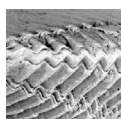


A new species of *Neopaulinella* (Brachiopoda, Terebratulida) from the Eastern Iberian Chains, Spain (Lower Devonian)

MENA SCHEMM-GREGORY



A new terebratulid brachiopod species, *Neopaulinella noguerasensis*, has been identified from the Nogueras Formation of the Eastern Iberian Chains (Spain). It is compared with the other known species of *Neopaulinella* from France and Spain, *N. guerangeri* and *N. gaudryi*, from which it differs in size of costae, dental plates, and dorsal adductor field including the dorsal median septum. Digitized three-dimensional reconstructions of the internal shell and the loop of the new species are presented. The life habit of *N. noguerasensis* is briefly discussed regarding its palaeoecological environment. The cladistical analysis shows an equal relationship to the other species of *Neopaulinella*. The phylogeny of the genus and migration paths of its species are demonstrated. The palaeobiogeographical distribution of *Neopaulinella* reflects the Early Devonian provincialism and suggests a migration path between Western and Central Europe during Siegenian time. • Keywords: *Paulinella*, Terebratulida, Brachiopoda, 3D reconstruction, palaeobiogeography, Lower Devonian, Spain.

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The Eastern Iberian Chains (Spain) belong to the northern Gondwanan regions within the Rhenohercynian and are characterized by Lower Devonian strata similar to successions in the Dra Valley (Morocco) represented by rhythmic sequences of limestone, sandstone, and clay (Jansen *et al.* 2007). In contrast to the strata in Morocco, strata of the Eastern Iberian Chains have undergone a complicate tectonic deformation. The intercalation of strata representing the hercynian (pelagic) facies and the rhenish (neritic) facies in the Eastern Iberian Chains allows correlation of Lower Devonian rocks between North Africa, Central and Western Europe, and Bohemia (*e.g.*, Jansen 2001, Jansen *et al.* 2007, Schemm-Gregory 2008a). Subsequently, the *Subcommission on Devonian Stratigraphy* (SDS) is paying special attention to their research. Although the Eastern Iberian Chains are important for correlation between today's North Africa, Central and Western Europe, the first studies of this mountain range began only 50 years ago. Since this time intensive geological and palaeontological research has been carried out. Detailed lithological and biostratigraphical divisions are published by Carls (1969, 1971, 1975, 1977, 1987, 1988, 1996a, b, 1999), Carls *et al.* (1972, 1982, 1993), Carls & Gandl (1967, 1969), and

Gandl (1972); special attention has been paid to the brachiopods by Carls (1974, 1985, 1986) and Carls *et al.* (1993), however, these studies focus mainly on spiriferids due to their biostratigraphic value.

The material used in this study has been collected within the frame of geological/palaeontological field trips by German and Spanish members of the SDS. The study area is situated in the Eastern Iberian Chains in the north-western part of the topographical mapsheet 466 (Moyuelo, ex Blesa) (Fig. 1). A detailed description of the collection locality is given in Carls (1987). The specimens studied occur in the d2c-beta bed of the Nogueras Formation which represents a time interval from the Late Gedinnian to the Early Siegenian (early to middle Early Devonian). It follows the Luesma Formation and is overlain by the Santa Cruz Formation (Fig. 2). The d2c-beta bed represents the uppermost part of the Formation of Early Siegenian age.

Most of the type regions of neritic Lower Devonian strata of Europe are in the Rheinisches Schiefergebirge (= Rhenish Slate Mountains) (Germany), or in the Ardennes (Belgium, France), however, these regions are characterized by the absence of fully marine biofacies from

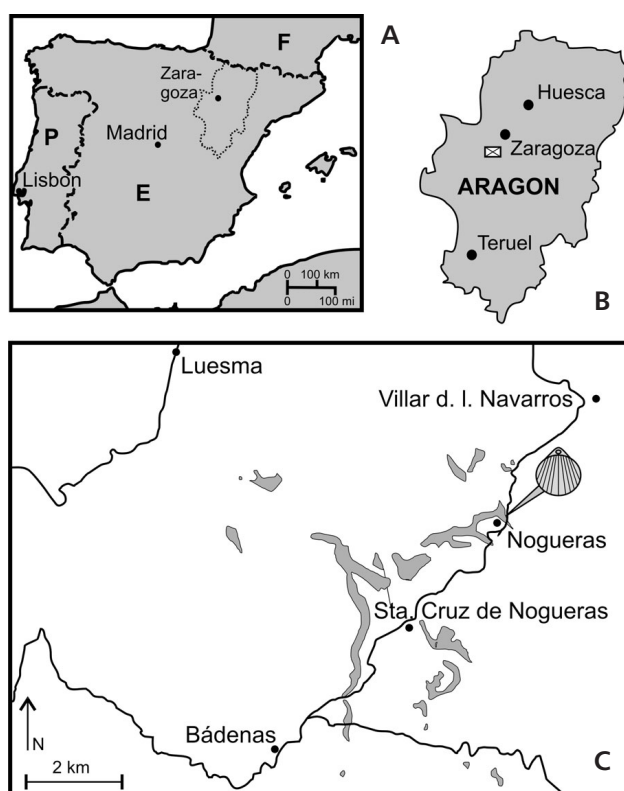


Figure 1. Topographical map of the Iberian Peninsula (A), the Province of Aragon (B), and the study area (C). Black lines represent streets. Outcrops of the Nogueras Formation highlighted in grey. Collecting locality indicated by the brachiopod symbol. Modified after Carls (1987); E = Spain, F = France, P = Portugal.

Late Gedinnian through most of Early Siegenian time. The last marine fauna before this gap is found on the *dumontianus* shelf in the Taunus Hills (Germany) and the Ardennes and describes a late Pridolian transgression (Carls 1987, Schemm-Gregory & Jansen 2009). The following transgression does not start before Middle Siegenian time. To study the stratigraphy and correlation of this time interval, special attention is paid to the Armorican Massif (France), the Cantabrian Mountains and Eastern Iberian Chains (both Spain) which contain extensive invertebrate faunas of this particular time interval. Several horizons with characteristic index fossils can be correlated within and also between these three regions. Especially the Eastern Iberian Chains show several faunal extinctions on a large geographical scale followed by re-settlements in local areas (Carls 1985), which can be described as allopatric speciation or punctuated equilibria, according to Johnson (1975) and Eldridge & Gould (1972). Carls (1987) argued that the rapid evolution and strong radiation of Early Devonian brachiopods found in sediments of turbid water with strong sediment transport in Western Europe is the result of rapid environmental changes and development of new ecological niches.

The brachiopods of the Eastern Iberian Chains have been briefly described by Carls (1999) with special focus on spiriferids for biostratigraphical purpose. The terebratulids of the d2c-alpha and beta beds of the Nogueras Formation have been mentioned under the name of *Globithyris* Cloud, 1942. Carls (1999) interpreted these forms as the phylogenetic ancestor of *Rhenorenselaeria* Kegel, 1913. In contrast, Schemm-Gregory (2008a) considered *Lievinella* Boucot, 1975 as their phylogenetic ancestors but could not study the terebratulids of the d2c-alpha beds for a phylogenetic interpretation of *Neopaulinella* (see Phylogeny section).

History of research

Species of the genus *Neopaulinella* Özdikmen, 2008 have been described since the 19th century; however, their systematic assignment is a long odyssey. The first described species was the type species, *N. guerangeri* (de Verneuil, 1851), under the name *Terebratula guerangeri*, followed a few years later by the second species of this genus *gaudryi* (Oehlert 1877). Until the erection of the genus *Neopaulinella* these two species have been assigned to various genera: *Terebratula* Müller, 1776, *Centronella* Billings, 1859, *Trigleria* Bayle, 1878, *Mutationella* Kozłowski, 1929, *Retzia* King, 1850, or *Xana* García-Alcalde, 1972.

