Paleobiogeographical relationships between North Gondwana and South Baltica: The *Ivanothyris havliceki* fauna (Cantabrian Zone, latest Emsian)

Paleobiogeografické vztahy mezi severní Gondwanou a jižní Baltikou: Fauna s *Ivanothyris havliceki* (kantabrická zóna, nejvyšší ems)

(5 figs, 2 plates)

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The relationships during the Late Emsian between the Ardenno-Rhenish (Belgium and Germany) area of South Baltica, and the Cantabrian Zone (northern Spain) of North Gondwana are analyzed according to a comparison of the articulate brachiopod faunas of the Cantabrian Faunal Intervals 14 to 16 and the equivalent Ardenno-Rhenish faunas. The value of the systematic determinations of the Cantabrian species are weighted through the abbreviation system proposed by the IGCP 421 leaders. Two new Cantabrian forms, *Ivanothyris havliceki* sp. nov. and *Moniellocyrtina orthoclina* gen. et sp. nov. characterize the Faunal Intervals considered and are described and figured.

Key words: Paleobiogeography, systematics, Baltica, North Gondwana, articulate brachiopods

Introduction

The separation between the main Devonian paleocontinents and their tectonostratigraphic units has been discussed at great lenght. The French geologists (Paris – Robardet 1990, Robardet et al. 1990, 1993, Plusquellec et al. 1996, Morzadec 1998, among others) relying mainly on sedimentologic and paleontologic data, carried out valuable efforts to show the cohesion among the North Gondwanan units and the narrowing of the so-called "Rheic ocean" during the Devonian. As a result the cartographic representation of North Gondwana and Baltica in the considered period has considerably changed and both continents are shown very close to one another on recent paleogeographic maps (compare Smith et al. 1973, Scotese et al. 1979 with Scotese – McKerrow 1990, Robardet et al. 1990, 1993 and Plusquellec et al. 1996, among others).

"Compact" reconstructions that integrate continents separated in the Paleozoic, are mainly based on the taxonomic analysis of biological groups with meager dispersion abilities such as articulate brachiopods. The increasing occurrence of common species and genera, and to a lesser extent of families and larger taxa of that group in different paleogeographic units, has thus been interpreted as indicating the progressive disappearance of previous barriers between these units. However, the present situation is unsatisfactory insofar comprehensive and precise systematic studies of many critical fossil groups are still lacking. The International Geological Correlation Project IGCP 421 "North Gondwana mid-Palaeozoic bioevent/biogeography patterns in relation to crustal dynamics" has promoted an excellent initiative involving the creation of databases where competent specialists analyze the taxonomic status of different fossil species cited in scientific papers after a common abbreviation system. This method would allow the fair selection of taxa to be processed by similar quantitative techniques.

In this paper the association of Lower Devonian articulate brachiopods that occurs in Faunal Intervals 14 to 16 (García-Alcalde 1996) of the Moniello (Fig. 1) and Santa Lucía Formations in the Cantabrian Mountains is analyzed. These Faunal Intervals belong to the conodont *Icriodus corniger* zone (only the Upper Emsian part of the biozone). The general paleontological study carried out by García-Alcalde et al. (1979) allowed the correlation of the corresponding stratigraphical levels of the Ardenno-Rhenish units such as the Kondel Group and Heisdorf Formation, in Germany, and the St. Joseph and Eau Noire (Co1a and Co1b pars) Formations, in Belgium, developed in the southern part of the Baltica paleocontinent. Aside from the data corresponding to the brachiopod faunas studied below, it is noteworthy to recall the complementary information on the occurrence of sublittoral, shallow marine ostracode faunas belonging to the "Eifel Ekotype" (Becker, in Bandel – Becker 1975) in Faunal Intervals 14–16. These faunas have been considered by Becker – Sánchez de Posada (1977) to be very close to those of the "Tentaculitenschiefer" level III of Thuringia (Zagora 1968) and show also close resemblance with the Heisdorf Formation ostracod faunas (Becker – Groos-Uffenorde 1982).

Cantabrian brachiopod species of the Faunal Intervals 14–16, together their abundance and taxonomic status (after the abbreviation system explained in the figure legende) are shown on Fig. 2. On the right hand side of the figure are indicated the identical (or related) species that are also found in the Ardenno-Rhenish region (Germany and Belgium) during the same period. The great number of common generic and even specific forms (50 to 52 common genera from the 70 determined Spanish genera and 37 common species from the 91 determined spe-

