

Late Devonian (Frasnian) bivalves from the Nocedo Formation – the results of Wilhelm Kegel's 1927 field trip to northern Spain

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During a field trip to the Peña-Corada Unit of the southernmost Esla region of the Cantabrian Mountains in 1927, the German stratigrapher Wilhelm Kegel sampled brachiopods and bivalves from a section in the Laoz valley near La Ercina. The stratigraphic position is believed to be part of the Nocedo Formation of Frasnian age. This fauna includes poorly preserved steinkerns of a near-shore bivalve fauna that was prepared for publication including labels and proposed names, but never published. The fauna represents only a very small and random part of the former community. But as information on Frasnian bivalves is scarce, the few specimens add important information on the distribution and palaeogeographic occurrence of near-shore, that is, Rhenish Facies bivalves within the south Laurussian – Rheic Ocean Realm. In the systematic part, seven bivalve taxa are described and discussed, most of which previously unknown from Palaeozoic Iberia and two of which are new. The revised list of bivalve taxa now includes members of the Eupteriomorphia, Palaeoheterodonta and Anomalodesmata: *Leptodesma* (*Leptodesma*) *adaroi* [Kegel] sp. nov., *Pterinopectinella?* sp., *Aviculopecten?* sp., *Glossites* sp., *Eoschizodus?* *hispanicus* [Kegel] sp. nov., *Leptodomus?* sp. and *Edmondia?* sp.

Bei Räumarbeiten im Devonsaal des Naturkundemuseums Berlin ist eine Schublade mit paläozoischen Muscheln (10 Exemplare) und Brachiopoden aus Nord-Spanien entdeckt worden. Darunter befinden sich auch einige Muscheln, die als Holotypen auf den Etiketten bezeichnet sind. Gesammelt wurde das Material 1927 von Wilhelm Kegel während eines Geländeaufenthaltes im Kantabrischen Gebirge. Den Angaben auf den Etiketten folgend wurde das Material auch von ihm bearbeitet. Seine vollständige(?) Publikationsliste in seinem Nachruf enthält allerdings keine Publikation, in der die vorliegende Fauna beschrieben wurde. Angaben zur stratigraphischen Stellung der Stücke fehlen; als Fundort ist bei allen Stücken „Valle Laoz bei La Ercina“ angegeben, dazu noch eine Schichtangabe (N32). Der Fundort liegt in der Peña-Corada Einheit der südlichsten Esla Region des Kantabrischen Gebirges (Geol. Karte 1 : 50.000, Blatt 130 Vegas del Condado) in der Provinz León. Nach den Informationen auf den Etiketten und der Lithologie der Matrix könnte als stratigraphische Position der untere Abschnitt der Nocedo-Formation (Frasnium) in Frage kommen. Im systematischen Teil werden sieben Taxa beschrieben, darunter zwei neue Arten. Die revidierte Liste der Bivalven-Taxa enthält Vertreter der Eupteriomorphia, Palaeoheterodonta und Anomalodesmata, *Leptodesma* (*Leptodesma*) *adaroi* [Kegel] sp. nov., *Pterinopectinella?* sp., *Aviculopecten?* sp., *Glossites* sp., *Eoschizodus?* *hispanicus* [Kegel] sp. nov., *Leptodomus?* sp. und *Edmondia?* sp. Trotz der wenigen Exemplare liefert die Fauna wichtige Hinweise zu paläogeographischen Beziehungen am Südrand von Laurussia während des späten Devons.

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Introduction

During curation work in the Naturkunde Museum Berlin, Henning Scholz discovered Devonian bivalve and brachiopod specimens labelled as having been collected by Wilhelm Kegel in 1927 in the Laoz valley near La Ercina in the Cantabrian Mountains, northern Spain. Kegel was a stratigrapher and later mapping geologist of the Preussische Geologische Landesanstalt at Berlin, who specialized in Devonian and Carboniferous geology, palaeontology of the Rheinisches Schiefergebirge and related topics.

Detailed research and inquiries to various colleagues failed to find any publication related to this fauna. In an obituary to Wilhelm Kegel, Putzer (1971, p. xv) listed all publications written by Kegel and none includes a description of or even a note on this fauna. A single piece of information related to these specimens is a note that Kegel visited the Cantabrian Mountains in 1927 (Putzer, 1971, p. xiv) following the International Geological Congress in Madrid in 1926, where he studied the tectonics of the Cantabrian Orogen and Early Devonian trilobites, published in the same year (Kegel, 1927), and a note by Kegel himself (1928, p. 82). But nowhere is given any indication to the Devonian bivalves and brachiopods collected by him in Asturias and León. In a later paper, Kegel (1929) described 'Gotlandian' (Silurian) faunas from northern León and added some information concerning the overlying Devonian sedimentary rocks, but did not mention any Devonian sections, faunas or publications in preparation. Also, the annual reports of the Preussische Geologische Landesanstalt did not mention any palaeontological project of Kegel concerning the respective fauna between 1926 and 1939. A publication was in fact intended by Kegel, based on information derived from the accompanying labels to the specimens. Although these original labels are accurately written, they contain confusing information as some of them indicate the status as holotype for the respective species (e.g., '*Modiomorpha cantabrica* n. sp. Holotyp'). Other labels, instead, refer to possibly existing species (e.g., '*Edmondia iberica* Kgl.'). In my opinion, it appears that not all specimens originally sampled by Kegel are present today and the latter labels were simply accompanying the paratypes, whereas the respective holotypes are lost. Further notes associated with the specimens include advice to illustrators or photographers, but do not contain taxonomic information.

Comparison of the host rocks with the regional geology of the collection area indicates that the small fauna almost certainly comes from the Frasnian Nocedo Formation, occurring in the southernmost part of the Cantabrian Mountains in northern León, and known to yield brachiopods, bivalves, bryozoans and echinoderms. This assumption is supported by the overall character of the fauna and the information

given from the original labels where Kegel indicated 'to I', meaning 'Upper Devonian I'. Frasnian bivalves from northern Spain have not yet been studied, although they would provide important information concerning bivalve evolution prior to the Kellwasser extinction event, especially relating to shallow marine benthic species, and to palaeo(bio) geography.