In his revision of Devonian Terebratulida Waagen, 1883, Cloud (1942, p. 119) pointed out that with the assignment of Bayle's *Trigleria Adrieni* de Verneuil, 1845 as type species of *Trigleria*, *Trigleria* became an objective synonym of *Retzia*, which is a rhynchospirid brachiopod. Due to the lack of material, he left the species *guerangeri* and *gaudryi* as well as several other European terebratulid species without generic assignment. In the same year Renaud (1942) described *N. guerangeri* from the Siegenian Taunusquarzit and the Upper Emsian Emsquarzit formations from Germany.

I have studied the brachiopod fauna of these formations and can confirm the presence of mutationellid brachiopods in the Taunusquarzit Formation. However, I have never seen these forms in the Emsquarzit Formation. A terebratulid from the Lower Emsian Vallendar Formation with similar outline and similar costae, but of much larger size, is stored in the Boucot collection in the Smithsonian Institution, Washington D.C. It is surely not *N. guerangeri*, but a taxonomic study of this form is strongly recommended to clarify its systematic position (pers. unpubl. data). The erection of *Paulinella* helped to solve part of the *Trigleria* problem (Boucot & Racheboeuf 1987a), although the genus name was recently replaced by *Neopaulinella* (Özdikmen, 2008). The same authors provided a detailed description of the two *Neopaulinella* species, *guerangeri* and *gaudryi*. Binnekamp (1965) studied terebratulids from

the Cantabrian Lebanza Limestone and assigned the species *guerangeri* to *Mutationella*. However, as Boucot & Racheboeuf (1987b) pointed out, these Cantabrian *guerangeri* forms lack dental plates and show fewer costae than *N. guerangeri*, but they surely belong to *Neopaulinella*. García-Alcalde (1972) assigned *N. guerangeri* to his new genus *Xana*. In accordance with Boucot & Wilson (1994), I consider this as erroneous because species of *Xana* show a sulcate dorsal valve and a short loop, whereas *Neopaulinella* shows a flat dorsal valve which never shows a sulcus. Mergl (1986) described *Mutationella* cf. *guerangeri* from Bohemia but did not give any information on the interior, so that the assignment to *Neopaulinella* is doubtful. Özdikmen (2008) suggested to replacing *Paulinella* with *Neopaulinella* Özdikmen, 2008 due to homonymy with *Paulinella* Lauterborn, 1895, a genus within the Rhizipoda (see ICZN 1999, art. 23).

Material and methods

The material is preserved as articulated and isolated shells. Plaster casts were made of specimens studied by serial sections. Up to several hundred serial sections of each articulated shell were prepared using a WOKO 50P grinding machine with slice-spacing of 50 and 100 µm (GZG.INV.35007: 235, GZG.INV.35008: 277, GZG.INV.35009: 313, GZG.INV.35010: 344, SMF 85615: 59, SMF 85616: 84, SMF 85617: 128, SMF 85618: 149). Acetate peels were used to record the morphological information from each slice; these were subsequently digitized using a digital camera. Three-dimensional reconstruction methods are those of Sutton *et al.* (2001, 2005), implemented using the custom SPIERS software suite for registration, virtual preparation, and interactive visualization. The digitized acetate peels were subsequently manually aligned with SPIERS-align and in a second step redrawn using different masks in SPIERSedit in order to reconstruct a 3D model of the internal shell morphology and the loop. The 3D images are copied out of SPIERSview and arranged in Photoshop. Furthermore, a 3D image of the internal mould of the articulated shell is shown and drawings of selected peels in order to ease comparison with data in older literature. Drawings were done with help of a camera lucida. Measurements were taken with digital calipers and rounded to 0.1 mm. Specimens were coated with ammonium chloride prior to photography. The phylogenetic analysis was performed with the heuristic search modus of PAUP 4.10 beta (Swofford 2002). All characters are coded as ordered, regarded as Wagner characters (Wagner 1961), and are of equal weights. Consistency index (CI), retention index (RI), and rescaled consistency index (RCI) are given. A fictitious outgroup was chosen in order to assure an independent analysis. The systematics follows Lee *et al.* (2006) in

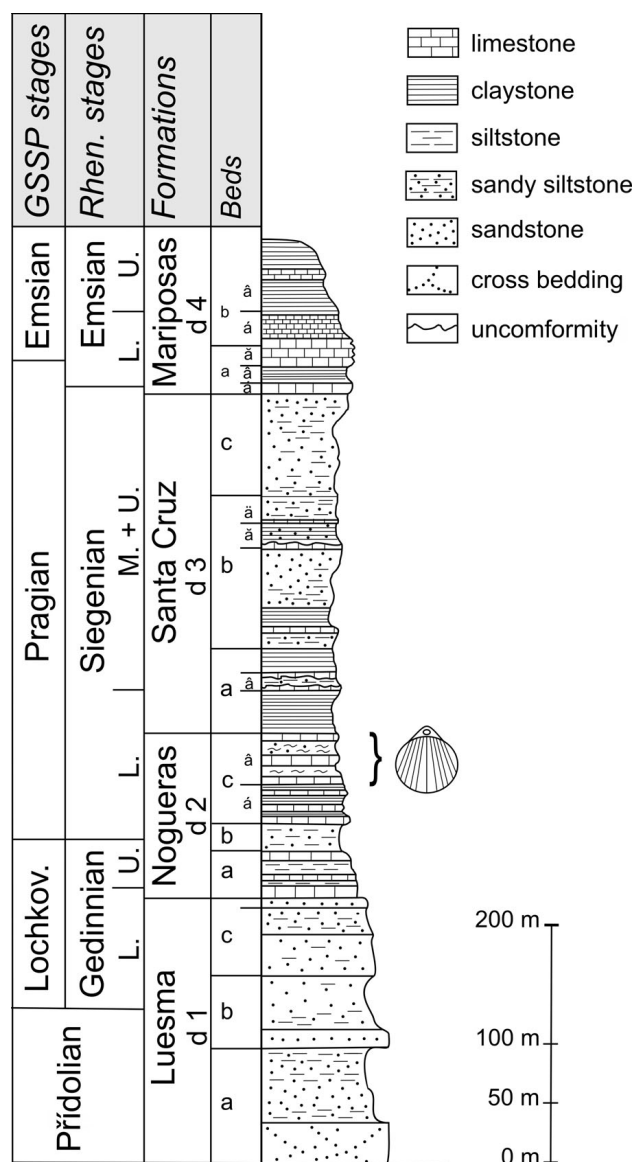


Figure 2. Lithology of the Lower Devonian in the Eastern Iberian Chains (Spain). Beds yielding *Neopaulinella noguerasensis* sp. nov. are marked by the brachiopod symbol. Modified after Carls (1987). Abbreviations: L. – Lower, Lochkov. – Lochkovian, M. – Middle, Rhen. – Rhenish, U. – Upper.

the revised *Treatise on Invertebrate Paleontology*. For stratigraphic assignment, the stages “Siegenian” and “Emsian” are used in their traditional German sense because taxa of *Neopaulinella* occur only in the neritic facies of the Rhenohercynian. A correlation with the GSSP subdivision is given in Fig. 2.

