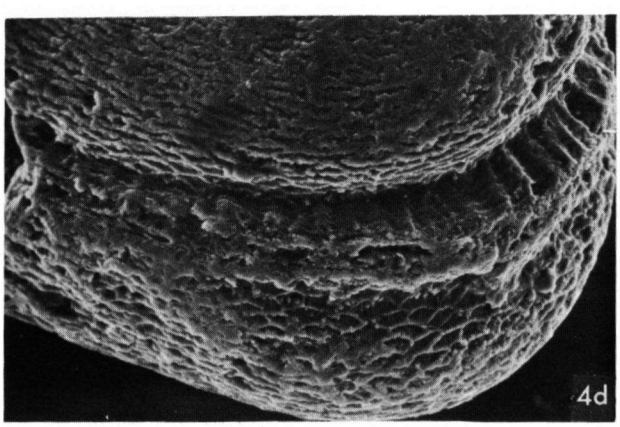
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PLATE III

III–1. *Polyzygia kroemmelbeini.* Carapace. STP/Mi. 72–3. Prendes, Asturias, Spain. Anterior view. LV = left valve; RV = right valve. x170.

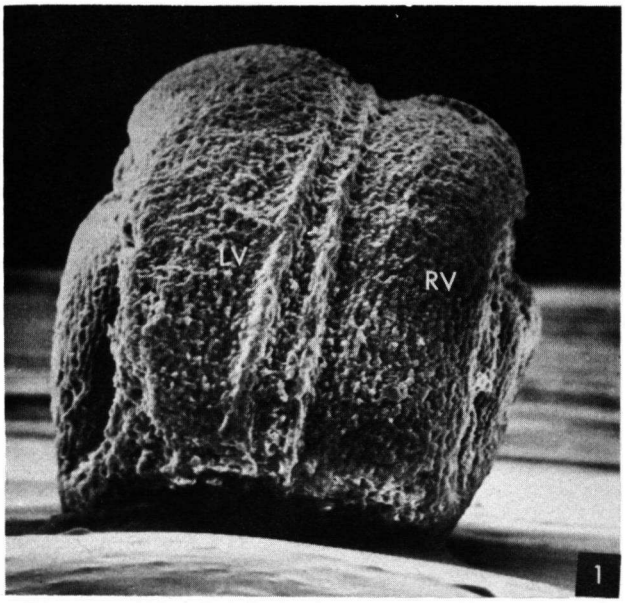
III–2. *Polyzygia kroemmelbeini.* Left valve. STP/Mi. 72–6. Llamoso, Asturias, Spain. Interior view. Note the narrow groove in the hinge bar. x95.

III–3. *Polyzygia kroemmelbeini.* Carapace. Prendes, Asturias, Spain. Transversal cross section. Note the smoothness of the inner surface. x185.

III–4. *Polyzygia kroemmelbeini.* Carapace. STP/Mi. 72–4. Prendes, Asturias, Spain. Posterior view. Note the overlap of the right valve over the left valve in the hinge area on the dorsal side. LV= left valve; RV= right valve. x95.

III–5. *Polyzygia kroemmelbeini.* Right valve. STP/Mi. 72–7. Llamoso, Asturias, Spain. Interior view, detail of the hinge area. Note the wide hinge groove with the narrow central list. x230.

III–6. *Polyzygia kroemmelbeini.* Çarapace. Prendes, Asturias, Spain. Longitudinal cross section. Note the marginal ridges and the gap between them. x125.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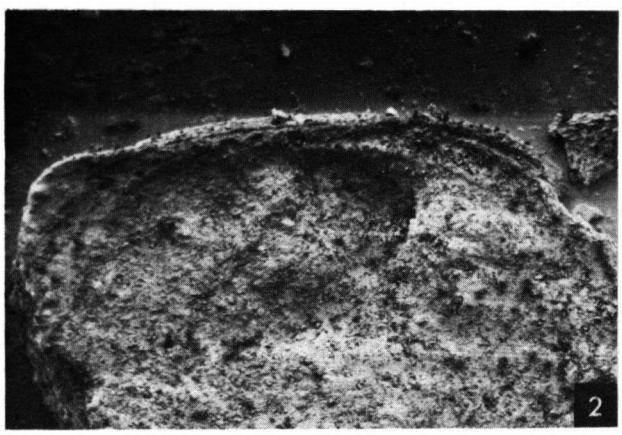
RV
1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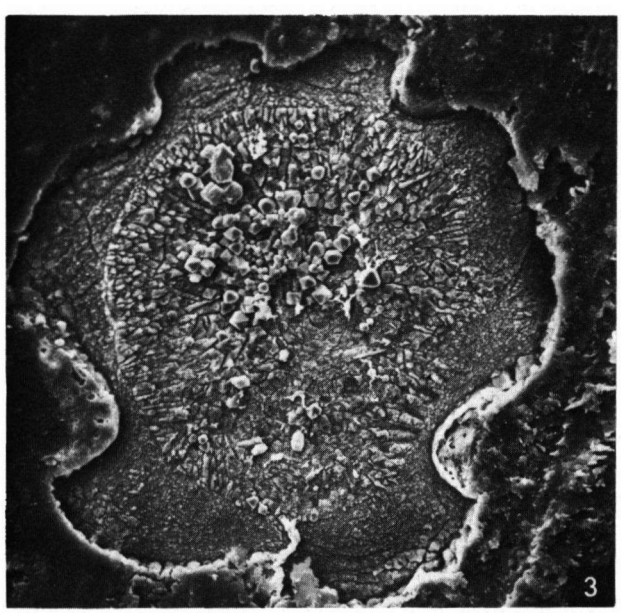
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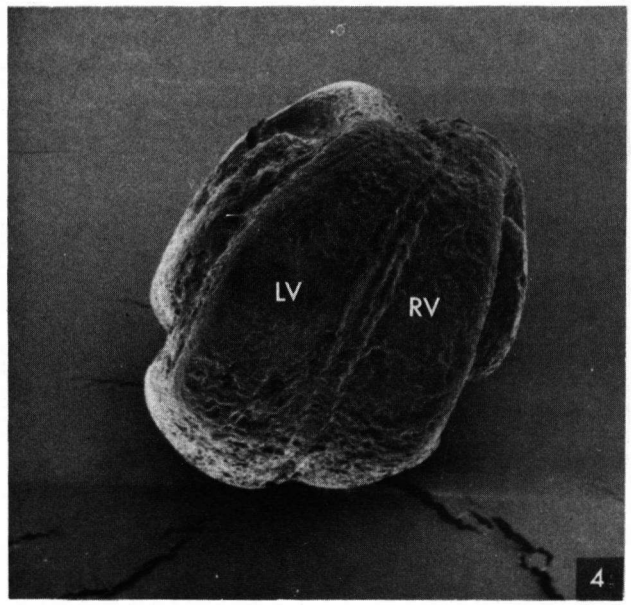
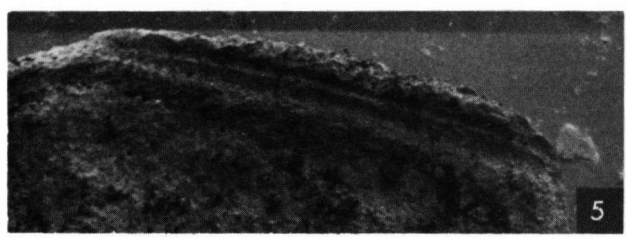

LV
RV
4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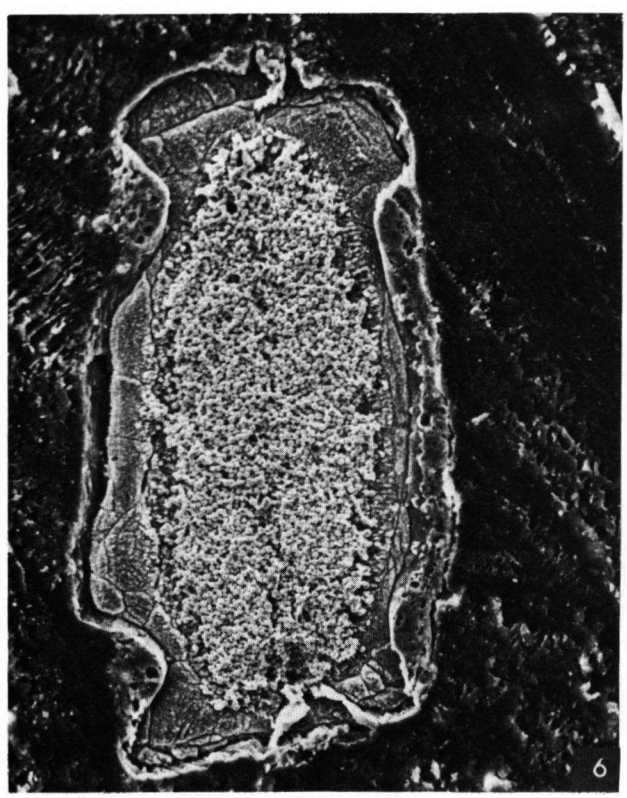
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PLATE IV

IV–1. *Polyzygia vinea.* Left valve. STP/Mi. 72–8. Paratype. La Vid, León, Spain. Lateral view. x85.

IV–2. *Polyzygia vinea.* Right valve, immature specimen. STP/Mi. 72–9. La Vid, León, Spain. Ventral view. Note the sharp posterior ledge. x60.

IV–3a, b, c, d and e. *Polyzygia vinea.* Carapace. STP/Mi. 72–10. Holotype. La Vid, León, Spain.