Most of the lithostratigraphic units presently distinguished in the Cantabrian Mountains were defined by various authors between 1960 and 1990. Many are based on the geological and stratigraphic account of the Palaeozoic succession in the Asturo-Leonesa and Palentian areas of the Cantabrian Mountains by Comte (1963). But, although he mentioned some brachiopods related to the presumed age of the 'Grès de Nocado', Comte did not refer to any bivalves nor did he indicate that he knew Kegel's visit to the region.

The thirty years of investigation between 1960 and 1990 have included extensive mapping campaigns carried out by working groups from Oviedo, Madrid (Instituto Tecnológico GeoMinero de España ITGE) and Leiden (de Sitter, 1962; Boschma, 1969; Boschma & van Staaldunin, 1969; Savage & Boschma, 1980; Sánchez de Posada *et al.*, 1990). They have been supplemented by studies on palaeontology, stratigraphy, sedimentology and tectonics of other universities (Sheffield, Tübingen and Würzburg), as well as more recent research by working groups from Cologne, Erlangen, Marburg, Kiel and Heidelberg. This research focussed on interrelations between sedimentary sequences, subsidence and orogenesis as well as basin analysis and modelling (Dallmeyer & Martínez García, 1990), but not specifically on Palaeozoic bivalves. Consequently, the aim of the present paper is threefold – to give notice of the fauna, to add some taxonomic and palaeobiogeographic information to Late Devonian bivalves, and to encourage colleagues working in the Cantabrian Mountains to collect further material.

Material and stratigraphy

Based on the information given by the original labels, Kegel sampled the bivalve specimens from a single locality in the Cantabrian Mountains in the province of León, Valle (= valley) Laoz near La Ercina, León, Spain (c. 42° 49' N 5° 13' W). This valley is neither indicated on the geological 1:50,000 sheet 130 Vegas del Condado of the Instituto Geológico y Minero de España (IGME, now Instituto Tecnológico GeoMinero de España ITGE; Rodríguez Fernández, 1982) nor on sheet 130-II La Ercina of the Mapa Topográfico Nacional de España, but is expected to stretch north-south in the very northeastern corner of the latter map.

All of the specimens are said to come from 'Schicht N 32', that is, bed N 32, of a section not known today, as we have no information about the outcrops and sections near La Ercina studied by Kegel during his field studies in 1927. The host sedimentary rock is a medium- to coarse-grained, pale reddish to pale brownish sandstone. All the fossils are preserved as internal or external moulds. Grain size does not allow detailed study of internal characters, but some features of hinge development are visible. The bivalves are accompanied by some spiriferids, rhynchonellids and chonetids, also not yet described. For this group he also created unpublished new names (*nomina nuda*), e.g., *Spirifer ercinensis* Kegel and *Chonetes leonesa* Kegel, which only appear on the accompanying labels.

According to the regional geology north of La Ercina, it appears most plausible that the host rocks belong to the Nocedo Formation which crops out 3 km north of La Ercina in a narrow band from southeast of Boñar in the west to north of Cistierna in the east. The Nocedo Formation was described by Evers (1968) and van Loevezijn (1982, 1986a, b). The latter studied the sedimentary environments, facies and stratigraphy of the Devonian sequence in the southern Cantabrian Mountains, and distinguished several facies belts. But as long as the precise location of the fauna as well as its stratigraphic level remain unknown, it cannot be attributed to one of the sedimentary facies of the External Zone distinguished by van Loevezijn (1986a, b). Furthermore, van Loevezijn studied biostratigraphic important groups only without recognizing bivalves in detail. Consequently, we can only assume that the studied bivalves come from the Gordon Member of the Nocedo Formation.

Late Devonian bivalves

Knowledge on Late Devonian bivalves of southern Laurussia is patchy, and full of gaps in systematic and taxonomic details, while also lacking any general account or overview. This is rather surprising as this time span includes the Kellwasser Crisis, one of the most important extinction events in Earth history. Descriptions of Frasnian or Famennian bivalve faunas are scattered in the literature, in local accounts on faunas or certain horizons of the Rhenohercynian or Saxothuringian zones of central Europe, most of which from the 19th and early 20th centuries. Even if types survived World War II, the material is mostly insufficiently preserved or unassignable to the correct stratigraphic levels. Even the extensive collections of fossils from the Rhenish Lower and Middle Devonian of central Europe or the siliciclastic North American Devonian are only occasionally precisely dated, and only a very limited number of specimens has been collected from Upper Devonian localities in central Europe.

Most of the taxa described from western and central European Rhenish (near-shore clastic) facies were erected by Goldfuss (1833-1841), Phillips (1841), Roemer (1843, 1850, 1855, 1860), de Ryckholt (1847, 1853), Sandberger & Sandberger (1849-1856), M'Coy (1851-1855), Kayser (1873, 1882), Frech (1891), Beushausen (1895), Whidborne (1889-1892, 1892-1907, 1896-1907) and Drevermann (1902); very few were added from northern Spain by Mallada (1875) and Barrois (1882). A limited number of bivalve assemblages from near-shore clastic facies of Late Devonian age are well studied in the last decades. McAlester (1962, 1963) revised North American bivalve faunas (mostly of Hall, 1885) from the Chemungian (~ Frasnian); Maillieux (1936) described bivalves from the Matagne Shale (Upper Frasnian); and I revised and analyzed the bivalve fauna from the Strunian Pilton-Velbert Facies of western and central Europe (Amler, 1993, 1995, 1996a, b, 2004).

If compared interregionally, the discovery of biogeographic connections between the Appalachian and the Rhenish or Hercynian Devonian combined with current plate tectonic reconstructions has increased advances in the taxonomy and distribution of faunas (e.g., Bailey, 1978, 1983; Nagel-Myers & Amler, 2007; Nagel-Myers *et al.*, 2008, 2009, for bivalves). These intercontinental studies allow comparison of the extensive North American faunas with our often badly preserved central and western European faunas across microplate faunas of the Iberian and/or Armorican terranes. From the Spanish Devonian,

few bivalves have been listed or described, although several formations, especially from the Middle Devonian, yield these molluscs in abundance. Due to their palaeoecological interdependences, they offer potential for biogeographic analyses.

