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Palaeobiogeography of the Late Carboniferous brachiopoda from Velebit Mt. (Croatia)

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Abstract

An abundant and diverse Late Carboniferous brachiopod fauna from Velebit Mt. (Croatia) comprises 63 brachiopod taxa dominated by Productida and Spiriferida. The Spiriferinida, Athyridida, Orthotethida and Rhynchonellata are less common, while the Orthida, Dictyonellida and Terebratulida occur in very small numbers. Brachiopods are mostly preserved as casts and moulds in shales, limestones and sandstones. Associated fusulinid foraminifera and calcareous algae indicate a Kasimovian to Gzhelian age for the brachiopod–bearing deposits. The global biogeographic distribution of brachiopod taxa indicates the probable seaways and brachiopod migration routes, along the Euramerican shelves.

1. INTRODUCTION

Brachiopods are common marine macrofossils in the Late Carboniferous sedimentary rocks of Velebit Mt. They have been collected since the beginning of the 19th century and stored in the Croatian Natural History Museum.

Upper Carboniferous (Pennsylvanian) sedimentary rocks from Velebit Mt. crop out in an elongate belt, 40 km long and up to 6 km wide, representing the core of an anticline, with a NW–SE strike (Fig. 1). They exhibit a variety of ancient environments varying from shoreline forests and swamps, through coastal and shallow shelf biomes (SREMAC, 2012; CLEAL et al., 2015). Carboniferous shelves were densely populated with foraminifera (mostly fusulinids), calcareous algae, brachiopods, crinoids, bry-

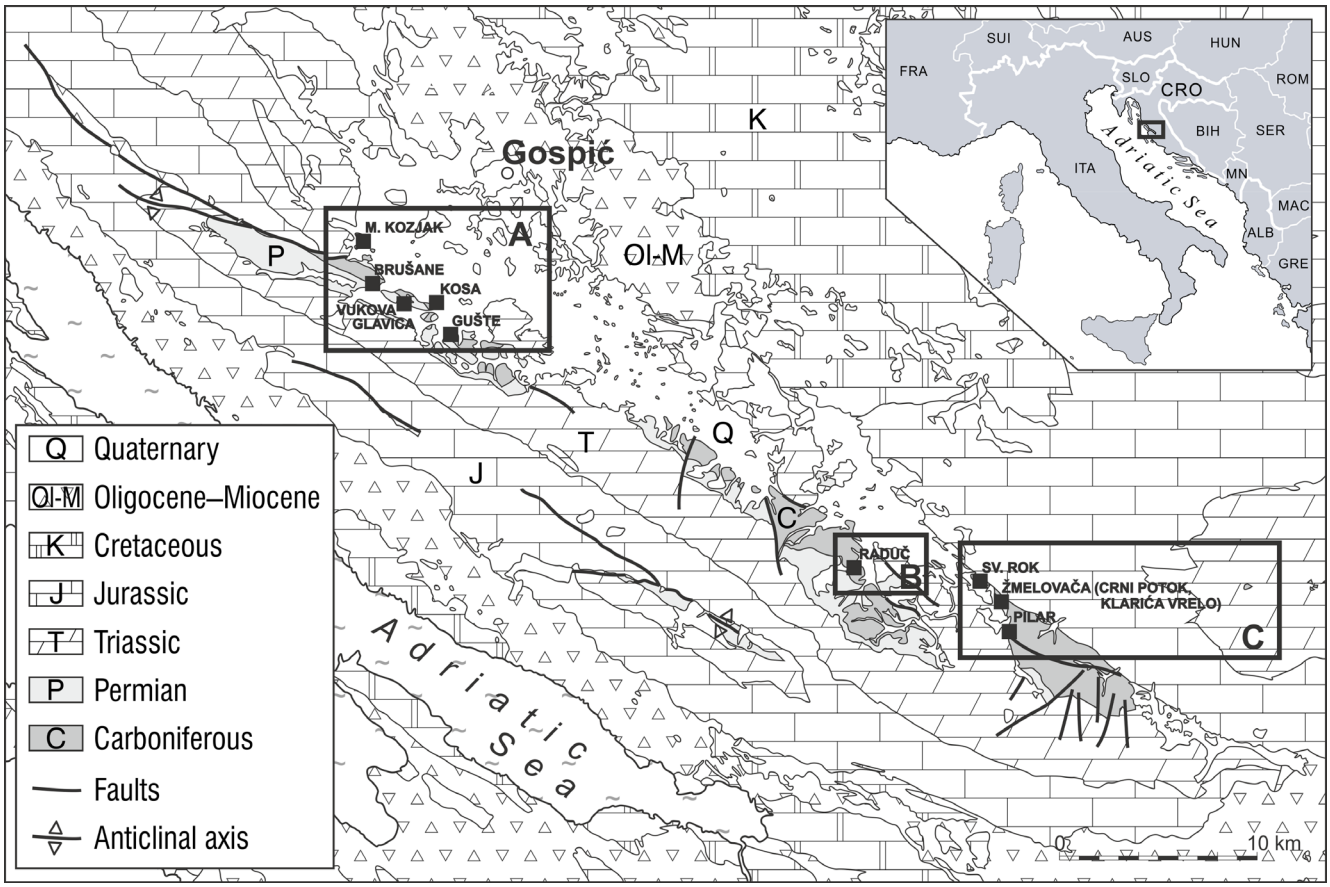

Figure 1. Simplified geological map of the research area, with the location of brachiopod observations (black squares?) (after CLEAL et al., 2015).

