

Lower Carboniferous marine bivalves from the Cantabrian Mountains (Spain)

M.R.W. Amler & C.F. Winkler Prins

Amler, M.R.W. & C.F. Winkler Prins. Lower Carboniferous marine bivalves from the Cantabrian Mountains (Spain). — *Scripta Geol.*, 120: 1-45, 3 figs., 5 pls, Leiden, December 1999.

Michael R.W. Amler, Institut für Geologie und Paläontologie, Fachbereich Geowissenschaften der Philipps-Universität Marburg, Hans-Meerwein-Strasse, D-35032 Marburg, Germany; Cor F. Winkler Prins, Nationaal Natuurhistorisch Museum Naturalis, Postbus 9517, NL-2300 RA Leiden, The Netherlands.

Key words — Bivalves, Lower Carboniferous, Vegamián Fm., Genicera Fm., Ricacabiello Fm., Cantabrian Mts.

The Lower Carboniferous bivalves of the Vegamián and Genicera formations are described, followed by a brief discussion on palaeoenvironmental and palaeogeographical aspects.

The black shales of the Vegamián Fm. (Tournaisian) yield a peculiar association of euchondriid taxa (*Euchondria wagneri* sp. nov., *Eu. cf. losseni*, *Eu. cf. bilstonensis*, and euchondriids under open nomenclature) and *Chaenocardia? carbonifera*. This association displays Central-European Kulm-type character, but other typical taxa from the German Kulm are missing in this environment, especially the posidoniids, actinopteriids and pterinopectinids.

The light coloured sediments of the Genicera (or Alba) Fm. yield bivalves in slightly greater diversity which include rare palaeotaxodonts, parallelodontids, euchondriids, *Limatulina?*, *Chaenocardia*, large *Posidonia*- or *Posidoniella*-like forms, posidoniids, *Chaenocardiola*, and possibly edmondiids; members of the heteroconchs are missing.

Los Lamelibranchios del Carbonífero Inferior (Formaciones Vegamián y Genicera) se describen y se comentan en cuanto a sus aspectos paleoambientales y paleogeográficos.

Las pizarras negras de la Formación Vegamián (Tournaisiense) contienen una asociación peculiar de euchondriidos (*Euchondria wagneri* sp. nov., *Eu. cf. losseni*, *Eu. cf. bilstonensis*, e euchondriidos en nomenclatura abierta) y *Chaenocardia? carbonifera*. Esta asociación muestra un aspecto típico del Kulm centroeuropeo, pero algunos taxones típicos del Kulm alemán faltan en este ambiente, sobre todo los posidoniidos, actinopteriidos y pterinopectinidos.

Los sedimentos de colores claros y rojos de la Formación Genicera (o Alba) contienen una fauna mas variada de lamelibranchios con algunos palaeotaxodontos, parallelodontidos, euchondriidos, *Limatulina?*, *Chaenocardia*, grandes formas parecidas a *Posidonia* o *Posidoniella*, posidoniidos, *Chaenocardiola*, y posiblemente también edmondiidos; faltan las heteroconchas.

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Introduction

The initial Carboniferous sea-level rise in the Early Tournaisian induced a facies differentiation into the Baleas Limestone Formation and the argillaceous Vegamián

Formation which both overlie the preceding clastic sediments of the Ermita Formation. A further sea level rise started in late Chadian times and caused widespread uniform facies conditions that occur in most parts of the Cantabrian Orogene and which are known as the 'Marbre griotte' or 'Griotte Limestone' (variously called Genicera, Alba, or Villabellaco Formation). This facies type persisted until the end of the Lower Carboniferous (mid-Carboniferous boundary) and is succeeded by more differentiated facies types which developed from Chokierian times onward.

Apart from stratigraphically important faunal elements many fossil groups of the Vegamián and Genicera Formations have not been described up to now. These faunas include representatives of nearly all Carboniferous invertebrate classes but are never abundant. Their affinities to other contemporaneous faunas offer interesting data for an interpretation of palaeobiogeographical relationships.

A full description of the Carboniferous bivalve faunas of the Cantabrian Mountains is envisaged starting with the present paper. Apart from regional faunal descriptions including a few bivalves (Barrois, 1882; van Amerom, in van Amerom et al., 1970; van Amerom, in van Loon, 1971), the bivalves of the Cantabrian Mts have received no special attention. Thus, our present knowledge on Carboniferous bivalves of the Cantabrian Mts is limited to — mainly unpublished — previous studies by one of us (CFWP) and our more recent studies. The present paper describes the Tournaisian, Viséan and Serpukhovian bivalves of the Vegamián and Genicera Formations, carried out by one of us (MRWA) during a six months research sabbatical at the NNM in Leiden (The Netherlands) in 1997, and some additional specimens from the Marsdenian Ricacabiello Formation. The results of this study have been presented at the annual meeting of the Paläontologische Gesellschaft in Berlin (Amler, 1998a).

Repository and abbreviations — The fossil material described in this paper is housed in the collection of the Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands (catalogue numbers prefixed RGM).

The following abbreviations are used throughout the text: LV = left valve, RV = right valve, ext. = external, int. = internal, mld. = mould, loc. = locality, dam. = damaged, dist. = distorted, O.D. = original designation, S.D. = subsequent designation; in the Tables: laa = length of anterior auricle, lpa = length of posterior auricle, R2 = total number of costae at 2 mm shell height, R10 = number of costae per 5 mm shell width at 10 mm shell height.

Geological setting and previous research

Most of the lithostratigraphical units presently distinguished were defined by various authors between 1960 and 1990, and these are based on the geological and stratigraphical account of the Palaeozoic succession in the Asturian-Leonese and Palencian areas of the Cantabrian Mts by Comte (1959). During the thirty years of investigation extensive mapping campaigns were carried out by working groups from Leiden, Oviedo and IGME (now ITGE, Madrid) (cf. de Sitter, 1962; Boschma, 1968; Boschma & Staalduin, 1968; Savage & Boschma, 1980; Sánchez de Posada et al., 1990), which have been completed by palaeontological, stratigraphical and sedimentological studies of other universities (a.o. Sheffield, Tübingen and Würzburg).

This research focused on interrelations between sedimentary sequences, subsidence and orogenesis as well as basin analysis and modelling (cf. Dallmeyer & Martínez García, 1990) and it provides the basis for chronostratigraphic interpretations (Wagner & Winkler Prins, 1985)

Shortly after the publication of Comte's (1959) report on the geology of northern León, Brouwer & van Ginkel (1964) introduced the term 'Sella Formation', comprising the complete sequence of Lower Carboniferous (Mississippian) strata, uniting the sediments overlying the clastic Ermita Formation, i.e. the 'Griotte à Goniatites crenistria' (= 'Griotte de Puente de Alba' and 'Couches de Vegamián'). This was later revised and, based on lithological and palaeontological evidence, the formal stratigraphic units 'Vegamián Formation' and 'Alba Formation' were introduced (van Ginkel 1965). Winkler Prins (1968) subdivided the Alba Formation into three members (Gete Mbr, Valdehuesa Mbr and La Venta Mbr). The Vegamián Formation was formally established by Wagner et al. (1971), whilst the Alba Formation was replaced by the Genicera Formation by these authors who pointed out that the Alba type locality shows an incomplete development of the formation. They introduced the Gorgera, Lavandera and Canalón members for the different parts of the formation in the genicera type section. Wagner et al. (1971) also rejected the Villabellaco Formation of Palencia, introduced by Wagner & Wagner-Gentis in 1963, because of incomplete development in its type locality. The Alba Formation is most commonly used, apparently as a result of inertia (cf. Gandl, 1977; Savage & Boschma, 1980; Raven, 1983; Sánchez de Posada et al., 1990 a.o.) but Genicera Formation has been employed for the official Spanish maps (IGME, ITGE).

Vegamián Formation

In most of the Asturian-Leonese Domain of the eastern Cantabrian Zone (N Palencia, N León and Asturias) sediments of the Vegamián Formation succeed the nearshore clastics of the Ermita Formation (Late Famennian — Early Tournaisian) disconformably. Most authors claim a hiatus and reworking at the base of the Vegamián Formation (Raven, 1983). Higgins et al. (1964) and Higgins (1971) report sandy and even conglomeratic beds at the base of the sequence with phosphatic nodules and conodonts. Locally, the Vegamián Formation interfingers with or is replaced by the Baleas Limestone Formation (Wagner et al., 1971; García-Alcalde et al., 1985; Rodríguez Fernández et al., 1985). A conformable succession upwards from the underlying Vidrieros Formation into the Vegamián Formation in the Palentine Domain as presumed by van Adrichem Boogaert (1967) has been contested by Raven (1983: 297).

The Vegamián Formation consists of mainly black, sometimes grey to slightly greenish laminated shales and cherts, containing phosphatic and markasite nodules. The sediments are described in many papers on the regional geology of the Asturo-Leonese Domain, most comprehensively in Sjerp (1967), Wagner et al. (1971) and Raven (1983). Within the sequence, even in sections with reduced thickness, erosional surfaces were observed (Raven, 1983). The general thickness of the Vegamián Formation is small but variable and ranges from some 5-10 m in N León (Comte, 1959; Wagner, 1963; Winkler Prins, 1968) to 30-50 m in the Palentine Area (van Ginkel, 1965;

Savage & Boschma, 1980). The latter figures are certainly exaggerated since grey silty shales are included (cf. Raven, 1983: 296) that are quite different from the true Vegamián Shales and should be differentiated (cf. Wagner & Winkler Prins, in prep.). Van Adrichem Boogaert (1967: 163) even included greenish and reddish cherts and ironstone concretions and layers at the top of the succession which should definitely be separated and combined with the overlying limestones generally assigned to the Genicera Formation.

The Vegamián Shales are generally poorly exposed due to weathering, forming hollows between the competent sandstones of the Ermita Formation and the limestones of the Genicera and Barcaliente Formations. They are also quite often partly or completely eliminated by tectonic shearing.

Based on the faunas discussed in the following chapter and especially on the conodonts (cf. Higgins, 1971; Higgins, in Higgins & Wagner-Gentis, 1982; Raven, 1983), a mainly Tournaisian age (most probably middle-late Tournaisian; *Si. cooperi*-*Pol. communis* to *Sc. anchoralis*-*Do. latus* Zone) can be assigned to the Vegamián Formation. If the black shales interfingering with black limestones in the southern part of the Alba Syncline are explained as an alternation of the Baleas and Vegamián Formations and not as part of the Baleas Formation (cf. Rodríguez Fernández et al., 1985), then the Vegamián Formation locally starts in the early Tournaisian. At most localities, the Vegamián Formation can only be dated indirectly since fossils are usually lacking but there is no positive evidence for a younger (early Viséan) age, unless one intends to include the silty shales of the Palentine area mentioned above (see also Winkler Prins & Martínez Chacón, 1999).

A complete account on previous research and a detailed revised lithostratigraphy is given in Wagner et al. (1971), Raven (1983) and Winkler Prins & Martínez Chacón (1999); a lithostratigraphical correlation scheme of previously published units can be found in Winkler Prins (1968: fig. 1).

Genicera Formation

The black shales and cherts of the Vegamián Formation are overlain by red and grey nodular limestones, cherts and shales of the 'marbre griotte' (Barrois, 1882), today either defined as Alba or Genicera Formation. The basal contact to the underlying Vegamián Formation is usually disconformable in the Asturian-Leonese Domain, as far as can be ascertained. In certain areas the hiatus at the base of the Genicera Formation caused by erosion is even greater, and the griotte limestones rest upon Upper Famennian — Lower Tournaisian sediments (Higgins, 1971; Raven, 1983: 299; Eichmüller & Seibert, 1984; Wagner & Winkler Prins, in press).

Sediments of the Genicera Formation are widely distributed in the Cantabrian Chain, especially in the Asturian-Leonese Domain; in the Palentine Domain normally a different type of condensed limestone is developed (Wagner & Winkler Prins, in prep.). The strata and the sedimentary structures have been described in detail by Sjerp (1966), Winkler Prins (1968), Wagner et al. (1971) and Raven (1983). After Wagner et al. (1971) the formation is divided into three members, the basal (griotte limestones and shales) Gorgera Member, the middle (cherty) Lavandera Member and the upper (main griotte) Canalón Member. The mudstones replacing the top of the for-

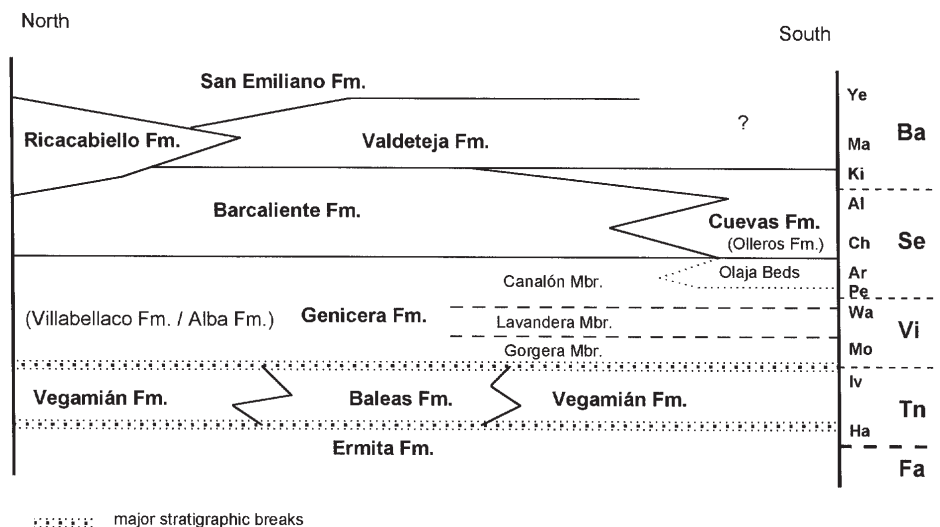


Fig. 1. General stratigraphic scheme of the Lower Carboniferous (Mississippian) succession in the southern part of the Cantabrian Mts.

mation in the southwestern part of the Cantabrian Mountains were separated as the Olaja Beds. The thickness of the Genicera Formation is generally small and measures at the type locality c. 25 m. Comte (1959) noted some 25-40 m, van Ginkel stated a maximum thickness of some 30 m, and Gandl (1977) mentioned only 20-25 m.