Systematic palaeontology

Repository — All specimens described in this paper are housed in the collection of the Museum für Naturkunde, Berlin, and bear the collection numbers MB.M.5337–5346. The systematics used herein follows Amler (1999). There are other opinions concerning the systematics (e.g., Carter *et al.*, 2000; Neveeskaja, 2009), but as I do not intend to discuss higher level taxa, any misplacements do not affect the discussion of species. The common abbreviations for left valves (LV) and right valves (RV) in bivalve descriptions are used consistently. In the measurements, a “+” indicates that the specimen is damaged and larger than the measured size.

Superorder Eupteriomorpha Boss, 1982 [Anisomyaria Neumayr, 1883]

Order Pterioida Newell, 1965

Suborder Pteriina Newell, 1965

Superfamily Pterioidea Gray, 1847

Family Pterineidae Miller, 1877

Genus *Leptodesma* Hall, 1883

Subgenus *Leptodesma* (*Leptodesma*) Hall, 1883

Type species — *Leptodesma potens* Hall, 1883/1884, by subsequent designation of Miller (1889, p. 484).

Diagnosis — See Amler (1995, p. 38).

Leptodesma (*Leptodesma*) *adaroi* [Kegel label] sp. nov.

Fig. 1.

Etymology — Very certainly after Luis de Adaro y Magro (1849 – 1915), a Spanish mining engineer who also published the first geological maps of Asturias. It is the name given by W. Kegel on the label with the specimen.

Material — Damaged steinkern (lacking posterior wing) and external mould (margins damaged) of a LV; MB.M.5344a, b (holotype).

Measurements — Height 25+ mm; length 30+ mm; length of posterior auricle *c.* 3 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

Description — Outline characteristically triangular-pteriiiform; hinge margin long, straight, but not preserved along posterior wing; central part of shell posteroventrally increasing in breadth; line of maximum convexity (= oblique length) slightly curved;

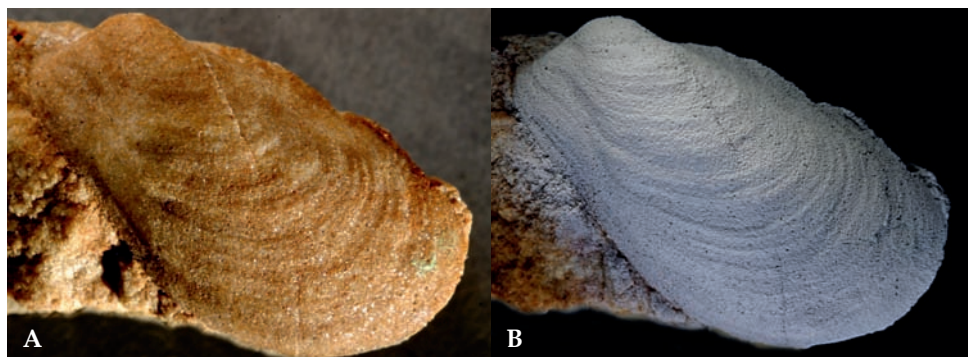


Fig. 1. *Leptodesma (Leptodesma) adaroi* [Kegel] sp. nov. Incomplete steinkern of a LV; MB.M.5344 (holotype). Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Length of specimen 30 mm. (A) Uncoated. (B) Coated with magnesium oxide.

angle between hinge margin and oblique length about 30°; posterior wing only visible on external mould, triangular, flattened, marked off from central body of shell with a gently curved slope, posterior margin strongly concave; anterior auricle nasute, separated from central body of shell by a narrow sulcus, forming a gentle sinus in anterior part of ventral margin. Central body of shell well inflated. Surface of shell covered by thin, closely spaced comarginal growth lines and six prominent comarginal rugae.

Remarks — According to the information given on the original label, Kegel intended to introduce the new species '*Leptodesma adaroi* Kegel'. Although not complete the specimen is fairly well preserved, if compared with the other material from the Laoz Valley. The palaeogeographical position of the locality without comparable species within this realm justifies the introduction of this species. Future studies of better preserved and more numerous material does not exclude the possibility to lower its rank to subspecies. There may be close relationships to European and North American species of *L. (Leptodesma)* within the south Laurussian Realm as pointed out by Bailey (1978, 1983) and Amler (1995), but as the phylogenetic concept of *Leptodesma* and allied pterineids is still poorly understood it remains uncertain whether 'species' are ecological variants or biological entities (McAlester, 1962; Amler, 1987). Several 'taxa' have been named from the Middle and Late Devonian, which resemble the specimen from La Ercina (Frech, 1891), particularly *Leptodesma (L.) bodanum* (A. Roemer, 1860), *L. (L.) anatinum* Whidborne, 1896, and *L. (L.) spinigerum* (Conrad, 1842). For discussion of taxonomic difficulties, see Amler (1995, pp. 38-46).

Order Pectinoidea Newell & Boyd, 1995 (= Pectinina Waller, 1978)
Superfamily Pterinopectinoidea Newell, 1938
Family Pterinopectinidae Newell, 1938
Genus *Pterinopectinella* Newell, 1938

Type species — *Pterinopectinella welleri* Newell, 1938, by original designation.

Diagnosis — See Newell (1938, p. 41), Newell & Boyd (1995, p. 29) and Amler (1995, p. 56).

Pterinopectinella? sp.

Fig. 2.

Material — Damaged and broken steinkern of a LV, subsequently glued, MB.M.5338.