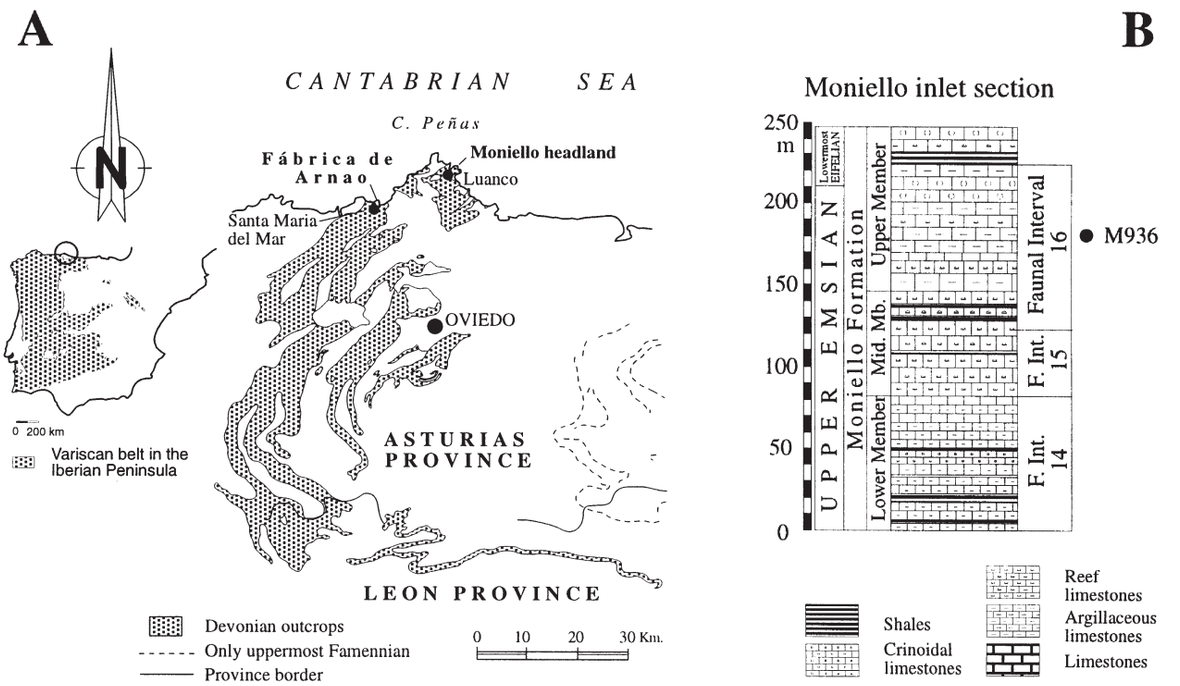

Fig. 1. A – Geographical situation of the stratotypes of *Ivanothyris havliceki* sp. nov. and *Moniellocyrtina orthoclina* gen. et sp. nov.; B – Stratigraphical situation of the Faunal Intervals 14 to 16 and the stratotype of *Ivanothyris havliceki* sp. nov. in the Moniello Formation, Moniello inlet section, southeast of Moniello headland.

cies; with the similarity increasing further if only abundant genera and species are considered), is in agreement with the minor importance of the Rheic ocean as a barrier between North Gondwana and Baltica in Late Emsian time (García-Alcalde 1993, 1995). Most of the cited brachiopods also occur in Aragón (in the eastern Cantabrian-Celtiberian area) where they are mainly represented in the Castellar and Ramblar Formations (García-Alcalde et al. 1979, Carls 1988).

In the studied association two very distinctive taxa of Spiriferida are worthy of mention and are described and figured here, *Ivanothyris havliceki* sp. nov. and *Moniellocyrtina orthoclina* gen. et sp. nov. *Ivanothyris havliceki* belongs to a genus widespread in Baltica [*I. trisecta* (Kayser 1883), Ardenno-Rhenish region], Gondwana [*I. gibbosa* (Barrande 1879), Bohemia, ?*I. gibbosa* sensu Brice 1970, Afghanistan], Siberia [*I. khalfini* (Alekseeva et al. 1981), Mongolia] and Kazakhstan (*I. grandis*, *I.* ? *kazachstanica*, and *I.* ? *subgrandis*; cf. Kaplun, in Senkevich – Kaplun 1982, Talent et al. 1987). *Moniellocyrtina orthoclina* is an external homeomorph of *I. havliceki* known presently only from northern Spain.

Systematic paleontology

Suborder Delthyridina Ivanova, 1972
Superfamily Delthyridoidea Phillips, 1841
Family Delthyrididae Phillips, 1841
Subfamily Delthyridinae Phillips, 1841

Genus *Ivanothyris* Havlíček, 1957

Remarks: Havlíček's (1959) original description of *Ivanothyris* states that the ventral median septum is completely "overgrown" within the shell by adventitious deposits which accumulate on both sides of the septum. However, Boucot's (1962) emendation established that the septum is thickened posteriorly by deposition of secondary material, but remains thin anteriorly. As this character is shown by the specimen of the type species *I. gibbosa* figured by Boucot (1962, Pl. 52, Fig. 19) and also by *I. trisecta*, *I. khalfini*, *I. grandis* and the new species described here, Boucot's above-mentioned emendation seems completely pertinent.

Ivanothyris havliceki sp. nov

Figs 3–4; Pl. I, Figs 1–9, 15

v. 1996 *Delthyris aculeata*; García-Alcalde, Fig. 2.
v. 1996 *Ivanothyris* cf. *trisecta*; García-Alcalde, Fig. 2.

Etymology: Species named after the Czech paleontologist Vladimír Havlíček for his invaluable contribution to the knowledge of Paleozoic stratigraphy and paleontology.

Material: 94 variably preserved specimens, most of which are silicified. Holotype DPO 32823 (Pl. I, Figs 1–5), 26 Paratypes, DPO 32762-32781 (DPO 32781 sectioned to show the internal structure, Fig. 4), 32818-32820, 32822, 32824-32825 (Pl. I, Figs 6, 8, 15) and 47 poorly preserved specimens DPO 32782-32816, 32821, 32826-32836 from the locality and stratum typicum (Fig. 1). 15 specimens, DPO 32745-32759 (Pl. I, Figs 7, 9) of the Upper Member of the Moniello Formation, cliffs north of Fábrica de Ar-