Institutional abbreviations. – GZG.INV.: Geowissenschaftliches Zentrum der Universität Göttingen, Museum, Invertebrate Collection, Göttingen, Germany; SMF: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806
Subphylum Rhynchonelliformea Williams *et al.*, 1996
Class Rhynchonellata Williams *et al.*, 1996
Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Stringocephaloidea King, 1850
Family Meganterididae Schuchert & Le Vene, 1929
Subfamily Mutationellinae Cloud, 1942

Genus *Neopaulinella* Özdikmen, 2008

Type species. – *Terebratula guerangeri* de Verneuil, 1851, p. 780.

Emended diagnosis. – Mutationellids with deeply impressed dorsal adductor field, a deeply or moderate impressed ventral muscle field, and a well-developed dorsal median septum. Ventral median septum weakly to strongly developed, rarely lacking. [Modified after Boucot & Racheboeuf 1987a, p. 99.]

Species assigned. – *Terebratula guerangeri* de Verneuil, 1851; *Terebratula gaudryi* Oehlert, 1877; *Neopaulinella noguerasensis* sp. nov.

Species questionably assigned. – *Centronella bergeroni* Oehlert, 1885; *Trigeria sarthacensis* Renaud, 1942; *Mutationella* cf. *guerangeri* Mergl, 1986.

Remarks. – Differences with other genera within the Mutationellinae are discussed in Boucot & Racheboeuf (1987a, b).

Geographic and stratigraphic occurrence. – Western and ?Central Europe, ?England, ?Turkey; Siegenian to Emsian in the traditional German sense (middle to upper Lower Devonian).

Neopaulinella noguerasensis sp. nov.

Figures 3–9, Tables 1–4

Derivation of name. – After “Nogueras”, the village near the collecting locality.

Holotype. – Articulated shell stored in the Senckenberg Forschungsinstitut und Naturmuseum under the inventory number SMF 85608. Length 20.0 mm, width 20.0 mm, and thickness 19.3 mm.

Type horizon and locality. – Bed d2C-beta, upper part of the Nogueras Formation (Lower Siegenian, middle Lower

Devonian), Fuente de Nogueras (Eastern Iberian Chains, Aragon, Spain). A detailed description of the collecting locality is given in Carls (1987).

Material. – 29 articulated shells (GZG.INV. 34999, 35000, 35004–35010, 35012, 35013; SMF 85607–85608, 85612–85618, 85620, 85622–85629) [8 of them used for serial sections (GZG.INV.35007–35010, SMF 85615–85618)], 6 isolated dorsal shells (GZG.INV.35001–35003; SMF 85609, 85610, 85630), and 6 ventral external shells (GZG.INV.35011, 35014, 35015; SMF 85611, 85619, 85621). Measurements of the material are listed in Table 1.

Diagnosis. – A neopaulinellid with a crenulate anterior margin, short and thin dental plates, clearly separated dorsal anterior and posterior adductor pairs which are strongly impressed at their posterior end, and a low and anterior faint dorsal median septum.

Description. – Form and size: Mutationellid-like small to medium-size shells that are ventribiconvex in longitudinal section, and subcircular in outline with maximum width at midlength of shell or shortly anterior of it. The ventral valve is strongly convex, and the dorsal valve almost flat. Exterior: The surface of the ventral shell is covered by 28 to 30 fine and simple costae, in rare cases up to 36. The dorsal shell shows one or two costae less. All non-medial costae are of equal size, however, the two ventral median costae and the corresponding median costa of the dorsal shell are coarser than adjacent ones (Fig. 3P–Q). Costae and furrows are of same size and rounded to angular in cross section. The anterior margin is rectimarginate, in some specimens it may be weakly sulcate. The ventral beak is gently erect, narrow, and elongate. The ventral interarea is low and small, with a large and submesothyrid foramen (Fig. 4B–C). The delthyrium is open and restricted by well-developed deltidial ridges (Fig. 4O). Concentric growth lamellae are developed at the anterior margin of both valves and overhang the youngest anteriormost portion of the shell. Interior of ventral valve: Hardly any development of secondary shell material is present in the ventral apical region. Fillings of the lateral apical cavities almost reach the posterior end of the filling of the umbo (Fig. 4H). Rare specimens show strong development of secondary shell material in the apical region that almost completely fills the apical cavities (Fig. 5). Dental plates are short and thin, leading to small knob-like teeth which point in an antero-dorsal direction (Figs 4O, 6K–M). The ventral muscle field is not imbedded into the shell material and ranges from barely to not impressed. Its outline is hardly recognizable in 3D reconstructions (Fig. 4H). Interior of dorsal valve: The dorsal apical region is characterized by almost no development of secondary shell material. Dental sockets are cone-shaped, pointing in a posterior