Measurements — Length 20.1 mm; height 20.0 mm; length of anterior auricle 3.0 mm; length of posterior auricle 5.0 mm; length of hinge line *c.* 7.0 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

Description — Shell small, slightly prosocline; outline obliquely oval with small auricles not clearly separated from disc (= central body of shell); anterior margin well rounded, ventral margin less convex; hinge margin short, straight; auricles unequal in size and outline, difficult to observe; anterior auricle small, triangular, posterior auricle relatively long, mostly parallel to posterior margin of disc, but its posterior and posterodorsal margins not preserved; both auricles nearly flat. Umbo small, proximate to hinge margin; umbonal angle approximately 105-110°; disc slightly convex. Surface of shell covered by numerous coarse, irregularly spaced, radiating ribs, secondary ribs appear at different distance from umbo, some of them very close to primary ribs, others well between interspaces. Growth lines hardly visible in umbonal region, being more distinct in postero-central region. Posterior auricle nearly smooth, anterior auricle with three or four indistinct radial riblets.

Remarks — The preserved original label with the specimen as '*Aviculopecten* n. sp. a (Kegel)' indicates that Kegel intended to erect a new Spanish species under open nomenclature based on this steinkern. The obliquely oval outline combined with a relatively large posterior auricle and the external ornamentation compares favourably with several members of *Pterinopectinella* Newell. Unfortunately, neither the morphology of

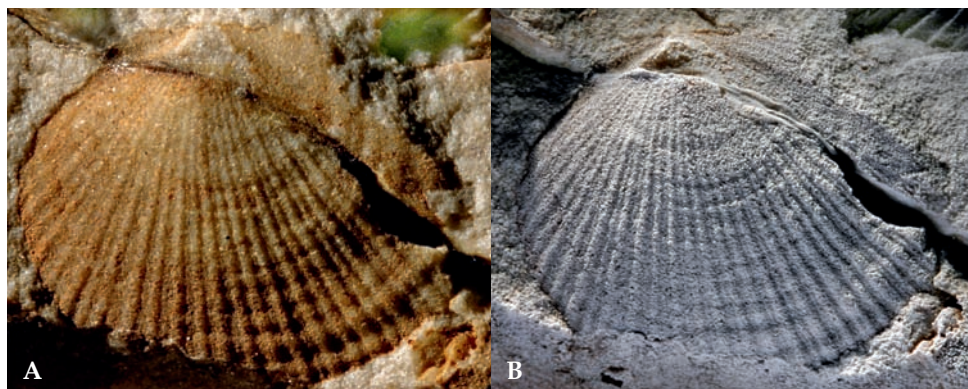


Fig. 2. *Pterinopectinella?* sp. Damaged and broken steinkern of a LV; MB.M.5338. Presumably Nocado Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Length of specimen 20 mm. (A) Uncoated. (B) Coated with magnesium oxide.

the auricles nor the hinge characters are sufficiently visible. As long as no material is available for the study of hinge characters, it remains open as to whether the specimen should be assigned to pterinopectinids or aviculopectinids. There is some resemblance to '*Aviculopecten' pelmensis* Frech, 1891, from the upper Middle Devonian of Germany and, particularly, '*Aviculopecten' aviformis* Whidborne, 1892, from the Middle Devonian of southwest England; the latter species is also mentioned from the upper Frasnian Matagne Shale of Belgium by Maillieux (1936). Both seem to be species of *Pterinopectinella*. Pterinopectinids crossed the Frasnian-Famennian boundary, and were common pectinoids in Devonian and Mississippian open shelf environments.

Superfamily Aviculopectinoidea Meek & Hayden, 1864 (Waller, 1978)

Family Aviculopectinidae Meek & Hayden, 1864

Genus *Aviculopecten* M'Coy, 1851

Type species — *Aviculopecten planoradiatus* M'Coy, 1851, by subsequent designation of Hind (1903).

Diagnosis — See Amler (1995, p. 62) and discussion in Waterhouse (1969, p. 1179; 2008, p. 72).

***Aviculopecten?* sp.**

Fig. 3.

Material — Damaged steinkern and external mould of a RV?; MB.M.5346_{1,2}.

Measurements — Length 31.0+ mm; height 33.0 mm; length of anterior auricle 12.0 mm; length of posterior auricle 12.0 mm; length of hinge line *c.* 27.1 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

Description — Shell small, nearly acline; outline not precisely reconstructable, somewhat subcircular or slightly obliquely oval; hinge margin long, straight; auricles of nearly equal size, relatively long, separated from central body of shell by narrow, deep sulci; anterior ear anteroventrally bounded by a rounded V-shaped byssal notch; posterior ear triangular with concave posterior margin; umbo small, proximate to hinge margin; umbonal angle approximately 100-110°; disc (= central body of shell) nearly flat; distinct and sharp oblique ridge extending from umbo to central part of posterior margin; ventral margin moderately rounded, posterior and anterior margins more convex. Surface of shell covered by numerous delicate paired radiating ribs, closely spaced, and minute growth lines. Posterior auricle only comarginally striated, anterior auricle with three or four indistinct radial ribs.

Remarks — The second pectinoid specimen from the Laoz Valley preserved as a steinkern with matching external mould was called '*Aviculopecten* n. sp. b' by Kegel.