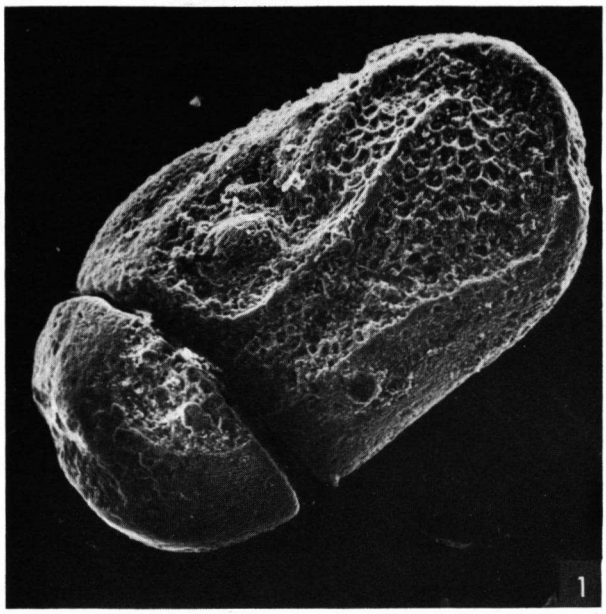
IV–3a. Detail of the first-order reticulation in the posterior part of the valve. Note pore upon murus. x2400.

IV–3b. Detail of the first-order reticulation with a pore within a fossa; posterior part of the right valve. x4400.

IV–3c. Right lateral view. x65.

IV–3d. Ventral view. x70.

IV–3e. First-order reticulation in the posterior half of the right valve. x220.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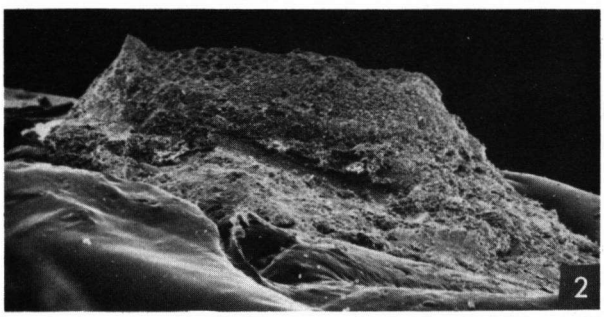
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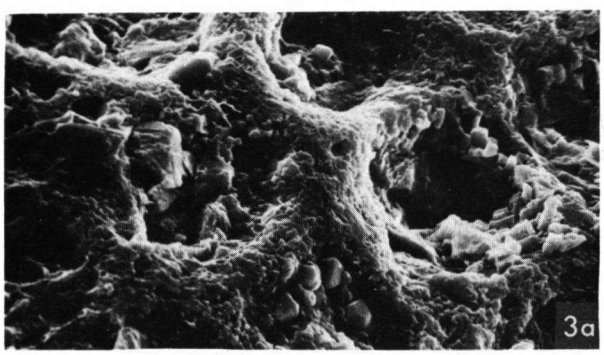
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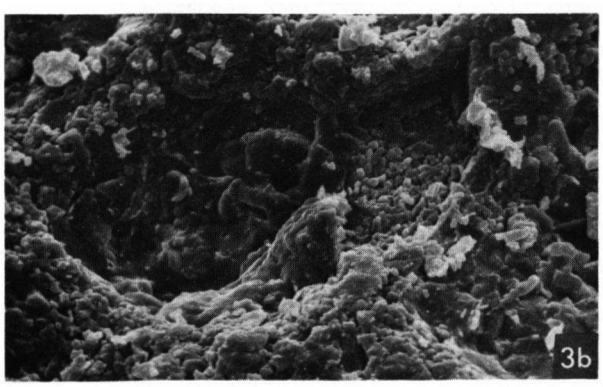
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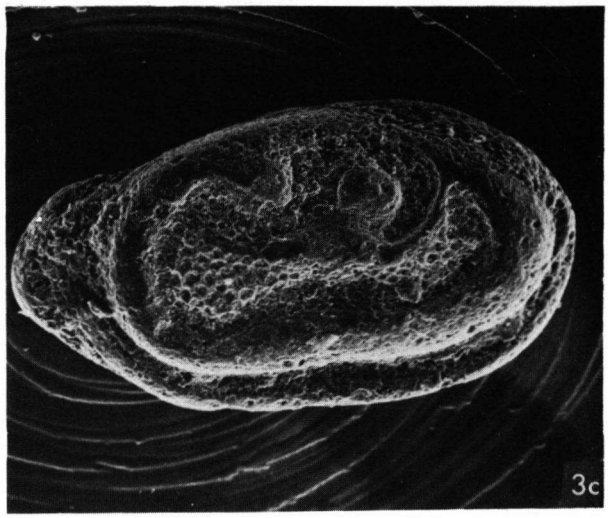
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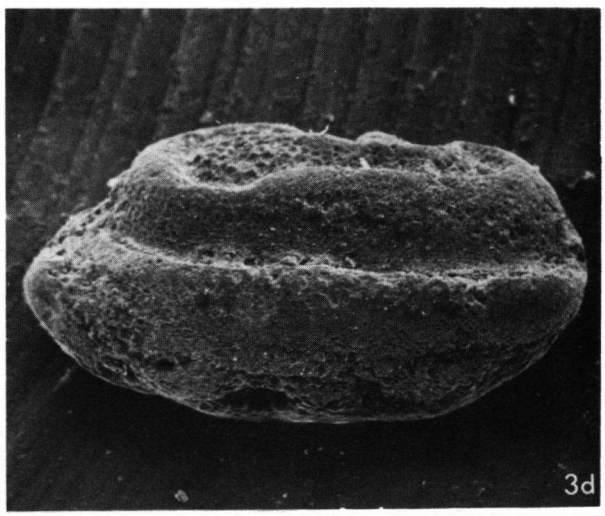
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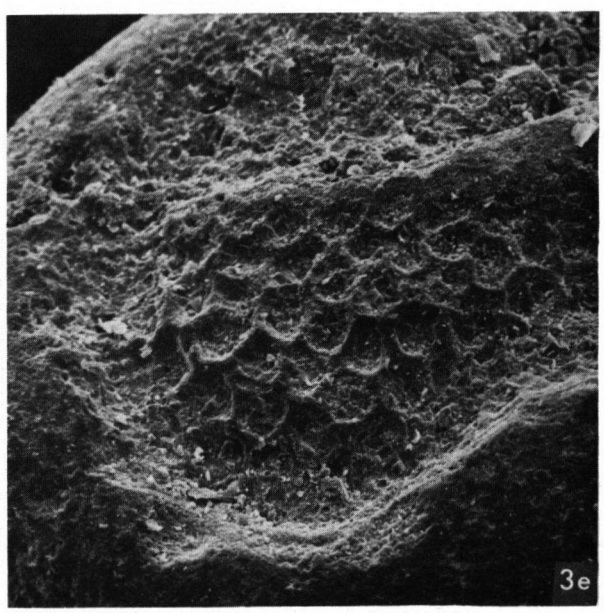

3e

PLATE V

V–1. *Polyzygia vinea.* Carapace. STP/Mi. 72–10. Holotype. La Vid, León, Spain. Detail of the ventral border. Second-order reticulation. Note the variation in outline of the fossae. x235.

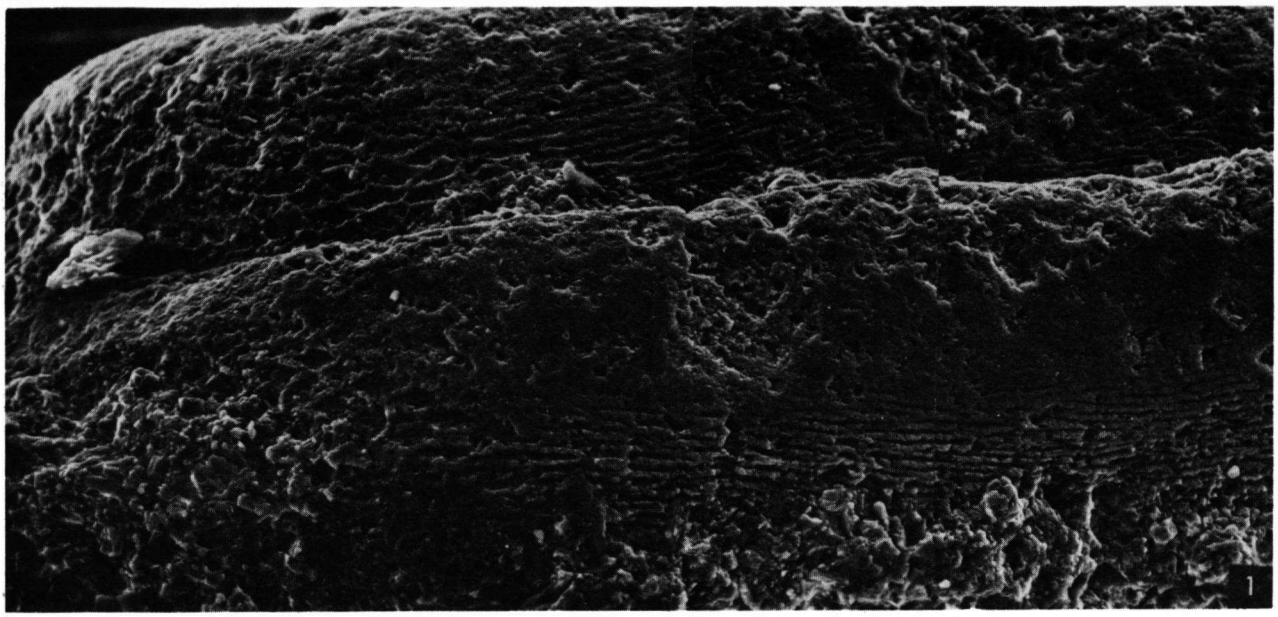
V–2. *Polyzygia vinea.* Left valve. STP/Mi. 72–8. Paratype. La Vid, León, Spain. Detail of the ventral border. Note the extremely elongated fossae. x400.

V–3a and b. *Polyzygia* sp. *A*. Half an external mould of the left valve. STP/Mi. 72–11. Locality unknown, province of León, Spain.

V–3a. Lateral view. Compare with V–3b which shows the photographical replica. x100.