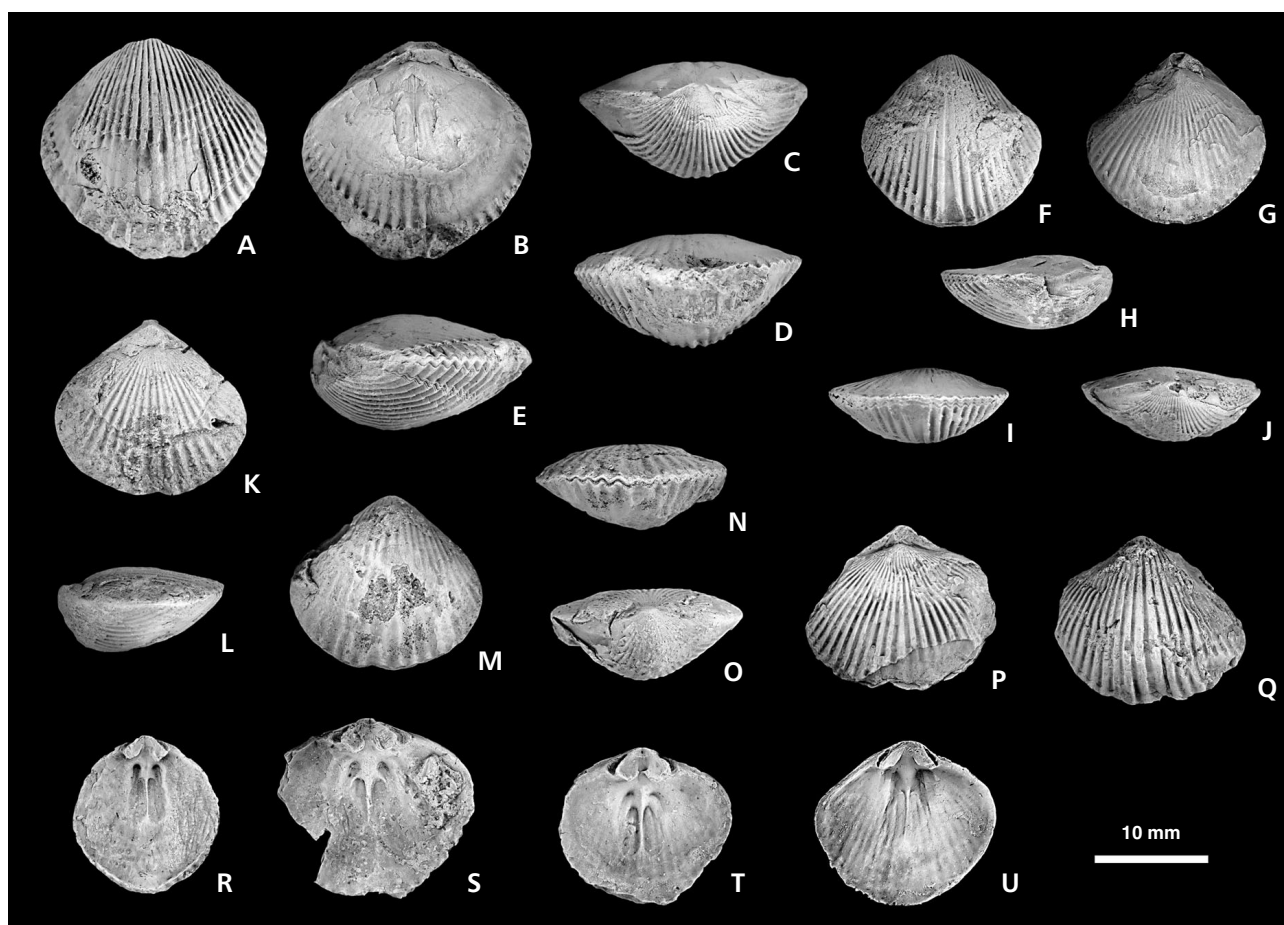


Figure 3. *Neopaulinella noguerasensis* sp. nov. • A–E – SMF 85608, holotype. Ventral (A), dorsal (B), posterior (C), anterior (D), and lateral (E) views of articulated shell. • F–J – SMF 85607. Ventral (F), dorsal (G), lateral (H), anterior (I), and posterior (J) views of articulated shell. • K–O – SMF 85613. Dorsal (K), lateral (L), ventral (M), anterior (N), and posterior (O) views of articulated shell. • P–Q – SMF 85613. Dorsal (P) and ventral (Q) views of articulated shell. • R – GZG.INV.35001. Upper view on internal dorsal shell. • S – GZG.INV.35002. Upper view on internal dorsal shell. Note impressions of adductor scars. • T – GZG.INV.35003. Upper view on internal dorsal shell. Note muscle scars and cardinal plate. • U – SMF 85610. Upper view on internal dorsal shell. All figures $\times 1.5$.

direction. Inner walls of socket ridges are thick and curved over dental sockets (Fig. 5G). The cardinal plates are medially separated, triangular, thick, foraminate at posterior end, and situated almost parallel to commissural plane (Figs 3R–U, 4M, 6N). Inner hinge plates are short and connected at their anterior ends, forming a thin and transversely oriented cardinal process (Fig. 6M). Outer hinge plates are thick and laterally curved in a ventral direction. The dorsal median is septum thin, low, posteriorly coarse and anteriorly blade-like, reaching at least to the midlength of the dorsal shell, and separating the dorsal adductor field. The adductor field is, especially with respect to the posterior margin, deeply impressed into the shell material; its posterior and anterior pairs of adductor scars are clearly differentiable (Fig. 4B, R–U). The posterior adductor pair is more deeply impressed than the anterior pair, thin and elongate anteriorly, with a paddle-like outline. The anterior adductor pair is larger, elongate, and elliptical in outline.

The posterior margin of both pairs of adductor scars is distinct and rounded posteriorly. The anterior margin is less visible but bordered by a faint ridge. A deltidiform and long loop extends over 2/3 of valve length anteriorly (Fig. 7). Crural processes are situated at the anterior end of the posterior 1/3 length of loop, sharply triangular, oriented parallel to each other, and pointing perpendicular to commissural plane in a ventral direction. Descending lamellae are parallel to one other and fused at the anterior end (Fig. 8K–L).

Discussion. – The morphological differences of *Neopaulinella noguerasensis* justify the erection of a new species (Table 2). The new species differs from the type species, *N. guerangeri*, in a crenulate anterior margin and lack of a sulcus. The anterior margin of *N. guerangeri* is weakly unisulcate. The dental plates in *N. noguerasensis* are short and thin, in *N. guerangeri* relatively long. The dorsal adductor

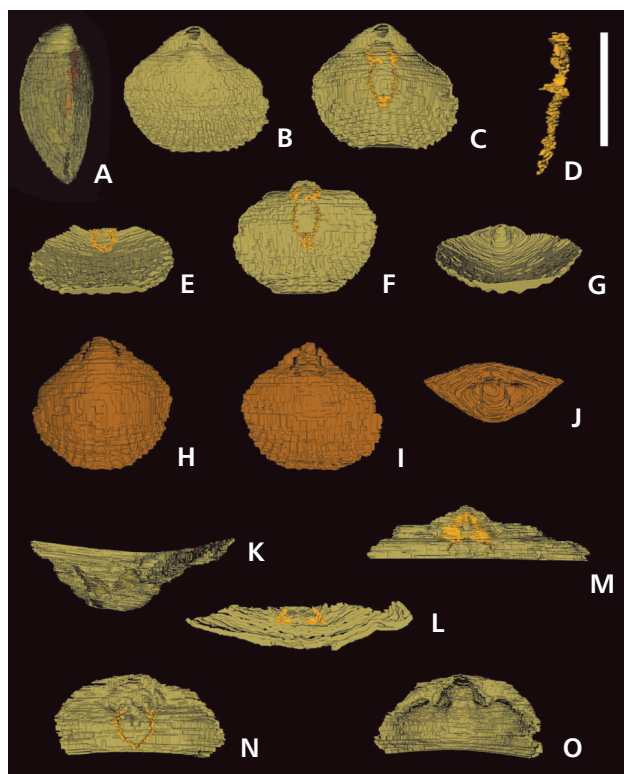


Figure 4. Three-dimensional reconstructions of *Neopaulinella noguerasensis* sp. nov. based on serial sections. • A–J – GZG.INV.35007. • A – lateral view of articulated shell with loop. Shells 50% transparent. Note orientation of loop. • B – dorsal view of external articulated shell. • C – upper view of ventral internal shell with loop. • D – lateral view of loop ($\times 3.0$), scale bar represents 5 mm. • E – oblique anterior view of dorsal internal shell with loop. • F – upper view of dorsal internal shell with loop. • G – oblique anterior view of ventral internal shell. • H – ventral view of internal mould of articulated shell. • I – dorsal view of internal mould of articulated shell. • J – posterior view of internal mould of articulated shell. • K–M – SMF 85617. K – oblique lateral view of ventral internal shell. Note teeth and dental plates. L – anterior view of dorsal internal shell with loop. M – upper view of posterior dorsal internal shell with fragment of posterior end of loop. Note cardinal plate. • N–O – SMF 85618. N – upper view of posterior dorsal internal shell with loop. Note short length of loop with crural processes situated almost at anterior end of cardinal plate. O – upper view of posterior ventral internal shell. Note thickness of dental plates, deltidial ridges, and teeth. All figures $\times 1.5$, if no other indication.

field of the new species is clearly separated by a coarse median ridge into a posterior and an anterior pair of muscle scars, whereas these are hardly recognizable in the type species. Furthermore, the margin of the dorsal adductor field of *N. noguerasensis* is well defined by a fine ridge and the whole muscle field is more strongly impressed into the dorsal valve than in *N. guerangeri*, in which the anterior margin of the dorsal adductor field is unknown. The dorsal median septum of the new species is shorter than in *N. guerangeri* and posteriorly strongly thickened. Its anterior part, however, is low and fine. In *N. guerangeri* the dorsal median septum is high and of equal size throughout its whole length or rarely weakly thickened at the posterior

Table 1. Measurements of *Neopaulinella noguerasensis* sp. nov. Numbers in brackets show extreme values. Abbreviations: ht – holotype, INV – Inventory number, L/mm – length in mm, R/DS – number of costae on dorsal shell, R/VS – number of costae on ventral shell, T/mm – thickness in mm, W/mm – width in mm, + x – maximum number of costae unknown.