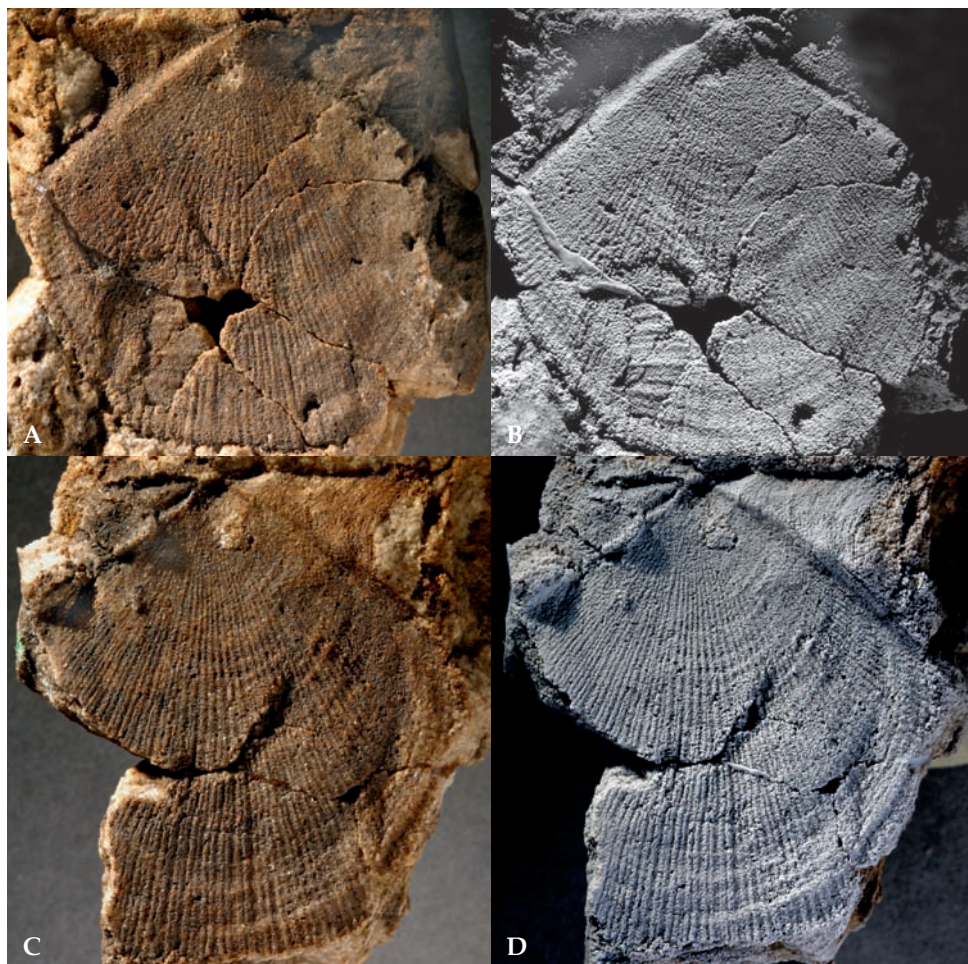


Fig. 3. *Aviculopecten?* sp. Damaged steinkern and external mould of a RV?; MB.M.5346_{1,2}. Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Height of specimen 33 mm. (A, B) Steinkern. (C, D) External mould (A, C, uncoated; B, D, coated with magnesium oxide).

Outline and ornamentation of the single specimen are poorly preserved, leaving the description in a fragmentary state. Especially, the lack of details of hinge characters excludes a confident generic assignment. The distinct, sharp, oblique ridge extending from the umbo to the central part of the posterior margin may allow comparison with members of the genus *Euchondria* Meek, 1874, but in this genus the ridge is confined to right valves, which are smooth (Amler, 1995). In addition, members of *Euchondria* possess a crenulated hinge line which is absent, as far as visible, in the present specimen. Devonian 'aviculopectinid' evolution and taxonomy are not yet revised, and for most taxa virtually nothing is known about hinge morphology. Consequently, any generic assignment remains provisional. Late Devonian 'aviculopectinids' were described, for example, by Frech (1891), Whidborne (1892-1907, 1896-1907), Maillieux

(1936), McAlester (1962) and Amler (1995), but, in contrast to the pterinopectinids, almost nothing is known of aviculopectinid evolution across the Frasnian-Famennian boundary (Kellwasser Event) and geographical distribution. If compared with broadly or supposedly contemporaneous taxa, such as '*Pseudaviculopecten striatus* (Hall, 1843), '*Aviculopecten aviformis* Whidborne, 1892, '*A. polytrichus sensu* Frech, 1891 (non Phillips, 1841), '*A. oceani* (Goldfuss, 1844), '*A. pelmensis* Frech, 1891, and '*A. neptuni* (Goldfuss, 1844), none shows a closely similar morphology.

Superorder Palaeoheterodonta Newell, 1965
Order Trigonioidea Dall, 1889
Superfamily Trigonioidea Lamarck, 1819
Family Eoschizodidae Newell & Boyd, 1975
Genus *Eoschizodus* Cox, 1951

Type species — *Megalodus truncatus* Goldfuss, 1837, by original designation.

Diagnosis — See Cox (1951, p. 369) and Neumayr (1891, p. 788) for diagnosis of *Kefersteinia* (preoccupied and replaced by *Eoschizodus*), and Newell & Boyd (1975, p. 91).

***Eoschizodus? hispanicus* [Kegel label] sp. nov.**

Fig. 4.

Etymology — After Hispania, the Latin name for the Iberian peninsular. It is the name given by W. Kegel on the label with the specimen.

Material — Damaged steinkern of a RV; MB.M.5341 (holotype).

Measurements — Length 45.0 mm; height 43.0 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

Description — Shell outline nearly subquadrate; posterior and ventral margins very slightly convex, anterior margin gently convex, only posteroventral margin well rounded; dorsal margin angular at 130°; umbo prominent, beak acute, slightly prosogyrate; hinge margin distinctly thickened with traces of one anterior and one posterior lateral tooth, but cardinal tooth not visible (hidden under beak). Valve moderately



Fig. 4. *Eoschizodus? hispanicus* [Kegel] sp. nov. Damaged steinkern of a RV; MB.M.5341 (holotype). Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Length of specimen 45 mm.

inflated, diagonal ridge weak. Valve smooth in umbonal region, with weak comarginal growth lines and rugae marginally.

Remarks — The single specimen was labelled '*Myophoria hispanica* Kegel' and intended to represent a new species. Anyhow, Devonian trigonoids are poorly understood and described, mostly based on absence of taxonomic features beyond hinge characters. Assignment of Devonian species to *Eoschizodus* Cox and Permo-Carboniferous species to *Schizodus* de Verneuil & Murchison, 1844, is rather a matter of convention than proper systematic background. For palaeobiogeographical reasons I make the species available, although it could have been also described under open nomenclature. Newell & Boyd (1975) briefly discussed and compared Devonian trigonoid genera, whereas Johnston (1993) described and discussed Australian taxa in more detail. Compared with the limited data on Devonian *Eoschizodus*, *Schizodus*-like trigonoids are relatively well documented in Carboniferous strata (de Koninck, 1885; Hind, 1898; see discussion in Amler, 1987, p. 218), but no taxonomic and evolutionary concept has yet been provided. To some extent, the Cantabrian species can be compared with specimens of *Eoschizodus? chemungensis* (Conrad, 1842) in McAlester (1962, p. 66), and it also resembles specimens figured as '*Myophoria' deltoidea* Phillips, 1841, and '*M.' trigona* F.A. Roemer by Whidborne (1896-1907) from upper Devonian strata. In contrast, most of the German Devonian trigonoids come from the near shore Emsian Rhenish Facies, such as '*Myophoria' circularis* Beushausen, 1895, and '*M.' roemeri* Beushausen, 1895.

