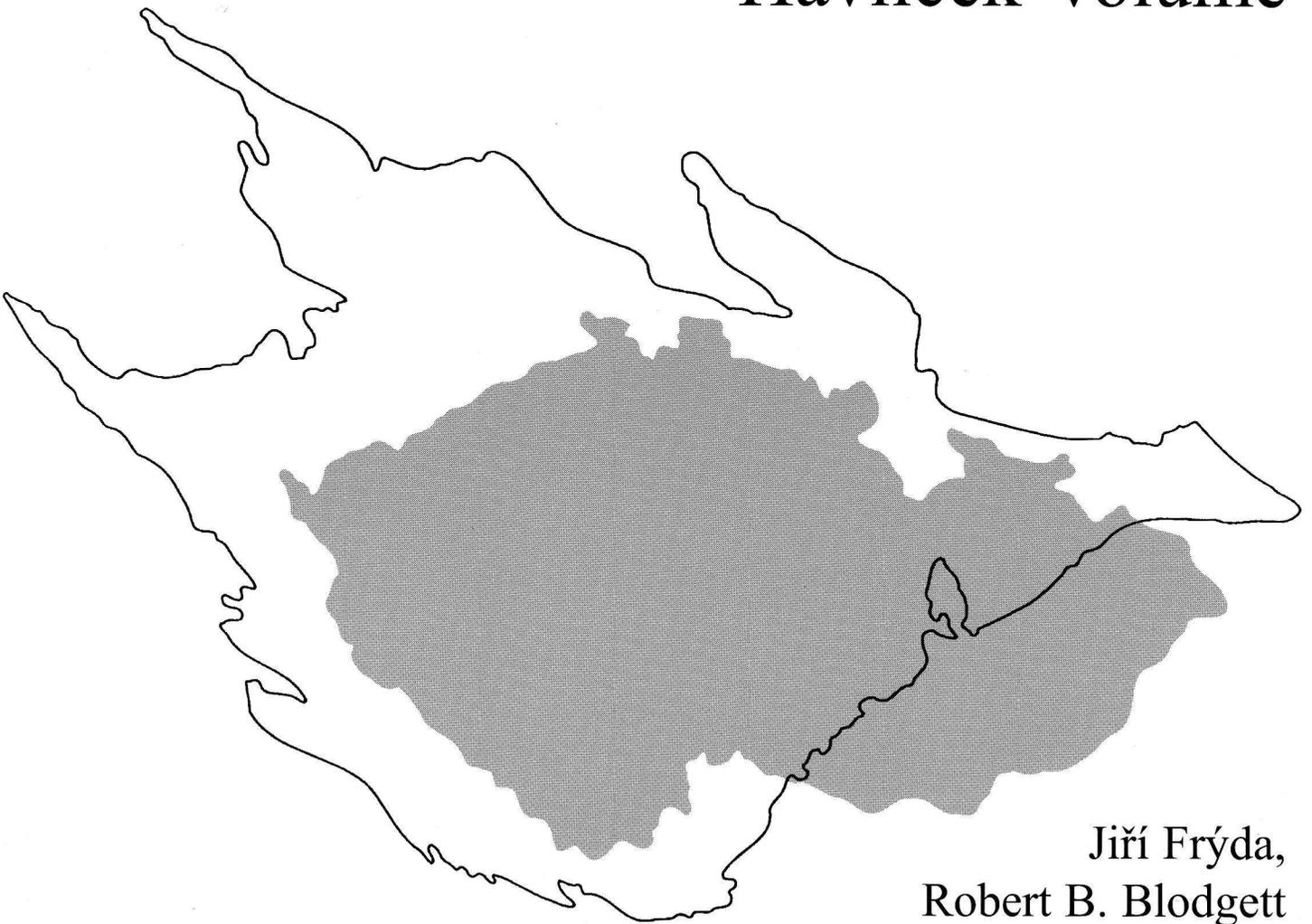


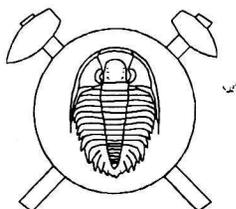
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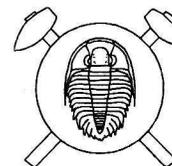


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New Lower Devonian (upper Emsian) *Myriospirifer* (Brachiopoda, Eospiriferinae) species from Alaska and northern Spain and the paleogeographic distribution of the genus *Myriospirifer*



Nové druhy rodu *Myriospirifer* (Brachiopoda, Eospiriferinae) se spodního devonu (svrchní ems) z Aljašky a severního Španělska a paleogeografické rozšíření rodu *Myriospirifer*