INV	W/mm	L/mm	T/mm	R/DS	R/VS
GZG.INV.34999	18.42	17.97	9.81		26
GZG.INV.35000	21.72	18.84	10.60	30	28
GZG.INV.35001	15.17	13.75		30	
GZG.INV.35002	12.98	14.00		36 + x	
GZG.INV.35003	17.29	15.82		30	
GZG.INV.35004	17.40	15.75	9.10	24	26
GZG.INV.35005	16.65	14.50	8.41	28	30
GZG.INV.35006	17.77	14.83	9.10	22	24
GZG.INV.35007	12.87	12.14	6.50	28	26
GZG.INV.35008	17.43	15.93	8.58	32	30
GZG.INV.35009	15.55	16.05	7.29	28	30
GZG.INV.35010	14.75	17.04	7.56	28	30
GZG.INV.35011	16.99	16.13	10.27		28
GZG.INV.35012	19.60	18.57	10.25	34	32
GZG.INV.35013	18.53	17.08	6.07	28	
GZG.INV.35014	14.03	13.13		20 + x	
GZG.INV.35015	20.83	11.52		28	
SMF 85607	15.78	14.87	6.52	23	22
SMF 85608 (ht)	20.00	20.04	19.34		26
SMF 85609	12.63	10.81			
SMF 85610	10.05	14.43		24	
SMF 85611	14.19	13.87	8.11		28 + x
SMF 85612	13.67	16.33	8.32		24 + x
SMF 85613	16.87	15.08	7.56	18	18
SMF 85614	19.46	18.46	9.99		
SMF 85615	16.40	19.00	10.40	28	30
SMF 85616	15.50	16.10	8.50	22	24
SMF 85617	23.40	21.3	11.60	34	36
SMF 85618	15.00	14.1	9.00	26	28
SMF 85619		10.88		32	
SMF 85620				30	28 + x
SMF 85621	17.97	20.00			20 + x
SMF 85622	16.53				
SMF 85623	17.24	17.21	6.58	28	28
SMF 85624	13.82	14.11	7.22		36
SMF 85625	20.99	20.7	11.30	20	20
SMF 85626	16.21	18.09	9.75	28	30
SMF 85627	18.66	19.52	13.15	30	32
SMF 85628	20.20	18.94	6.63	30	32
SMF 85629					28
SMF 85630	Fragment of posterior dorsal shell				

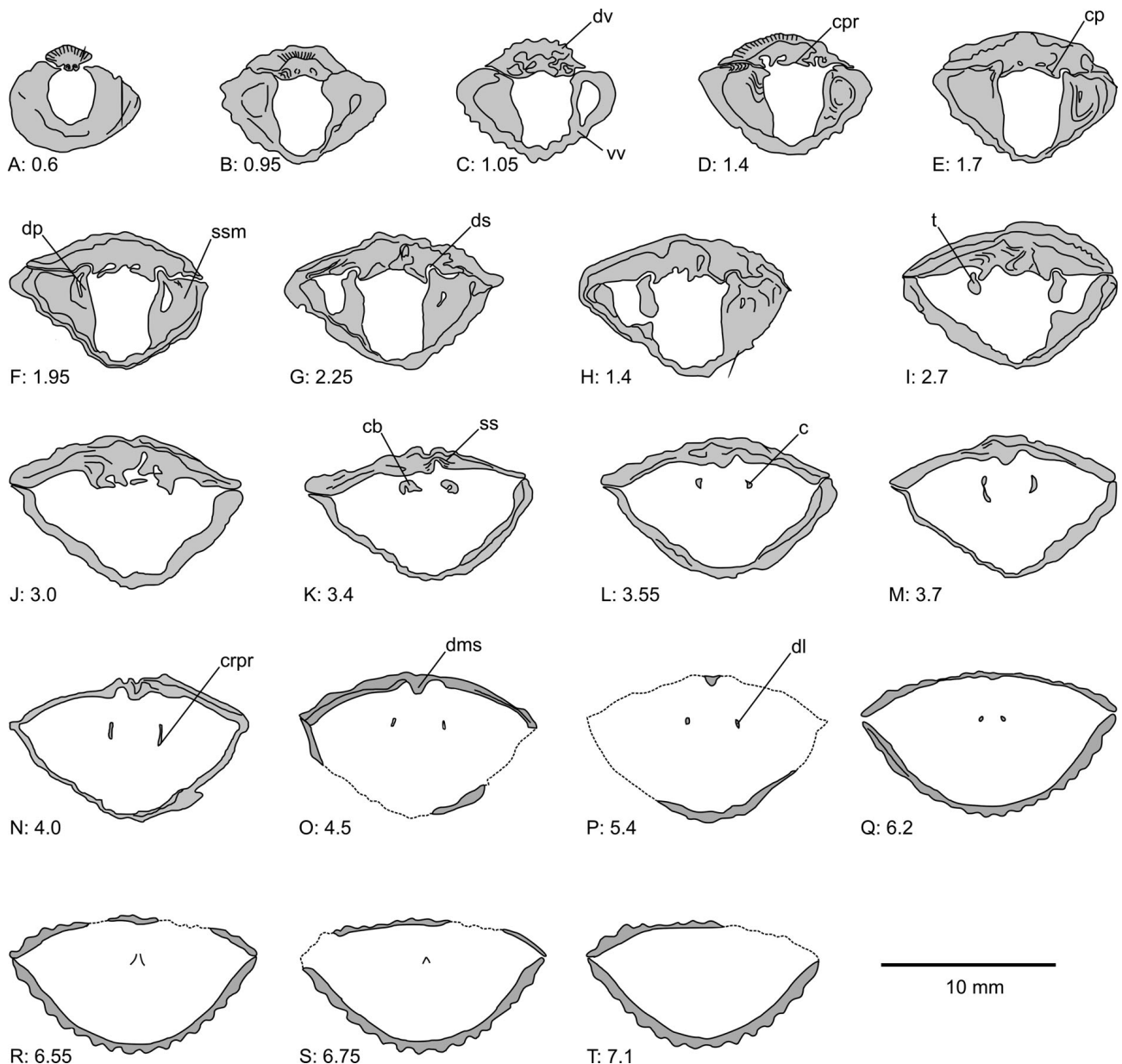


Figure 5. Serial sections of *Neopaulinella noguerasensis* sp. nov. SMF 85618. All figures magnified ($\times 2.5$). Sectioning perpendicular to commissural plane, sectioning distance in mm from posterior. Dotted line represents abraded shell. Abbreviations: c – crus, cb – crural base, cpr – cardinal process, cp – cardinal plate, crpr – crural process, dl – decending lamella, dms – dorsal median septum, dp – dental plate, ds – dental socket, dv – dorsal valve, ss – shell structure, ssm – secondary shell material, t – tooth, vv – ventral valve.

margin. The angle of the ventral umbo is about 20° larger and the angle of the dental plates about 12° to 16° larger in *N. noguerasensis* than in *N. guerangeri*. The new species differs from *N. gaudryi* in having less costae and thin dental plates. Its dorsal adductor field is short and narrow with an oval outline and the posterior and anterior pairs of adductor muscle scars being clearly divided by a coarse ridge, whereas it is large and coarse with tear-drop outline in *N. gaudryi* and the border between anterior and posterior muscle scar pairs is hardly recognizable. The dorsal median

septum is lower in *N. noguerasensis* and posterior thickened, but high and of equal thickness in *N. gaudryi*. The ventral umbonal angle of *N. noguerasensis* is slightly smaller and the angle between dental plates wider than in *N. gaudryi*.

It has to be stated that for statistical analyses fewer specimens were measured than in the work by Boucot & Racheboeuf (1987a), and as far as these data says, the ratio of length to thickness is not as low as in *N. guerangeri* and *N. gaudryi* which means that specimens of *N. noguerasensis* are slightly less curvate, however, the line of

Table 2. Morphological comparison of species of *Neopaulinella* Özdikmen, 2008.