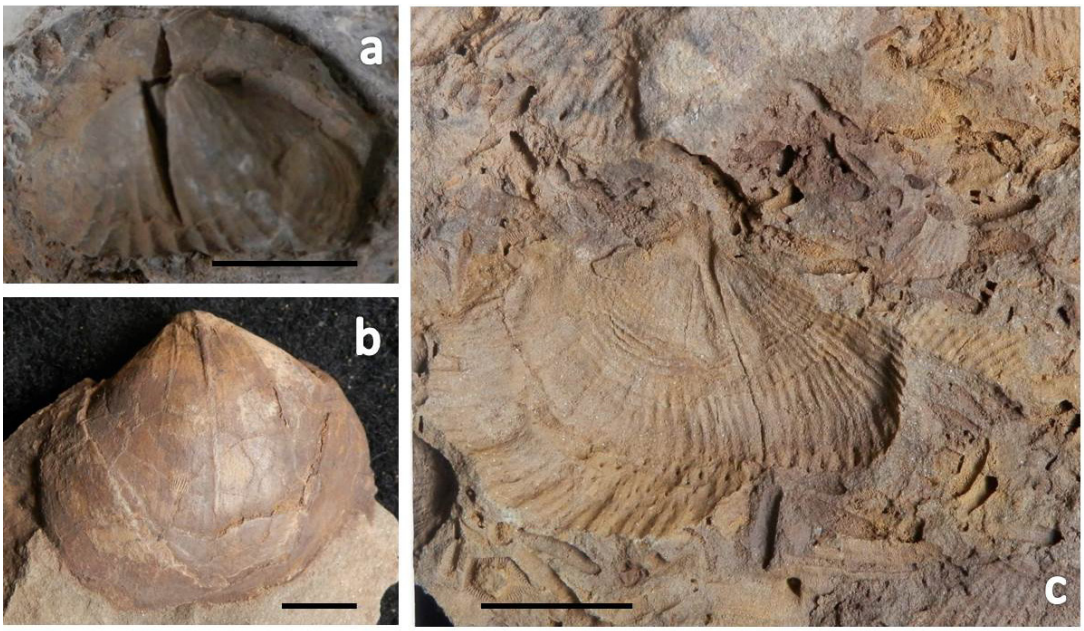

Figure 2. Modes of preservation of Late Carboniferous brachiopods in the Velebit Mt.: a) inner cast (with gaps in places of dissolved median septa) – area C; b) partly preserved shell and inner cast with visible median septum – area C; c) cast with visible external ornamentation, surrounded with fusulinid casts – area C. (Scale bar 1cm)

ozoans and other macrofossils (SALOPEK, 1942, 1948; KOCHANSKY-DEVIDÉ, 1955, 1970; SREMAC, 2005, 2012).

A rich fossil assemblage from these deposits has been collected during mapping campaigns undertaken by M. Salopek and his students between 1935 and 1938 (SALOPEK, 1942, 1948). The geological setting of the wider area is described in Basic Geological maps of Yugoslavia on the 1:100000 scale and Basic Geological Map of Croatia 1:300 000 (IVANOVIĆ et al., 1973, 1976; SOKAČ et al., 1974, 1976a, b, c; VELIĆ et al., 2009).

Mixed siliciclastic-carbonate deposition is typical for the Late Carboniferous of this region. The stratigraphic age (late Kasimovian or earliest Gzhelian) was determined from microfossils and land megaflora (KOCHANSKY-DEVIDÉ, 1955, 1970; SREMAC, 2012; CLEAL et al., 2015).

Different lithological units in the Carboniferous of Velebit Mt. were recognized quite early by SALOPEK (1942, 1948). Marine macrofossils, including the brachiopods (SIMIĆ, 1935), were discovered in three lithological types: yellowish-brown shales and siltstones (**cau**, equivalent to the Auernig Beds according to SALOPEK, 1942, 1948), limestones (**cv,** according to SALOPEK, 1942, 1948) and greywackes („fusulinid sandstones", **cf,** according to SALOPEK, 1942, 1948). „Fusulinid sandstones" are more common in the lower horizons of the Late Carboniferous sequences, estimated to be of Kasimovian age, with overlying yellowish shales and siltstones of Late Kasimovian to Gzhelian age (KOCHANSKY, 1955; SREMAC, 2012). The diversity of marine fossils, including brachiopods increases from the Kasimovian to Gzhelian horizons (SREMAC, 2012).

2. MATERIALS AND METHODS

Carboniferous brachiopods from this study were collected by SALOPEK (1942, 1948) and by the present authors between 2012-2014. The brachiopod collection is stored in the Croatian Natural History Museum (under 96 inventory numbers).

All together 110 brachiopod specimens were determined and/or revised (SELDEN, 2007; EMIG et al., 2013; Paleobiology Database; www.fossilworks.org and references therein; August 2015) and asserted to 63 taxa.

The Carboniferous palaeogeographic map chosen to present the Carboniferous brachiopod localities is based upon Blakey's (2015) reconstruction.

3. BRACHIOPOD TAXA

Brachiopods were discovered in Carboniferous sedimentary rocks forming the core of the anticline on the continental slopes of Velebit Mt. (SIMIĆ, 1935; SALOPEK, 1942, 1948).

Brachiopods are in most cases preserved as casts and moulds (Fig. 2), and it is not always possible to determine them to species level.