The transition from the Vegamián Formation into the Genicera Formation is dated as Late Tournaisian (*Gn. pseudosemiglaber* Zone) in the Esla area; in other regions the basal sedimentation started at the time of the *Sc. anchoralis-Do. latus* Zone (Higgins, 1971; Higgins, in Higgins & Wagner-Gentis, 1982; Raven, 1983). In the Palentine Domain, the griotte limestone started in the Middle Viséan (*Gn. bilineatus* Zone). In its type region, the Gorgera Member has yielded non-determinative goniatites, e.g. *Merocanites applanatus*, *Dzhaprakoceras hispanicum* and *Eurites corpulentissimus*, which suggest Early Viséan rather than Late Tournaisian (written commun. by J. Kullmann, Tübingen). The Canalón Member is dated independently (e.g. Kullmann, 1963 and written commun.; Winkler Prins, 1968; Wagner et al., 1971) by goniatites as (Late) Viséan (pink part) and early Serpukhovian (Lower Namurian, Arnsbergian, E2; grey part and Olaja Beds).

Lower Carboniferous faunas of the southern Cantabrian Mountains

Vegamián Formation

Notwithstanding the fact that remains of many fossil groups have been noted from some localities, the fossil content of the Vegamián Formation is low compared with other Carboniferous units. Fossils are mostly restricted to distinct layers but, then, may cover complete bedding planes. The dominant group is that of the ostracodes followed by brachiopods and bivalves. The brachiopods include frequent Lin-

gulfiformea (Winkler Prins & Martínez Chacón, 1999) of the genera *Lingula*, *Lachrymula* and *Orbiculoidea* as well as Rhynchonelliformea (Winkler Prins & Martínez Chacón, in prep.) of the (sub)orders Orthida (*Rhipidomella*), Strophomenida (*Drahanorhynchus*), Chonetidina (*Tornquistia*, *Rugosochonetes*, *Globosochonetes*, *Plicochonetes*), Productidina (*Chonetipustula*, *Parmephrix?*), Rhynchonellida (*Propriopugnus?*), and Spiriferidina (*Crurithyris*). These taxa show very close relationships to the Central European Kulm facies (cf. Nicolaus, 1963; Winkler Prins, 1971; Amler, 1998b; see also chapter on palaeogeography).

Ostracodes occur frequently, sometimes as shell layers. Their taxonomic composition (*Kirkbya*, *Richterina*, *Amphissites*, *Shishaella*, *Healdia*, *Kloedenia*, *Triplacera*, *Graphiodactylis*) agrees well with contemporaneous associations in Central and Western Europe (Jordan & Bless, 1971; Sánchez de Posada, 1976; Becker, 1982), apart from the endemic genus *Maternella*, and stresses the connecting palaeogeographic situation at that time.

Gandl (1973) described several trilobite taxa of the Proetacea (families Otarionidae, Brachymetopidae and Proetidae), from a few localities of the Vegamián Formation and claimed affinities with the Franconian Lower Carboniferous.

Radiolaria occur widespread but foraminifers were not recorded by van Ginkel (1965). Furthermore, crinoid ossicles, bryozoan fragments, solitary corals, vermes (*Campylites*) and fish remains have been noted (own observations, CFWP), not to mention the conodonts discussed above.

Cephalopods are present with *Pericyclus* sp., *Muensteroceras arkansanum* and orthoconic forms (Wagner-Gentis, in Wagner et al., 1971). Gastropods are rare or simply undeterminable fragments.

Bivalves occur only occasionally in the Vegamián Formation. The composition of the black shale bivalve fauna is restricted to only a few taxa. The association is characterized by three taxa of euchondriid aviculopectinaceans with *Euchondria wagneri* sp. nov. as the dominant species, *Eu.* cf. *losseni* and *Eu.* cf. *bilstonensis* being known only as single specimens. The euchondriids reach an average size (shell height) of 12-14 mm which is comparable to that known from the Kulm Shales of Herborn (Dill Syncline, Rheinisches Schiefergebirge, Germany), but totally different from the size of specimens of *Eu. aprathensis* Rathmann & Amler, 1994 from the Kulm Shales (Kulm-Tonschiefer) of the famous Aprath locality near Wuppertal (Germany) in the westernmost part of the Rheinische Schiefergebirge near the transition between the Carboniferous Limestone facies and the central European Kulm Basin. The euchondriids are accompanied by a few specimens of *Posidonia*-like bivalves which are assigned provisionally to *Chaenocardia? carbonifera* (Hind, 1904). Other taxa characteristic of the German Kulm are missing in this environment, especially the posidoniids, actinopteriids and pterinopectinids.

Genicera Formation

The first compilation of the fauna from the Viséan and lower Namurian was presented by Winkler Prins (1968, table II), after Delépine (1943) had summarized fossils (but no bivalves) from the 'Griotte limestone' of Asturias. The formation is moderately rich in fossils, which are however sometimes poorly preserved; cephalopods, trilo-

bites, corals, crinoids, brachiopods, gastropods, bivalves, and conodonts have been mentioned. Its fossil content increases towards the top of the formation.

Gorgera Member (red and green shales and griotte limestone)

Up to now, no bivalves are recorded from this member. Thus, we have no data on the change in bivalve diversity during the change of biofacies conditions from the black mudstones to the grey mudstones and limestones that lead into the basal griotte limestones of the Gorgera Member. The few brachiopods are related to the Vegamián taxa; the cephalopods invaded the basin gradually, and only pelmatozoans (crinoid ossicles) seem to have been more or less widespread at that time. At present are known: small brachiopods (Winkler Prins, 1968: table II, and unpublished information): small orthids, *Tornquistia*, *Rugosochonetes*, and *Crurithyris*), goniatites (Wagner-Gentis, in Higgins et al., 1964: *Merocanites subhenslowi*, *Muensteroceras* sp.), trilobites (Gandl, 1977: Archegonidae), crinoids (mainly disarticulated columns), sponges, tabulate corals (*Cladochonus*, *Pseudofavosites?*), zaphrentid solitary corals (cf. de Groot, in Winkler Prins, 1968: table II), large, smooth-shelled ostracodes, and conodonts.

Lavandera Member (cherts)

From this chert member only a few bivalves were recorded from a locality south of Triollo (see below). These are *Limipecten* sp. and *Euchondria* sp. A, both reaching a considerable size. They are associated with small brachiopods (*Rhipidomella*, *Tornquistia*, *Rugosochonetes*, *Aseptella*, *Crurithyris*), trilobites (Archegonidae), crinoids (mainly disarticulated ossicles), sponges, tabulate corals (*Cladochonus* type), zaphrentid solitary corals, and large, smooth-shelled ostracodes. Conodonts were rarely found in the Lavandera Member, and up to now no goniatites have been reported. The association is comparable to that of the 'Kieselige Übergangsschichten' (Lower Brigantian) of Central Europe (Nicolaus, 1963; Amler, 1998b) and, to a certain extent, that of the 'couches de passage' of Belgium (Demagnet, 1938).

Canalón Member and Olaja Beds

The calcareous and marly parts of the Canalón Member and the time-equivalent Olaja Beds have yielded a considerable number of fossils, which may reach a relatively large size. Preservation is not always favourable due to dissolution during fossilization. Cephalopods are quite frequent and include *Asturoceras subdivisum*, *Delepinoceras bressoni*, *D. cantabricus*, *D. thalassoide*, *Dobarocanites chancharensis*, *Eumorphoceras mediolobum*, *Euroceras latior*, *Glaphyrites subangulatus*, *Kazakhoceras yanshini*, *Parafayettevillea prior*, *Praedaraelites dangeardi*, *P. postculmiensis*, *P. saharensis*, *P. simulans*, *Proshumardites delepinei*, *Stenopronorites occidentalis*, *Syngastrioceras cadiconiforme*, *S. pseudomalhamense*, *Tympanoceras getinoi*, *T. ibericum*, *Zephyroceras asturicum*, *Z. promodestum*, *Z. rauserae* (Kullmann, 1961-1963; GONIAT programme of J. Kullmann, Tübingen), and orthoconic forms. The brachiopods include large *Martinia glabra*, and the top part of the succession contains faunas that display strong affinities to the Central European Kulm Facies, including the genera *Orbiculoidea*, *Tornquistia*, *Rugosochonetes*, *Aseptella*, *Chonetipustula*, *Parmephrix?*, *Productella*, *Crurithyris*, and *Phricodothyris* (cf. Winkler Prins & Martínez Chacón, in prep.). Similar relationships are visible in the trilobites, which can reach large dimensions (cf. Gandl, 1977), and ostra-

codes (Becker, 1982: *Truyolsina*). The bivalves occur in greater diversity compared with the older parts of the Carboniferous succession and include members of all subclasses apart from heteroconchs. Rare palaeotaxodonts are recorded, parallelodontids, euchondriids, *Limatulina?*, *Chaenocardia*, large *Posidonia*- or *Posidoniella*-like forms of uncertain taxonomic relationships, posidoniids, *Chaenocardiola*, and possibly edmondiids. Additional faunal elements are gastropods, rare anthozoans (de Groot, in Winkler Prins, 1968: table II: *Ufimia* sp.; Kullmann, 1966 and pers. comm.; Rodriguez et al., 1986) and crinoids (Herbig, 1994: *Baleaocrinus*).

Ricacabiello Formation

For comparison, a few bivalves from the Ricacabiello Formation (= 'Meré Beds'; for information on its fauna see Martínez Chacón & Winkler Prins, 1977; Martínez Chacón et al., 1985), which are considered to be at least partly equivalent in age with the Valdeteja Formation (Kinderscoutian?-Marsdenian), are included in this study because these also show a typical Kulm character (Martínez Chacón & Winkler Prins, in press).

Localities

The following list of localities is arranged according to data from the data base kept in the Nationaal Natuurhistorisch Museum Naturalis and established by one of us (CFWP).

Table 1. Localities of Lower Carboniferous bivalves from the Cantabrian Mts (Abbreviations of authors: WP = Winkler Prins, Wa = Wagner, Ku = Kullmann).

loc. code	loc. no. others	loc.	specific site	town	prov.	formation	age
Ge	WP14 Wa1165B Ku5737	Genicera	1 km SW of, E side Canalón Brook	NE La Robla	León	Vegamián	Late Tn
OS	WP17	Oseja de Sajambre	on main road 1 km S of Oseja	N Cistierna	León	Vegamián	Late Tn
OV	WP59 Wa372	Sta Olaja de la Varga	750 m NE of Sta Olaja	N Cistierna	León	Genicera Olaja Beds	Arnsbergian
BG	WP53 Wa1227, 1229	Barrios de Gordón	1.35 km S of Barrios	N La Robla	León	Genicera Olaja Beds	Arnsbergian
TI	WP89, 89''	Triollo	quarry 1.5 km S of E bank reservoir	W Cervera	Pal.	Genicera Lavandera Mbr	Late? Vis.
III	WP89A	Triollo	1.5 km S of W bank reservoir	W Cervera	Pal.	Genicera Lavandera Mbr	Late? Vis.
RS	Wa1711	Revilla de Santullán	quarry W of Revilla	S Barruelo	Pal.	Genicera Canalón Mbr	Arnsbergian
HE	WP60	Hoces de Entrago	quarry S of road	SE Oviedo	Ast.	Genicera Canalón Mbr	Arnsbergian
PE	WP82	Nozaleda W Perlora	quarry Tudela Veguín S.A.	NW Gijón	Ast.	Genicera Canalón Mbr	Arnsbergian
Me	WP629	Meré		SW Llanes	Ast.	Ricacabiello	Marsdenian

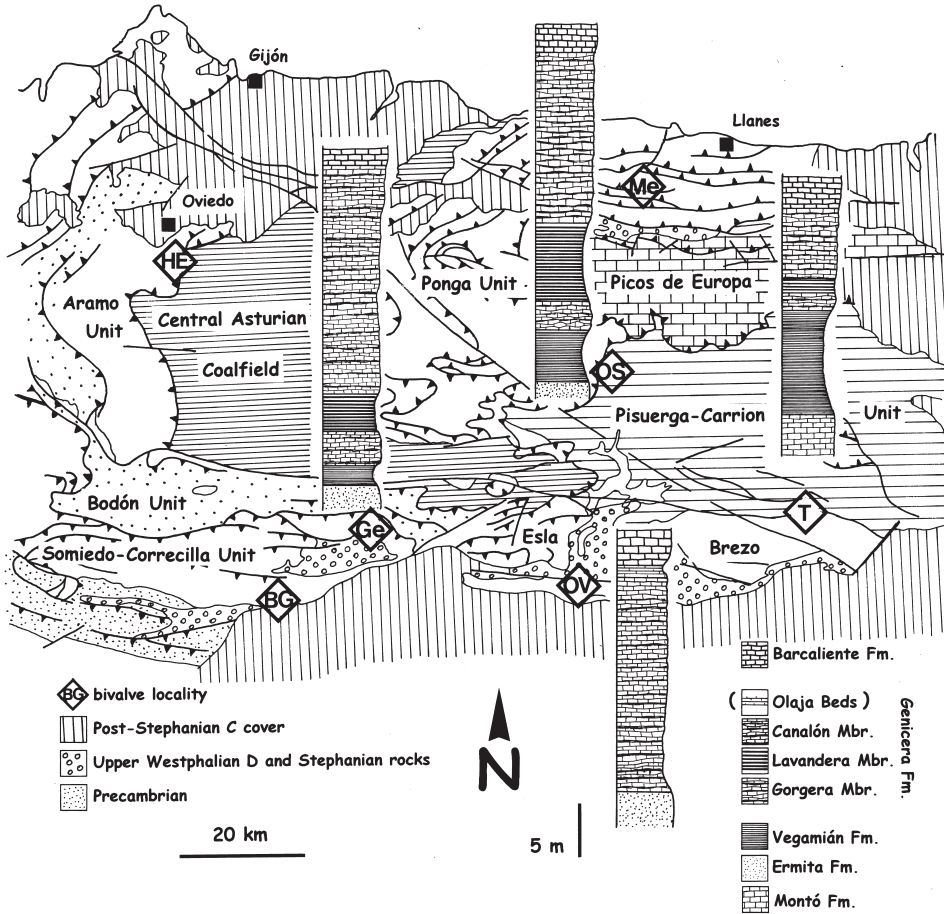


Fig. 2. Simplified structural map of the Cantabrian Mts with localities (abbreviations in diamonds) listed in Table 1.