	<i>Neopaulinella noguerasensis</i> sp. nov.	<i>Neopaulinella guerangeri</i> (de Verneuil, 1851)	<i>Neopaulinella gaudryi</i> (Oehlert, 1877)
curvature	equi- to ventribiconvex	ventribiconvex	equibiconvex
number of costae on ventral valve	28–30	(22–44) 30–32	58–76 (92)
anterior margin	crenulate	weakly unisulcate	crenulate
ventral muscle field	unknown	deeply impressed	deeply impressed
dental plates	short, thin	long, thin	short, thick
dorsal adductor field	short, narrow with oval outline	short, narrow, anterior margin unknown	large, broad with oval to tear-drop outline
posterior and anterior pair of dorsal adductor field	clearly separated by a coarse ridge	border between muscle pairs hardly recognizable	border between muscle pairs hardly recognizable
dorsal median septum	low, posteriorly thickened, anterior faint	high, posteriorly weakly thickened or of equal thickness	high, equally thick
ratio length/thickness	2.6–1.7	1.4–2.7	2.4–1.6
ratio length/width	0.85–1.3	1	0.83–0.9
ventral umbonal angle	102°–106°	86°	111°–125°
angle between dental plates	57°–61°	45°	32°–35°
geographic occurrence	Spain (Eastern Iberian Chains)	France, Spain, ?Belgium, ?Germany, ?England, ?Turkey	France (Armorican Massif)
stratigraphic occurrence	Lower Siegenian (middle Lower Devonian)	Middle Siegenian to ?Emsian (middle to upper Lower Devonian)	Middle to Upper Siegenian (middle Lower Devonian)

tendency is closer to that of *N. gaudryi*. The ratio of length to width varies a little more in *N. noguerasensis* than in the other two species, and overall the line of tendency is less steep. The ratio of length to thickness is almost the same in both species, however, the ratio of length to width varies more in the new species than in *N. guerangeri* (Fig. 9).

Geographical and stratigraphical occurrence. – See type locality and type horizon.

Cladistical analysis of *Neopaulinella*

In this work, an attempt for cladistical analysis on species level of *Neopaulinella* is made, even though up to now only 3 species are described for which sufficient morphological data is given. Species questionably assigned or in open nomenclature were omitted because of the lack of morphological information. Due to the few characters available and the few taxa used, the resulted cladogram shows evolutionary tendencies rather than a reliable lineage. Description and coding of characters are given in Table 3. Table 4 shows the matrix for the cladistical analysis. The cladogram demonstrates the closer relationship of *guerangeri* to *noguerasensis* (Fig. 10). The high consistency index (CI = 0.9) indicates the lack of homoplasy and supports the definition of taxa by morphological differences discussed above and given in Table 2. The retention index is rather low for the lack of homoplasy (RI = 0.67), subsequently, the rescaled consistency index is RCI = 0.6.

Phylogeny

Revision is recommended for the other reported finds of *Neopaulinella* and its questionably assigned species in order to improve the evolutionary lineage. However, I believe without doubt that the phylogenetic origin of *Neopaulinella* is somewhere in small mutationellid brachiopods as it was already suggested by Boucot & Wilson (1994). An attempt at the phylogeny of taxa of *Neopaulinella* is given in the following: The root of *Neopaulinella* lies in small mutationellid brachiopods in the Eastern Iberian Chains out of which *N. noguerasensis* probably originated (see Boucot & Wilson 1994, fig. 6). The new species represents the oldest species within this genus. The rather small median septa in both shells, the short and thin dental plates, the coarse ridge in the dorsal adductor field, and the posteriorly thickened dorsal median septum are interpreted as conservative morphological features. The ventral umbonal angle is widest in the new species, however, more material of all taxa of *Neopaulinella* should be measured to prove this argument. The increasing thickness of the dorsal median septum and the loss of the ridge separating the posterior and anterior pair of dorsal adductors are interpreted as changes to an advanced morphology within the phylogenetical lineage of the genus. During the Middle and Late Siegenian, *N. guerangeri* and *N. gaudryi* developed out of *N. noguerasensis*. The lineage of *N. gaudryi* became extinct during the Late Siegenian, whereas forms or descendents of *N. guerangeri* are also found in Emsian strata. Subsequently, if forms reported from the lowermost Upper Emsian Emsquartzit

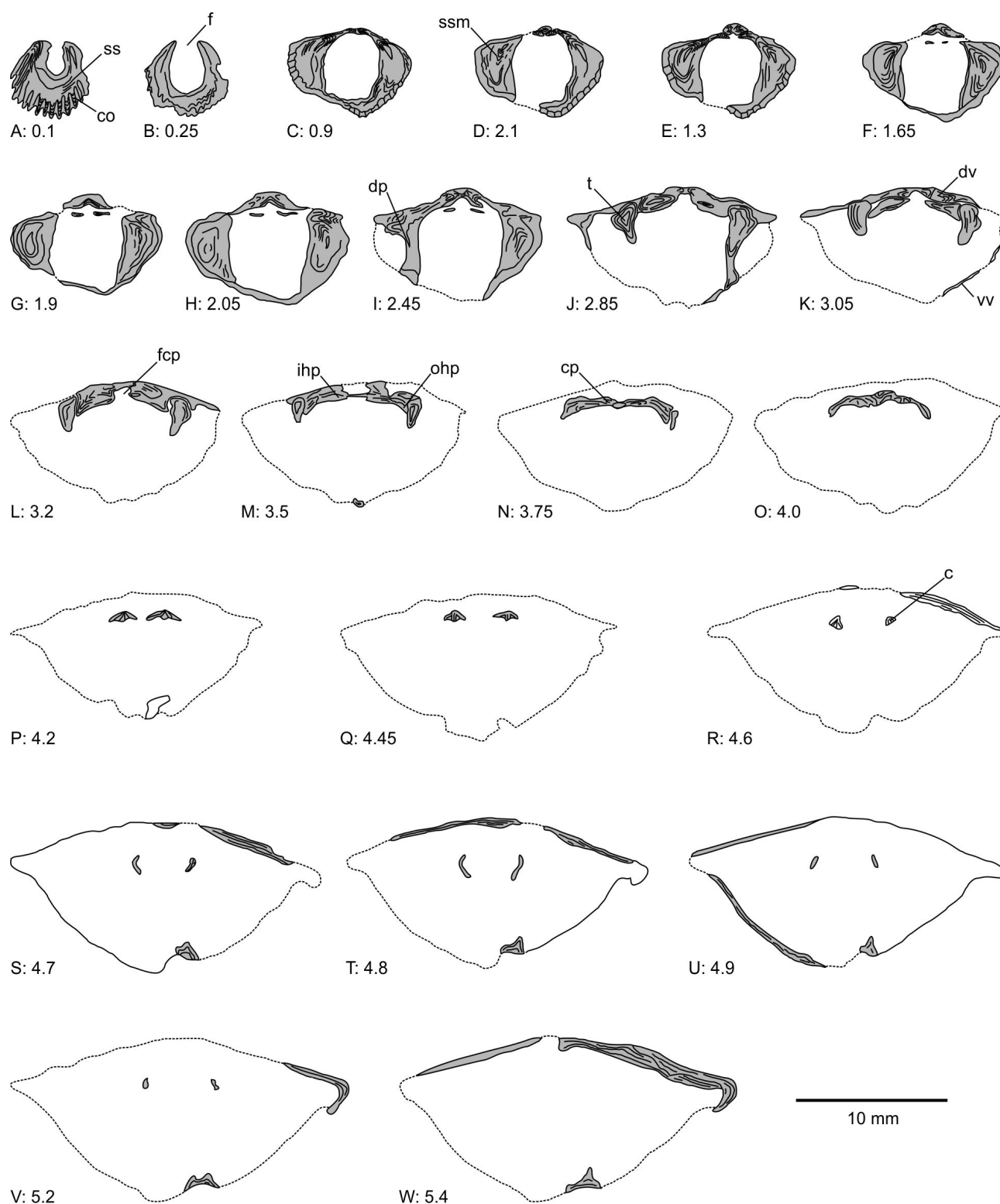


Figure 6. Serial sections of *Neopaulinella noguerasensis* sp. nov. SMF 85617. All figures magnified ($\times 2.5$). Sectioning perpendicular to commissural plane, sectioning distance in mm from posterior. Dotted line represents abraded shell. Abbreviations: c – crus, co – brachiofovea, cp – cardinal plate, dp – dental plate, ds – dental socket, dv – dorsal valve, f – foramen, fcp – foramen in cardinal plate, ihp – inner hinge plate, ohp – outer hinge plate, ss – shell structure, ssm – secondary shell material, t – tooth, vv – ventral valve.