The determined taxa belong to nine taxonomic groups: Productida, Orthothetida, Athyridida, Spiriferinida, Spiriferida, Rhynchonellida, Orthida, Dictyonellida and Terebratulida (Table 1.). Initial brachiopod taxonomy studies were based upon several published papers (e.g. VON SCHLOTHEIM, 1816; WAAGEN, 1884; SCHELLWIEN, 1892, 1900; MOORE, 1979). Taxa are revised according to the Treatise on Invertebrate Palaeontology (SELDEN, 2007). Localities with carboniferous brachiopods can be grouped into three clusters (A, B and C) with different brachiopods (Fig. 1, Tab 1., 2. Figs. 1, 3–7)

The westernmost localities (A) are dominated almost completely by productids (*Linoproductus lineatus*, *Neochonetes granulifer*, *Paramesolobulus latesinuata*, with small *Dielasma* (Tab. 1.; Fig. 3 a, 4). Altogether, 6 brachiopod specimens from this area are stored in the Natural History Museum. Moving eastwards (B), brachiopod diversity increases and, the first orthotethids and rhychonellids occur (Tabs. 1., 2.; Figs. 3 b, 5). The Eastern part of the Carboniferous belt in Velebit Mt. and the Lika region (C) comprises highly variable brachiopod assemblages, with almost a hundred specimens of productids, orthotethids, athyridids, spiriferinids, spiriferids, rhynchonellids, orthids and dictyonellids (Tabs. 1., 2.; Figs. 3 c, 6).

All the aforementioned facies types occur in all three sampling areas (SALOPEK, 1942, 1948; SREMAC, 2012), but greywackes („ Fusulinid sandstones") are more common in the older horizons, while shales and scarce limestones prevail in the younger horizons. Brachiopod fossils are particularly numerous

Table 1. List of Carboniferous brachiopod taxa grouped through localities in the Velebit Mt. and facies types. (SIMIĆ, 1935; SALOPEK, 1942, 1948 and own research revised).

CLASS/ORDER/GENUS/SPECIES	LOCALITIES (W→E)			FACIES		
	A (1-4)	B (5-6)	C (7-11)	cau	cv	cf
STROPHOMENATA						
PRODUCTIDA						
Breileenia echidniformis (GRABAU in CHAO)						
Chaoiella gruenewaldti (KROTOV)						
Chonetes mamontovi						
Chonetes papilionacea (PHILLIPS)						
Chonetes sp.						
Comuquia curvirostris (SCHELLWIEN)						
Cubacula subpunctata (NIKITINO)						
Echinoconchus elegans NORWOOD and PRATTEN						
Echinoconchus punctatus (MARTIN)						
Incisius incisus (SCHELLWIEN)						
Linoproductus lineatus WAAGEN						
Linoprodutus sp.						
Marginifera pusilla SCHELLWIEN						
Megousia aagardi (TOULA)						
Neochonetes granulifer (OWEN)						
Neochonetes variolata (d'ORBIGNY)						
Neochonetes (Sommeriella) strophomenoides WAAGEN						
Paramesolobus latesinuata SCHELLWIEN						
Plicatifera sp.						
Productus mölleri						
Productus transversalis TSCHERNYSCHEW						
Productus sp.						
Productus cf. *longispinus SOWERBY*						
Transennatia gratiosa (WAAGEN)						
Vediproductus punctatiformis CHAO						
Waagenoconcha sp.						
ORTHOTHETIDA						
Derbya (Derbyia) altestriata WAAGEN						
Derbya (Derbyia) cf. *grandis WAAGEN*						
Derbya (Derbyia) sp.						
Meekella sp.						
Streptorhynchus pelargonatus SCHLOTHEIM						
Streptorhynchus semiplanus (WAAGEN)						
Streptorhynchus sp.						
RHYNCHONELLATA						
ATHYRIDIDA						
Retzia sp.						
Hustedia mormoni (MARCOU)						
SPIRIFERINIDA						
Callispirina ornata Waagen						
Spiriferellina cristata (SCHLOTHEIM)						
Spiriferina sp.						
Spiriferina laminosa (McCOY)						
SPIRIFERIDA						
Alphachoristites trautscholdi STUCKENBERG						
Ambocoelia sp.						
Bajkuria rostrata KUTORGA						
Choristites fritschi (SCHELLWIEN)						
Choristites sp.						
Elinoria carnica (SCHELLWIEN)						
Eliva lyra (KUTORGA)						
Martinia semiplana (WAAGEN)						
Martinia sp.						
Neospirifer cameratus (MORTON)						
Neospirifer fasciger (KEYSERLING)						
Plicatocyrtia zitteli (SCHELLWIEN)						
Reticularia lineata (MARTIN)						
Reticularia sp.						
Spirifer sp.						
Squamularia sp.						
RHYNCHONELLIDA						
Hustedia mormoni (MARCOU)						
Rhynchonella aff. confinensis SCHELLWIEN						
Stenoscisma alpinum (SCHELLWIEN)						
Uncinunellina timorensis (BEYRICH)						
ORTHIDA						
Rhipidomella pecosi (MARCOU)						
Enteletes sp.						
DICTYONELLIDA						
Isogramma paotechovensis GRAB						
TEREBRATULIDA						
Dielasma sp.						