ABUNDANCE	FAUNAL INTERVALS 14–16, CANTABRIAN ZONE (N GONDWANA)	ARDENNO-RHENISH REGION (BALTICA)
a	***Platyorthis opercularis*** (no Fig.)	*Platyorthis opercularis*
c	***Schizophoria*** aff. ***interstrialis*** (no Fig.)	*Schizophoria antiqua*
r	***Schizophoria beaumonti*** (insufft. mat., no Fig.)	*Schizophoria vulvaria*
c	***Schizophoria*** sp. nov. (no Fig.)	*Schizophoria* spp.
rr	***Prokopia*** cf. ***bouskai*** (insufft. mat., no Fig.)	*Prokopia eichenbergi*
c	***Resserella*** aff. ***triangularis*** (no Fig.)	*Resserella triangularis*
a	***Parmorthina*** ? ***clariondi*** (?gen., ?int., no Fig., no int. Fig.)	
c	***Dalejina*** ? ***hamoni*** (?gen., no Fig.)	*Dalejina* ? *hamoni*
c	***"Rhipidomella" subcordiformis*** (?gen., no Fig.)	"*Rhipidomella*" *subcordiformis*
a	***Tyersella tetragona*** (no Fig.)	*Tyersella tetragona*
c	***Arbizustrophia*** aff. ***diaphragmata*** (no Fig.)	*Strophodonta* spp.
c	***"Leptaena" dicax*** (?gen., sp. nov.)	"*Leptaena rhomboidalis*"
c	***Plicostropheodonta*** cf. ***steiningeri*** (no Fig.)	*Plicostropheodonta* ? *steiningeri*
r	***Plicostropheodonta diffusa***	*Plicostropheodonta acutiplicata*
c	***Fascistropheodonta*** aff. ***sedgwicki*** (no Fig.)	*Fascistropheodonta sedgwicki*
r	***Strophodonta*** ? cf. ***piligera*** (?gen., insufft. mat., no Fig., no int., species inquerendum)	*Strophodonta* ? *piligera*
a	***Teichostrophia lepis*** (no Fig.)	*Teichostrophia lepis*, *T. lepis* emsii
c	***Teichostrophia*** ? ***tricornuta*** (?gen, no Fig.)	*Teichostrophia* spp.
r	***Mesoleptostrophia explanata*** (no Fig., no int.)	*Mesoleptostrophia explanata*
r	***Rhytistrophia sowerbyi*** (no Fig., no int.)	*Rhytistrophia sowerbyi*
rr	***Asturistrophia*** ? sp. nov. **A** (?gen., insufft. mat., no Fig., no int.)	
r	***Protodouvillina*** ? cf. ***taeniolata*** (?gen., insufft. mat., ?int., no Fig., no p. v.)	*Protodouvillina* ? *taeniolata*
r	***Cymostrophia*** ? ***bertrandi*** (basic prob., ?gen., insufft. Fig., insufft. mat., ?int., no b. v. int., no int., nondescript.)	
a	***Douvillinella (Douvillinella) fibula***	*Douvillinella* (*Crinistrophia*) *elegans*
c	***Douvillinella (Douvillinella)*** aff. ***filifer*** (no Fig., no p. v.)	*Douvillinella* (*Douvilinella*) *filifer*
c	***Telaeoshaleria*** sp. 2 (insufft. Fig., nondescript, sp. nov.)	*Telaeoshaleria subtetragona*
c	***Telaeoshaleria subtetragona***	*Telaeoshaleria subtetragona*
rr	***Eoschuchertella*** ? sp. (?gen, insufft. mat., no Fig., no int., no int. Fig.)	
c	***Iridistrophia*** aff. ***hipponyx*** (no Fig., no int.)	*Iridistrophia hipponyx*
a	***Chonetes bediae***	*Chonetes sarcinulatus*
r	***Plebejochonetes semiradiatus*** (no Fig.)	*Plebejochonetes semiradiatus*
a	***Plebejochonetes moniellensis***	*Plebejochonetes plebejus*
c	***Plicanoplia (Plicanoplia) ?*** aff. ***heddebauti*** (?gen., insufft. mat., no Fig., ?int., no int., no int. Fig.)	
c	***Longispina*** ? sp. (?gen, insufft mat., no int.)	"*Devonaria minuta*"
c	***Luanquella cantabriensis***	
a	***Luanquella alcaldei***	
c	***Loreleiella jahnkei***	*Loreleiella dilatata, L. extensa*
r	***Gypidula*** ? sp. (?gen., insufft. mat., no Fig., no int.)	*Gypidulinae* spp.
a	***Zdimir hercynicus*** (no Fig., no int.)	*Zdimir hercynicus*
a	***Iberirhynchia santaluciensis***	"*Trigonirhynchia*" spp.
a	***Glossinulus mimicus*** (nondescript)	*Glossinulus mimicus*
r	***Uncinulus*** ? cf. ***suborbignyanus*** (?gen., insufft. mat., no Fig.)	*Uncinulus* ? *gr. orbignyanus*
a	***Uncinulus*** ? ***orbignyanus*** (?gen.)	*Uncinulus* ? *orbignyanus*
a	***Uncinulus*** ? aff. ***lodanensis*** (?gen., no Fig.)	*Uncinulus* ? *lodanensis*
a	***Chlupacitoechia intermedia***	*Chlupacitoechia intermedia*
c	***Oligoptycherhynchus*** ? ***hexatoma*** (?gen., no Fig., no int.)	*Oligoptycherhynchus* ? *hexatoma*
c	***"Tetratomia" parvula*** (nondescript.)	"*Tetratomia*" *parvula*
a	***Atrypa (Planatrypa)*** ? cf. ***westfalica*** (?subgen, no Fig., no int.)	*Atrypa westfalica*
c	***Atrypa (Kyrtatrypa)*** ? sp. (?subgen., insufft. mat., no Fig., no int.)	*Atrypa* (*Kyrtatrypa*) *culminigera*
r	***Spinatrypina*** sp. (insufft. mat., no Fig., no int.)	*Spinatrypina* spp.
r	***Desquamatia (Desquamatia)*** cf. ***varistriata*** (insufft. mat., no Fig., no int.)	*Desquamatia* (*Desquamatia*) spp.
c	***Desquamatia (Synatrypa)*** sp. (no Fig., no int.)	*Desquamatia* (*Synatrypa*) *microzonata*
c	***Retzia prominula***	*Retzia prominula*