V–3b. Photographical replica of the specimen figured in V–3a. In order to see the exact relief the photo has been turned. x100.

V–4. *Polyzygia* sp. *A*. Right valve. STP/Mi. 72–12. La Vid, León, Spain. Lateral view. Note the narrow remaining edge between S_5 and S_4. x125.



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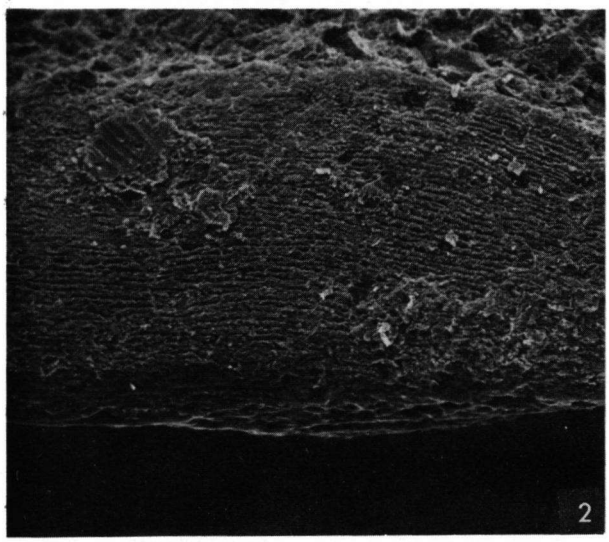

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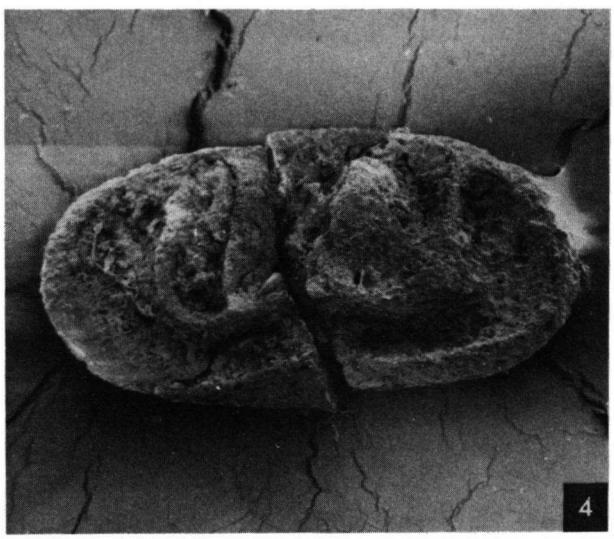

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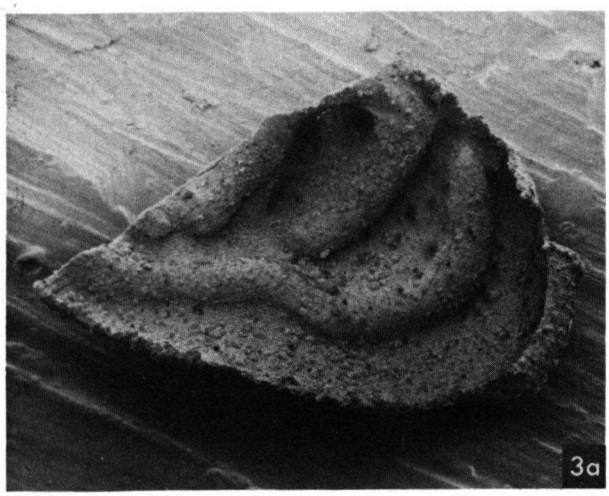


3a

3b

PLATE VI

VI–1. *Polyzygia normannica.* Right valve. STP/Mi. 72–13. La Vid, León, Spain. Lateral view. x120.

VI–2a and b. *Polyzygia normannica.* Left valve. STP/Mi. 72–14. La Vid, León, Spain.

VI–2a. Ventral view. Note the faintly visible second-order reticulation. x90.

VI–2b. Dorsal view. x105.

VI–3a and b. *Polyzygia normannica.* Left valve. STP/Mi. 72–15. La Vid, León, Spain.

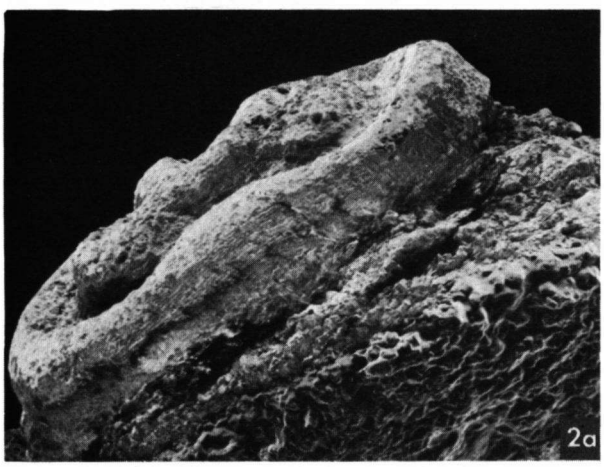
VI–3a. Detail of the first-order reticulation. Note the almost hexagonal outline of the fossae. x445.

VI–3b. Detail of posterior half of the valve. Note the fading out of the S_4. x380.

VI–4. *Polyzygia normannica.* Left valve. STP/Mi. 72–45. La Vid, León, Spain. Lateral view. x85.


1


4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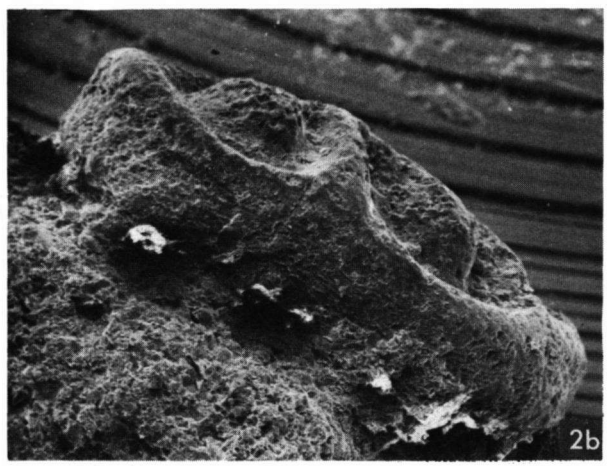
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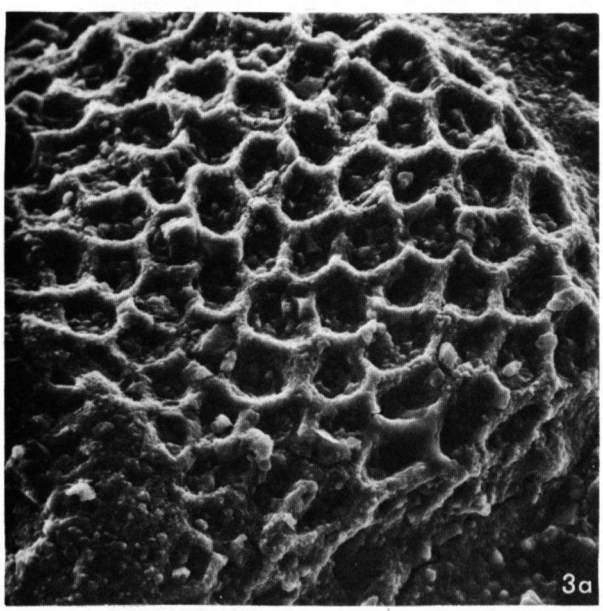
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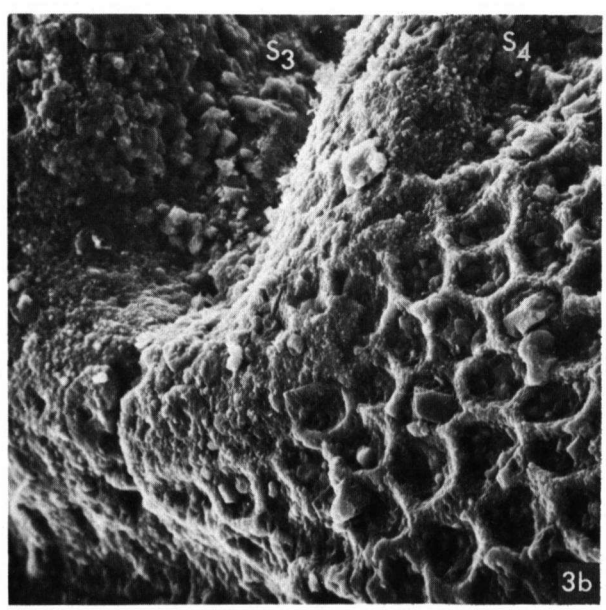


3b

PLATE VII

VII–1. *Polyzygia beckmanni.* Carapace. STP/Mi. 72–13. Refrath, W. Germany. Left lateral view. Note the undulating marginal ridge and the posterior ledge which dorsally terminates in a spine. x95.

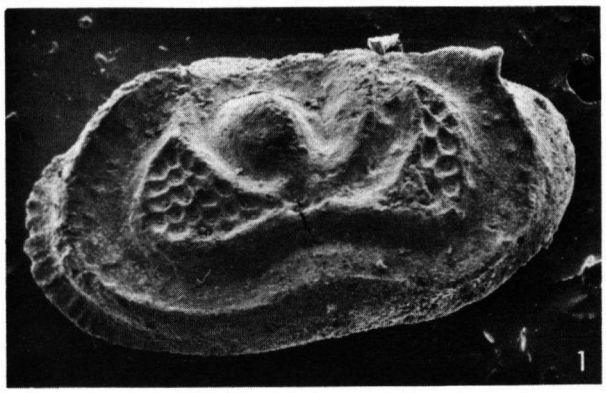
VII–2. *Polyzygia beckmanni.* Carapace. STP/Mi. 72–14. Refrath, W. Germany. Ventral view. x108.