Superorder Anomalodesmata Dall, 1889

Order Modiomorphoidea Newell, 1969

Superfamily Modiomorphoidea Miller, 1877

Family Modiomorphidae Miller, 1877 (= Modiolopsidae Fischer, 1887)

Genus *Glossites* Hall, 1885

Type species — *Glossites lingualis* Hall, 1885, by original designation.

Diagnosis — See Hall (1885, p. xlix), Williams & Breger (1916, p. 143) and Cox *et al.* (1969, p. N820); see also discussion in McAlester (1962, p. 45).

***Glossites* sp.**

Fig. 5.

Material — Damaged steinkern of a LV; MB.M.5343 ('holotype' of *Modiomorpha cantabrica* n. sp. (Kegel) *nomen nudum*, label with specimen).

Measurements — Length 44+ mm; height 24.0 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

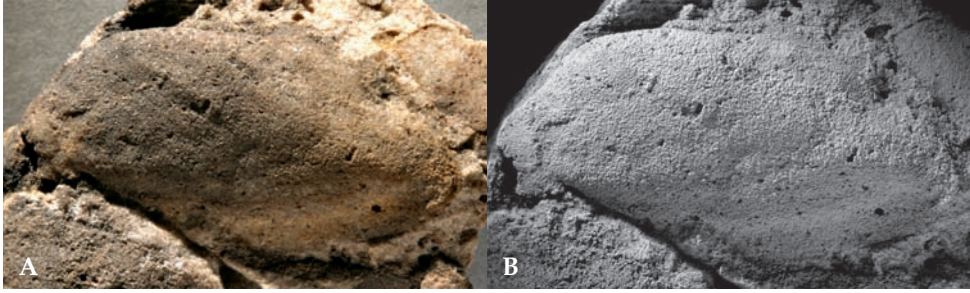


Fig. 5. *Glossites* sp. Damaged steinkern of a LV; MB.M.5343 ('holotype' of *Modiomorpha cantabrica* [Kegel] *nomen nudum*). Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Height of specimen 24 mm. (A) Uncoated. (B) Coated with magnesium oxide.

Description and remarks — Anterior, anterodorsal and posterior margins are incomplete, and do not allow proper reconstruction of the shell outline, which is more or less transversely oval with subparallel dorsal and ventral margins. Unfortunately, nothing can be observed about hinge characters. A weak diagonal ridge characteristic (but not exclusively) of modiomorphid taxa is apparent. The umbonal region is only very slightly inflated.

The overall morphology appears modiomorphid-like, but the more elongate outline allows comparison with members of *Glossites* Hall. *Glossites* and, especially, *Modiomorpha* are common and cosmopolitan genera, but their morphology and taxonomy are poorly understood (see Pojeta *et al.*, 1986; Bradshaw, 1999). The whole group of modiomorphoids *sensu lato* of still uncertain systematic position is in a rather dubious state of knowledge. Some spot data are available (Carter 1990, p. 266; Carter *et al.*, 1990, p. 391), but the entire group appears as a 'waste basket' for morphologically similar forms without distinct characters. Pojeta *et al.* (1986, p. 71) grouped the modiomorphids within the order Mytiloida based on similarities in ligamental features. In contrast, Carter *et al.* (2000, table 2) retained the position within the Anomalodesmata. Consequently, Kegel's new specific name, '*Modiomorpha cantabrica* n. sp. (Kegel)' as indicated by the corresponding label, is not formally introduced here, as further specimens need to be collected for proper description of a new taxon.

Order Pholadomyoidea Newell, 1965
Superfamily Pholadomyoidea Gray, 1847
Family Sanguinolitidae Miller, 1877
Genus *Leptodomus* M'Coy, 1844

Type species — *Leptodomus fragilis* M'Coy, 1844, by subsequent designation of Stoliczka (1870-1871, p. xix).

Diagnosis — See M'Coy (1844, p. 66), Stoliczka (1870-1871, p. 270) and Miller (1889, p. 485).

Leptodomus? sp.

Fig. 6.

Material — Damaged steinkern of a LV; MB.M.5342.*Measurements (distorted)* — Height 25+ mm; length 42+ mm.*Locality* — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.*Age* — Frasnian.

Description — Shell morphology partly reconstructable; outline of valve compact to elongate trapezoidal, posteriorly truncated; anterior region damaged; hinge margin posterior to umbo apparently straight; ventral margin slightly convex; posteroventral angle about 80° causing posterior margin to run obliquely (*c.* 100°) from posterodorsal margin. Umbo prominent, orthogyrous to slightly prosogyrous, distinctly raised above hinge margin, placed in anterior part of dorsal margin; prominent postumbonal carina (keel) running slightly S-shaped to posteroventral angle. Original valve inflation disguised by strong post-depositional distortion, apparently moderate anterior to carina; posterodorsally sloping abruptly. Internal mould covered with traces of weak growth lines visible in posterior area. Internal structures lacking; no traces of hinge teeth or ligament preserved.