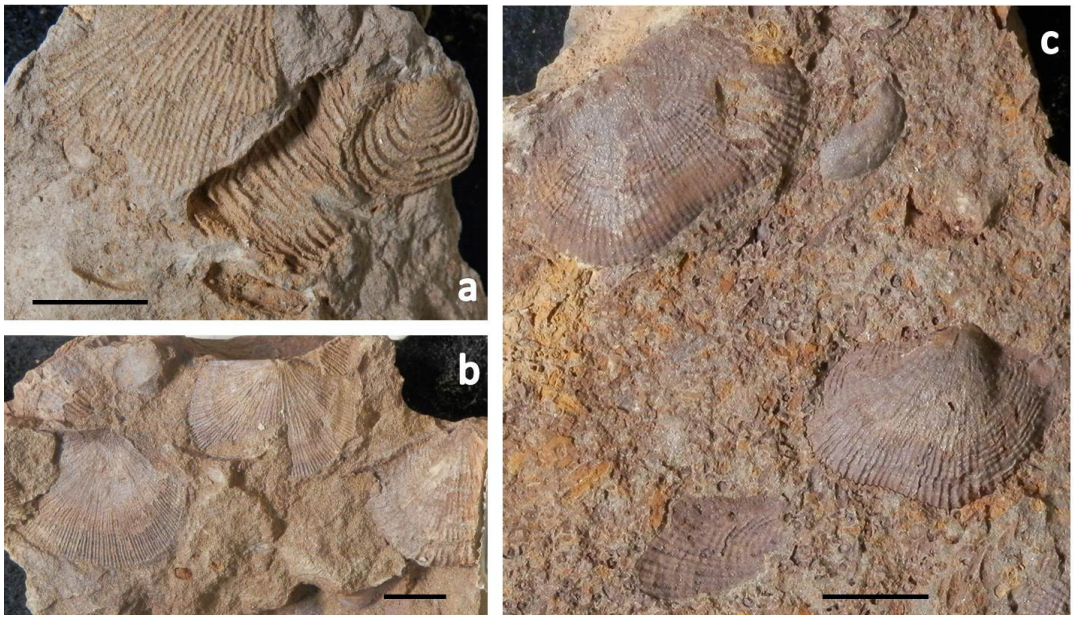

Figure 3. Differentiation of facies and brachiopod assemblages in the three examined areas with Carboniferous deposits in Velebit Mt.: a) Westernmost area (A) comprises large fenestellid casts and rather small brachiopods; b) Central area (B) is characterized by the domination of flattened orthotethids; c) Eastern localities (area C) comprise an abundant and variable brachiopod fauna, with the predomination of Productida. (Scale bar 1cm)

and diverse in the shales and siltstones (**cau**, equivalent to the Auernig Beds according to SALOPEK, 1942, 1948). A different fossil assemblage is preserved in the limestones (**cv,** according to SALOPEK, 1942, 1948). Only a few brachiopod taxa were observed in the greywackes („fusulinid sandstones", **cf,** according to SALOPEK, 1942, 1948) (Tab. 1.).

4. DISCUSSION

4.1. Palaeoecology and the local distribution of brachiopod genera

Brachiopod finds are clearly grouped into three areas with different fossil assemblages (Tabs. 1., 2., Fig. 3). Palaeobiodiversity evidently increases towards the East (Tab. 2., Fig. 8). It is important to note that these three areas very rarely comprise the same taxa (Tab. 1). The exceptions are several tolerant taxa, capable of adapting to a variety of marine environments, such as *Linoproductus lineatus* (present in all three areas and in all lithological units – shales and siltstones, greywackes and limestones), or *Transennatia gratiosa*, present in the central and eastern areas, and in two of the three lithological units (shales and siltstones; limestones) (Tab. 1.).

The western area (A, Fig. 1) is characterized by several small productid taxa, with the exception of the larger *Linoproductus* (Tabs. 1., 2., Figs. 4 a, b). They lived anchored by spines on the soft bottom, with low depositional rates. Their low diversity and small size probably indicate restricted food sources.

The central area (B, Figs. 1, 3 b, 5 a-d), comprises some orthotethids and rhyncnonellids (Tabs. 1., 2; Figs. 5 b, c) in addition to the productids. *Linoproductus* and *Transennatia* (Figs. 5 a, d) discovered in this area could have lived in different marine environments, from open subtidal, to basinal areas.

The presence of *Neochonetes variolata* (Fig. 4 a) indicates a most probable deep subtidal depositional area (KALASHNIKOV, 1993). *Rhynchonella confinensis* seems to be endemic, occurring only in Velebit Mt. and in the Permian deposits in neighbouring Slovenia (SCHELLWIEN, 1892).

The eastern area (C, Fig. 1) is generally rich in fossils. A well preserved terrestric megaflora indicates the vicinity of land (SREMAC, 2012; CLEAL et al., 2015). Marine fossils are diverse, with a predomination of fusulinids and crinoid ossicles, together with calcareous algae, brachiopods (Figs. 6 a-h), bryozoans (Fig. 7 a), bivalves (Fig. 7 b) and gastropods (SIMIĆ, 1935; SALOPEK, 1948; KOCHANSKY-DEVIDÉ 1955, 1970; SREMAC, 2012).

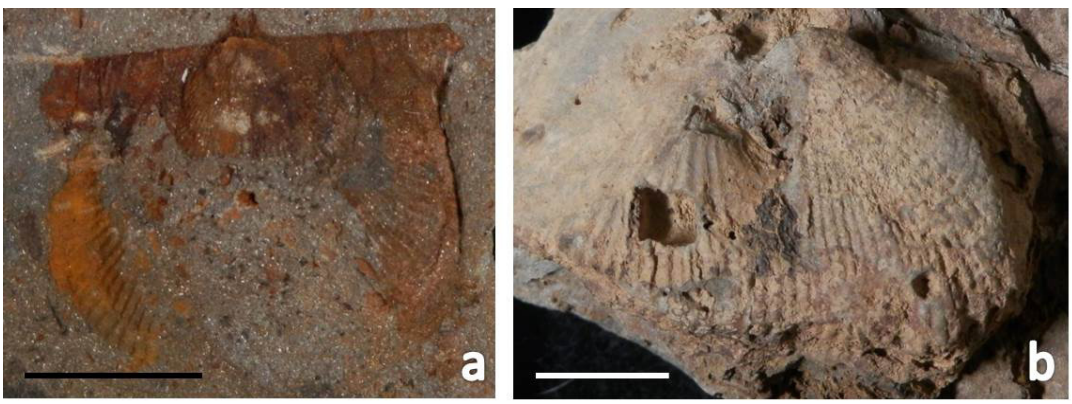

Figure 4. Mould of a *Linoproductus* brachial valve (a) and bioeroded cast of *Productus transversalis* TSCHERNYSCHEW (b) from locality cluster A. (Scale bar 1cm)