VII–3. *Polyzygia beckmanni.* Left valve. STP/Mi. 72–15. Refrath, W. Germany. A detail of the first-order reticulation in the anterior part of the valve. x1450.

VII–4. *Polyzygia beckmanni.* Carapace. STP/Mi. 72–16. Refrath, W. Germany. Right lateral view. x120.

VII–5. *Polyzygia beckmanni.* Carapace. STP/Mi. 72–17. Refrath, W. Germany. Dorsal view. Note the backward directed spines on the right valve; these are extensions of the posterior ledge. x130.

VII–6. *Polyzygia beckmanni.* Carapace. STP/Mi. 72–13. Refrath, W. Germany. A detail of the first-order reticulation in the anterior part of the valve. Note the roundness of the fossae. x570.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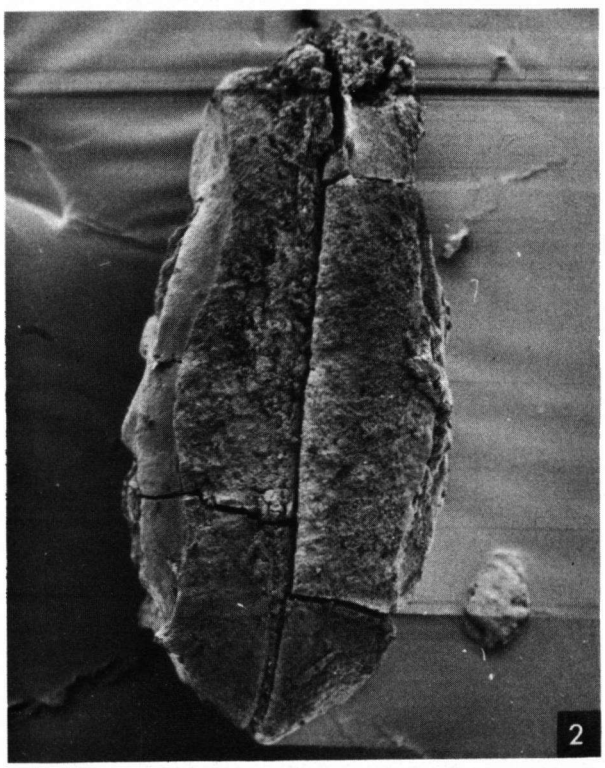
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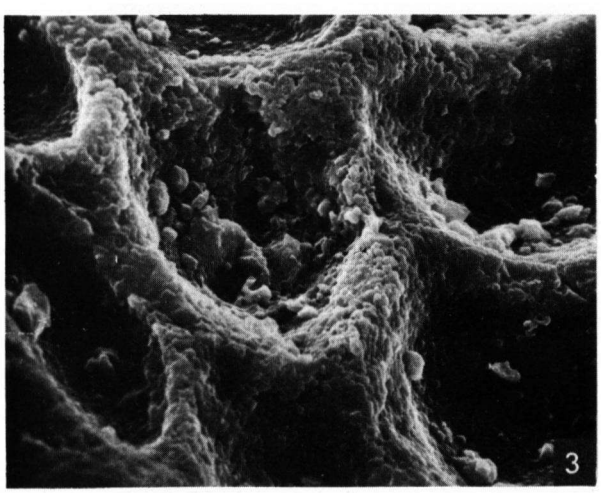
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4


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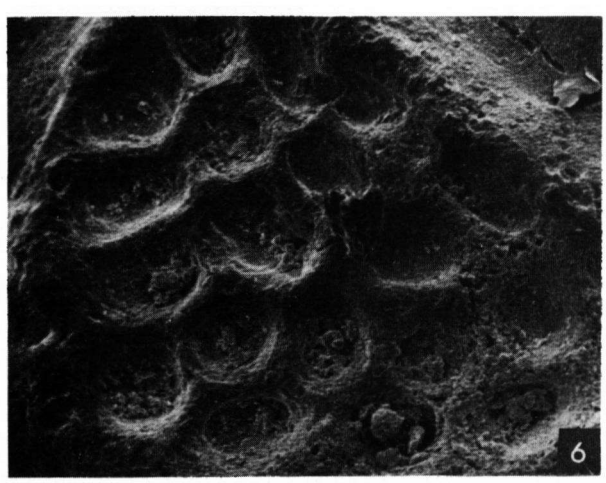
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PLATE VIII

VIII–1. *Polyzygia beckmanni.* Fragment of left valve. STP/Mi. 72–18. Refrath, W. Germany. Interior view. Note the muscle scar consisting of many small scars in the area between S_2 and S_3. M= muscle scar. x160.

VIII–2a and b. *Polyzygia beckmanni.* Broken carapace. STP/Mi. 72–19. Refrath, W. Germany.

VIII–2a. Interior view of the hinge area, posterior half. Note the hinge tooth of the right valve and the corresponding socket in the left valve. T= tooth; S= socket. x170.

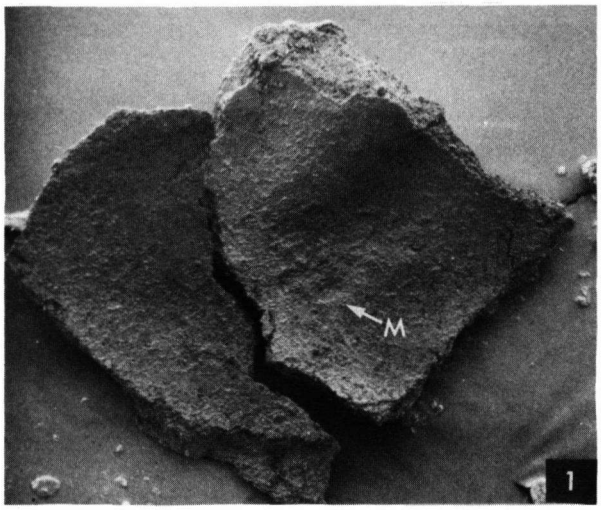
VIII–2b. Interior view of the hinge area. Posterior part of the right valve. T= tooth; G= groove. x150.

VIII–3a and b. *Polyzygia beckmanni.* Fragment of left valve. STP/Mi. 72–20. Refrath, W. Germany.

VIII–3a. Interior view of the anterior and ventral part of the valve. Note the contact groove which mid-ventrally is less deep. x150.

VIII–3b. Interior view of the ventral and anterior area of the valve. Note the contact groove and the undulating marginal ridge. x170.

VIII–4. *Polyzygia beckmanni.* Fragment of right valve. STP/Mi. 72–21. Refrath, W. Germany. Interior view. Detail of the mid-ventral area. x500.


M
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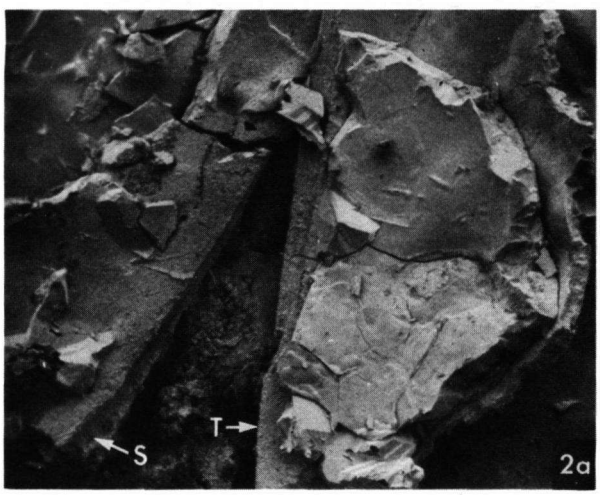
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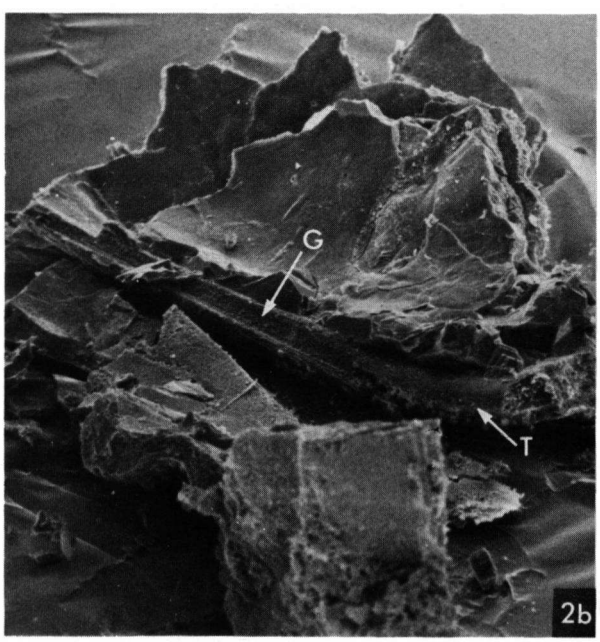
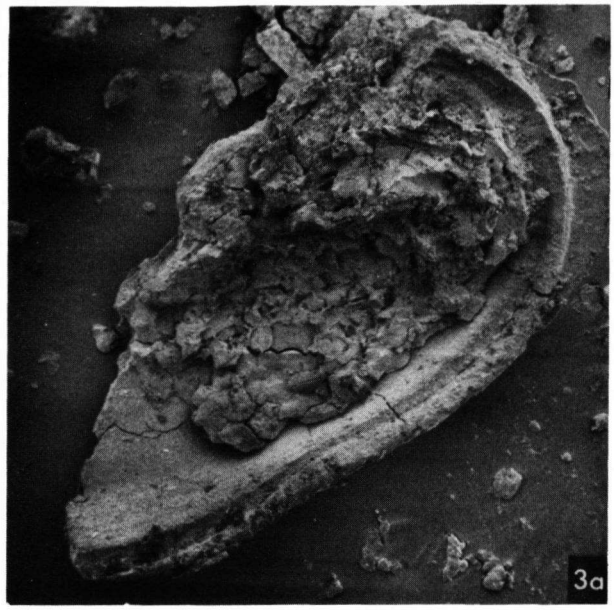
T
2a