Systematic palaeontology

- Subclass Pteriomorpha Beurlen, 1944
- Superorder Prionodonta McNeil, 1937
- Order Arcoida Stoliczka, 1871
- Superfamily Arcoidea Lamarck, 1809
- Family Parallelodontidae Dall, 1898
- Parallelodon* Meek & Worthen, 1866

Type species — *Macrodon rugosus* Buckman, 1845.

Diagnosis — See Amler (1995: 34) and Amler (1989).

Range — Middle Devonian — Late Cretaceous.

Discussion — See Amler (1987, 1989, 1995).

Parallelodon sp.

Pl. 5, fig. 6.

Material — RGM 346 494, RV/LV int.mld. tectonically distorted.

Description — Shell outline parallelodontid; ventral margin generally convex but slightly sinuous mid-ventrally; posterior margin (after re-distortion) oblique, straight or slightly concave; hinge margin straight; umbones broad, blunt, prosogyrous and slightly raised above hinge margin; oblique ridge from umbo to posteroventral angle distinct, posterodorsal area depressed.

Shell surface only tentatively reconstructable: main shell body with traces of medium coarse radial ribbing, obviously limited to external shell surface. Posterodorsal area with 5-6 coarse radial ribs which may be nodose (visible on small shell remains in postumbonal region). No traces of growth lines visible, but 5-6 concentric undulations (growth varices?) present.

Discussion — At present, no precise determination is possible for the Spanish parallelodontids as the whole group is under revision (Amler, in prep.); our specimen does not show the complete morphology of external surface.

Occurrence — Loc. BG, Genicera Formation, Olaja Beds, Arnsbergian.

Superorder Eupteriomorpha Boss, 1982

Order Pectinoidea Newell & Boyd, 1995

Superfamily Aviculopectinoidea Meek & Hayden, 1864

Family Euchondriidae Newell, 1937

Euchondria Meek, 1874

Type species — *Pecten neglectus* Geinitz, 1866, O.D.

Diagnosis (after Newell & Boyd, 1995: 48; see also Amler, 1995: 71 and Rathmann & Amler, 1992: 48) — Shell inequivalve, discordant, nearly equiconvex; valves infracrescent (acline) or retrocrescent (proscloine), higher than long, characteristically obliquely oval in outline or sometimes suboval; auricles triangular. Shell sculpture of RV and LV are different: LV multicostate, with concentric crossed lamellar inner ostracum, and homogeneous outer ostracum, growth lines closely spaced, only visible in interspaces between slender costae; RV with minute concentric fila or smooth, outer ostracum prismatic. Hinge plate long and slender, slightly thickened, adult hinge pseudotaxodont (crenulated); ligament alivincular external, with small, symmetrical or slightly asymmetrical ligamental groove.

Range — Late Devonian — Middle Permian.

Discussion — Although the genus is mentioned in many papers on Late Palaeozoic bivalve faunas and is discussed in Newell (1937) and Newell & Boyd (1995), knowledge on these peculiar aviculopectioids is rather fragmentary. This is also a result of poor preservation of the type material of the type species, *Eu. neglecta*. Newell (1937) included the doubtful genus *Crenipecten* together with *Euchondria* in the subfamily Euchondriinae, both differing in the presence (*Euchondria*) or absence (*Crenipecten*) of a central ligamental groove in the characteristically pseudotaxodont hinge plate. We refrain from discussing at length the question, whether or not both taxa may be synonyms because our Spanish material does not exhibit further details of the hinge morphology. But, ignoring the fact that in most euchondriid specimens preservation of the hinge is generally insufficient to discriminate between both genera, studies on aviculopectinoids have shown that even within single taxa or populations the size and development of a ligamental groove is subject to a large degree of variation and may be, therefore, only weakly developed. This seems even more likely because the function of the crenulation is re-interpreted as neotenic conservation of the crenulated provinculum of the prodissoconch II according to observations on Recent bivalve larval stages, instead of being multiple ligamental grooves (Newell in Cox et al., 1969; Newell & Boyd, 1987). Another serious difficulty involves the differing external sculpture of euchondriid shells. Most 'species' are based on radially ribbed left valves only, but in only one (!) taxon (*Eu. aprathensis* Rathmann & Amler, 1992) the morphology of both valves is properly known. Apart from one specimen (Ve18), here assigned provisionally to *Eu. densistria*, this difficulty also applies to our Spanish material and even in this case only a fragment of the matching right valve internal mould is preserved (Fig. 3). For pragmatic reasons we have decided to describe the few right valves from our collection under open nomenclature because no characters are present to assign isolated left and right valves correctly to a named taxon and because the right and left valves of one species do not necessarily match in outline (discordance of valves; cf. Kegel, 1951).

Apart from hitherto known species assigned to *Euchondria* or *Crenipecten*, some undescribed euchondriids may still be grouped with *Aviculopecten* or *Pecten*, especially but not exclusively in older literature (see discussion below).

Euchondria wagneri sp. nov.

Pl. 1, figs. 1-7; Pl. 2, figs. 2, 4-5.

cf. 1929 *Pterinopecten* cf. *granosus*. — de Voogd: 28, pl. 4, fig. 13.

cf. 1956 *Euchondria levicula*. — Sulga: 148, pl. 5, fig. 65.

cf. 1956 *Aviculopecten gentilis*. — Sulga: 143, pl. 5, figs. 55-56.

cf. 1962 *Euchondria* aff. *E. levicula*. — Yates: 399, pl. 58, figs. 1-2.

Derivatio nominis — Named after Dr Robert Wagner, Córdoba, who was the first to investigate in detail the region between the rivers Torío and Porma in the province of León and who collected part of the material.

Type specimen — Holotype LV RGM 143 376, figured on Pl. 1, figs. 5-6, housed in the collection of the Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands. Paratypes see Table 2.

Type locality — Loc. W1162 of Winkler Prins (1968); section immediately east of the canyon 'el Canalón' 1000 m southwest of Genicera, province of León, Spain (cf. Wagner, 1963: 54; Winkler Prins, 1968: 45; Gandl, 1973: 25).

Type stratum — Upper part of the Vegamián Formation, Late Tournaisian.

Diagnosis (left valve only) — Characters of the genus *Euchondria* with the following features: Shell outline remarkably retrocrescent; both auricles triangular, the posterior auricle ventrally narrowing and merging with the posterior margin of the disc; external ornament multicostate consisting of 13-17 thin, filiform primary costae and intercalating secondary and tertiary costae summing up to 45-55 costae in specimens of 10 mm shell height; interspaces broad, flat, covered with sharp, closely spaced growth lines; anterior auricle with 3-4 primary and 3-4 secondary costae, posterior auricle with 4-6 thin costae.

Remarks — This new species is based on left valves only because no specimen is present showing both valves in close contact to confirm a correct assignment of isolated right and left valves. New material may lead to a revision of the description and a unification of taxa. Isolated right valves are described under open nomenclature as *Euchondria* sp. A.

Material and measurements — See Table 2.

Description (left valves only) — Shell small (average height 10 mm), almost certainly inequivalve; retrocrescent (prosocline), higher than long, characteristically obliquely oval in outline with distinct posteroventral prolongation. Umbo triangular, pointed, central or somewhat anterior to midline, umbonal angle 90°; anterior auricle triangular, separated by narrow auricular sulcus, anterior margin very gently convex, anterior auricular sinus nearly perpendicular; posterior auricle triangular, acuminate, less distinctly separated, slightly longer than anterior auricle, its posterior margin concave and ventrally merging with posterior margin of disc in a nearly straight line.

Sculpture multicostate: 13-16 primary costae, very thin, filiform, secondary and tertiary costae intercalate at various distance from umbo (see chapter on ontogeny), at H = 10 mm 15-17 costae in 5 mm length, shells of 10 mm shell height with altogether 45-55 costae; interspaces unequal, generally wide, flat, but less wide in posterior region of disc. Growth lines sharp, closely spaced, developed only in interspaces, giving the exterior shell surface a characteristic reticulate appearance. Anterior auricle with 3-4 primary and 3-4 secondary costae (the latter not visible on internal moulds), posterior auricle with 4-6 thin costae.

Interior: Impressions of adductor or pallial line not preserved. The characteristic crenulation of the hinge margin is seldom visible if at all; at best in specimens RGM 143 376 and 346 523.

Ontogenesis (observations based on specimens RGM 346 510, Ve12, Ve14) — The samples yielded some immature (3 mm shell length and height) and few exceptionally well preserved mature specimens, where the development of the external shell ornamentation could be observed. Shells of that size have 11-13 primary costae and

Table 2. Material and measurements (in mm) of *Euchondria wagneri* sp. nov.

RGM	preservation	length	height	laa	lpa	R2	R10	loc.
142 653	LV int.mld. dam.	9.0	8.9	2.2	3.0	13-14	13/5	Ge
142 658	LV ext.mld.	14.9	16.5	—	—	—	—	Ge
142 692	LV int.mld.	8.0	8.8	2.1	3.0	—	16/5	Ge
143 376	LV int.mld.	15.7+	15.6	3.8	5.8	15	16/5	Ge ?
143 377	LV ext.mld.dam.	12.0+	14.0	2.8	4.1	15	15/5	Ge ?
143 378	LV ext.mld. fragment	—	—	—	—	—	—	Ge ?
346 501	LV int.mld.	13.3	13.5	—	4.1	18	14-15/5	Ge
346 502	LV int.ext.mld.	13.0+	15.0+	3.3+	—	13+	16/5	Ge
346 503	LV int.ext.mld.	17.0	16.2	3.6	—	14	16/5	Ge
346 506	LV int.mld. upon RV ext.mld. dam.	—	—	—	—	16	12-14/5	Ge
346 507	LV int.ext.mld. dam.	14.2	14.2	1.8+	4.0	14-15	15/5	Ge
346 508	LV int.mld.	13.9	15.0	3.5+	4.8	15	18/5	Ge
346 509	LV int.mld.	10.8	10.2	3.0	4.2	14-15	15/5	Ge
346 510	LV int.mld.	5.9	5.8	2.0	2.3	15	—	Ge
346 513	LV ext. mld. dam.	12.0+	15.8	3.6	—	14	12-13/5	Ge
346 514	LV int.mld. dam.	15.5+	16.7	—	4.0+	—	17/5	Ge
346 518	LV int.mld.	11.0	11.2	2.9	3.9	17	15-16/5	Ge
346 521a	LV ext.mld.	12.9	12.1	—	3.5+	16	16/5	Ge
346 521b	LV int.mld.	6.5	7.0	2.0	—	—	—	Ge
346 521c	LV int.mld.	13.1	12.5	2.8	4.0	—	17/5	Ge
346 523*	LV int.ext.mld.	11.0	10.0+	2.7	3.7	16	16-17/5	Ge
346 524	LV ext.mld. fragment	—	—	—	—	—	—	Ge
346 526	LV ext.mld.	14.9	14.9	3.4	4.1	—	—	Ge
346 527	LV int.mld. dam.	11.5+	15.9	4.0	—	15	15/5	Ge
346 528	LV int.mld., ext.mld.	12.0	10.8	3.0	3.8	13-14	14/5	Ge
Ve12	LV int.mld.	3.5	3.0	—	—	13	—	Ge
Ve31	LV int.ext.mld.dam.	10.0+	11.3	—	4.2	16	15-16/5	Ge
For comparison:								
346 485	LV int.mld.	—	—	—	—	—	—	Me
346 486	LV int.mld.	—	—	—	—	—	—	Me

as well as 30 fragments of LV.

* Holotype.

10 first order intercalated costae. Starting from the umbo, these primary costae are developed up to a shell height of 2 mm, where the interspaces become extremely wide, because only the interspaces but not (never) the costae increase in size (height and breadth). At 2 mm shell height, the breadth of the interspaces reaches up to twenty times the width of the costae. Then, the first intercalated secondary costae appear, some quite sharp and instantly, others, especially in later growth stages, more gradually and not necessarily centred within the interspaces but often asymmetrically situated between the primary costae. This leaves further interspaces of different width and induces the intercalation of new third order costae in the wider interspaces.