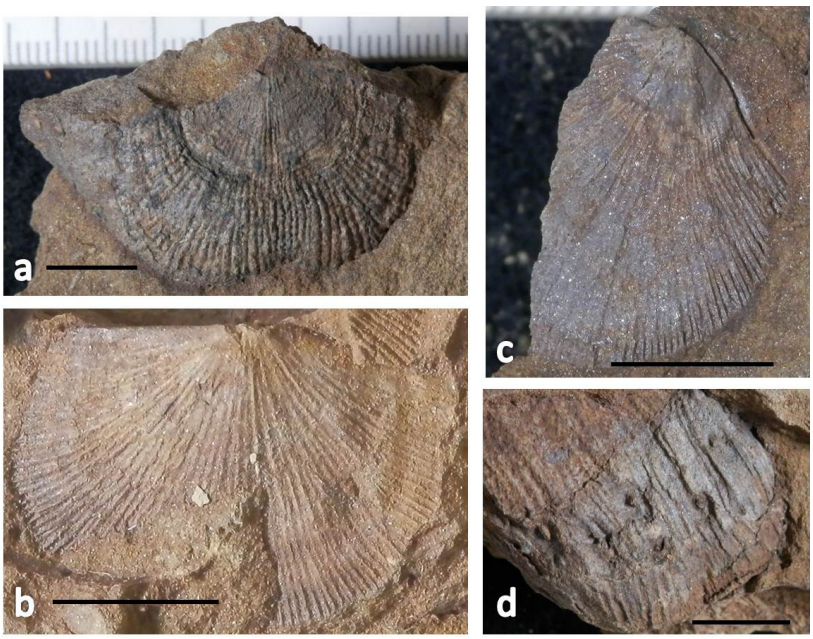

Figure 5. *Transennatia* (a), *Derbya*, (b,c) and segment of *Linoproductus* (d) with visible spine bases from the locality B. (Scale bar 1cm)

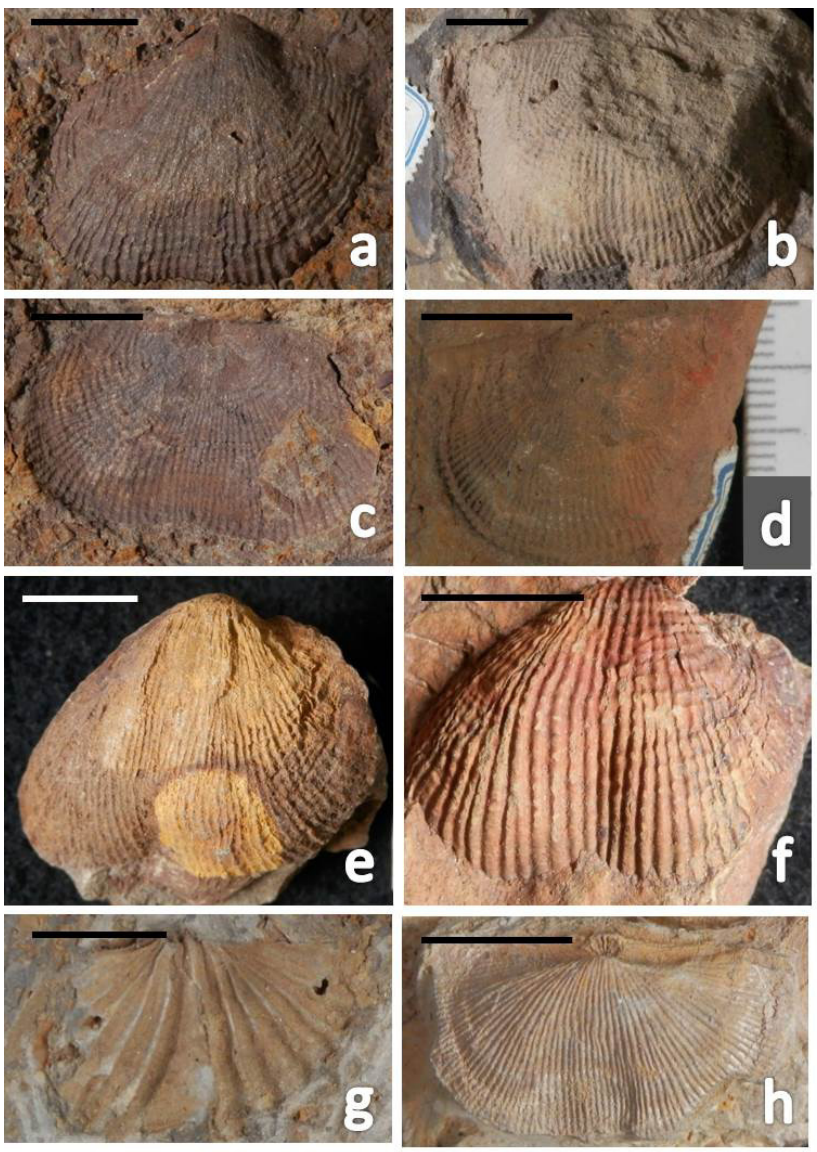

Figure 6. Productid genera (a-f): *Productus* (a, c, e), *Dictyoclostus* (b), *Linoproductus* (d) and *Marginifera* (f), spiriferinid (*Spiriferina* sp.) (g) and the spiriferid (*Choristites*) (h) brachiopoda from locality group C. (Scale bar 1cm)