G
T
2b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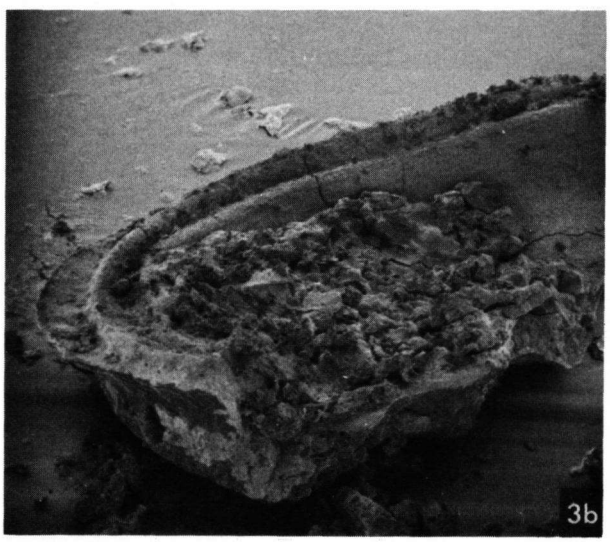
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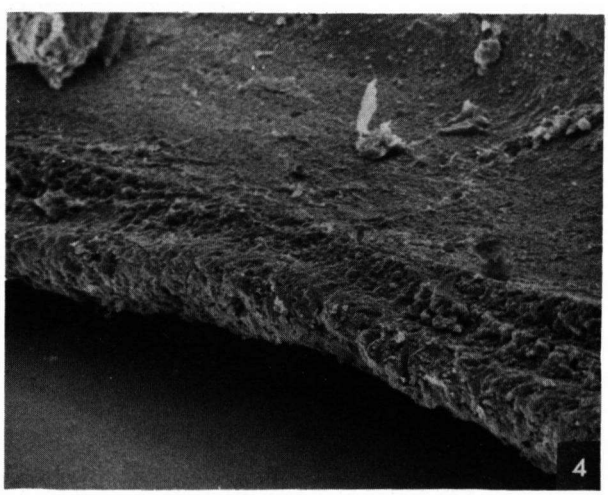
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PLATE IX

IX–1a and b. *Polyzygia beckmanni.* External mould of a right valve. STP/Mi. 72–22. Locality unknown, León, Spain.

IX–1a. Interior view. Compare with IX–1b which is the photographic replica. x100.

IX–1b. Photographic replica of the specimen shown in IX–1a. x100.

IX–2a, b and c. *Polyzygia beckmanni.* External mould of a left valve. STP/Mi. 72–23. Locality unknown, León, Spain.

IX–2a. Detail of the mid-ventral area. Note the 'negative' second-order reticulation. x700.

IX–2b. Interior view. Compare with IX–2c which is the photographic replica. x95.

IX–2c. Photographic replica of the specimen shown in IX–2b. x95.

IX–3a and b. *Polyzygia trigonata.* Left valve. STP/Mi. 72–24. Luanco, Asturias, Spain.

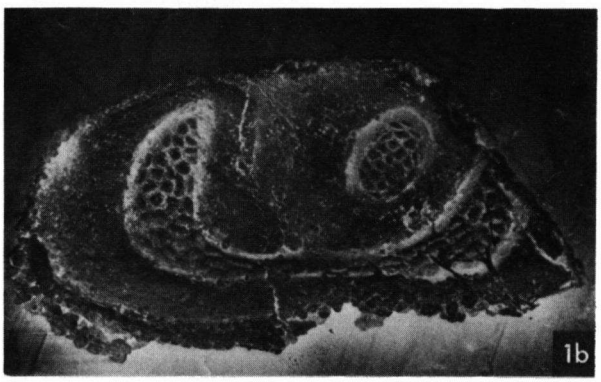
IX–3a. Ventral view. x110.

IX–3b. Dorsal view. x110.

IX–4. *Polyzygia trigonata.* Carapace. STP/Mi. 72–25. Perlora, Asturias, Spain. Tilted anterior view of the right valve. Note the weak ventral connection between S_2 and S_3. x75.


1a


2b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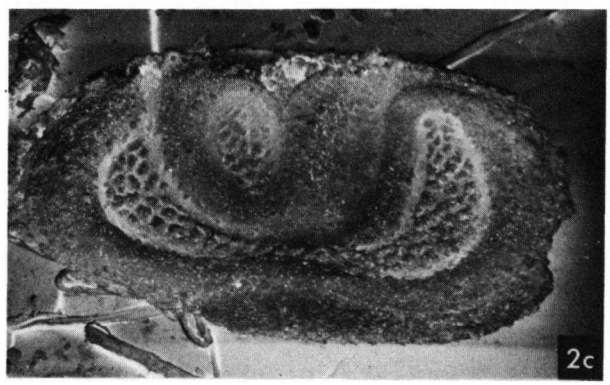
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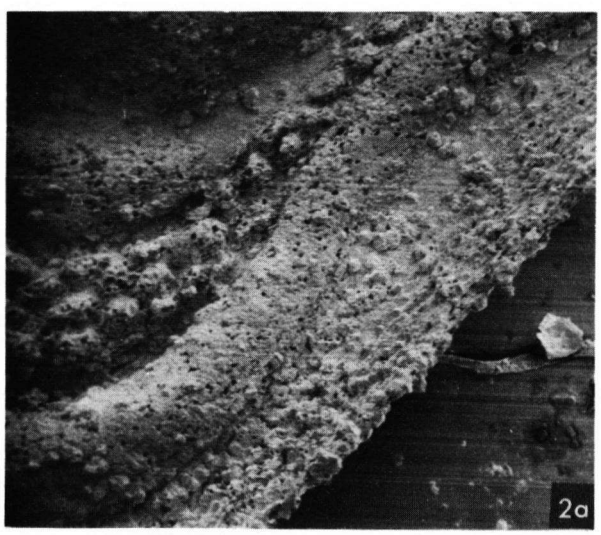
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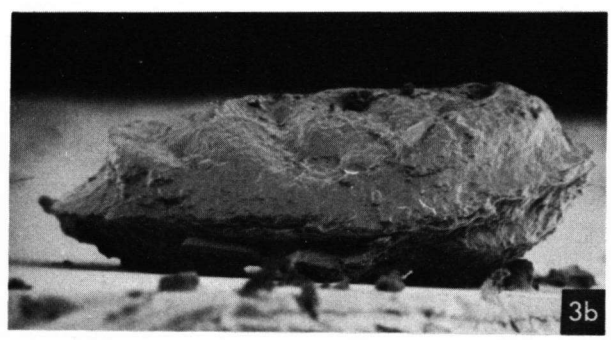
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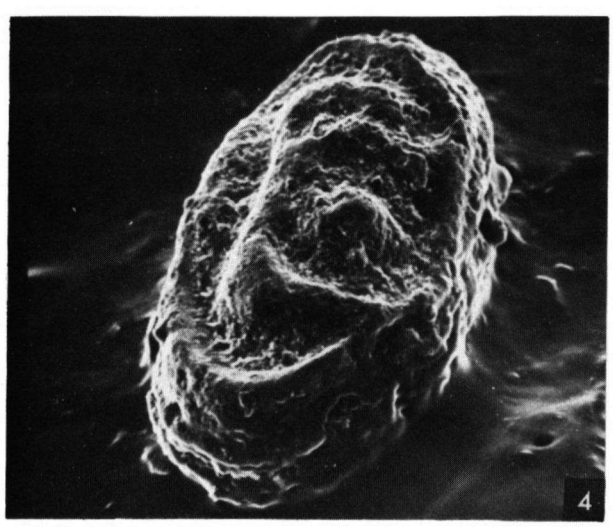
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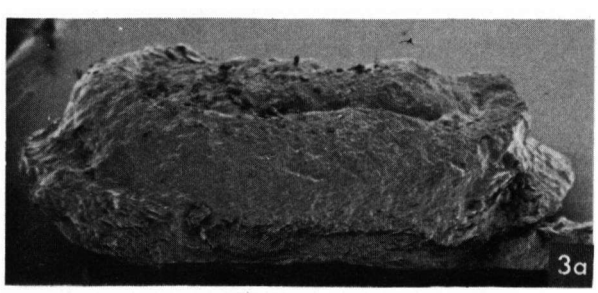

3a

PLATE X

X–1a, b and c. *Polyzygia insculpta insculpta.* Carapace. STP/Mi. 72–26. Luanco, Asturias, Spain.

X–1a. Left lateral view. x90.

X–1b. Right lateral view. x80

X–1c. Dorsal view. x90.

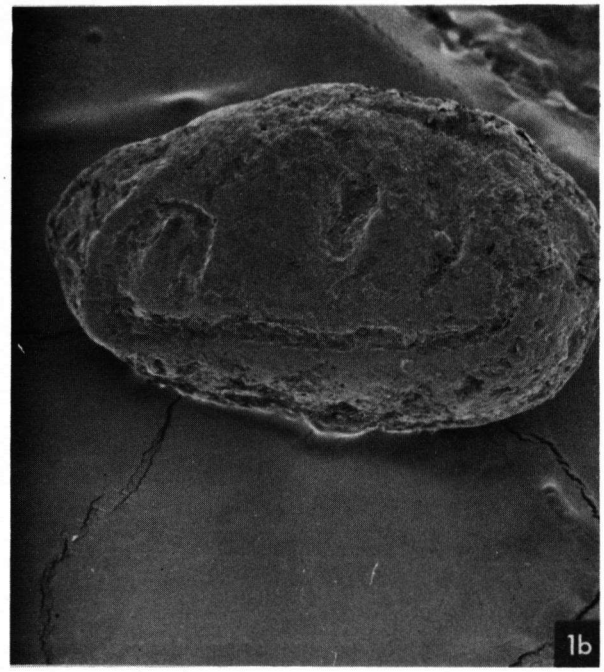
X–2a, b and c. *Polyzygia insculpta insculpta.* Carapace. STP/Mi. 72–27. Luanco, Asturias, Spain.