Remarks — Based on information provided by the accompanying label this specimen was identified as *Leiopteria* n. sp. by Kegel. In fact, the specimen is torted like Triassic species of the genus *Hoernesia* Laube, 1866, a phenomenon discussed at length by McGhee (1978), and resembles deformed specimens of *Leptodesma* from the Late Devonian Pilton Facies of southwest England described by Whidborne (1896-1907). Thus, its original inflation is difficult to estimate. It was obviously misinterpreted by Kegel as a member of *Leptodesma* (*Leiopteria*) Hall, 1883, and is here transferred to *Leptodomus* M'Coy based on the trapezoidal outline, the prominent postumbonal carina and the lack of radial ornamentation with some hesitation. Faint comarginal growth lines indicate that a true posterior wing or auricle characteristic of pteroids is absent. The general morphology also suggests some affiliation to *Goniophora* (*Goniophora*) Phillips, 1848, but members of this genus (and subgenus) are characterized by distinctly prosogyrous umbos. In a general sense, *Leptodomus* is a tentatively used taxon for Ordovician to Permian modiomorphid-like bivalves lacking precise diagnoses for the species included. In general shape, the studied specimen also resembles short species of *Mecynodon* Keferstein, 1857, a



Fig. 6. *Leptodomus? sp.* Damaged and distorted steinkern of a LV; MB.M.5342. Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Length of specimen 42 mm.

genus widespread in the Rhenish Early and Middle Devonian (Beushausen, 1895; Haf-fer, 1959). Members of these genera show broad overlap in external morphology, but *Mecynodon* has prominent cardinal and lateral hinge teeth, which are absent in *Lepto-domus*, *Goniophora* and the studied specimen. Within this group of unclassified taxa also some species of *Cardiomorpha sensu* Beushausen (1895) can be included.

Family Edmondiidae King, 1850
Genus *Edmondia* de Koninck, 1842

Type species — *Isocardia unioniformis* Phillips, 1836, by original designation.

Diagnosis — See Amler (1987, p. 220) and discussion in Runnegar & Newell (1974, p. 5).

***Edmondia?* sp.**

Fig. 7.

Material — Incomplete steinkern of a LV?; MB.M.5339 ('holotype' of *Edmondia iberica* Kegel *nomen nudum*, label with specimen).

Measurements — Length 27.0 mm; height 20.0 mm.

Locality — Bed N 32, Valle Laoz near La Ercina, Leon, Spain.

Age — Frasnian.

Description — Due to the sparse morphological characters and the incomplete preservation, this short description follows some suggestions presented by Bailey (2009) for fossil bivalves where correct orientation of the valves remains uncertain for various reasons. Outline of the shell transversely oval with breviterminus (presumed

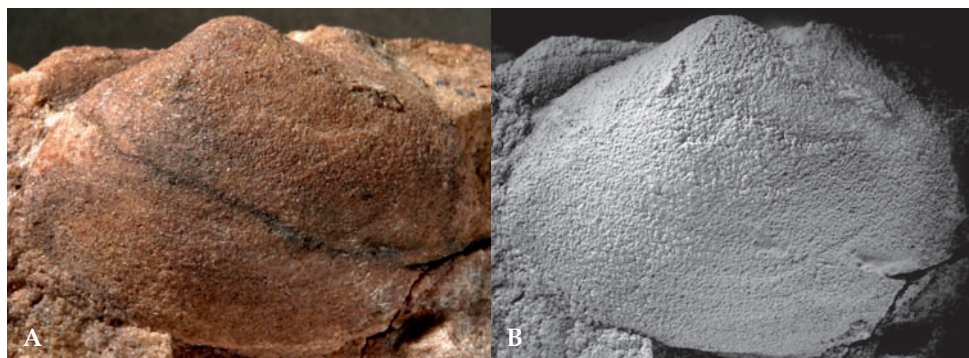


Fig. 7. *Edmondia?* sp. Incomplete steinkern of a LV; MB.M.5339 (holotype of *Edmondia? iberica* [Kegel] *nomen nudum*). Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Height of specimen 20 mm. (A) Uncoated. (B) Coated with magnesium oxide.

anterior) margin more convex than longiterminus (presumed posterior) margin; hinge margin slightly angled and hinge covered by prominent, more or less orthogyrate, centrally placed umbo. Shell markedly inflated and covered by few, weak comarginal growth rugae.

Remarks — The accompanying original label clearly indicates that Kegel chose this specimen as the holotype for his new species '*Edmondia iberica* Kgl.' The overall morphology resembles Late Devonian members of *Edmondia*, which is widespread in Mississippian shelf environments (see de Koninck, 1885). Its Devonian representatives, mentioned, for example, by Hall (1885), Whidborne (1896-1907), McAlester (1962) and Amler (1996a), are not well known, as *Edmondia* and allied genera lack precise diagnoses and include many 'species' of insufficient preservation. But the observed morphology of the specimen at hand fits rather well into the variation of '*Edmondia philipii* Hall & Whitfield, 1870, as described and discussed by McAlester (1962, p. 64). As there is no further, better preserved material available, I refrain from making the 'species' available.

Incertae sedis

Remarks — The following specimens were separated from their labels when found in the cabinet. Thus, our curation work was not successful in assigning correctly the names proposed by Kegel to the respective specimens. All steinkerns are inadequately preserved and need additional specimens from the type locality for proper erection of new species. The current combination of labels and specimens is as follows.

Glossites pradoi sp. nov. (Kegel label) (Fig. 8) [here: gen. et sp. indet. 1] *nomen nudum*. Damaged steinkern of a LV; MB.M.5337 (labelled as 'holotype'); very low inflation of the valve, which is covered with delicate, closely spaced growth lines.

Glossites simplex Kgl. [here: gen. et sp. indet. 2] *nomen nudum*. On the same label as *Spirifer ercinensis* Kgl.; no specimen discovered so far.