(8 figs)

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The paleogeographic range of the Silurian-Devonian eospiriferine brachiopod genus *Myriospirifer* is analysed. The genus appears in South Baltica during Early Silurian time and spread subsequently along both margins of the Rheic Ocean. During the Devonian it was widespread within Gondwana and Baltica reaching as far as Siberia. During the Early Devonian, this genus was found throughout much of the Old World Realm, but is notably missing from cratonic faunas of western and Arctic North America (Cordilleran Region of the Old World Realm), as well as the Eastern Americas and Malvinokaffric realms. Two new Emsian species, *M. breasei*, from south-central Alaska, and *M. crassus*, from northern Spain are described and figured. One of the Emsian species, *M. breasei* sp. nov. was transported in an accreted terrane rifted from Siberia, and subsequently joined to North America during late Mesozoic time.

Key words: Paleogeography, Brachiopods, Eospiriferinae, *Myriospirifer*, Silurian, Lower Devonian, Alaska, N Spain

Introduction

The subfamily Eospiriferinae Schuchert et LeVene, 1929 constitutes the basal trunk of the important articulate brachiopod group Spiriferida. The Eospiriferinae are represented in Late Ordovician to Devonian age beds of all continents except Antarctica. They have been studied by Boucot (1963) and Havlíček (1980) and include a great number of genera characterized mainly by their non-spinose, radial, capillate micro-ornament, the so-called “eospiriferid” micro-ornament (Gourvenec 1989b).

Lack of suitable micro-ornament descriptions in most older Eospiriferinae references makes it difficult to ascertain the true generic affiliation of the described or figured taxa and consequently, to establish the biostratigraphic and palaeogeographic range of some genera within the group. This fact noticeably occurs when a revision of the older references to *Eospirifer* Schuchert, 1913 is attempted because the non-costate forms of this genus differ from *Myriospirifer* Havlíček, 1978 only in the form of the micro-ornament. *Eospirifer* has intercalary, angular to subangular radial capillae narrower than the interspaces, whereas *Myriospirifer* has bifurcating, flattened capillae larger than interspaces. Based on these ornamental differences, Havlíček (1978, 1980), re-assigned several *Eospirifer* species to *Myriospirifer*. However, the complete revision of the older *Eospirifer* references has not yet been undertaken, and indeed, the number of *Myriospirifer* species concealed within *Eospirifer* is not yet known.

An analysis of the stratigraphic and paleogeographic range of *Myriospirifer* is made in this paper (Fig. 1), based mainly upon a bibliographic study. In addition, two new Lower Devonian species, *M. breasei* and *M. crassus*, are established from south-central Alaska and northern Spain (Fig. 2) respectively. The specimens illustrated here are deposited in the following repositories: *M. breasei* sp. nov. in the University of Alaska Museum (abbreviation UAM), Fairbanks, Alaska, USA; and *M. crassus* sp. nov. in the Department of Geology (Paleontology) of the University of Oviedo (abbreviation DPO), Oviedo, Asturias, Spain.

Paleogeographic and stratigraphic distribution of *Myriospirifer*

Myriospirifer appeared in Early Silurian (Llandoveryan) time (Sheehan – Baillie 1981, Rong et al. 1994) in southern Baltica. According to the distribution of the oldest eospiriferines (Rong et al. 1994), *Myriospirifer* evolved from some non-costate form of *Eospirifer*, because the latter genus served throughout the history of the subfamily as the source of both costate and non-costate eospiriferine taxa (Boucot 1963, Havlíček 1980). During latest Llandoveryan and Wenlockian time, *Myriospirifer* proliferated on both sides of the Rheic Ocean, mainly in Baltica. The immigration into peri-Gondwanan areas would perhaps be facilitated by the Bohemian (Perunica) prolongation of the supercontinent proposed by Havlíček et al. (1994). The Silurian *Myriospirifer* stock is