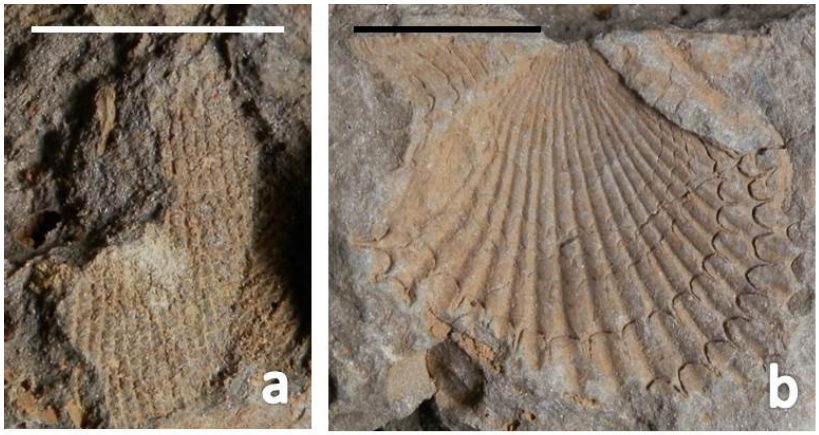

Figure 7. Cast of a fenestellid bryozoan (a) and a scallop *Acantopecten* sp.(b) from locality group C. (Scale bar 1cm)

Trace fossils are common in the sandstones and siltstones, present on bedding surfaces, but also within the layers, and can be attributed to the Scolithos ichnofacies.

Well sorted conglomerates and the aligned orientation of fusulinids in some sandstone layers indicate a the coastal environment. Partial or complete dissolution of fusulinid tests (SALOPEK, 1948; KOCHANSKY, 1955) indicate a probable fresh-water influence (SREMAC, 2012). Brachiopods, although numerous and highly diverse, are also mostly present as casts or moulds (Figs. 1-6). All these features indicate a variety of environments, from beaches to the more favourable subtidal niches.

Erosion of the uplifted Variscan Mountains provided nutrients and enabled the significant diversification of marine biota. Similar trends were described from Spain (WINKLER PRINS, 2007; MERINO-TOMÉ et al., 2009).

4.2. Palaeobiogeographic studies

The Late Carboniferous was a time of a slight increase in brachiopod diversity (SHU-ZHONG et al., 2006) and these organisms were present in all seas and oceans. Their geographic distribution was closely related to the position of continental shelves and possible sea-ways and climate gradients, recently studied by several authors (ANGIOLINI et al., 2007; BERRA & ANGIOLINI, 2014). During the Late Carboniferous, the study area was a part of NE Gondwana, situated near the equator (VOZAROVA et al., 2009; SREMAC, 2012; CLEAL et al., 2015)

Table 2. Total number of brachiopod taxa in three different Carboniferous areas in Velebit Mt.

		LOCALITY GROUP A,B, C			FACIES		
BRACHIOPOD GROUP	TAXA	A (1–4)	B (5–6)	C (7–11)	cau	cv	cf
Productida	26	5	3	24	23	9	1
Orthothetida	7	0	3	4	5	2	0
Athyridida	2	0	0	2	2	0	0
Spiriferinida	4	0	0	4	3	1	0
Spiriferida	16	0	0	16	15	4	0
Rhynchonellida	4	0	1	3	2	0	1
Orthida	2	0	0	2	2	0	0
Dictyonellida	1	0	0	1	1	0	0
Terebratulida	1	1	0	0	1	0	0
	63	6	7	56	54	16	2

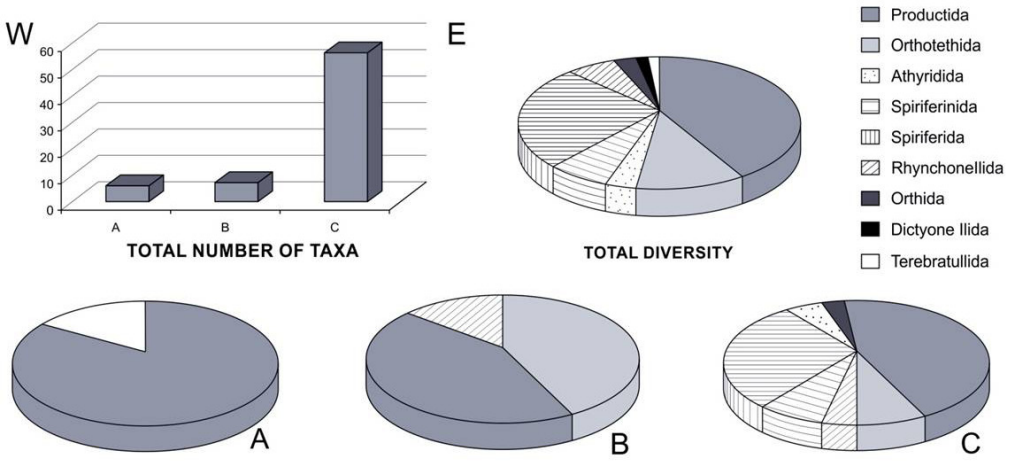

Figure 8. Total brachiopod diversity and area specific diversity for the three Carboniferous areas in Velebit Mt.