X–2a. Ventral view. x80.

X–2b. Anterior view. x135.

X–2c. Posterior view. x130.


1a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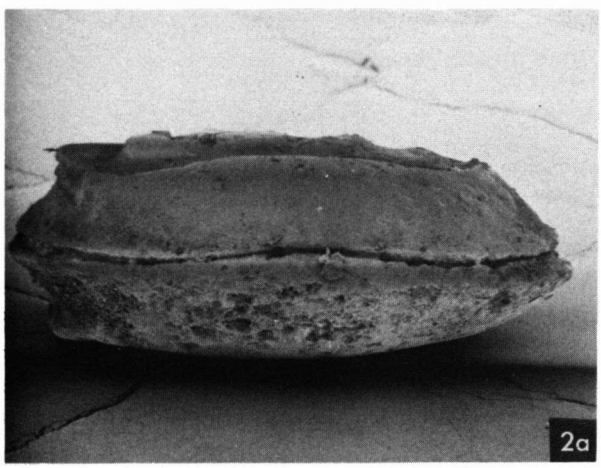

2a


1c


2b


2c

PLATE XI

XI–1a–h. *Polyzygia insculpta beckeri.* Carapace. STP/Mi. 72–28. Prendes, Asturias, Spain.

XI–1a. Left lateral view. Note that S_2 and S_3 are connected dorsally. x85.

XI–1b. Dorsal view. Note the posterior edge. Note the connections of S_2 and S_3 on both valves. x80.

XI–1c. Anterior view. Note the small lip in the mid-ventral part of the left valve which is indicated by an arrow. x145.

XI–1d. Detail of the mid-posterior region of the valve showing a pore. x2000.

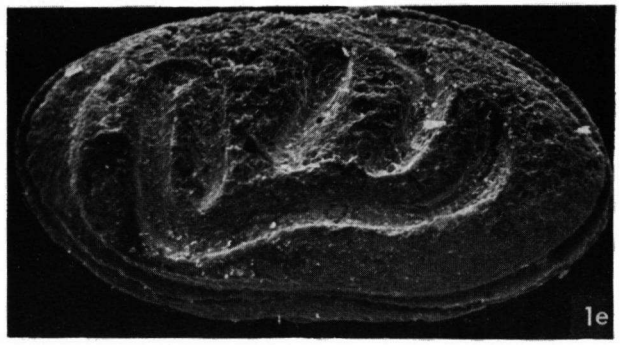
XI–1e. Right lateral view. Note that S_2 and S_3 are not connected. x85.

XI–1f. Ventral view. Note the small lip in the mid-ventral region of the left valve. x85.

XI–1g. Posterior view. The arrow indicates the overlap of the right valve in the hinge area. x180.

XI–1h. Detail of the mid-ventral border. Note the lip of the left valve which does not interrupt the marginal ridge of the right valve. x190.


1a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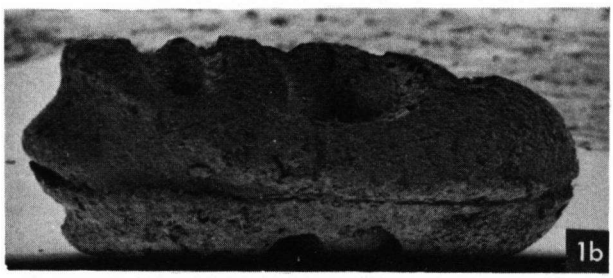
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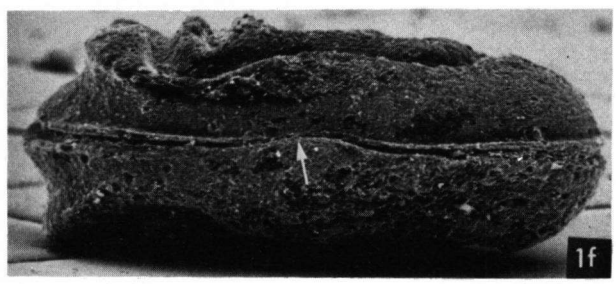
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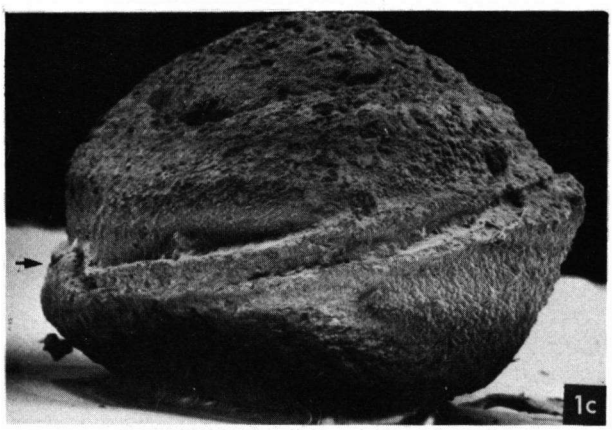
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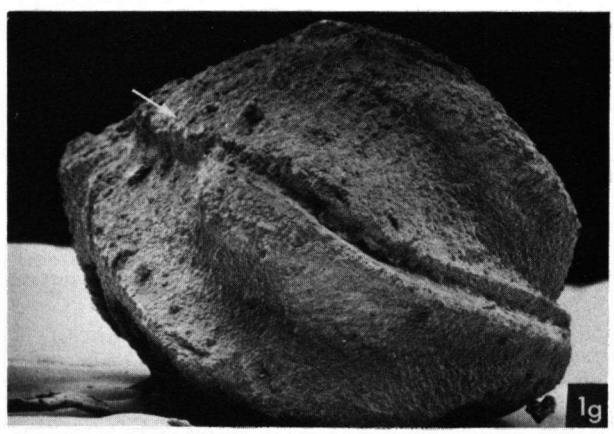
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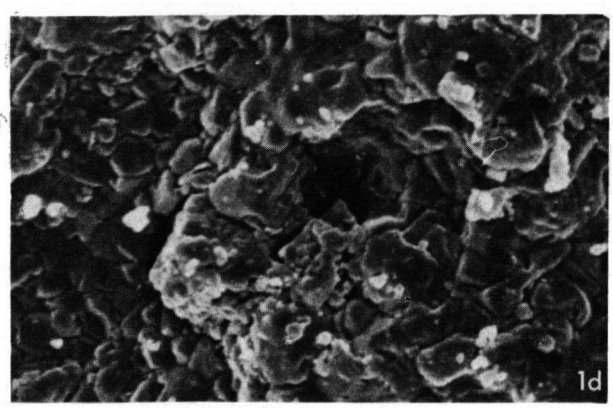

1d


1h

PLATE XII

XII–1a, b and c. *Polyzygia symmetrica.* Left valve. STP/Mi. 72–29. Luanco, Asturias, Spain.

XII–1a. Left lateral view. x110.

XII–1b. Dorsal view. x110.

XII–1c. Ventral view. x130.

XII–2. *Polyzygia symmetrica.* Right valve (pyritized). Accidentally destroyed in the SEM. Renanue, Spanish Pyrenees, Spain. x120.

XII–3a, b and c. *Polyzygia symmetrica.* Carapace. STP/Mi. 72–30. Skały, Holy Cross Mountains, Poland. From Gürich's type locality.

XII–3a. Left lateral view. x70.

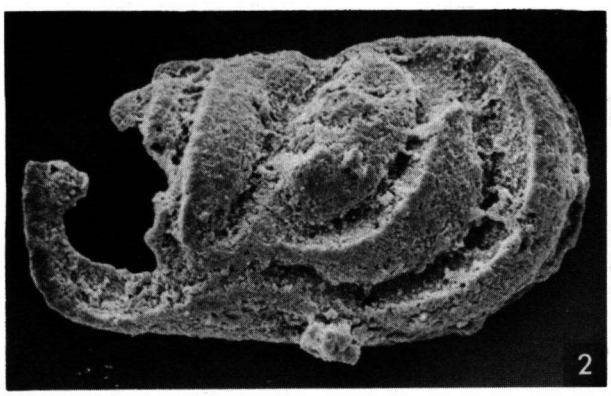
XII–3b. Ventral view. Second-order reticulation faintly visible. x65.

XII–3c. Detail of the mid-ventral border of the left valve. Second-order reticulation. x500.

XII–4. *Polyzygia trigonata.* Left valve. STP/Mi. 72–24. Luanco, Asturias, Spain. Left lateral view. Note the short triangular S_4. x95.


1a


3a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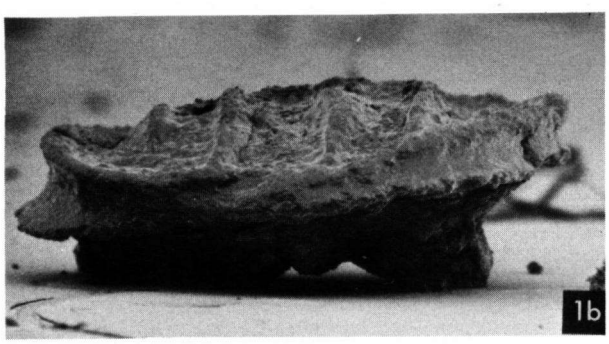
3b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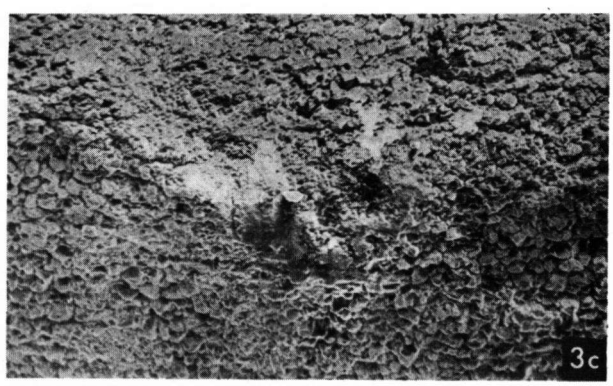
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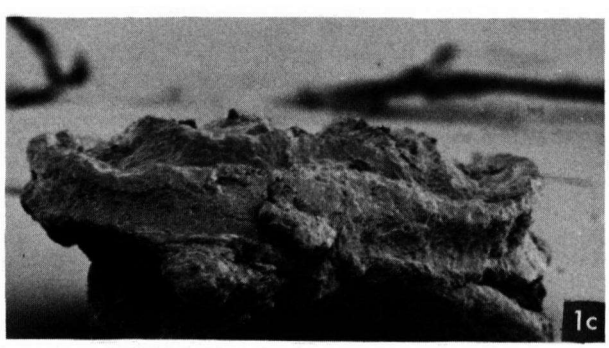

1c


4

PLATE XIII

XIII–1. *Polyzygia neodevonica.* Carapace. STP/Mi. 72–31. Nismes, Ardennes, Belgium. From Matern's type locality. Left lateral view. x85.