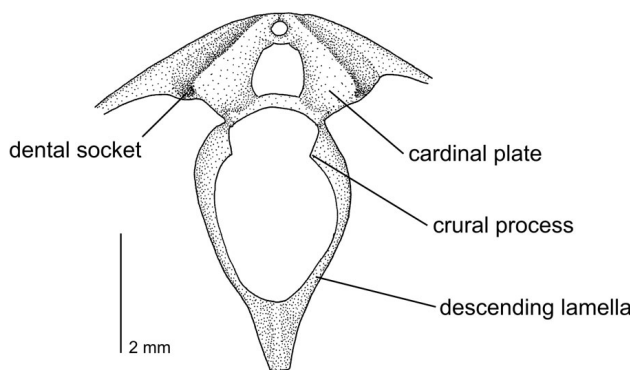


Figure 7. *Neopaulinella noguerasensis* sp. nov. Reconstruction of the loop and cardinalia after sectioned specimens (see Fig. 4).

Table 3. Description and coding of characters used for character matrix.

Number	Character description	Character coding
1	number of costae	below 50 (0), above 50 (1)
2	anterior margin	crenulate (0), unisulcate (1)
3	pairs of dorsal adductors	not recognizable (0), recognizable (1)
4	dorsal median septum	posteriorly thin (0), posteriorly thick (1)
5	dorsal medium septum	low (0), high (1)
6	length of dental plates	short (0), long (1)
7	thickness of dental plates	thin (0), thick (1)
8	angle of ventral umbo	below 100° (0), above 100° (1)
9	angle between dental plates	below 50° (0), above 50° (1)

Table 4. Character matrix used for cladistics. See Table 3 for description of characters.

	1	2	3	4	5	6	7	8	9
<i>N. guerangeri</i>	0	1	0	0	1	1	1	0	0
<i>N. gaudryi</i>	1	0	0	0	1	0	1	1	0
<i>N. noguerasensis</i>	0	0	1	1	0	0	0	1	1
Outgroup	0	0	0	0	0	0	0	0	0

Formation are related to *Neopaulinella*, the genus extends up to earliest late Emsian time.

Palaeoecology

The life habit of *Neopaulinella* is interpreted to be somewhat similar to the life habit of *Rhenorensellaeria* Kegel, 1913 and *Crassirensellaeria* Schemm-Gregory & Jansen, 2007 (Schemm-Gregory & Jansen 2007). *Neopaulinella* probably lived in clusters (pers. comm. F. Langenstrassen 2009, GZG) attached by a pedicle on hard substrate, e.g., shell material, and oriented perpendicular to the seafloor with their anterior part oriented upwards. In contrary to the

life habit of *Rhenorensellaeria*, I do not believe that shells of *Neopaulinella* were partly buried in the sediment because the shell material studied lacks a line marking the upper sediment boundary. Furthermore, in a carbonate environment more hard substrate is available, represented by isolated shells or reef hardground, than in the clayey seafloor and turbid water with hardly any hard substrate in which the rhenorensellaerid genera lived.

The zigzag commissure of brachiopods results in a longer commissure in comparison to an unfolded shell. Nutrient water is rather poor in carbonate environments (Rupke 1965) and a longer commissure provides a greater surface of exchanges and more nutrient water could be filtered (Schemm-Gregory 2010). The brachiopod could have benefited from this physiological advantage, too. In a second step the zigzag commissure reduced the distance between the valve margins so that coarse particles could not enter into the mantle cavity (Rudwick 1964). If taxa identified as *N. guerangeri* from the Taunusquarzit or Emsquarzit formations turn out to be forms of *Neopaulinella*, it would support the theory of the zigzag commissure mentioned above. *Neopaulinella guerangeri* shows a quite coarse ornamentation within the genus and these two formations represents environments of turbid “dirty” water with much suspension (Stets & Schäfer 2002).

Palaeobiogeography

The Early Devonian is characterized by an increasing endemism that gets lost step-by-step with the beginning of the Late Emsian. The different Early Devonian faunal provinces have been described by Boucot (1975), Boucot & Blodgett (2001), and Schemm-Gregory (2007, 2009). Boucot & Wilson (1994) pointed out that the Early Devonian provincialism is reflected by the European terebratulid forms *Xana* and *Paulinella* (now *Neopaulinella*). I agree with these authors and consider these forms as Gondwanan forms because Spain and France belong to former Gondwana (today’s North Africa and Western Europe) which are distinct from today’s Central Europe (Jansen 2001, Schemm-Gregory 2008a). However, forms described as *Neopaulinella guerangeri* from Central Europe and Turkey have to be revised in order to prove the Gondwanan endemism of *Xana* and *Neopaulinella*. It has to be stressed that the Istanbul Basin from where *guerangeri* forms are reported belongs to the northern Gondwanan terrane, too, as already discussed by Schemm-Gregory (2008b). On the other hand a migration pathway between Central and Western Europe existed during the Middle Siegenian and the Siegenian/Emsian boundary interval reflected by the terebratulid genus *Rhenorensellaeria* (Schemm-Gregory 2008a). Faunal affinities between the Armorican Massif and the Eastern Iberian Chains were shown by Carls (1987)