The development of the auricles is not well shown in the specimens because the growth lines are extremely faint. But it is noted that the posterior auricle is already

quite high, being connected with the posterior portion of the disc in long distance as in later growth stages where the posterior margin of the disc and the posterior auricle merge for a considerable distance. The anterior auricle is triangular with an acute anterodorsal angle which becomes gradually wider and may reach nearly 90°.

The immature specimens do not show traces of the crenulated hinge line.

Discussion — No complete specimen is available with fully visible left and right valves still in contact. In RGM 346 506 some 1 mm of the dorsalmost portion of the RV (umbo with both auricles) is preserved as an external mould just dorsal to the internal mould of the LV (Pl. 1, fig. 3). Thus, presently no reconstruction of the RV morphology is possible. For that reason some uncertainty exists whether or not all the isolated LVs and RVs belong to one taxon only, especially because at least two other euchondriid taxa occur contemporaneously. In euchondriids, LVs and RVs do not necessarily match because the marginal portion of RVs may not be entirely calcified during its lifetime. Consequently, the shell outline of the corresponding LVs is no aid for a proper reconstruction of RVs. The find of specimens with both valves in contact and displaying both their morphology is necessary to solve this problem. Provisionally, we describe the isolated RVs under open nomenclature as *Euchondria* sp. A.

Euchondriids are widespread among Carboniferous bivalve faunas worldwide. They have been mentioned by various authors in the past as species of either *Aviculopecten*, *Acanthopecten*, or *Pecten*, but in most cases these were misinterpreted and/or misidentified. Thus, more than 40 species of Carboniferous aviculopectinoids have been erected during the past 100 years that are more likely euchondriids. Serious difficulties are caused by the different ornamentation of right and left valves and the lack of preserved hinge plates. Additionally, we will not discuss the question whether or not *Euchondria* and *Crenipecten* are synonyms, because the present material does not show further details to describe hinge characters for discrimination. Pending complete revision of euchondriid taxa which will be carried out in the near future, the Carboniferous 'species' (in original binomina) listed in Table 3 are here assigned to *Euchondria* or *Crenipecten* for various reasons as discussed below.

This list is far from being complete but intends to demonstrate, how many euchondriid forms exist within the wide range of aviculopectinoid taxa. Descriptions and figures of these taxa already reveal unsolvable difficulties for the comparison of these species. One important reason is that internal moulds (Steinkerne), composite moulds (Skulptur-Steinkerne) and external moulds (or, of course, replicas of them) of the same specimen not necessarily show identical morphology. Thus, the comparison of specimens preserved in different kinds is not always satisfying and may lead to the wrong assumptions. Even more misleading is the possible overprinting and tectonic distortion which, in some cases, can create slight differences that may be misinterpreted as different morphology.

Additionally, further members of the Euchondriidae may not have been discovered because 1) the hinge line morphology is visible only occasionally when the shell is preserved or the embedding matrix is argillaceous to allow the impression of the structure which 2) may not be fully developed in immature specimens, 3) the discordance and different ornamentation of allied RV and LV cannot be discerned and 4) the different specimen sizes and variability are not recognized.

Table 3. List of taxa definitively or tentatively assigned to *Euchondria* (or *Crenipecten*).

species	author and year	original genus	age
<i>alsaticus</i>	Tornquist, 1896	<i>Aviculopecten</i> (<i>Aviculopecten</i>)	Viséan
<i>altaicus</i>	Muromzeva & Turbanov, 1974	<i>Crenipecten</i>	Early Tournaisian
<i>aprathensis</i>	Rathmann & Amler, 1992	<i>Euchondria</i>	Brigantian
<i>areolatus</i>	Cooper, 1900	<i>Aviculopecten</i>	Kinderhookian
<i>aurilaevis</i>	Roemer, 1852	<i>Pecten</i>	Brigantian
<i>belgica</i>	Drevermann, 1902	<i>Euchondria</i>	Early Tournaisian
<i>beushauseni</i>	Drevermann, 1902	<i>Euchondria</i>	Strunian
<i>bilstonensis</i>	Wilson, 1961	<i>Euchondria</i>	Namurian
<i>businovensis</i>	Sergeeva, 1971	? <i>Euchondria</i>	Viséan
<i>cancellatus</i>	Herrick, 1888	<i>Aviculopecten</i> (<i>Lyriopecten?</i>)	Mississippian
<i>caneyanus</i>	Girty, 1909	<i>Euchondria?</i>	Chesterian
<i>circularis</i>	Maslennikow & Muromzeva, 1971	<i>Aviculopecten</i>	Tournaisian
<i>clathratus</i>	M'Coy, 1844	? <i>Pecten</i>	Viséan
<i>concentricostriatus</i>	M'Coy, 1844	<i>Pecten</i>	Viséan?
<i>densistria</i>	Sandberger & Sandberger, 1856	<i>Pecten</i>	Brigantian
<i>elsahensis</i>	Worthen, 1884	<i>Aviculopecten</i>	Kinderhookian
<i>europaea</i>	Tornquist, 1897	<i>Euchondria</i>	Brigantian
<i>flabelliformis</i>	Muromzeva, 1974	<i>Crenipecten</i>	Early Tournaisian
<i>gentilis</i>	J. de C. Sowerby, 1840	<i>Pecten</i>	Namurian-Westphalian
<i>hallanus</i>	Walcott, 1884	<i>Crenipecten</i>	Kinderhookian
<i>intercostatus</i>	M'Coy, 1844	? <i>Pecten</i>	Viséan
<i>laevis</i>	Weller, 1899	<i>Crenipecten</i>	Kinderhookian
<i>leiotis</i>	M'Coy, 1844	<i>Pecten</i>	Viséan?
<i>levicula</i>	Newell, 1937	<i>Euchondria</i>	Missourian
<i>limaeformis</i>	White & Whitfield, 1862	<i>Aviculopecten</i>	Lower Mississippian
<i>losseni</i>	von Koenen, 1879	<i>Pecten</i>	Brigantian
<i>menardi</i>	Worthen, 1884	<i>Lima?</i>	Desmoinesian?
<i>micropterus</i>	M'Coy, 1844	<i>Pecten</i>	Viséan?
<i>neglectus</i>	Geinitz, 1866	<i>Pecten</i>	Virgilian
<i>neilsoni</i>	Wilson, 1966	<i>Euchondria</i>	Brigantian
<i>obliquatus</i>	de Koninck, 1885	<i>Aviculopecten</i>	Hastarian
<i>ohioensis</i>	Mark, 1912	<i>Acanthopecten</i>	Missourian?
<i>ottonis</i>	Goldfuss, 1840	<i>Pecten</i>	Brigantian?
<i>pellucida</i>	Meek & Worthen, 1860	<i>Euchondria</i>	Desmoinesian
<i>perplexa</i>	Hutchinson & Stumm, 1967	<i>Euchondria</i>	Kinderhookian
<i>schulzi</i>	Frech, 1891	<i>Aviculopecten</i>	Strunian
<i>semicircularis</i>	M'Coy, 1844	<i>Pecten</i>	Viséan?
<i>senilis</i>	Herrick, 1888	<i>Crenipecten</i>	Kinderhookian
<i>smithwickensis</i>	Newell, 1937	<i>Euchondria</i>	Morrowan
<i>subcancellata</i>	Newell, 1937	<i>Euchondria</i>	Desmoinesian
<i>subcardiformis</i>	Herrick, 1888	<i>Crenipecten</i>	Kinderhookian
<i>sublevis</i>	Muromzeva & Turbanov, 1974	<i>Crenipecten</i>	Early Tournaisian
<i>subradiatus</i>	Roemer, 1852	<i>Pecten</i>	Brigantian
<i>tenuidentatus</i>	Cramer, 1910	<i>Crenipecten</i>	Brigantian-Namurian
<i>tenuisculptus</i>	Janischewskyi, 1900	<i>Aviculopecten?</i>	Serpukhovichian
<i>vera</i>	Drevermann, 1902	<i>Euchondria</i>	Strunian
<i>winchelli</i>	Meek, 1875	<i>Aviculopecten</i>	Kinderhookian-Osagean

Most of the taxa listed show one or more euchondriid left valve characters, i.e. the oblique disc shape, the thin and thread-like external costae with broad, flat interspaces or the sharp, narrow-spaced growth lines that are only visible in the interspaces. Apart from *Eu. aprathensis*, none of the species is completely known or described or figured, especially concerning hinge development, and even in that taxon not all characters are fully shown and possibly not yet observed.

Several authors have dealt with single taxa within the genus and have often created confusion rather than clarity in the distinction and characterisation of the taxa involved, which have rarely been compared directly with the type material. Additionally, most descriptions including the accompanying photographs do not permit comparison of the relevant morphological details, so we are faced with presently insurmountable discrepancies.

In Central Europe, members of the genus *Euchondria* were first recognized by Tornquist (1896; 1897) who erected *Eu. europaea* Tornquist, 1897 based on a shell from the Kulm-Tonschiefer (Warnantian) of Herborn (Germany). He observed the characteristic hinge structure but did not recognize the differing shell sculpture of RV and LV because his species was based on a single LV. From that locality, two other pectinoid taxa had been described earlier, *Pecten densistria* Sandberger & Sandberger, 1856, based on comarginal ornamented RVs, and *Pecten losseni* von Koenen, 1879, based at least on three specimens with RV and LV in close but not matching contact (von Koenen, 1879). Tornquist (1897) already assumed the synonymy of *P. losseni* and *Eu. europaea*, and Kayser (1900) united both species after the examination of further material from the type locality (see under *Eu. cf. losseni*). Drevermann (1902) compiled a first overview on Central European euchondriids, which had been almost entirely overlooked or/and placed in the genus *Aviculopecten* (or even *Pecten*). He erected three additional species, *Eu. belgica* Drevermann, 1902, *Eu. vera* Drevermann, 1902 and *Eu. beushauseni* Drevermann, 1902. The first is a replacement name for a misidentified Tournaisian shell of *Aviculopecten tornacensis* de Koninck, 1885, the second is the first known representative of the genus from the Late Devonian (Strunian) of W Germany, whereas the latter is based on insufficient type material and may be a synonym of *Crenipecten granulatus* (Phillips, 1841) (cf. Amler, 1995). *P. losseni* and *Eu. europaea* were regarded as separate species by Drevermann because he questioned the postulated synonymy of both species; *P. densistria* was not regarded as a member of euchondriids at that time. Later, Weigelt (1919) assumed that *P. densistria* and *P. losseni* could be conspecific, and consequently, Paul (1941) united all three taxa, a procedure which was followed by Nicolaus (1963) and Rathmann & Amler (1992) who collected and revised material from the type locality at Herborn and additional material from Aprath (near Wuppertal, W Germany).

In contrast, Demanet (1936, 1938) and Demanet & van Straelen (1938) who identified material from the Warnantian and Pendleian of Belgium as *Aviculopecten losseni* (not confirmed by Demanet, 1941) ignored the re-assignment to *Euchondria*.

Hind (1903), without having seen original material from Herborn, misinterpreted *P. losseni* von Koenen, 1879 and used that name for shells of different shape and ornamentation from the Carboniferous Limestone facies of Laurussia, an error which created a series of misidentifications by most subsequent authors since they used Hind's monograph as basis. He regarded *Euchondria* as a synonym of *Aviculopecten* and was

apparently unaware of Tornquist's and Kayser's observations on *P. losseni*. Accordingly, he assigned *P. losseni* to *Aviculopecten*, as he also did with *Pecten gentilis* Sowerby, 1840, a comparable form from the Silesian of the British Isles. He failed to comment on the possible relationships between *A. losseni* and *A. gentilis*, although both species occur at similar stratigraphic horizons and display an almost identical morphology. In several collections from the British Isles many specimens are labelled either as *A. losseni*, *A. gentilis* or as closely related to these species. From our present knowledge, it appears likely that both taxa are conspecific, whereas *A. losseni* sensu Hind is a different species, possibly conspecific with *Eu. bilstonensis* Wilson, 1961. A further species from the British-Irish Carboniferous with smooth RV and costate LV is *Pecten clathratus* M'Coy, 1844 which was also grouped with *Aviculopecten*. It resembles the euchondriids but does not show the crenulated hinge.

A few years later, Hind (1908) described shells from the Namurian of Scotland as *Aviculopecten neglectus* (Geinitz, 1866), claimed affinities to North American faunas, and noted the difficulties of generic assignment caused by the attribution to *Aviculopecten*, if the American material had the different, crenulated hinge characters. In a revision of this fauna, Wilson (1961) denied the American affinities and erected the taxon *Euchondria bilstonensis* Wilson, 1961, based on Hind's syntypes. Later, he added *Eu. neilsoni* Wilson, 1966, known only from a few incomplete specimens from the Scottish Brigantian.