Fig. 2 *(continued next page)*

ABUNDANCE	FAUNAL INTERVALS 14–16, CANTABRIAN ZONE (N GONDWANA)	ARDENNO-RHENISH REGION (BALTICA)
r	***Rhynchospirina*** ? sp.	
	(?gen., insufft. mat., no Fig., no int., poor mat.)	*Rhynchospirina* spp.
a	***Anoplotheca lapparenti***	*Anoplotheca venusta*
c	***Bifida lepida*** (no Fig., no int.)	*Bifida lepida*
r	***Coelospirina*** sp. (insufft. mat., ?int., no Fig., no int.)	
r	***Plectospira*** cf. ***ferita***	
	(insufft. Fig., insufft. mat., ?int, sp. nov.)	*Plectospira ferita*
r	***Plectospira longirostris***	
	(insufft. mat., no int., nondescript.)	*Plectospira longirostris*
rr	***Plectospira*** sp. nov. (insufft. mat., no Fig., no int., sp. nov.)	*Plectospira* spp.
c	***Meristina*** ? aff. ***iconensis*** (?gen., ?int., no Fig., no int.)	*Meristina* ? *iconensis*
a	***Nucleospira*** sp. (no Fig., sp. nov.)	*Nucleospira* spp.
r	***"Athyris"*** cf. ***concentrica***	"*Athyris*" cf. *concentrica*
a	***Pachyplax gyralea***	
r	***Plicathyris ezquerrai***	
c	***Plicathyris collensis***	
rr	***Hexarhytis bonarensis***	
a	***Hexarhytis glomerosa***	"*Athyris undata*"
c	***Hexarhytis minor***	
a	***Pradoia lehmani***	
c	***Adolfia cabedana cabedana***	
rr	***Ambocoelia*** ? sp.	
	(?gen., insufft. mat., ?int., ?micro, no Fig., no int.)	*Ambocoelia* spp.
rr	***Echinocoelia*** ? sp.	
	(?gen., insufft. mat., ?int., no Fig., no int., poor mat.)	
c	***Alatiformia alatiformis*** (no Fig.)	*Alatiformia alatiformis*
a	***Alatiformia*** cf. ***alatiformis*** (no Fig., sp. nov.)	*Alatiformia* spp.
r	***Mediospirifer*** ? ***luciae*** (basic prob., ?gen., insufft. Fig, insufft. mat., ?int., ?micro, no int., nondescript, poor Fig.)	*Mediospirifer* spp.
c	***Subcuspidella*** aff. ***subcuspidata alata***	
	(basicprob., ?int., ?micro, no int., nondescript.)	*Subcuspidella subcuspidata alata*
a	***Ivanothyris havliceki*** sp. nov.	*Ivanothyris trisecta*
c	***Arduspirifer mosellanus***	*Arduspirifer mosellanus*
r	***Arduspirifer intermedius***	*Arduspirifer intermedius*
c	***Euryspirifer pellicoi***	*Euryspirifer* gr. *pellicoi*
r	***Euryspirifer*** cf. ***pellicoi***	
	(insufft. mat., no Fig., no int., no micro)	*Euryspirifer gr. pellicoi*
a	***Paraspirifer sandbergeri***	*Paraspirifer sandbergeri*
r	***Fimbrispirifer*** ? ***boulei*** (gen. nov., no int., no micro)	*Struveina daleidensis*
c	***Reticulariopsis dereimsi***	"*Reticulariopsis*" *curvata*
a	***Cyrtina intermedia***	*Cyrtina* gr. *heteroclita*
a	***Moniellocyrtina orthoclina*** gen. et sp. nov.	
r	***Meganteris archiaci***	*Meganteris archiaci*
r	***Micidus*** cf. ***shandkyddi***	
	(no Fig., no int., no shell structure, poor mat., sp. nov.)	
a	***Cimicinella loxogonia***	*Cimicinella loxogonia*, *C. granulosa*, *C. eifliensis*
r	***Cryptonella*** sp.(insufft. mat., no Fig., no int.)	*Cryptonella* spp.

Fig. 2 Articulate brachiopod species that occur in the Cantabrian studied intervals and equivalent or related species in the Ardenno-Rhenish region. The abundance in number of specimens of the Cantabrian Zone species is indicated by: **a**: abundant (50 specimens or more in collection), **c**: common (species known in several levels, 15–50 specimens in collection), **r**: rare (up to 15 specimens in collection), **rr**: very rare (1 or 2 specimens in collection, that often occur in residues of conodont analysis). The taxonomic status of the Cantabrian material as analyzed by the author is indicated by the abbreviation system proposed by the IGCP 421 leaders and adopted by the IGCP 421 Spanish Working Group, as shown: species accepted: non diacritical marks. **aff**: "close to"; in many cases possibly conspecific with the specified taxon but identification not possible on basis of documentation presented; **basic prob.**: problem of species definition needing resolution with type or topotype materials; **cf**: "similar to".; **?gen**: generic position questioned; **?subgen.**: subgeneric position questioned; **gen. nov**: apparently representative of a new genus; **insufft. Fig.**: insufficient illustration; **insufft. mat.**: insufficient or inadequate material, in many cases one incomplete specimen; **?int.**: clarification of internal structures desirable; **?micro**: microsculpture uncertain; **no b. v. int.**: inadequate or no data on taxonomically critical interior of brachial valve; **no Fig.**: description or brief descriptive citation without supporting illustration, in many cases only the name in synonymy lists; **no int.**: inadequate data on both valve interiors; **no int. Fig**.: no figure of taxonomically critical interior; **no micro**: inadequate data on microsculpture; **nondescript.**: a form so lacking in documented characters that definition with respect to other species is problematic; **no p. v.**: pedicle valve not known; **no shell structure**: absence of information on taxonomically critical shell structure, e.g. for retziids and terebratulids; **poor Fig.**: illustrations inadequate for useful taxonomic evaluation; **poor mat.**: material poorly preserved or inadequate in other ways; **species inquerendum**: a species in need of re-investigation of type or topotype materials to determine (or confirm) taxonomic characters that might enable identification of materials from elsewhere on the globe; **sp. nov.**: believed to represent an unnamed species; **""**: inverted commas around a generic name imply that either generically critical characters are not known, or delineation of genus needs clarification compared with previously proposed genera.

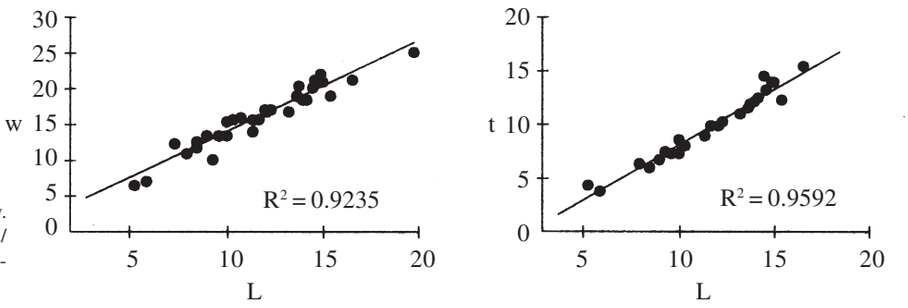

Fig. 3 *Ivanothyris havliceki* sp. nov. Lenght/Width (L/w) and Lenght/ /Thickness (L/t) dispersion diagrams.

nao (Castrillón, Avilés). 2 specimens, DPO 32760-32761 of the same stratigraphic level, Xivares beach (Gijón). 3 specimens, DPO 32837-32839 of several Santa Lucía Formation localities in the Leon province, Faunal Intervals 15–16 (García-Alcalde 1996).

Type locality and type horizon: Moniello inlet (Luanco, Gijón). Moniello Fm., Upper Member, Faunal Interval 16, bed M936. Latest Emsian. (Fig. 1).

Diagnosis: Small and moderately inflated *Ivanothyris*, with few lateral costae (up to 3). Short dental plates. Umbonal ventral secondary shell deposition developed only up to half of the delthyrial chamber. Ventral middle septum very long reaching up to near the anterior margin of valve. Short crural plates.