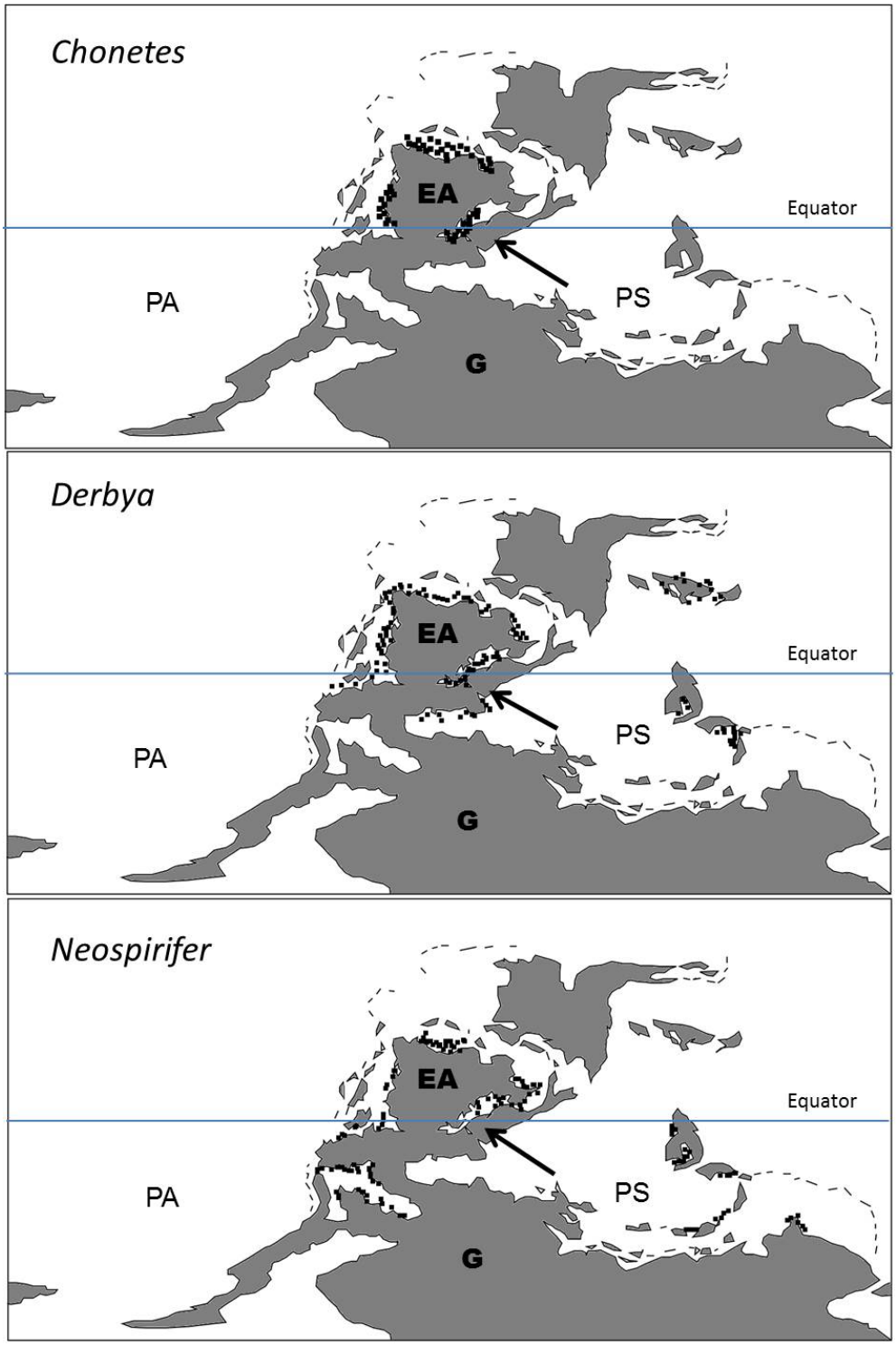

Figure 9. The Distribution of the Late Carboniferous cosmopolitan brachiopod genera (*Neospirifer*, *Derbya*, *Chonetes*, observed in Velebit Mt. (records from: PEDERSON, 1954; SUTHERLAND, 1991; KORA, 1995; KALASHNIKOV, 1998; SOBOLEV et al., 1998; WENDT et al., 2001; SCHNEIDER, 2003; GONG et al., 2007; http://fossilworks.org/ and references therein). Palaeobiogeography based upon Blakey's (2016) reconstruction. Grey colour: continents; white colour: oceans/seas; PS: Palaeotethys; PA: Panthalassa; G: Gondwana; EA: Euroamerica. Study area indicated by the arrow.

In order to identify possible migration routes, some of the common Carboniferous brachiopod genera from Velebit Mt. were selected for further palaeobiogeographic studies.

Tolerant brachiopod taxa (*Neospirifer, Derbya*) were widely spread. Disocveries of *Neospirifer* have been recorded in almost a thousand Carboniferous and Permian collections all over the world (PEDERSON, 1954; SUTHERLAND, 1991; KORA, 1995; KALASHNIKOV, 1998; SOBOLEV et al., 1998; WENDT et al., 2001; SCHNEIDER, 2003; GONG et al., 2007; http://fossilworks.org, 2016 and references therein). They lived all along the continental shelves of Euramerica, but also on the shelves of the southern continents and islands (Fig.9). It is possible that they had a rather long-lived swimming larval stage. The genus *Chonetes* was also widespread, present all around Euramerica (Fig. 9). However, the geographic range of the genus *Echinoconchus* is very peculiar (Fig. 10) indicating possible migrations along the shelves of Panthalassa, rather than those of Palaeotethys. The genus *Megousia* was common on the northern shelves of Euramerica and its ap-