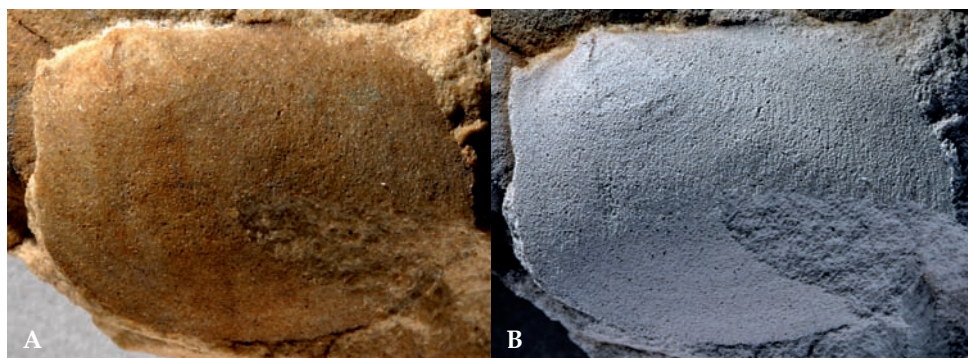


Fig. 8. Gen. et sp. indet. 1. Damaged steinkern of a LV; MB.M.5337. Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Height of specimen 24 mm. (A) Uncoated. (B) Coated with magnesium oxide.

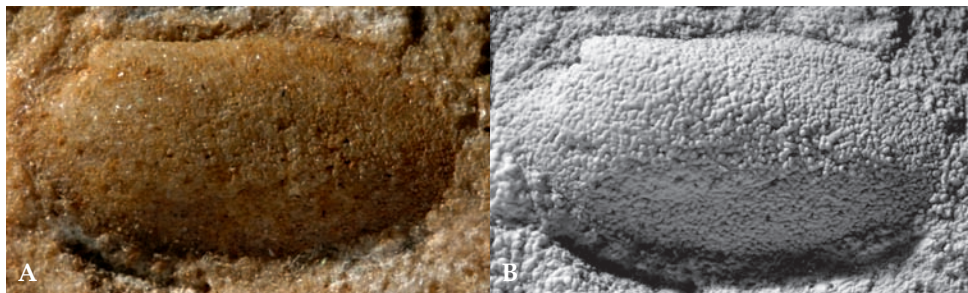


Fig. 9. Gen. et sp. indet. 4. Rather complete steinkern of a LV; MB.M.5340. Presumably Nocedo Formation, Frasnian. Valle Laoz near La Ercina, Leon, Spain. Length of specimen 11.5 mm. (A) Uncoated. (B) Coated with magnesium oxide.

Tellinopsis? sp. nov. Kegel [here: gen. et sp. indet. 3]. Incomplete steinkern of a LV; MB.M.5345; this specimen rather looks like a juvenile *Leptodesma* sp. and shows some affinities to '*Avicula*' *languedociana* Frech, 1891, but could also be compared with specimens of *Streblopteria* M'Coy, 1851.

Limoptera (*Paropsis*) sp. nov. (Kegel label) (Fig. 9) [here: gen. et sp. indet. 4]. Rather complete steinkern of a LV; MB.M.5340; measurements: length 11.5 mm; height 6.5 mm. Obviously, this specimen is not connected with its correct label, as the characteristic morphology of *Limoptera* Hall & Whitfield, 1869, does not match the elongate, transversely oval outline of the specimen. It may turn out that this specimen refers to the label of *Glossites simplex*.

Conclusions

The revised list of bivalve taxa now includes members of the Eupteriomorphia, Palaeoheterodonta and Anomalodesmata, namely *Leptodesma* (*Leptodesma*) *adaro* [Kegel] sp. nov., *Pterinopectinella?* sp., *Aviculopecten?* sp., *Eoschizodus?* *hispanicus* [Kegel] sp. nov., *Glossites* sp., *Leptodomus?* sp. and *Edmondia?* sp., as well as few additional indeterminable taxa. Due to the short sampling period during Wilhelm Kegel's field trip to northern Spain in 1927, the fauna is a random association without any indication of the original community. However, compared with similar or contemporaneous faunas it appears rather puzzling that palaeotaxodonts are completely missing. In Devonian and Carboniferous biotopes, assemblages of palaeotaxodonts are associated not only with near-shore marine muds, but also with mixed sediments of grain sizes ranging between silt and medium-grained sand (Beushausen, 1895; Whidborne, 1896-1907; Amler, 1995, 1996a, 2004). The overall impression is that of a typical near-shore, 'Rhenish Facies type' fauna from medium grained clastic sedimentary rocks. Judged from its composition and preservation, the La Ercina fauna sampled by Wilhelm Kegel is very similar to typical Rhenish Facies bivalve faunas from the central European ('German') late Early Devonian, the siliciclastic North American Devonian, the Late Devonian Pilton-Velbert facies or the siliciclastic Early Devonian of New

Zealand – as far as studied. The very limited number of specimens only tentatively allows comparison with these areas, but near-shore shallow water bivalves need continuous shelf areas for dispersal, contrasting with pelagic, Hercynian type bivalves, which obviously had long-term larval stages. That implies that most of the different shelf areas, such as western Europe, eastern North America, Armorica (Brittany) and Iberia, as well as parts of Morocco, seem to have been quite close to each other during Frasnian and Famennian time. This is supported by observations on Famennian bivalves from North America, Morocco and western Europe (Amler, research in progress).

The few bivalves collected by Wilhelm Kegel cannot be analyzed for palaeoecological conclusions. With respect to life habits, some of them were rather shallow endobenthic and semi-endobenthic, others like the eupteriomorphs were epibyssate. But we have no information on taphonomic circumstances inevitable for proper conclusions or on accompanying biota apart from few spiriferoid brachiopods. Thus, I do not intend to compare the composition of the La Ercina fauna with bivalve associations described and defined by Bowen *et al.* (1974) from the Late Devonian of New York State and of rather similar facies, nor the Strunian Pilton-Velbert shelf association as described some years ago (Amler, 1995, 1996a). However, the La Ercina bivalves need completion through intensive future collection plus additional data from other biota instead of simple faunal lists. These data sets will allow proper facies belt definition beyond simple sedimentary environment discrimination. Furthermore, future taxonomic studies based on sufficient material may provide more detailed information on palaeogeographic connections and relative position of microplates during the late Devonian – still debated among palaeomagnetists, geologists and palaeontologists. As a preliminary result, we can conclude from the small fauna studied that western Europe, Iberia and the region of present day New York State as well as Armorica seem to have been closely related without large scale separating oceans.

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