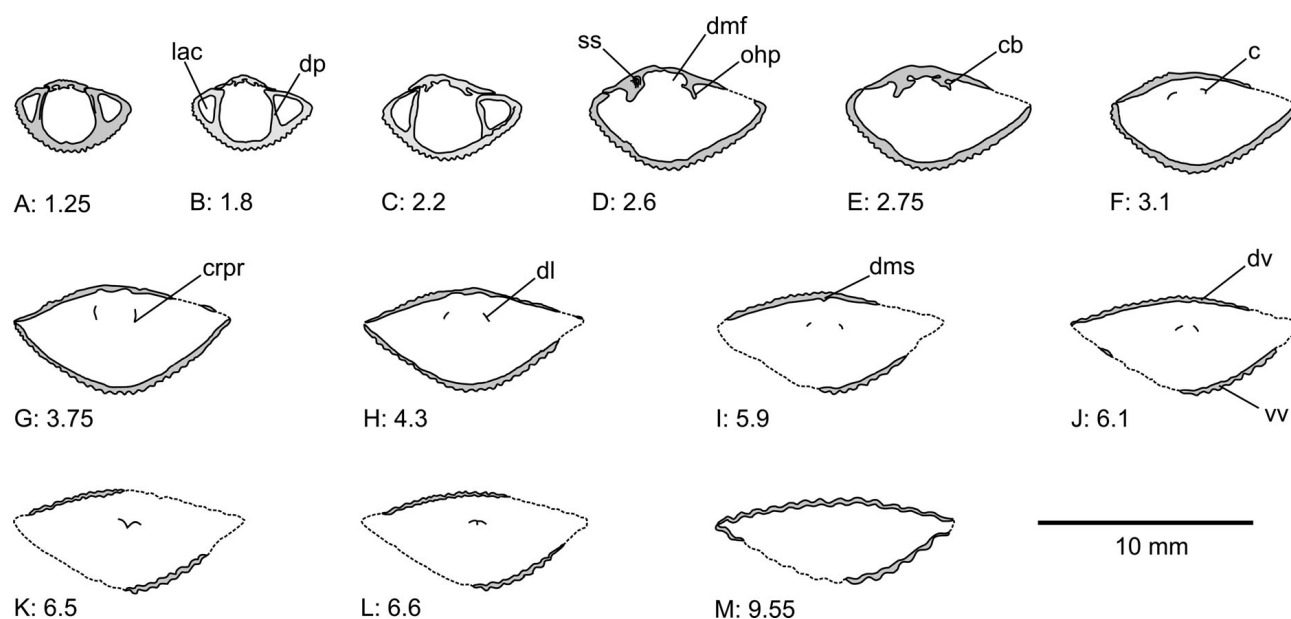


Figure 8. Serial sections of *Neopaulinella noguerasensis* sp. nov. GZG.INV.35007. All figures magnified ($\times 2.5$). Sectioning perpendicular to commissural plane, sectioning distance in mm from posterior. Dotted line represents abraded shell. Abbreviations: c – crus, cb – crural base, crpr – crural process, dl – descending lamella, dp – dental plate, dmf – dorsal muscle field, dms – dorsal median septum, dv – dorsal valve, lac – lateral apical cavity, ohp – outer hinge plate, vv – ventral valve.

and Gourvennec (1989) who discussed the occurrence of *Torosospirifer* Gourvennec 1989, resp., spiriferids of the *roussai* group, *Athyris undata* (Defrance, 1828), and *Vandercammenina trigeri* (de Verneuil, 1850). Jahnke (1971) correlated the Erbslochgrauwacke of the Kellerwald (Rheinisches Schiefergebirge, Germany) with the Eastern Iberian Chains due to the presence of *Vandercammenina trigeri* and *Mauispirifer* sp. H, however, he considered the Erbslochgrauwacke as part of today's Central Europe. The occurrence of *Filispirifer fallax* (Giebel, 1858) proves that the Erbslochgrauwacke is part of the northern Gondwana terranes and presents a block that probably slipped northward (Jansen 2001, Schemm-Gregory 2008c). The Lower Devonian of Western Europe can also be correlated with the Meguma Zone (Nova Scotia) with the presence of *Vandercammenina* Boucot, 1975 and *Ovetensispirifer* Schemm-Gregory, 2008b in both regions, however, *Neopaulinella* has not yet been reported from Nova Scotia (Bouyx *et al.* 1992; Boucot 1960, 1975; Schemm-Gregory 2008b).

Neopaulinella appears in Siegenian and Emsian strata. The new species occurs only in the Eastern Iberian Chains where it is restricted to the Early Siegenian. During Middle and Late Siegenian time the genus migrated to the Cantabrian Mountains and the Armorican Massif. It is represented by the species *guerangeri* in both regions but only by *gaudryi* in the Cantabrian Mountains. In the latest Siegenian and Early Emsian it is questionably reported from Central Europe, southern England, and Turkey; as mentioned above, this material has to be revised to prove

the identification and confirm the systematic position. I have briefly studied material from the Siegenian and Emsian of Devon and Cornwall (southern England) and the Istanbul Basin (Turkey). Externally similar but much smaller specimens resemble *Mutationella* Kozłowski, 1929 rather than *Neopaulinella*, however, I have not seen the material identified as *Neopaulinella guerangeri* yet. Carls & Valenzuela-Ríos (1998) already showed close affinities between the Eastern Iberian Chains and the Rheinisches Schiefergebirge and argued for a Middle Siegenian transgression resulting in a faunal exchange between these regions. Schemm-Gregory (2008a) discussed migration paths of centronellid brachiopods which are widely related to *Neopaulinella*. The Middle Siegenian transgression would be the only possibility for a pathway between a northern Gondwana terrane and the Rheinisches Schiefergebirge through which forms related to *N. guerangeri* found in the Taunusquarzit Formation would have been able to migrate to Central Europe.

Conclusions

Neopaulinella noguerasensis represents the earliest species of *Neopaulinella* and proves the origin of the genus from mutationellid brachiopods in the Eastern Iberian Chains. With the Middle Siegenian transgression questionable forms of *Neopaulinella* have migrated to Central Europe, southern England, and Turkey and support the theory of a pathway between Western and Central Europe during

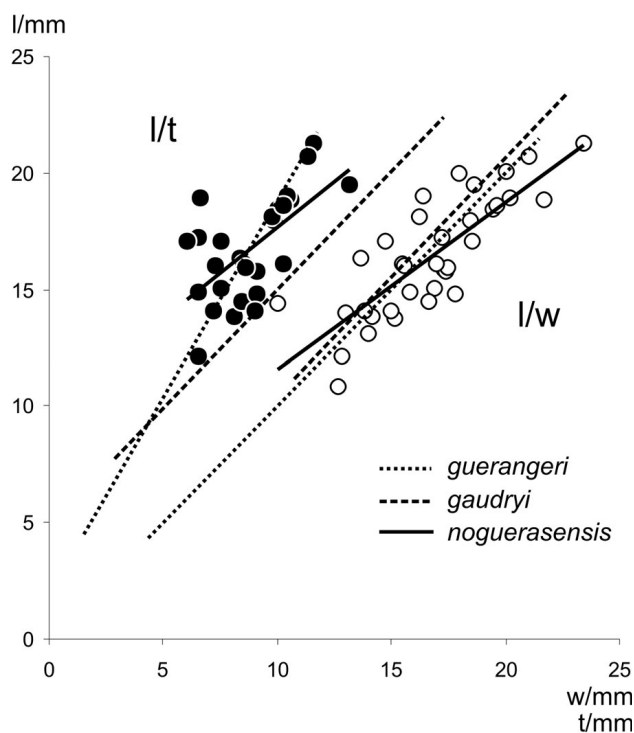


Figure 9. Diagram of the l/t and l/w ratios of species of *Neopaulinella* Özdikmen, 2008 based on measurement in Table 1. Abbreviations: l – length, t – thickness, w – width.

this time period. The morphological comparison and cladistical analysis demonstrate the independent coeval evolution of taxa of *Neopaulinella* which is another proof of Early Devonian endemism even on a regional scale within Western and Central Europe. The method of 3D reconstructions allows a detailed study of the shell interior including the development of the loop and justifies the erection of the new species. A revision of taxa questionably assigned to *Neopaulinella* using this method would be desirable to improve the knowledge of this genus.

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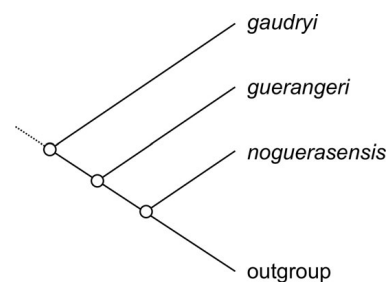


Figure 10. Cladogram showing the most plausible parsimonious tree resulting from an analysis of the character matrix in Table 4 with PAUP 4.10 beta (length = 10, CI = 0.9, RI = 0.67, RCI = 0.6).

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