Description: Small, biconvex to slightly ventribiconvex, inflated but not spheroidal (t 82 % of L), brachythyrid shell with rounded cardinal angles. Shell outline transversely elliptical (L less than 75 % of w); greatest width near hinge; greatest thickness in the posterior half of the shell lenght.

Well developed, strongly apsacline, concave ventral area with poorly defined lateral margins. Rather large delthyrium occupying 1/5 to 1/4 of the hinge width; perpendicular to the area, deltidial plates join below the ventral beak to form a small, convex deltidium. The ventral area is divided into two differently ornamented regions (palintrope and ventral interarea; sensu Krans 1969) separated by faint interareal edges (Pl. I, Figs 5, 8, 15). The interarea is smaller than the palintrope and is ornamented by well marked transverse and very fine longitudinal striae. The palintrope is laterally bounded by subdued umbonal edges and shows the same ornamentation than the rest of the valve, with overlapping growth lamellae and close growth lines frilled by small, numerous, sub-radial spine bases. Strongly curved (sometimes reaching an angle close to 180˚ over the interarea) to erect ventral beak (Pl. I, Fig. 4). Well developed, rather flat, anacline, transversely striated dorsal interarea, 5–6 times lower than the ventral interarea. Open nothothyrium. Small, slightly curved beak. No palintrope present. Rounded to flattened, rather deep ventral sinus starting at the apex of valve, up to 33 % of the shell width anteriorly. Flattened, convex dorsal fold bounded by rounded furrows stronger than the intercostal spaces. Short, concave, parabolic, dorsal to postero-dorsally turned tongue. Parasulcate frontal commisure (Pl. I, Fig. 3).

The shell flanks are ornamented by 2–3 very rounded, low and wide costae separated by similar interspaces. The first lateral pair of costae are well developed and start at the apex of valve, but the other costae originate further anteriorly and are very faintly developed, so much that sometimes they are only marked by subdued commisural folds. The sinus bounding costae sometimes form subangular indentations in the commisure. Fairly overlapping, growth lamellae. Numerous, close, regularly spaced, more or less strongly marked growth lines provided by many (more than 50 per 5 mm. near the anterior part of sinus in the specimen DPO 32745), strong, well aligned, subradially extended spine bases, diverging anteriorly from the intercostal spaces and ventral sinus towards the summit of the costae and median fold. In some silicified specimens occur spines which are more or less complete in anatomical connection. They occur in superimposed series, corresponding to several consecutive growth lamellae (Pl. I, Figs 7, 9). The lamellar edges are

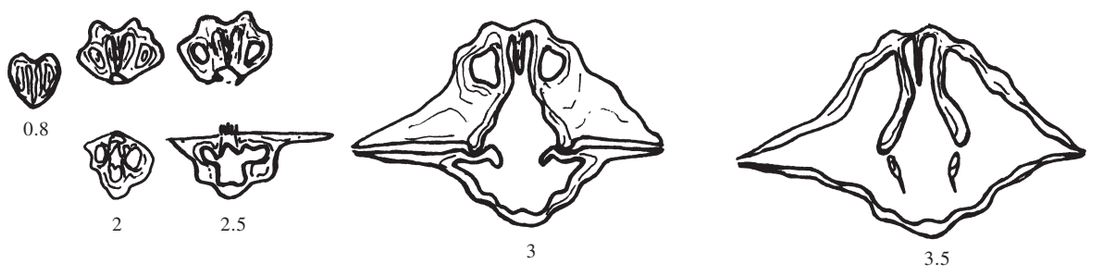

Fig. 4 *Ivanothyris havliceki* sp. nov. Paratype DPO 32781. Serial sections. x3.5. Figures: distances of the sections to the ventral apex.

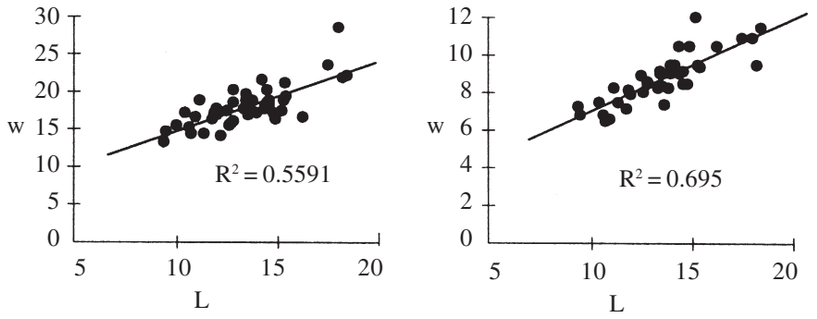

Fig. 5 *Moniellocyrtina orthoclina* gen. et sp. nov. Lenght/Width (L/w) and Lenght/ /Thickness (L/t) dispersion diagrams.

fringed by rather thick, apparently massive spines, that project anteriorly from the valve surface to form variable acute angles around 30˚. These spines are flanked by finer spines that sometimes are grouped together between and below the stronger spines. In specimen DPO 32751 (Pl. I, Fig. 7) fine, parallelepipedic spines up to 2 mm in lenght forming a dense and complex protective cluster are preserved. The spines are disposed in superimposed and intermingled series of diferently sized elements with faint longitudinal furrows. The spine section is more or less square.

Serial sections (Fig. 4), dissociated ventral valves (Pl. I, Fig. 6) and silicified specimens prepared by diluted hydrochloric acid etching show the characteristic internal ventral structure of *Ivanothyris*. The dental plates are short with its main body reaching only up to the hinge line; dorsally converging, near parallel and very close ventral adminicula and largely dorsally diverging dental bases. A strong (but not higher than the ventral adminicula) median septum occur between the dental plates. The thick posterior part of the median septum is included in a strongly developed apical callus that extends up to the mid-lenght of the delthyrial chamber. In front of the apical callosity the median septum becomes sharper and loses height anteriorly, reaching almost to the distal end of the valve. Narrow cardinal teeth. Excavated dental muscle field placed between the distal part of the ventral adminicula, not accesible to direct observation in the available material.

Crural bases, merging apically in the valve floor, are supported by short crural plates. Small cardinal process with a ctenoforidium composed of vertical platelets. Narrow and shallow dental cavities, situated high on the valve floor, partially covered by winged shell edges. Fairly long median myophragm. Brachidium coiled with laterally directed spiral cones composed of at least 12 rather circular whorls.