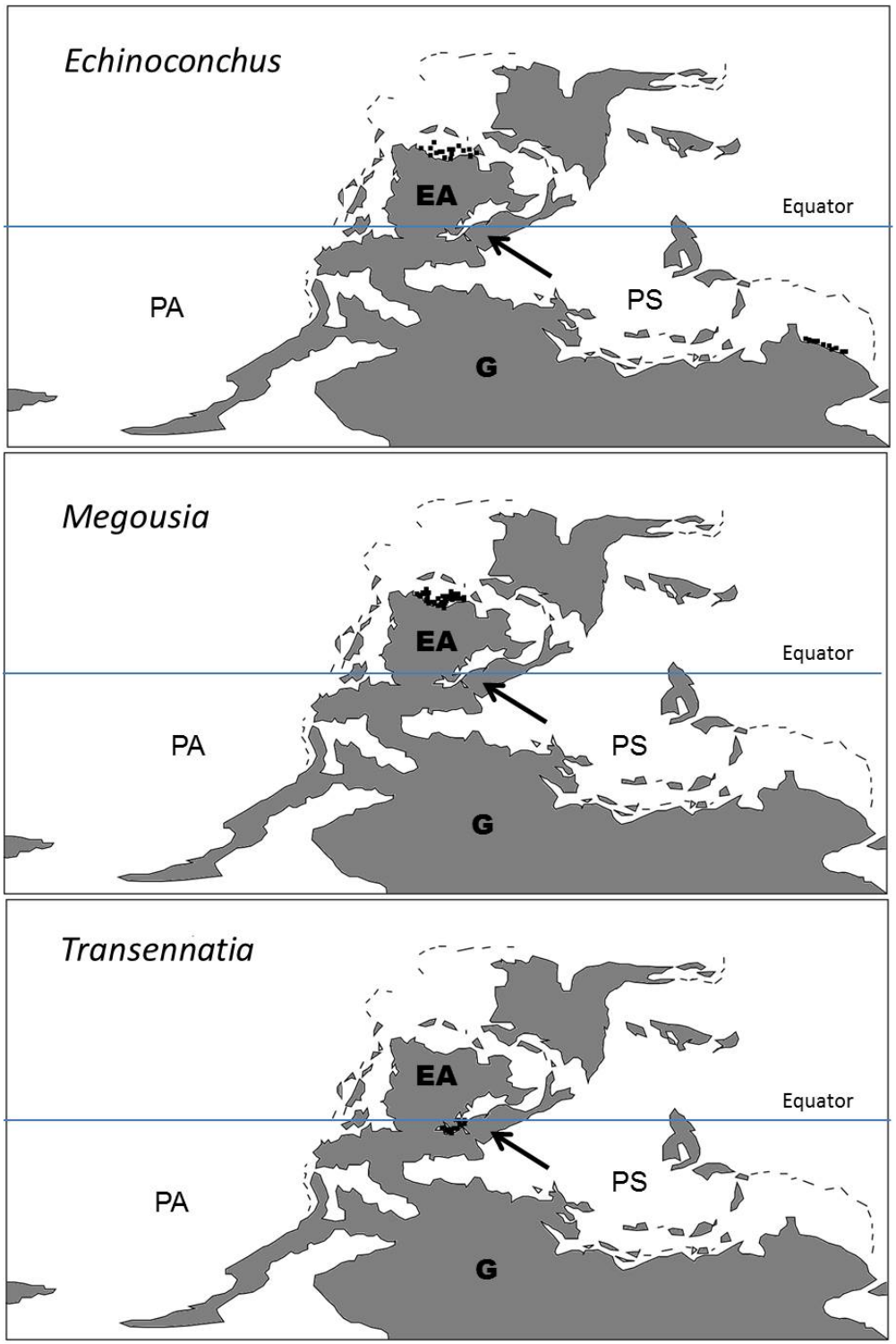

Figure 10. Distribution of the Late Carboniferous specialist brachiopod genera (*Echinoconchus*, *Megousia*, *Transennatia*, observed in Velebit Mt. (observations from: PEDERSON, 1954; SANDO et al., 1975; SCHNEIDER, 2003; GONG et al., 2007; HEIM et al., 2009; http://fossilworks.org/ and references therein). Palaeobiogeography based upon Ron Blakey's reconstruction (http://cpgeosystems.com/300Marect.jpg, July 2015). Grey colour: continents; white colour: oceans/seas; PS: Palaeotethys; PA: Panthalassa; G: Gondwana; EA: Euroamerica. Study area marked by arrow.

pearance near the equator is interesting (Fig. 10). Alternatively, the genus *Transenatia* is rather endemic, appearing on the eastern continental shelves of Euramerica, near the equator (Fig. 10).

5. CONCLUSIONS

The Carboniferous brachiopod fauna from Velebit Mt. is very rich and diverse. but in most cases not well preserved. All together 63 taxa were determined, belonging to nine brachiopod groups, with a predominance of productids and spiriferids.

Brachiopods were observed in the form of moulds and casts in shales and siltstones, limestones and graywackes, with the highest abundance in fine-grained clastic deposits. Three different areas with diverse brachiopod associations can be clearly recognized. The highest brachiopod diversity was observed in coastal fine-grained clastic deposits at the eastern part of the outcropping Carboniferous rock belt.

A Kasimovian to Gzhelian age was proposed on the basis of the associated fusulinid fauna.

During the Late Carboniferous, brachiopods were common along the continental shelves of Euroamerica. Southern hemisphere records are less common and represented by tolerant genera, e.g. the cosmopolitan *Neospirifer* and *Derbya*.

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