XIII–2. *Polyzygia neodevonica.* Left valve. STP/Mi. 72–32. Perlora, Asturias, Spain. Interior view. HS= hinge socket; HB= hinge bar. Note the narrow groove in the hinge bar. x85.

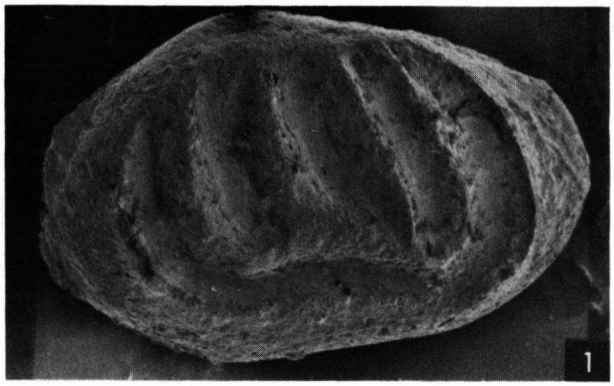
XIII–3. *Polyzygia neodevonica.* Carapace. STP/Mi. 72–33. Perlora, Asturias, Spain. x75.

XIII–4. *Polyzygia neodevonica.* Carapace of juvenile instar. Accidentally destroyed in the SEM. Luanco, Asturias, Spain. Pore on the area between S_4 and S_5. Same specimen figured on Pl. XIV–2. x2000.

XIII–5. *Polyzygia neodevonica.* Carapace. STP/Mi. 72–34. Perlora, Asturias, Spain. Right lateral view. x95.

XIII–6. *Polyzygia neodevonica.* Right valve. STP/Mi. 72–35. Luanco, Asturias, Spain. Interior view. Note the marginal ridge which broadens along the anterior border and the contact ridge which is slightly concave in the mid-ventral area. In the hinge groove the central list (=L) is faintly visible. M= muscle scar. x90.

XIII–7. *Polyzygia neodevonica.* Carapace. STP/Mi. 72–36. Luanco, Asturias, Spain. Dorsal view. x115.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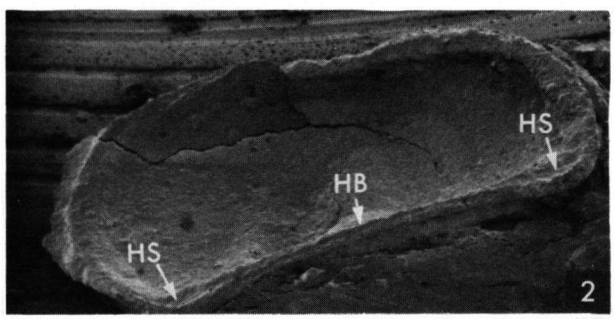

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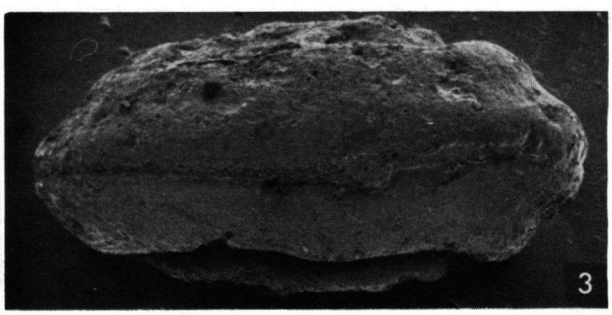
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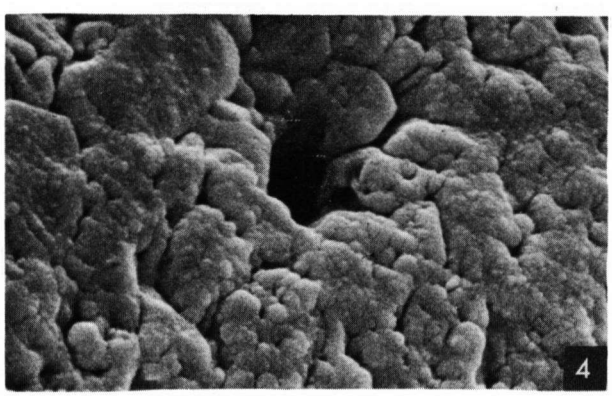
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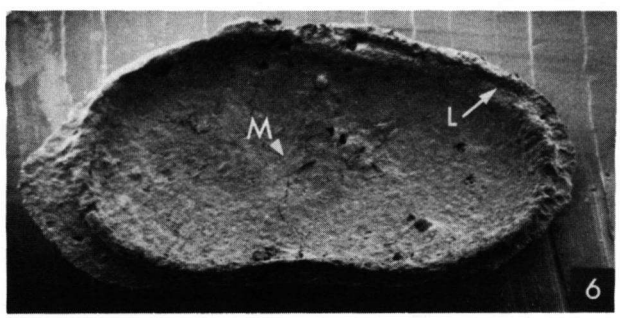
5



6

7

PLATE XIV

XIV–1a and b. *Polyzygia neodevonica.* Fragment of left valve. STP/Mi. 72–37. Luanco, Asturias, Spain.

XIV–1a. Interior view. Note the sculpture and its manifestation at the interior. Contact groove shows mid-ventrally a discontinuity. x100.

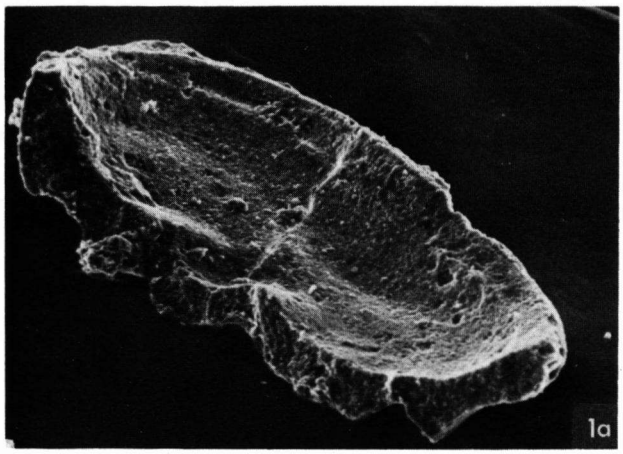
XIV–1b. Interior view. Note the contact groove. x 110.

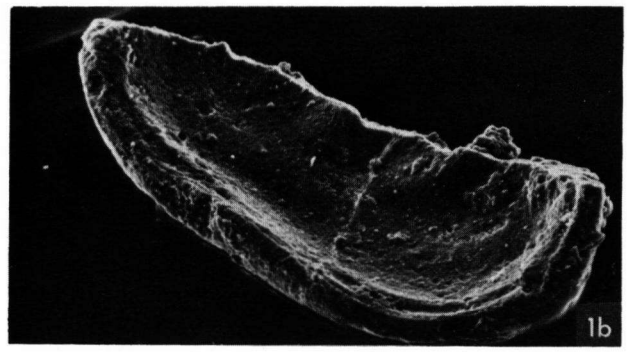
XIV–2. *Polyzygia neodevonica.* A–1 carapace. Accidentally destroyed in the SEM. Luanco, Asturias, Spain. Right ventro-lateral view. Note the marginal ridge, the absence of S_{vp} and the upwards curling of S_{va}. x115.

XIV–3. *Polyzygia neodevonica.* Fragment of left valve. STP/Mi. 72–38. Luanco, Asturias, Spain. Anterior view. Note the central thickening of the marginal ridge. x190.

XIV–4. *Polyzygia neodevonica.* Left valve. STP/Mi. 72–32. Perlora, Asturias, Spain. Interior view. Posterior part of the hinge. S= posterior hinge socket; B= hinge bar; G= narrow central groove. The same specimen is shown on Pl. XIII–2. x460.

XIV–5. *Polyzygia neodevonica.* Carapace. Luanco, Asturias, Spain. Transverse cross section between S_5 and S_4. Note the contact groove in the left valve and the overlap of the right valve in the hinge area (arrow). LV= left valve; RV= right valve. x190.