Discussion: The lack of suitable and abundant material allowing for the observation of the ventral internal structures and the morphologic external variability caused misidentification in the past of our species with *Delthyris aculeata* (Schnur, 1853) and *Ivanothyhris* cf. *trisecta* (Kayser, 1883) (García-Alcalde 1996). *D. aculeata* is easily differentiated from *I. havliceki* by the lack of umbonal callus including the ventral median septum. Compared with *I. trisecta,* our species is smaller, with less lateral costae, less developed umbonal secondary shell, more incurved dental plates and shorter ventral interarea.

I. gibbosa (Barrande, 1879) is larger, more inflated and has a higher tongue. Furthermore, it has more lateral costae, and the apical secondary shell deposit is more developed than in *I. havliceki*.

The Mongolian species, *Ivanothyris grandis* (Kaplun, 1961) and *I. khalfini* (Alekseeva et Mendbajar 1981) are larger; moreover, the latter species is more transverse and has more costae (6 or more on each flank).

Suborder Cyrtinidina Carter et Johnson, 1994
Superfamily Cyrtinoidea Frederiks, 1911
Family Cyrtinidae Frederiks, 1911

Genus *Moniellocyrtina* gen. nov.

Type species: *Moniellocyrtina orthoclina* sp. nov.
Etymology: After the name of the formation (Moniello Formation) where the type species of the genus occurs.
Included species: Only the type species, *M. orthoclina*.
Age and stratigraphical and geographical distributions: *M. orthoclina* sp. nov. occurs in beds of latest Emsian age in the Moniello Formation, Astur-Leonian domain of the Cantabrian Zone, northern Spain.

Diagnosis: Large-sized cyrtiniid with high, concave ventral interarea extending proximally in the commisural plane (orthocline) or even slightly dorsally. Strongly curved ventral beak largely roofing the ventral interarea or even the dorsal interarea in lateral view.
Discussion: The endopunctate shell, occurrence of a spondylium and a divided tichorhinum in the ventral valve interior, and the ventral interarea morphology with a pseudodeltidium bearing a subapical foramen permit the inclusion of *Moniellocyrtina* among the Cyrtinidae.

Nevertheless, the type-species of the new genus shows a very original feature that singles out it from other cyrtiniform taxa. All the known Cyrtinidae have flattened or faintly concave, strongly apsacline to catacline, even procline, ventral interareas, while that of *M. orthoclina* is faintly apsacline proximally, but rapidly becomes orthocline, or even anacline because of its curvature. This feature is deemed so important to propose a new genus.

***Moniellocyrtina orthoclina* sp. nov.**
Fig. 5; Pl. I, Figs, 10–14; Pl. II, Figs 1–10

? 1882 *Cyrtina heteroclita* var. *hispanica*; Barrois, p. 261, Pl. 10, Fig. 8a, b, f.

Etymology: After the ventral interarea orientation (orthocline) of most specimens of the species.

Material: 142 variably preserved, often silicified specimens. Holotype DPO 35514 (Pl. I, Figs 10–14) and 29 paratypes, DPO 35510-35513, 35515-35529, 37480-37489 (Pl. II, Figs 4–10) from the locality and stratum typicum (Fig. 1). 21 specimens, DPO 35530-35544 (Pl. II, Figs 1–3), 35554-35558 and 36047, from other levels of the same locality. 5 specimens, DPO 32195-32199, from La Planadera (Cornellana, central Asturias), yac. I-108, Moniello Formation, late Emsian. 28 specimens, 35545-35553, 37733-37751, from Xivares (Gijón, northern Spain), middle member of the Moniello Formation, late Emsian. 58 specimens, 35559-35615, 36048, from the Moniello inlet, levels M928 a M932 Moniello Formation, late Emsian.

Locality and stratum typicum: Cliffs north of Fabrica de Arnao (Castrillón, Avilés, Asturias), level C-132, middle member of Moniello Formation, late Emsian (Fig. 1).

Diagnosis: Megathyrid cyrtiniid with an high, faintly apsacline to orthocline, even anacline, concave ventral interarea. Flattened ventral sinus and dorsal median fold. Macro-ornament composed of a few strong, rounded costae. Very faint, micro-capillate, microspinose micro-ornament with vaguely quinquncially arranged spine bases.

Description: Fairly large for the genus, megathyrid, alate, transverse (L 77 % of w), ventribiconvex, non inflated (t 63 % of L) shell (L_{max}=18,4 mm; w_{max}=28 mm). Shell outline rhomboidal. Greatest thickness near the mid-lenght.

Ventral interarea non-differentiated, very high, sometimes longer than the dorsal valve, slightly concave, faintly apsacline near the hinge to orthocline and even anacline later on (Pl. I, Fig. 13; Pl. II, Fig. 6), bounded by sharp interareal edges. The interarea surface is ornamented by transverse and longitudinal striae, the latter weaker than the former. Sometimes the interarea is slightly asymmetrical showing differently developed sides and a twisted beak (Pl. I, Fig. 11). Narrow delthyrium (1/9 to 1/10 of the hinge width) covered by a convex pseudodeltidium with a large submesothyrid, longitudinally oval foramen, oftenly separated from the ventral beak (Pl. I, Fig. 11; Pl. II, Fig. 9). Dorsal interarea faintly anacline to orthocline, almost linear, much lower than ventral interarea.

Faintly developed ventral umbo prolonged into an acute, semierect to erect beak that because of the interarea curvature appears to be roofing the ventral interarea, the hinge line and even the dorsal valve in lateral view (Pl. I, Fig. 13; Pl. II, Fig. 6). Small dorsal umbo with slightly curved beak.

Ventral sinus relatively large (27 % of the valve lenght at anterior margin), well defined, shallow, starting at the apex of the valve with a faintly rounded to flattened bottom. The sinus is bounded by costae higher and wider than the other costae situated laterally. Dorsal fold, fairly high, narrow, with a faintly convex to flattened, even faintly grooved summit. The median fold is bounded by furrows stronger than the costal interspaces.

Parasulcate anterior commisure (Pl. I, Fig. 12; Pl. II, Fig. 3). Strongly ventrally turned lateral commisure. Well developed, rounded trapezoidal, dorsal to posterodorsally turned tongue.