In his pioneering monograph on Late Palaeozoic pectinoid bivalves, Newell (1937/38) presented a revised concept for Palaeozoic pectinoid taxonomy and systematics where the status and generic concept of *Euchondria* were established. In an appendix, Newell (1937: 113ff) assigned the pectinoid taxa of Hind's monograph in accordance with his new taxonomy. Unfortunately, and obviously without having seen the specimens, he confirmed the assignment of *P. losseni* (sensu Hind, 1903) and *P. gentilis* to the genus *Aviculopecten*, a practice which has been wrongly followed by Russian authors (see below). Yates (1962) confirmed the presence of euchondriids in the Irish Namurian where she observed forms called *Euchondria* aff. *Eu. levicula* Newell, 1937 in calcareous shales. These seem closely related to or identical with the specimens from the Vegamián Formation. We intend to re-investigate later our assumption whether or not the Irish and the Spanish specimens are geographical subspecies of a single taxon. The relationships to *Eu. aprathensis* Rathmann & Amler, 1992 seem to be quite close as they share the same obliquity, but the German species reaches a gigantic size compared with the Spanish form and differs in the number of costae.

When we try to recognize faunal relationships to different palaeogeographic realms, it is important to stress the fact that Russian authors totally misunderstood the Central European species of *Euchondria* because they were unaware of the errors committed by W European palaeontologists. Apart from the erroneous assignment of taxa to *Aviculopecten* (see above), most specimens figured as *A. losseni* and *A. gentilis* do not belong to these taxa (cf. Sergeeva, in Aisenverg et al., 1983: pl. 55, figs. 18-20; pl. 56, figs. 4-5; Muromzeva, 1974: pl. 12, figs. 5-8; Muromzeva, 1975: pl. 19, figs. 30-31). In contrast, *Streblochondria tenuisculptus* (Janischewskyi, 1900) in Muromzeva & Alexandry-Sadova (1975) from the Serpukhovian of the Urals appears to be a member of the euchondriids and is close to the Vegamián species.

The North American Mississippian species of *Euchondria*, i.e. *Eu. winchelli*, *Eu. areolatus* and *Eu. perplexa*, are generally more infracrescent, semicircular and symmetrical; they do not show the characteristic retrocrescent outline (cf. Hutchinson & Stumm, 1967).

Occurrence — Loc. Ge, Vegamián Formation, Tournaisian; loc. Me, Ricacabiello Fm., Kinderscoutian (R1).

Euchondria cf. losseni (von Koenen, 1879)

Pl. 2, fig. 3.

cf.? 1856 *Pecten densistria* Sandberger & Sandberger: 296, pl. 30, fig. 12.

cf. 1879 *Pecten losseni* von Koenen: 324, pl. 6, fig. 1c-d; non? pl. 6, fig. 1a-b.

cf.? 1879 *Pecten densistria*. — von Koenen: 327, pl. 6, fig. 2a-b.

cf. 1882 *Pecten densistria*. — Kayser: 76.

non 1896 *Aviculopecten densistria*. — Tornquist: 32, pl. 18, fig. 1.

cf.? 1897 *Euchondria europaea* Tornquist: 445, figs. A-C.

cf. 1900 *Pecten losseni*. — Kayser: 132.

non 1903 *Aviculopecten Losseni*. — Hind: 80, pl. 18, figs. 1-2.

pt. 1941 *Euchondria densistria*. — Paul: 221.

pt. 1963 *Euchondria densistria*. — Nicolaus: 195, pl. 14, fig. 5a-c.

non 1974 *Aviculopecten losseni*. — Muromzeva: 58, pl. 12, figs. 7-8.

non 1975 *Aviculopecten losseni*. — Muromzeva: pl. 19, fig. 30.

See Rathmann & Amler (1992), Paul (1941) and Nicolaus (1963) for further synonymy.

Material and measurements — See Table 4.

Table 4. Material and measurements (in mm) of *Euchondria cf. losseni* (von Koenen, 1879).

RGM	preservation	length	height	laa	lpa	R2	R10	loc.
346 511	LV int.ext.mld. next to RV int.mld.	7.6	7.7	2.5	2.9	—	—	Ge
346 519	LV int.mld.	13.8	13.5	—	4.5	16	16-17/5	Ge
346 525	LV int.mld.	8.0+	9.0	2.0	2.5+	—	—	Ge

Description (left valves only) — Shell small, LV slightly retrocrescent; height and length nearly equal; obliquely oval in outline, with slight posteroventral prolongation; umbo triangular, in anterior half of dorsal margin; umbonal angle some 80-90°; anterior auricle triangular, separated by narrow auricular sulcus; posterior auricle larger, less well separated from disc. External surface multicostate; number of costae (primary/secondary/tertiary) indeterminate; costae thin, filiform, but somewhat nodose; interspaces between costae relatively narrow, only twice as broad as the radial costae.

In RGM 346 511, remains of the internal mould of the RV are rotated some 90° upon the external mould of the LV (see Fig. 3).

Discussion — Up to now, no revision of the type material of *P. losseni* and *P. den-*



Fig. 3. *Euchondria* cf. *losseni* (von Koenen, 1979), remains of the internal mould of the RV are rotated some 90° upon the external mould of the LV. RGM 346 511; loc. Ge, Vegamián Formation, Late Tournaisian.

sistria has been carried out. Present knowledge of these taxa relies on syntype material from the collection of the IGP University of Marburg (figured for comparison on Pl. 2, fig. 1; Pl. 3, figs. 6-7). *Eu. losseni* is based on radially costate LVs, *Eu. densistria* on comarginally striate RVs. Apart from statements of von Koenen (1879), Tornquist (1897) and Kayser (1900) who suggested uniting '*Pecten*' *losseni* and '*P.*' *densistria* as well as *Eu. europaea*, there is no convincing evidence that these differently ornamented RVs and LVs really belong to one taxon only. We have seen no specimen with both valves in direct contact, and information on shell outline variability is meagre. Thus, we assign the LVs provisionally to *Eu. losseni* and hope that further studies on European euchondriids may solve the difficulty of discriminating between these taxa. Very close to our material is *Eu. neilsoni* Wilson, 1966, of Brigantian age which is not well known due to its rare occurrence in Scotland. Interesting to note is the size of the Spanish specimens which is similar to the German specimens from the Dill Syncline of the Rheinische Schiefergebirge, whereas the average size of *Eu. aprathensis* Rathmann & Amler, 1992, from the Kulm Shales of Aprath near Wuppertal (Germany) is nearly six to ten times.

For further discussion on euchondriid taxa see *Eu. wagneri* sp. nov.

Occurrence — Loc. Ge, Vegamián Formation, Late Tournaisian.

Euchondria cf. *bilstonensis* Wilson, 1961

Pl. 2, figs. 6-7.

- cf. 1840 *Pecten gentilis* Sowerby: pl. 39, fig. 19.
- cf. 1903 *Aviculopecten losseni*. — Hind: 80, pl. 18, figs. 1-2.
- cf. 1908 ?*Aviculopecten neglectus*. — Hind: 341, pl. 1, figs. 4-7.
- non? 1930 *Aviculopecten gentilis*. — Dorlodot & Delépine: 83, pl. 7, figs. 8-9.
- cf. 1961 *Euchondria bilstonensis* Wilson: 516, pl. 66, figs. 8-10.
- cf. 1969 *Aviculopecten gentilis*. — Sergeeva: 55, pl. 5, figs. 7-8.

Material — RGM 142 686, LV int.ext.mld.fragment.

Measurements — Length 13.0+ mm, height 13.0 mm, length of anterior auricle 3.4 mm, total number of costae at 2 mm shell height = 33, number of costae per 5 mm shell length at 10 mm shell height = 30-31.

Description — The single left valve is small and slightly retrocrescent (proscloine), slightly higher than long and characteristically obliquely oval in outline. Umbo triangular, pointed, central, umbonal angle 90°; anterior auricle triangular, separated by narrow auricular sulcus, anterior margin very gently convex, anterior auricular sinus perpendicular; posterior auricle triangular, acuminate, its posterior margin concave and ventrally merging with posterior margin of disc in a continuous curve.

Sculpture multicostate: some 30 primary costae, very thin, filiform, secondary and tertiary costae intercalate at various distance from umbo, at H = 10 mm 30-31 costae in 5 mm length; interspaces generally narrow, flat. Growth lines sharp, closely spaced, developed only in interspaces, giving the exterior shell surface a characteristic reticulate appearance. Anterior auricle with some 6-7 thin costae, posterior auricle with 4-6 weak, thin costae.

Interior morphology not preserved.

Discussion — The single LV, although similar to *Eu. wagneri* sp. nov. in general outline, is covered with nearly twice the number of extremely fine costae as compared with this species. As long as only one specimen is at hand the range of variation cannot be observed but the difference to *Eu. wagneri* and most other euchondriids listed above is noteworthy. *Eu. bilstonensis* and *Eu. losseni* sensu Hind non von Koenen are the only forms described which display this extremely delicate type of external ornament close to *Eu. gentilis*. Revision of the type material is necessary for serious comparison. For further discussion on euchondriid taxa see *Eu. wagneri* sp. nov.

Occurrence — Loc. Ge, Vegamián Formation, Late Tournaisian.

Euchondria sp. A

Pl. 3, figs. 2-4; Pl. 4, fig. 5.

Material and measurements — See Table 5.

Table 5. Material and measurements (in mm) of *Euchondria* sp. A.

RGM	preservation	length	height	laa	lpa	loc.
131 032	RV int.ext.mld.	—	—	—	—	Ge?
143 379	RV ext.mld.	7.0	7.7	2.5	3.0	Ge
Ve5	RV int.mld.	5.1	5.9	2.1	2.6	Ge
346 489	RV int.ext.mld. dam.	11.3(+?)	14.5(+?)	—	—	Pe
346 500a	RV int.mld.dam.	8.0+	7.0+	3.8	4.0+	Ge
346 504	RV ext.mld.	8.8	9.2	3.0	3.5+	Ge
346 505	RV int.mld.	4.2	4.0+	1.8	2.0	Ge
346 515	RV ext.mld.	4.0	4.7	1.7	1.2	Ge
346 516	RV int.ext.mld.dam.	8.0	8.0	2.5+	3.0	Ge
346 520	RV int.ext.mld.dam.	6.0	6.8	2.0+	2.8 ?	

and 3 fragments of RV (a.o. RGM 142 579).

Description (right valves only) — Valves small, outline suboval to semicircular and

only slightly retrocurved; anterior auricle semilobate, anterior margin convex, anterior auricular sulcus sharp and narrow, byssal (auricular) notch deeply indented. Posterior auricle corresponding in outline with that of LVs (*Eu. wagneri* sp. nov.). External ornamentation of disc consisting of narrowly spaced, minute concentric fila (c. 30/mm); anterior auricle with sharp, strong, closely spaced comarginal growth lines and 3 radial costae; posterior auricle with a few, thin radial costae and closely spaced growth lines; intersections of comarginal and radial elements forming minute spines. Original valve inflation not visible.

The characteristic crenulation of the hinge margin is seldom visible if ever; at best in specimen RGM346 500a.

Discussion — As stated above, the right valves of the samples are here described as an informal taxon since no specimens have been found with both valves in close association or direct contact. There is no indication whether these right valves belong to only one or more of the taxa described above. They agree well with specimens described as *Eu. densistria* from the Central European Kulm facies, especially a right valve (cf. Pl. 3, figs. 6-7).

One tectonically deformed specimen resembles members of the genus *Pernopecten* (Pl. 4, fig. 5). Its outline is of common pernopectinid shape; its hinge margin is short and straight; the auricles are not elevated above the hinge margin; the umbonal folds are indistinct; the posterior auricle is characteristically triangular in outline; the hinge margin shows the faint crenulation typical for the genus and the shell surface is covered with minute, closely spaced comarginal fila, strengthened on auricle. Additionally, the shell surface shows parallel creased folds caused by tectonic pressure on the very thin shell. Some other specimens are indeterminable and have been assigned only tentatively to the genus *Euchondria* (Pl. 3, fig. 1).

Occurrence — Loc. Ge, Vegamián Formation, Late Tournaisian; loc. Pe, Genicera Formation, Canalón Member; Arnsbergian.

Euchondria sp. B
Pl. 3, fig. 5.

Material — RGM 346 487a, RV ext.mld.distorted.

Measurements — Length 11.0 mm, height 9.0 mm.

Description and discussion — One single right valve, slightly distorted by tectonic pressure, differs from other right valves by its great width. Although the specimen shows several characters of *Euchondria*, there is no convincing indication of the crenulated hinge margin. Thus, it may also be possible that this shell is an extremely delicate ornamented right valve of *Limipecten* which also occurs in the Lavandera Member.

Occurrence — Loc. TII, Genicera Formation, Lavandera Member, Late? Viséan.

Family Aviculopectinidae Meek & Hayden, 1864
Limipecten Girty, 1904

Type species — *Limipecten texanus* Girty, 1904; O.D.

Diagnosis — Shell pectiniform, sub-orbicular, infracrescent (acline), inequivalve: LV convex, RV nearly flat. External shell sculpture consisting of intercalate radial ribs on LV and delicate or missing intercalate ribs on RV which is often only comarginally ornamented. Growth lines imbricate with zig-zag arrangement, elevated in interspaces and/or on top of ribs as minute spines. Auricles of more or less equal length, aviculopectinid in outline, and more strongly ornamented than disc.

Range — Tournaisian — Early Permian.

Discussion — See Newell (1937/38), Waterhouse (1969, 1982) and Amler (1987).

Limipecten sp.
Pl. 4, figs. 1-2, 4, 6.

Material and measurements — See Table 6.

Table 6. Material of *Limipecten* sp.

RGM	valve	preservation	loc.
346 487b	LV	ext.mld. dam. dist.	TII
346 488a	LV	ext.mld. dam. dist.	TI
346 488b	LV	ext.+ int.mld. fragment	TI
346 493	LV	int.+ ext.mld. dam. dist.	TI

Description and discussion — Unfortunately, none of the specimens studied is complete in shell outline or can be reconstructed. Furthermore, all are somewhat damaged as a result of tectonic pressure, but the overall morphology suggests close affinities to the aviculopectinoids, and the characteristic development of growth lines in a 'zig-zag' pattern allows most likely an assignment to *Limipecten*.