1a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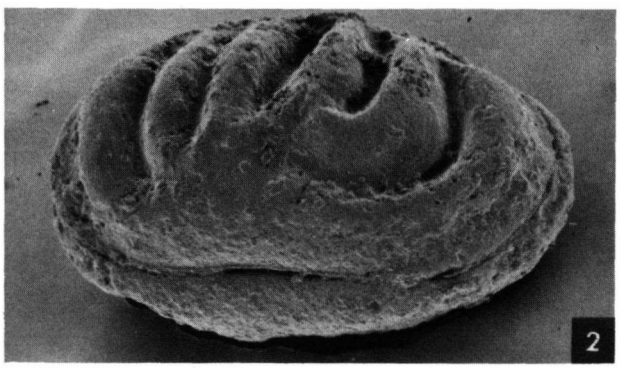
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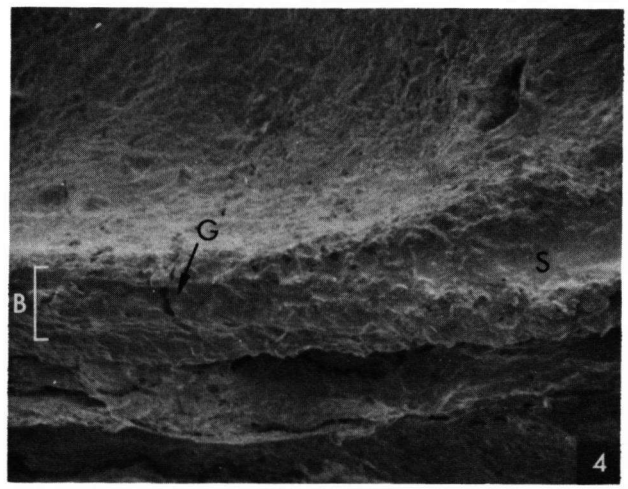

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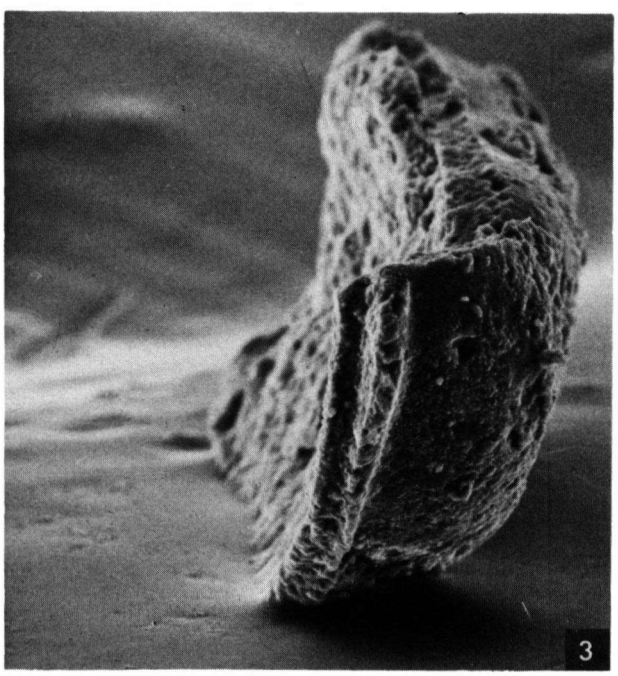
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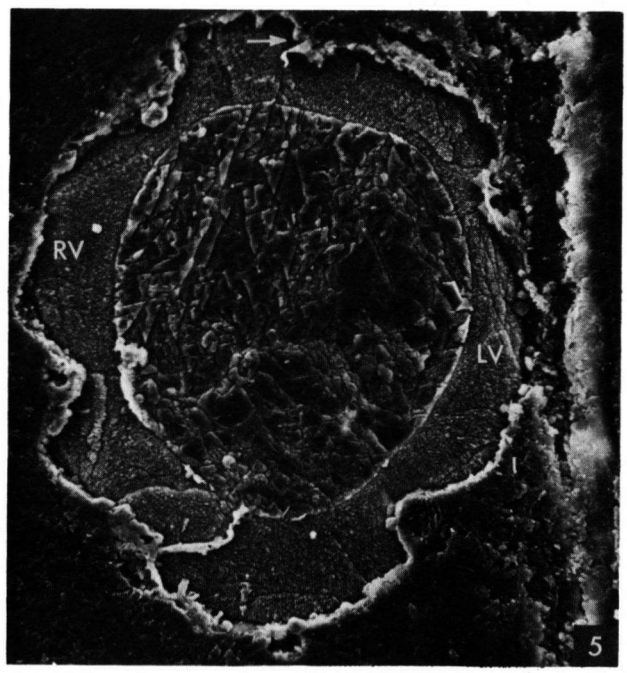


5

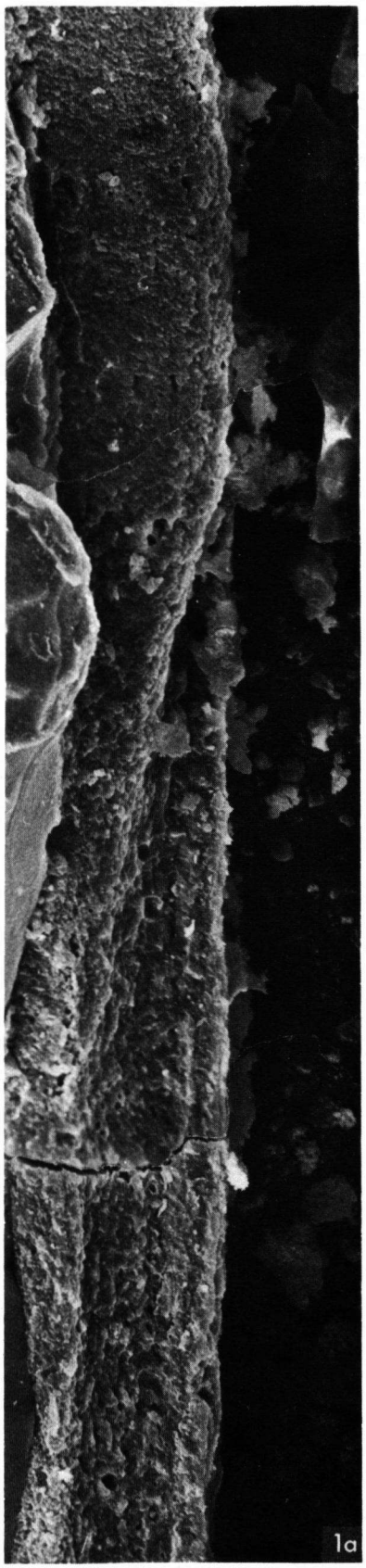
PLATE XV

XV–1a and b. *Polyzygia beckmanni.* Broken carapace. STP/Mi. 72–19. Refrath, W. Germany.

XV–1a. Detail of the posterior hinge tooth of the right valve. x1020.

XV–1b. Detail of the posterior hinge socket of the left valve. x1020.

XV–2. *Polyzygia neodevonica.* Left valve. STP/Mi. 72–32. Perlora, Asturias, Spain. Detail of the hinge area. x370.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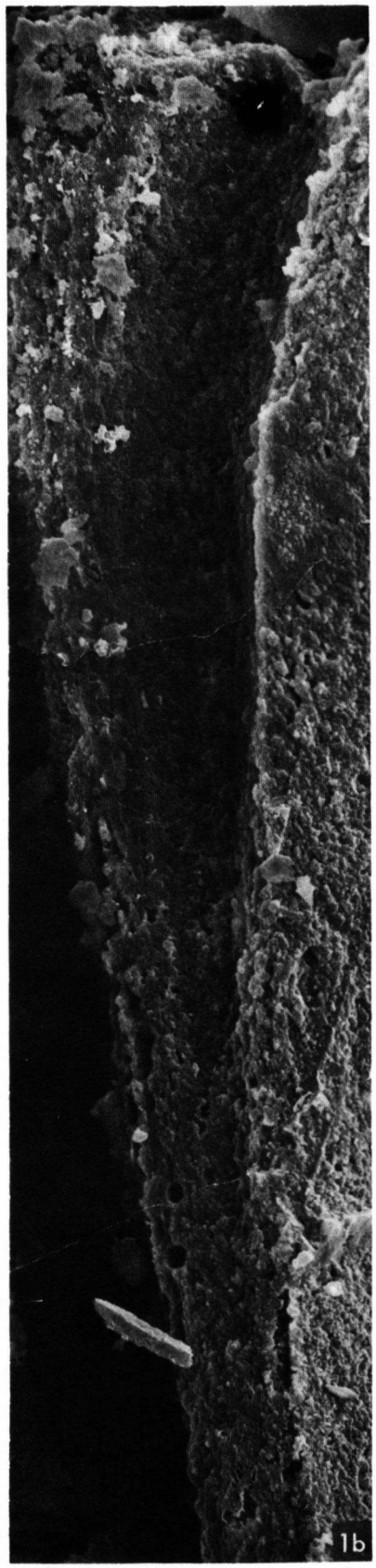
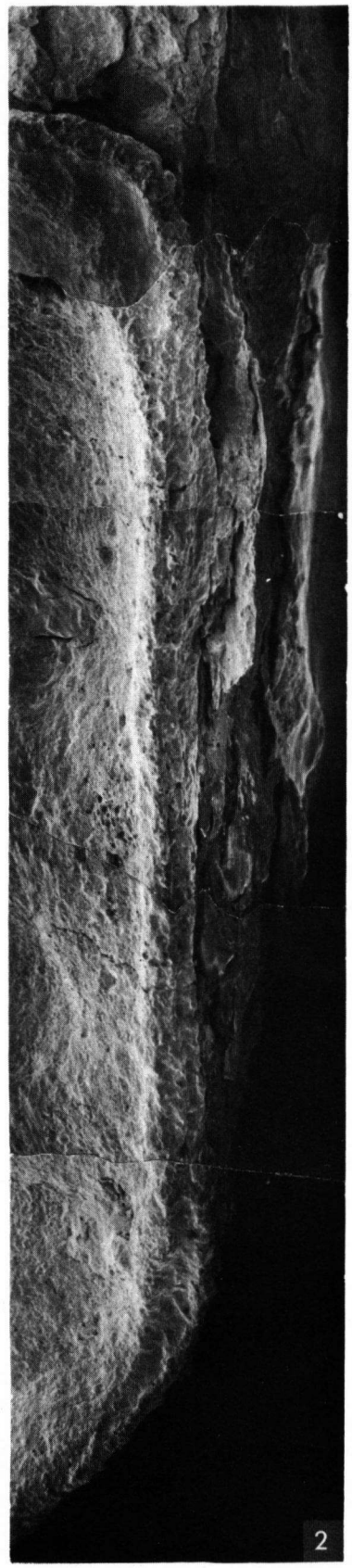

1b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