Flanks ornamented by 4–5 (89 % of the specimens) (min: 3; max: 6) straight, simple, narrow, rounded, relatively high costae separated by interspaces similar. The lateral costae lose height quickly so that the last pair are usually obsolescent.

Numerous, fairly strong and regularly spaced growth lamellae. The micro-ornament is very faintly developed and it is oftenly concealed by the strong silicification of the available material. Some specimens show extremely subdued, subradial microcostules, with minute teardrop granules irregularly distributed (vaguely in quinqunx) along them.

Densely endopunctate shell with minute, circular endopuncta (more than 250 by mm^2 near the front in the ventral sinus) (Pl. II, Fig. 8).

Shell interior poorly known. Dental plates joined to a high, sharp, long septum, forming a rather deep spondylium with an ovoidal tubular chamber divided by the ventral septum (tichorhinum) at the base of the spondylium. Cardinal process very high, clearly bilobate, lacking ctenophoridium, sometimes overhanging the inner socket ridges (Pl. II, Fig. 10).

Discussion: Orbigny's (1850) usage of the name "*hispanica*" to denote the Spanish Cyrtinidae has been extremely misleading for later authors. Mallada (1875) used *Cyrthia Hispanica*, D'Orb for forms determined by Verneuil – Archiac (1845, p. 474, Pl. 15, Fig. 4a–d) as *Spirifer heteroclitus*, var. *A*. Barrois (1882, p. 261, Pl. 10, Fig. 8) generally assigned the Spanish Cyrtinidae to *Cyrtina heteroclita*, Defr. although distinguishing within the species several varieties, among them *C. heteroclita* var. *hispanica*, from the Moniello Limestone of the Asturian coast. Barrois's figures (op. cit., Pl. 10, Fig. 8a, b, f) differ radically from those of Verneuil – Archiac (reproduced in Mallada). These figures are vaguely close to our *M. orthoclina* sp. nov., but it was not possible from them to firmly establish the identity of both forms. Finally the original specimens of Verneuil and Archiac's (1845) (reproduced in Mallada 1875) come from Ferroñes and their description and figures coincide rather with that of a probably new species of *Cyrtina* to be described in another paper.

For the above reasons we prefer to abandon the name "*hispanica*" and to call our new species as *M. orthoclina*.

The ventral interarea orientation separates clearly *M. orthoclina* of other known Cyrtinidae species.

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Submitted January 8, 2001

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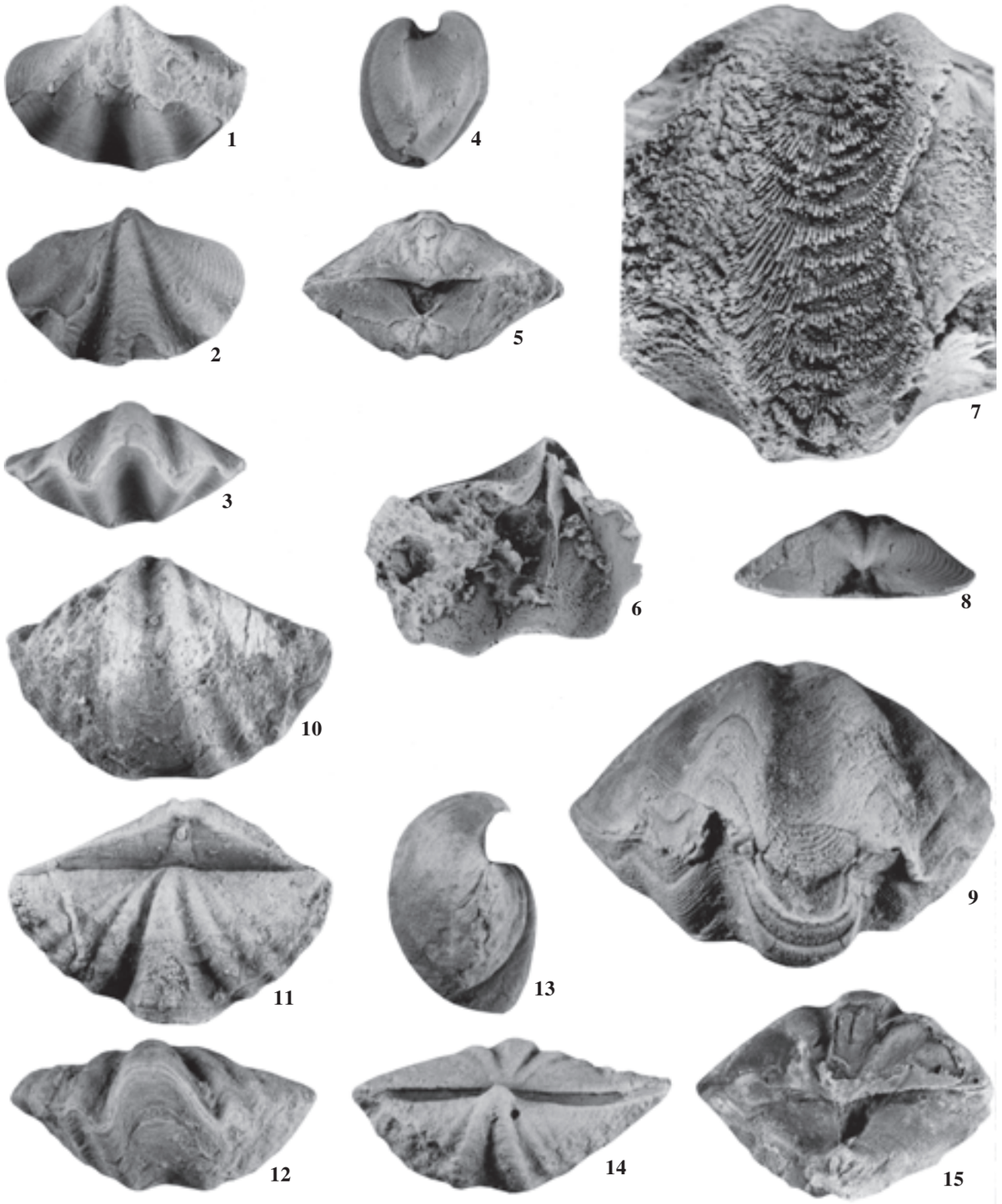
Paleobiogeografické vztahy mezi severní Gondwanou a jižní Baltikou: Fauna s *Ivanothyris havliceki* (kantabrická zóna, nejvyšší ems)