Occurrence — Loc. TI, TII, Genicera Formation, Lavandera Member, Late? Viséan.

Superfamily Buchioidea Waller, 1978
Family Chaenocardiidae Miller, 1889
Chaenocardia Meek & Worthen, 1869

Type species — *Chaenocardia ovata* Meek & Worthen, 1869; O.D.

Diagnosis (Newell & Boyd, 1995: 76) — Ovoid, retrocrescent to prorescent; higher than long; RV anterior auricle small and rounded; ligament variable, essentially opisthodontic, with long posterior bourrelet and vestigial anterior one.

Range — Viséan-Desmoinesian.

Discussion — As Newell & Boyd (1995) mentioned the genus is rare and not well known. In addition to the type species which was thought to be the only known species of the genus (Newell & Boyd, 1995: 79) we include *Megambonia carbonifera* in this taxon, and some Lower Carboniferous aviculopectinids may also prove to be members of *Chaenocardia*.

Chaenocardia? carbonifera (Hind, 1904)
Pl. 5, figs. 3, 7.

1904 *Megambonia carbonifera* Hind: 133, pl. 25, fig. 8.

1941 *Megambonia carbonifera*. — Paul: 138.

Material and measurements — See Table 7.

Tab. 7. Material and measurements (in mm) of *Chaenocardia? carbonifera* (Hind, 1904).

RGM	valve preservation	length	height	loc.
131 068	LV int.mld.dam.	13.5	13.2	Ge
143 380	LV int.mld.	17.1	16.6	Ge
346 500b	LV int.mld.	—	—	Ge
346 512	LV int.ext.mld.dam.	—	—	OS
346 517	LV int.ext.mld.dam.	—	—	Ge
346 529	LV int.mld.	18.0	17.9	Ge
Ve27	LV int.mld. fragment	—	—	Ge?

Description — Shell small, obliquely ovate; anterior end short, lobate; hinge line short, straight or very gently rounded; posterodorsal angle bluntly rounded; posterior margin very gently rounded or almost straight, ventral margin semi-circular; anterior margin with shallow byssal sinus. Umbones small, slightly raised above the hinge line, situated in anterior half of the hinge margin. Due to tectonic deformation, the former inflation of the valves and umbones is no longer visible. The external surface of the LV is ornamented with minute concentric fila; growth bands not clear; shell probably very thin.

Discussion — There is little doubt that the LVs under discussion show identical characters to the two shells figured and described by Hind (1904) as *Megambonia carbonifera*. Obviously, this taxon is very rare in the Carboniferous and its proper affinities have not yet been discovered. With some hesitation, we suggest that this species be placed in the genus *Chaenocardia*, the type species of which, *Ch. ovata* Meek & Worthen, 1869, was figured by Newell & Boyd (1995). Whereas LVs of *Megambonia carbonifera* and *Ch. ovata* match each other quite well in external morphology, no hinge characters have been observed in *M. carbonifera*. Furthermore, *Ch. ovata* is seemingly inequivalve with RVs of streblochondriid type having a well developed anterior auricle and a deeply indented byssal notch giving RVs of *Chaenocardia* an

Obliquipecten-like appearance. In contrast, the RVs of *M. carbonifera*, figured by Hind (1904), are a mirror image of its LV without any ear-like and notch-like structures.

Occurrence — Loc. Ge and OS, Vegamián Formation, Late Tournaisian.

Family Posidoniidae Frech, 1909

Posidonia Bronn, 1828

Type species — *Posidonia becheri* Bronn, 1828; by monotypy.

Diagnosis — See Weigelt (1922: 121) and Cox et al. (1969: 342).

Range — Carboniferous.

Discussion — See Weigelt (1922) and Ramsbottom (1959).

Posidonia cf. *becheri* Bronn, 1828

Pl. 5, figs. 8-9.

cf. 1828 *Posidonia Becheri* Bronn: 262, pl. 2.

cf. 1901 *Posidonomya Becheri*. — Hind: 27, pl. 6, figs. 11-15.

cf. 1941 *Posidonia becheri*. — Paul: 175.

For further synonyms see Paul (1941).

Material — RGM 346 496, ?RV int.mld.dam.; RGM 346 497, ?LV int.mld.dam.

Description and discussion — In both specimens the umbonal region and hinge line are missing. The overall shell shape and the concentric undulations fit into the unrevised and still uncertain concept of *Posidonia becheri*, one of the most widespread species of the Carboniferous. Both specimens are very similar to many specimens known to us from the Dinantian Kulm-Tonschiefer and Posidonien-Schiefer (*Posidonia* Shale) of Central Europe, not only in the size and shell shape but also in shell ornamentation. A wide range in variation is known with regard to these characters, but we cannot agree with the extremely broad species concept as admitted by Weigelt (1922).

Occurrence — Loc. BG, Genicera Formation, Olaja Member, Arnsbergian.

Order Pterioida Newell, 1965

Superfamily Ambonychioidea Miller, 1877

Family Myalinidae Frech, 1891

Posidoniella de Koninck, 1885

Type species — *Inoceramus vetustus* J. de C. Sowerby, 1829; by monotypy.

Diagnosis — See Weyer (1968: 565) and Semertzidis (1976: 130).

Range — Carboniferous.

Discussion — See Ramsbottom (1959) and Weyer (1968). It has to be mentioned that we do not agree with the view of Weyer who placed the genus in the family Posidoniidae. The group needs a thorough revision so as to eliminate synonyms and to define the proper taxa adequately.

Posidoniella? sp.

Pl. 5, fig. 4.

Material — RGM 346 490, RV int.mld.

Description and discussion — The single specimen available is incomplete and resembles oval-shaped representatives of the myalinids. The umbo is pointed and terminal; the ornamentation consists of concentric lines and undulations; the hinge margin and anterior portion of the shell are incompletely preserved, thus making confusion with pointed posidoniids a distinct possibility. Most palaeobiological characters of the group are uncertain and even the systematic position close to the ambonychioids or the mytilioids is a point of discussion.

Occurrence — Loc. OV, Genicera Formation, Canalón Member, Olaja Beds, Arnsbergian.

Order Limoida (Rafinesque, 1815) Waller, 1978

Superfamily Limoidea Rafinesque, 1815

Family Limidae Rafinesque, 1815

Limatulina de Koninck, 1885

Type species — *Avicula radula* de Koninck, 1842; S.D. by Newell, in Cox et al. (1969).

Diagnosis — See Newell & Boyd (1981: 62).

Range — Carboniferous.

Discussion — We disagree with the opinion of Newell & Boyd (1981) who placed the genus in the family Aviculopectinidae because these authors failed to revise the syntype collection of de Koninck and did not discuss any of the closely related species from the Dinantian of Belgium.

Limatulina? cf. *lima* (Holzapfel, 1889)

Pl. 4, fig. 3.

non 1844 *Lima alternata* M'Coy: 87, pl. 15, fig. 4.

cf. 1889 *Avicula lima* Holzapfel: 63, pl. 7, fig. 4

? 1912 *Limatulina alternata*. — Von Klebelsberg: 477, pl. 20, fig. 2.

non 1967 *Koninckopecten alternatus*. — Wilson: 476.

Material — 2 LV and 1 LV int.mlds, partly damaged, one with fragments of shell (RGM 346 498-499, Ge13).

Description — Shell outline obliquely oval; disc drop-shaped; hinge line short, straight; umbo situated in anterior half; anterior, posterior and ventral margin forming continuous line; auricles unequal: anterior auricle triangular, rounded, distinctly separated by shallow sulcus; posterior auricle elongate triangular, indistinctly separated from disc. Shell disc inflated, posterior auricle sloping and flattened; umbo prominent and swollen. External surface of shell covered with sharp radial costae and sharp growth lines which produce a reticulate appearance not visible on internal moulds. Intersections of comarginal and radial elements with small spiny projections. Auricles with similar ornament as the disc.

Discussion — Members of the limoids are rather unommon in Late Palaeozoic faunas and the few taxa are not well distinguished because most of them are based on insufficient type material. The type species of *Limatulina*, *L. radula* de Koninck, 1885, is more oblique and typically retrocrescent (see Newell & Boyd, 1981). The only taxon which agrees well in all morphological aspects with the Spanish material is '*Avicula*' *lima* Holzapfel, an endemic species from the Erdbach Limestone (probably of Ivorian age) of Germany (Holzapfel, 1889). At present, we neither follow Paul (1941) who united *L. alternata* M'Coy and *L. lima* Holzapfel, nor do we accept the assignment of both taxa to the genus *Streblochondria* as long as the internal characters are unknown. The specimens also resemble certain species of *Pseudomonotis* from the Late Palaeozoic and *Eumorphotis* from the Lower Triassic with less well pronounced posterior auricles.

Occurrence — Loc. RS and HE, Genicera Fm., Canalón Member; Arnsbergian.

Incertae sedis

? Family Lunulacardiidae Fischer, 1887

Chaenocardiola Holzapfel, 1889, emend. Beushausen, 1895

Type species — *Cardita haliotoidea* Roemer, 1850; S.D. by Beushausen (1895).

Diagnosis (after Beushausen, 1895) — Shell equivalve, inequilateral; outline somewhat triangular; umbones strongly incurved. External surface multicostate.

Range — Devonian?, Ivorian-Namurian.

Discussion — *Chaenocardiola* has been treated as a subjective junior synonym of *Lunulacardium* Münster, 1840 according to Newell & LaRocque, in Cox et al. (1969). No internal structures have been observed in either taxon, and more specifically it is noted that neither the hinge or ligament nor adductor scars or pallial line are known. The generic diagnoses of both species are imprecise from their inception, and both type species differ significantly. Serious difficulties concern the proper orientation of the shells, i.e. whether the umbo is curved opisthogyrous or prosogyrous, because no indications like ligamental area or lunule are present. Accordingly, we suggest differentiating between both taxa until a complete revision of the group may be possible.

Chaenocardiola cf. *haliotoidea* (Roemer, 1850)

Pl. 5, figs. 1-2, 5.

- cf. 1850 *Cardita* ? *haliotoidea* Roemer: 49, pl. 8, fig. 5.
 cf. 1941 *Chaenocardiola haliotoidea*. — Paul: 149.
 cf. 1962 *Chaenocardiola footii*. — Yates: 404, pl. 62, fig. 3.
 cf. 1962 *Chaenocardiola* cf. *haliotoidea*. — Yates: 406, pl. 61, fig. 3.
 cf. 1963 *Chaenocardiola haliotoidea*. — Nicolaus: 186, pl. 14, fig. 2a-b.
 cf. 1992 *Chaenocardiola haliotoidea*. — Rathmann & Amler: 54, pl. 1, figs. 14-16.
 For further synonyms see Paul (1941: 149) and Nicolaus (1963: 186).

Material and measurements — See Table 8.Table 8. Material and measurements (in mm) of *Chaenocardiola* cf. *haliotoidea* (Roemer, 1850).

RGM	preservation	length	height	loc.
346 492	RV? int.ext.mld.	29.4	18.5	BG
346 495	RV? fragment	17.8	14.5	BG
346 522	RV? int.mld.	—	—	Ge

Description — The overall shell outline equals that of the type species of *Chaenocardiola*, *Ch. haliotoidea* (Roemer, 1850), from the Erdbach Limestone of Germany, and that of *Ch. footii* (Baily, 1860) (see descriptions in Baily, 1860: 19; Yates, 1962: 404; and Rathmann & Amler, 1992: 54).

The shell surface is covered with 24 radial ribs which are well rounded in cross section and increase continuously in strength and width. The interspaces are very narrow furrows. The ribs are crossed by closely spaced growth lines, which are scaly and irregular near the ventral margin. They bend umbonally on top of the ribs and project marginally in the interspaces.

Discussion — Paul (1939: 170) was the first who considered *Ch. haliotoidea* and *Ch. footii* to be synonyms because both appeared to represent different developmental stages of one and the same species. This view was confirmed by Nicolaus (1963) after studying extensive collections from the Rheinische Schiefergebirge. Complete development of secondary costae corresponds to the '*footii*' stage whereas only marginally developed secondary costae have been called '*haliotoidea*' stage.

The Spanish material is similar to Irish and German specimens which have been studied for comparison in several collections but, as long as the whole group has not been revised, we prefer a 'cf.' determination.

Occurrence — Loc. Ge, Vegamián Formation, Late Tournaisian; loc. BG, Genicera Formation, Olaja Beds, Arnsbergian.

Palaeogeographical and palaeoecological implications

Facies conditions and distribution in the Early Carboniferous (Mississippian) of

Northwest Spain have been described by various authors, e.g. van Adrichem Boogaert (1967), Frankenfeld (1981), Eichmüller & Seibert (1984), Winkler Prins (1968), and Sánchez de la Torre et al. (1985). The black shale environment of the Vegamián Formation is generally interpreted as related to coastal upwelling currents which had been induced by a rise of sea level (Raven, 1983). A sea-level high stand is accepted for the Middle Tournaisian and Early Viséan (Ross & Ross, 1987). A poor oxygen content and a low rate of sediment accumulation seems to have led to the characteristic thin layering of condensed shales and cherts deposited in a relatively shallow sea below storm wave base. Environmental conditions, although generally equivalent, must have changed not only from the Vegamián black shales to the sediments of the Genicera Formation but also during the Viséan and Early Namurian when grey, green and red sediments of the succession were deposited. Apart from the oxygen content of the sediment and/or the bottom level of the seawater column, the sediments of both formations suggest quiet-water conditions as already assumed by Martínez-Chacón & Winkler Prins (1993). Similar and contemporaneous deposits are known from Central Europe as Kulm Facies.