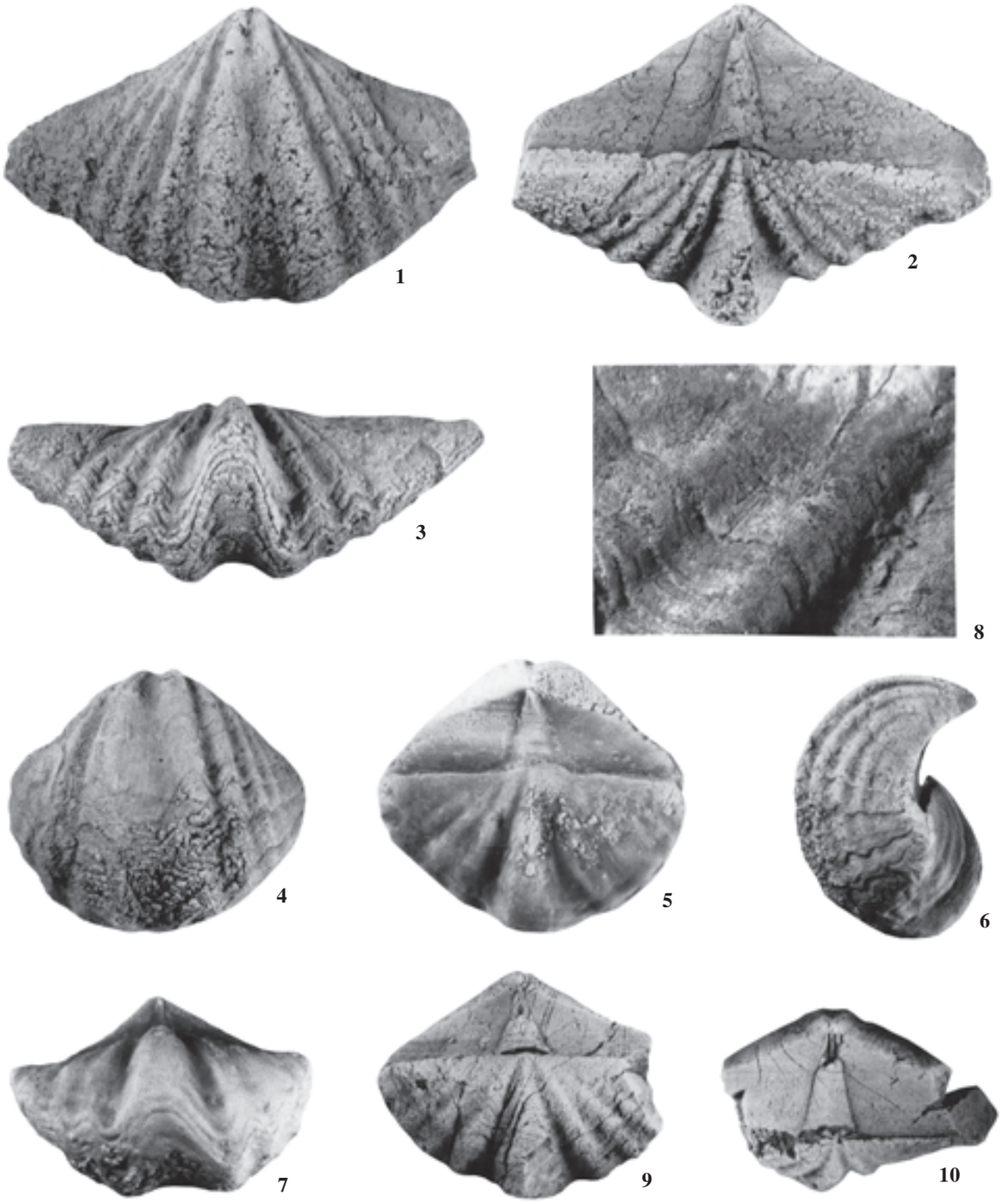
V práci jsou analyzovány vztahy mezi svrchně emskými faunami ardensko-rýnské oblasti (Belgie a Německo) patřící jižní Baltice a kantabrickou zónou v severním Španělsku patřící severní Gondwaně. Analýza je provedena srovnáním artikulátních brachiopodů kantabrické fauny v intervalu 14–16 a jeho faunistickým ekvivalentem v ardensko-rýnské oblasti. Význam systematické determinace druhů z Kantábrie je vyhodnocen podle systému zkratek navrženým vedoucími projektu IGCP 421. Dva nové druhy jsou popsány z Kantábrie: *Ivanothyris havliceki* sp. nov. a *Moniellocyrtina orthoclina* gen. et sp. nov., které charakterizují uvedený faunistický interval.

J. L. García-Alcalde: Paleobiogeographical relationships between North Gondwana and South Baltica: The *Ivanothyris havliceki* fauna (Cantabrian Zone, latest Emsian) (Pl. I)



Ivanothyris havliceki sp. nov.
1–5 – Holotype DPO 32823. Ventral, dorsal, frontal, lateral and posterior views, x3.
6 – Paratype DPO 32762. Ventral valve, x2.
7 – DPO 32751. Specimen showing spines in anatomical connection, x7.
8 – Paratype 38222. Posterior view showing the differentiated ventral area and delthyrium, x3.
9 – DPO 32745. Anteroventrally orientated specimen showing the spinose micro-ornament.
15 – DPO 32745. Posterior view showing the differentiated area and delthyrium, x2.

Moniellocyrtina orthoclina gen. et sp. nov.
10–14 – Holotype DPO 35514. Faintly asymmetrical specimen. Ventral, dorsal, anterior, lateral and posterior views. x3.



Moniellocyrtina orthoclina gen. et sp. nov.
1–3 – Ventral, dorsal and anterior views of an alate specimen, DPO 35536, x3.
4–7 – Paratype DPO 35510. Ventral, dorsal, lateral and anterior views, x3.
8 – Enlarging of the lateral part of paratype DPO 35523 showing endopunctae, x10.
9 – Paratype DPO 35515. Dorsal view showing the subapical foramen and pseudodeltidium, x3.
10 – Paratype DPO 35519. Posterior view showing the bilobate cardinal process, pseudodeltidium and middle ventral septum, x3.