With regard to palaeobiogeography, the Vegamián and Genicera faunas are difficult to interpret. It seems as if faunal connections were closer to the Pyrenees, the Ukraine and the Carnic Alps rather than Western and Central Europe (cf. Martínez Chacón & Winkler Prins, 1993; Kullmann, 1985) but the general composition of both faunas agrees well with Brigantian, Pendleian and Arnsbergian black shale faunas from Western and Central Europe (see Amler, 1998a,b; Wilson, 1967, 1989; Yates, 1962; Semertzidis, 1967). Similar relationships were also noted for trilobites (Gandl, 1973), brachiopods (Winkler Prins, 1968) and ostracodes (Becker, 1982). But, for the bivalves this appraisal is hampered by an unequal knowledge of faunas from the different regions. The sparse bivalve faunas from the Cantabrian Mts do not permit any decision in this matter as most of the marine bivalve faunas are not well preserved and poorly known as yet. If northern Spain had been an independent micro-continent at that time (e.g. Johnson & Tarling, 1985; Ziegler, 1989), palaeogeographical connections would have depended largely on palaeocurrents influenced by the closing of the Rheic Ocean (Palaeotethys). Relationships to both regions, the Ukraine and western Europe would have been possible at that time, and even closer ones to northern Africa.

Apart from these general assumptions, no conclusive model has been drawn for this biofacies yet. Few possibilities for ecological and depositional conditions have been discussed (Kammer et al., 1986 and references therein). The Vegamián Shale fauna is comparably low in biodiversity and is composed of a few benthonic organisms only. Most animals are nektonic or appear to have unknown life habits which also may include chemosymbiosis; bioturbation has not been observed. Some species occur in larger quantities but most appear in very few specimens only. Generally, the fossil content is restricted to certain layers, and most of the succession is unfossiliferous.

For an estimation of the oxygen content of ancient environments, especially, for discrimination between dysaerobic and anaerobic conditions, presence or absence and size of soft-bodied endofauna seems to be a requirement (Allison et al., 1995 and references therein). Accordingly, it seems that sedimentary conditions in Tournaisian

times were anaerobic because no ichnofauna has been observed in the Vegamián Shales. As the Vegamián Shale fauna is restricted to single layers and thus existed during certain time intervals rather than continuously during the Tournaisian, the term exaerobic biofacies may be applied in this case, especially, if additionally the associated fauna is considered (cf. Allison et al., 1995).

Dysaerobic faunas similar to modern examples are fairly common in Upper Palaeozoic successions. Characteristic faunal elements such as thin-shelled brachiopods including members of the Linguliformea, cephalopods and archaeogastropods occur in various black shale environments around Laurussia. In contrast, the composition of the Vegamián fauna does not agree well with the assemblage of macroinvertebrates of modern dysaerobic basins, as these largely contain deposit feeders (cf. Kammer et al., 1986).

Fossil preservation of the fragile shells and suggested life habits of the bivalves from the Vegamián and Genicera formations exclude long post-mortem transport and dislocation. However, the muddy and dysaerobic or anaerobic substrate would not have allowed a benthonic mode of life. Consequently, most of the bivalves as well as other faunal components are regarded as subautochthonous, some with a byssal attachment to floating or rooted algae. In particular, the thin-shelled euchondriids are well known to occur in a comparable manner in black shale biofacies of Central, Western and Eastern Europe of Carboniferous age. As long as we accept an epibyssate life habit on any substrate within the water column off the sediment for the eupteriomorphs, we do not need an extraordinarily specialized trophic condition, e.p. chemosymbiosis, for the euchondriids.

An important aspect for a characterization of the bivalve fauna is the question of trophic structures within that biofacies. In accordance with their modern counterparts, Late Palaeozoic eupteriomorphs are generally accepted as ciliary suspension feeders with a possible but unknown specialization. Additionally, Schmidt (1935) suggested a different life habit upon larger algal thalli for *Chaenocardiola* cf. *haliotoidea*. A comparable scenario was summarized by Amler (1998b) for the Kulm Basin of Central Europe based on more diversified bivalve faunas.

Acknowledgements

It is a great pleasure to acknowledge the help and advice of several colleagues in different institutions and museums who enabled access to type material and fossil collections — not only for this study. Above all I like to mention P.J. Brand and M.T. Dean (British Geological Survey, Edinburgh), W. Baird (Royal Scottish Museum, Edinburgh), P. Jeffery and J. Cooper (Natural History Museum, London), A. Dhondt and J. Godefroid (Institut Royal des Sciences Naturelles de Belgique, Bruxelles), W. Lindert and H.-U. Schlüter (Bundesanstalt für Geowissenschaften und Rohstoffe, Aussenstelle Berlin), P. Ensom (Yorkshire Museum, York), G. Flajs (Rheinisch-Westfälische Technische Hochschule, Aachen), E. Gröning (University of Clausthal-Zellerfeld), A. Gunning (Kelvingrove Art Gallery and Museum, Glasgow), J. Helms (Naturkundemuseum, Berlin), S. Tunnicliff (British Geological Survey, Keyworth), H. Jahnke (University of Göttingen), N.T. Monaghan (National Museum Ireland, Dublin), M. Dorling and R. Long (Sedgwick Museum, Cambridge), D. Siveter (Uni-

versity Museum, Oxford), U. Stottrop and U. Scheer (Ruhrlandmuseum, Essen), and G. Kauffmann (University of Marburg).

Furthermore, thanks are due to members of the staff of the NNM Naturalis, especially René Malherbe and Irma Regtien for photographic assistance, Wouter Wildenberg for laboratory help and Agnes Bavelaar-Dekker and Hidde Kingma Boltjes for bibliographic assistance. Very special thanks are due to J. Kullmann (University of Tübingen), D. Weyer (Naturkundemuseum Magdeburg), Nick Riley (BGS, Keyworth), Paul Wignall and Chris Peel (both University of Leeds) for discussions and information. The authors are indebted to R.H. Wagner, whose critical remarks helped to improve the manuscript.

One of us (MRWA) likes to thank the Prof. Dr K. Martin foundation for financial support of a five months sabbatical at the NNM Naturalis, Leiden.

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Manuscript received 2 December 1998.

Plate 1

Figs. 1-7. *Euchondria wagneri* sp. nov.; loc. Ge, Vegamián Formation, Upper Tournaisian.

1: RGM 346 518, LV internal mould, × 5; 2: RGM 346 509, LV internal mould, × 5; 3: RGM 346 506, LV internal mould upon RV external mould (arrow), × 3.9; 4: RGM 143 376, loc. Ge?, LV internal mould, × 3.3; 5: holotype RGM 346 523b, LV external mould, × 3.8; 6: holotype RGM 346 523a, LV internal mould, × 4.5; 7: RGM 143 377, loc. Ge?, LV external mould, × 4.

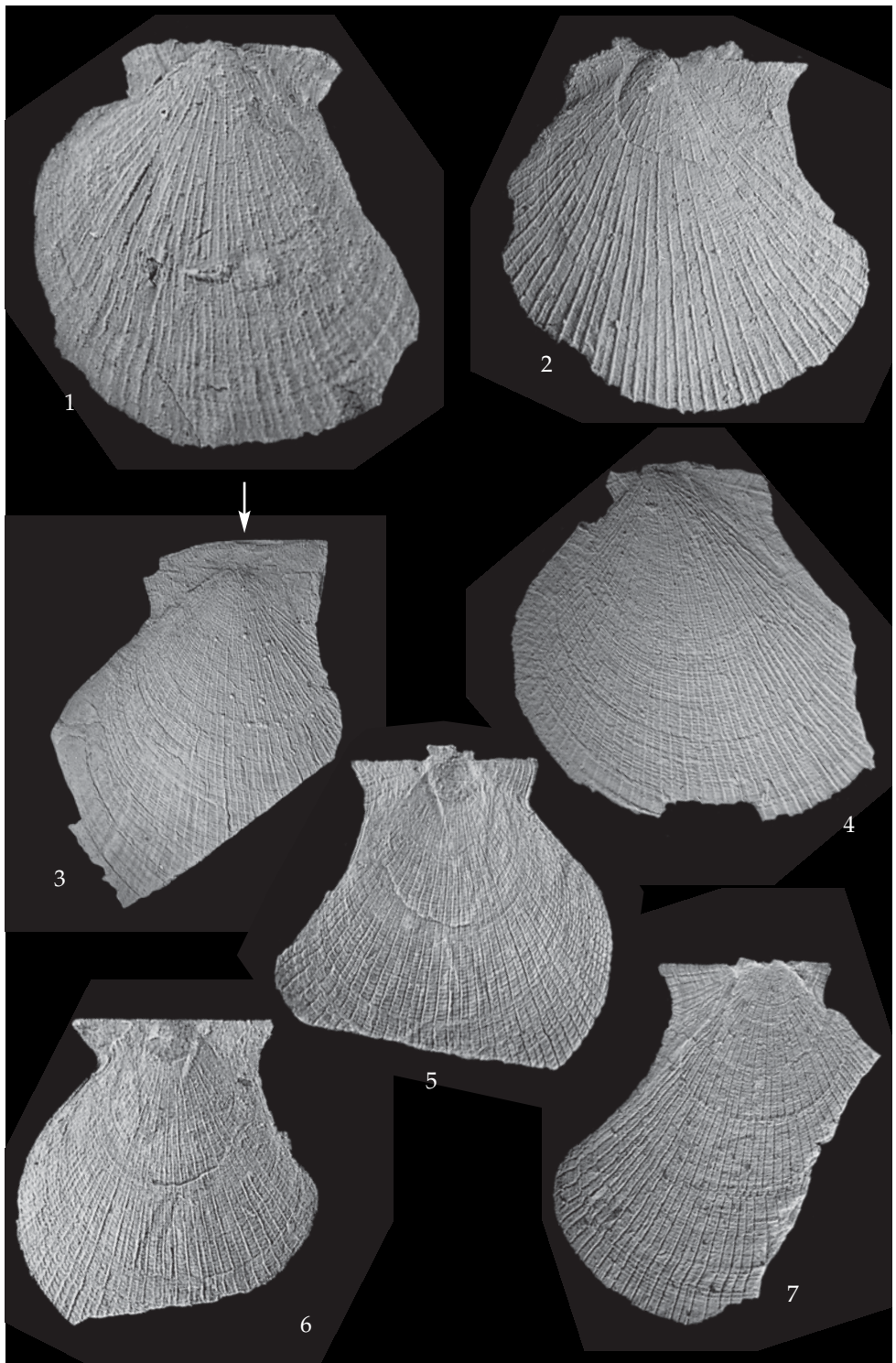


Plate 2

Fig. 1. *Euchondria losseni* (von Koenen, 1879), Mbg.Hb1, LV internal mould, loc. Herborn (Hessen, Germany), 'Kulm-Tonschiefer' (Kulm Shales), Lower Viséan, × 4.5.

Figs. 2, 4-5. *Euchondria wagneri* sp. nov.

2: RGM 142 692, LV internal mould, loc. Ge; Vegamián Formation, Upper Tournaisian, × 5.5; 4: RGM 346 486, LV internal mould, loc. Me, Ricacabiello Formation (= Meré Beds), Kinderscoutian?-Marsdenian, × 4; 5: RGM 346 485, LV internal mould, same loc., × 5.

Fig. 3. *Euchondria* cf. *losseni* (von Koenen, 1879), RGM 346 525, LV internal mould, loc. Ge, Vegamián Formation, Upper Tournaisian, × 6.

Figs. 6-7. *Euchondria* cf. *bilstonensis* Wilson, 1961, loc. Ge, Vegamián Formation, Upper Tournaisian, × 4.5.

6: RGM 142 686b, LV external mould; 7: RGM 142 686a, LV internal mould, × 4.2.

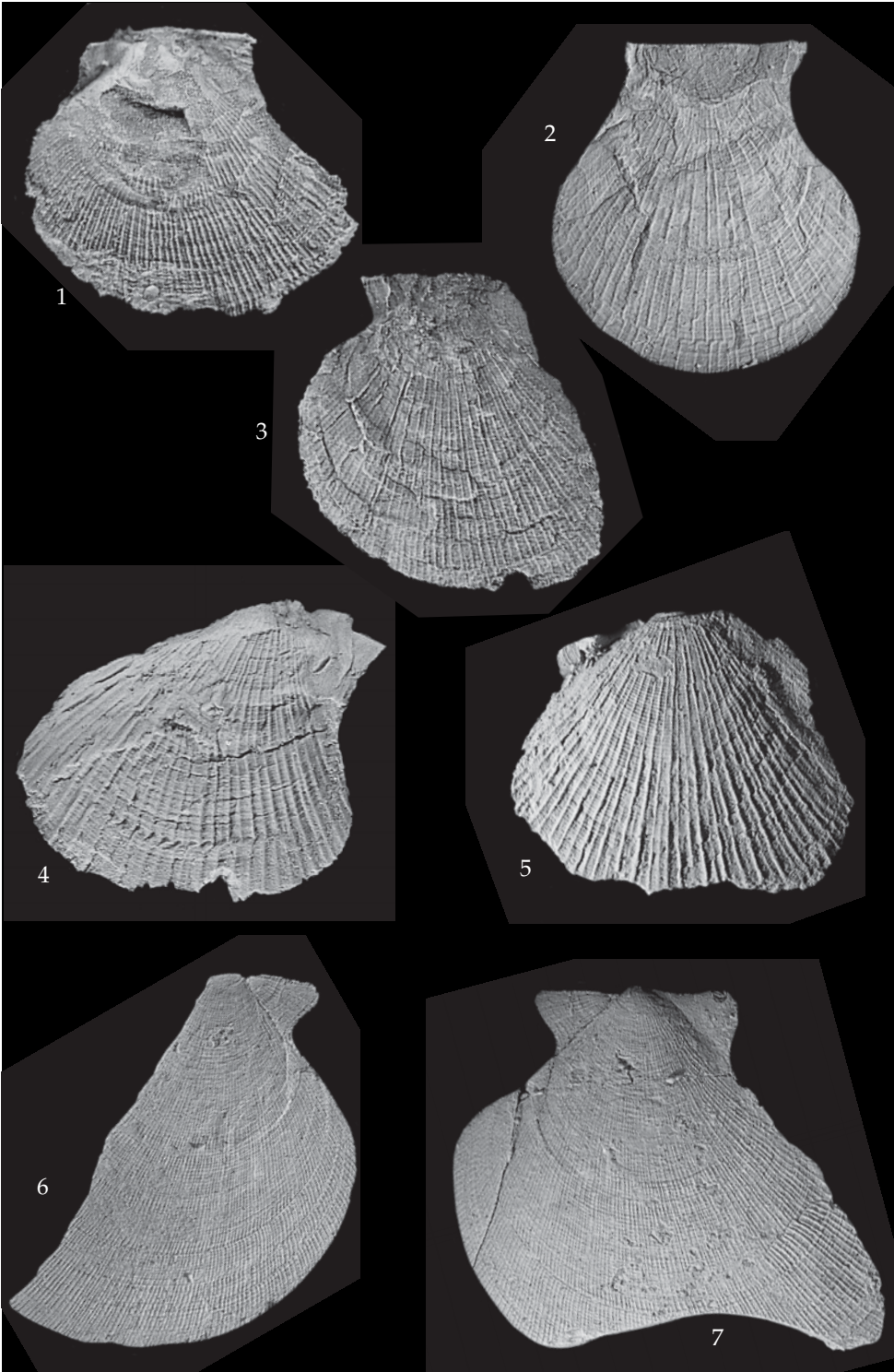


Plate 3

Fig. 1. *Euchondria* sp., RGM 346 491, RV internal mould, loc. OV, Genicera Formation, Olaja Beds; Arnsbergian, × 3.5.

Fig. 2-4. *Euchondria* sp. A, loc. Ge, Vegamián Formation, Upper Tournaisian.

2: RGM 346 516, RV external mould, × 4.5; 3: RGM 346 500a, RV internal mould, × 6.6; 4: RGM 143 379, RV external mould, × 6.

Fig. 5. *Euchondria* sp. B, RGM 346 487a, RV external mould, loc. TII, Genicera Formation, Lavandera Member, Upper? Viséan, × 6.

Figs. 6-7. *Euchondria densistria* (Sandberger & Sandberger, 1856); 6: SMF.Hb16, RV external mould, loc. Herborn (Hessen, Germany), 'Kulm-Tonschiefer' (Kulm Shales), Lower Viséan, × 4; 7: Mbg.Hb2, RV internal mould, same loc., × 5.2.

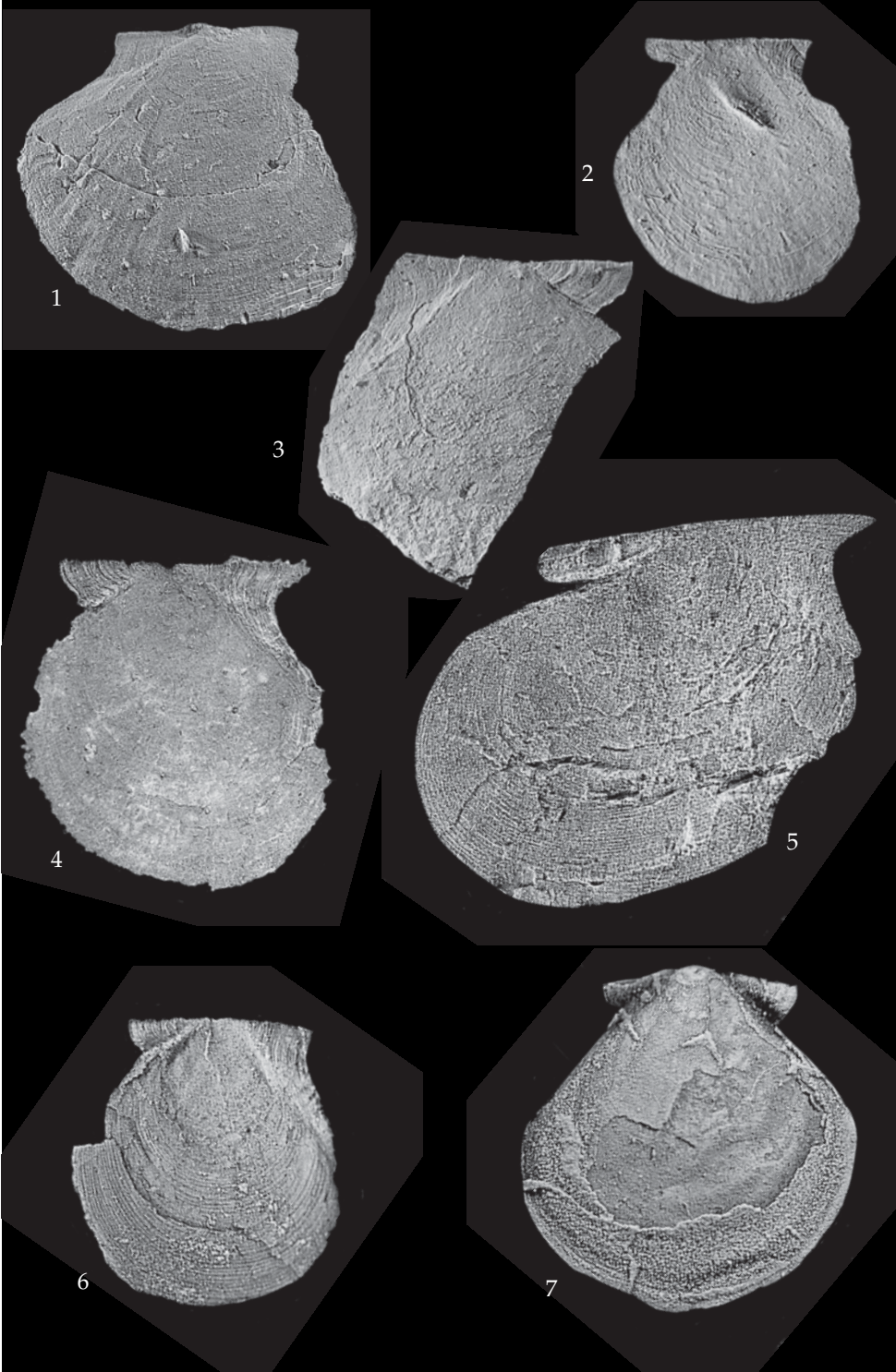


Plate 4

Figs. 1-2, 4, 6. *Limipecten* sp.

1: RGM 346 493a, LV internal mould, loc. TI, Genicera Formation, Lavandera Member, Upper? Viséan, × 1.2; 2: RGM 346 493b, LV silicone replica of external mould, same loc.; × 1.2; 4: RGM 346 487b, LV external mould, fragment, loc. TII, Genicera Formation, Lavandera Member, Upper? Viséan, × 1.6; 6: RGM 346 488a, LV external mould, fragment, loc. TI, Genicera Formation, Lavandera Member, Upper? Viséan, × 4.1.

Fig. 3. *Limatulina?* cf. *lima* (Holzapfel, 1889), RGM 346 499, LV internal mould with shell fragments, loc. RS, Genicera Formation, Arnsbergian, × 1.6.

Fig. 5. *Euchondria* sp. A, RGM 346 489, RV internal mould, loc. Pe, Genicera Formation, Canalón Member, Arnsbergian, × 3.5.

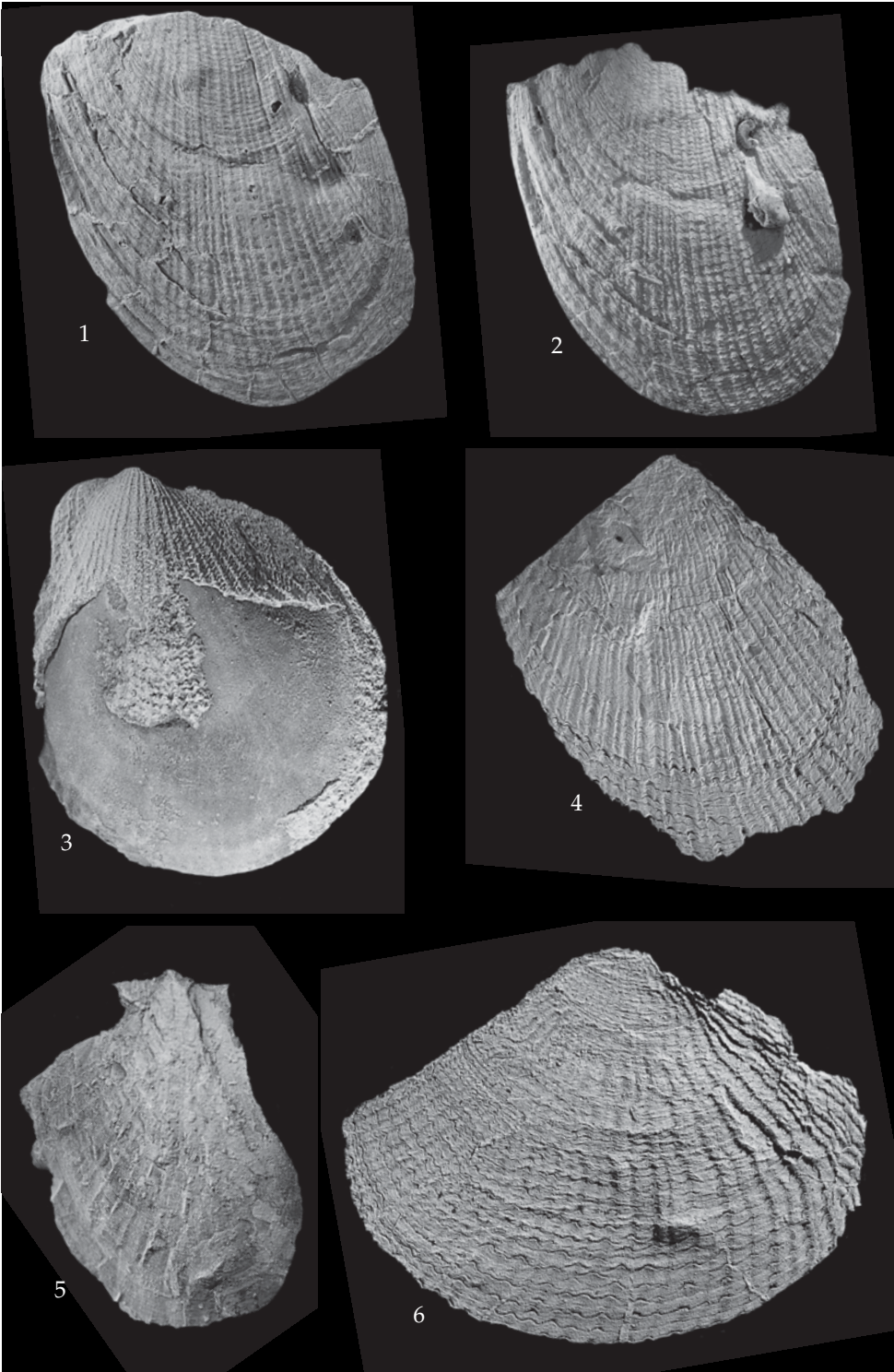


Plate 5

Figs. 1-2, 5. *Chaenocardiola cf. haliotoidea* (Roemer, 1850)

1: RGM 346 495, ?RV, loc. BG, Genicera Formation, Olaja Beds, Arnsbergian, × 3; 2: RGM 346 492, ?RV internal mould with shell fragments, same loc., × 2; 5: RGM 346 522, ?RV internal mould, loc. Ge; Vegamián Formation, Upper Tournaisian, × 4.

Figs. 3, 7. *Chaenocardia? carbonifera* (Hind, 1904)

3: RGM 143 380, LV internal mould, loc. Ge, Vegamián Formation, Upper Tournaisian, × 1.8; 7: RGM 346 512, LV internal mould, loc. OS, Vegamián Formation, Upper Tournaisian, × 4.

Fig. 4. *Posidoniella? sp.*, RGM 346 490, RV internal mould, loc. OV, Genicera Formation, Olaja Beds, Arnsbergian, × 4.

Fig. 6. *Parallelodon sp.*, RGM 346 494, RV+LV internal moulds with shell fragments, loc. BG, Genicera Formation, Olaja Beds, Arnsbergian, × 2.

Figs. 8-9. *Posidonia cf. becheri* (Bronn, 1828), loc. BG, Genicera Formation, Olaja Beds, Arnsbergian;

8: RGM 346 497, LV internal mould, × 3.2; 9: RGM 346 496, LV, × 2.