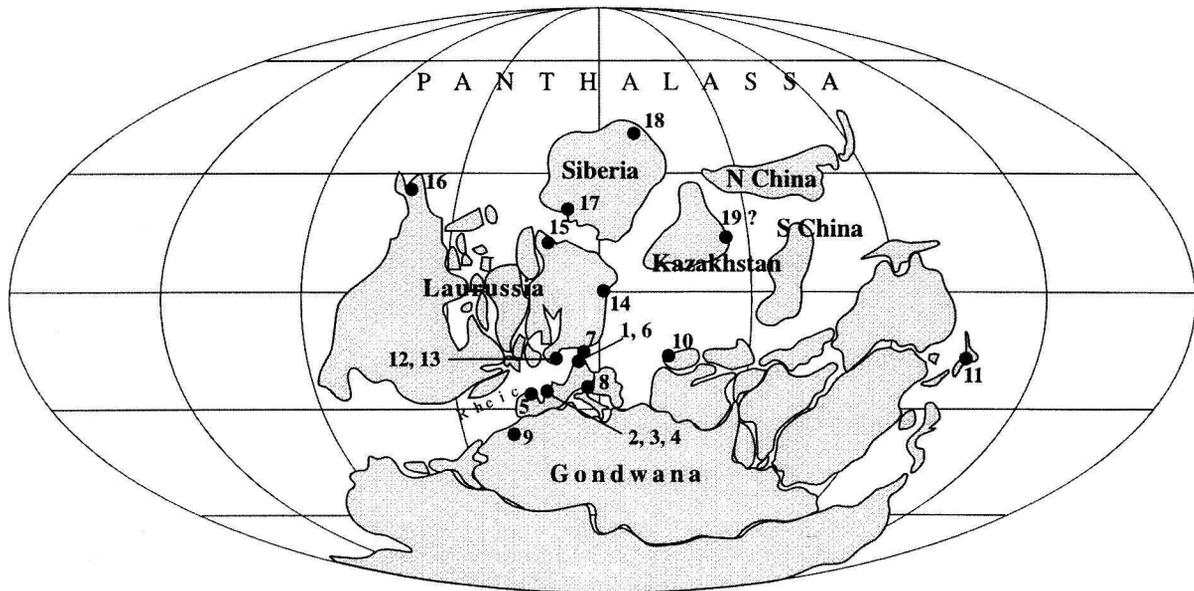


Fig. 1 Paleogeographic distribution of Early Devonian *Myriospirifer* species (cartographic base slightly modified from Scotese – McKerrow 1990). Localities: 1 – *Myriospirifer myriofila* Havlíček, 1978, Lochkovian-Pragian, central Bohemia; 2–4 – *Myriospirifer ceneratiensis* Gourvenec 1989a, *M. davousti* (Verneuil, 1850) and *M. sp.* Gourvenec 1989b, Pragian, Armorican Massif (France); 5 – *Myriospirifer crassus* sp. nov., upper Emsian, Cantabrian Mountains (northern Spain); 6 – *Myriospirifer insidiosus* (Barrande, 1879), upper Emsian-lower Eifelian, central Bohemia; 7 – *Myriospirifer* sp. Havlíček – Mergl 1990, Moravia; 8 – *Myriospirifer* sp. 1 (= *Spirifer togatus* sensu Heritsch – Wolsegger 1935, Scupin 1906), upper Emsian, Carnic Alps; 9 – *Myriospirifer* sp. 2 (= *Eospirifer* aff. *togatus insidiosus* sensu Drot 1964), upper Emsian, Morocco; 10 – *Myriospirifer* ? *togatoides* (Paeckelmann, 1925), upper Emsian, Boporus; 11 – *Myriospirifer* ? sp. 3 (= *Eospirifer togatus* sensu Shirley, 1938), upper Emsian, New Zealand; 12, 13 – *Myriospirifer* ? *subsinuatus* (F. A. Roemer, 1855) and *M. sp.* 4 (= *Spirifer togatus* sensu Kayser, 1878), Emsian, Harz Mountains (Germany); 14 – *Myriospirifer* sp. 5 (= *Eospirifer* aff. *togatus insidiosus* sensu Sapelnikov – Mizens 1985), upper Emsian, west-central Urals; 15 – *Myriospirifer* ? *karmanovi* (Khodalevich, 1951), upper Emsian, Polar Urals; 16 – *Myriospirifer breasei* sp. nov., upper Emsian, south-central Alaska (this occurrence is in an accreted terrane derived most probably from Siberia); 17 – *Myriospirifer* ? *kolymensis* (Rzhonsnitskaya, 1967), upper Emsian, Kolyma region of northeastern Siberia (because this species remains formally undescribed, it probably represents a nomen nudum); 18 – *Myriospirifer* sp. 6 (= *Eospirifer* (*Eospirifer*) aff. *secans* (Barrande, 1848) sensu Kulkov in Alekseeva et al. 1970), lower Emsian, northeastern Salair (southwestern Siberia); 19 – “*Eospirifer davousti*” (sensu Nalivkin, 1930), upper Emsian, Turkestan.

reliably represented by the upper Llandoveryan *M. marklini* (Verneuil, 1848) of Gotland, by *M. grandis* (Hedstrom, 1923) from the Wenlockian of Gotland, and also by *M. dichotomus* Havlíček, 1980, from the Wenlockian of Bohemia. Bassett – Cocks (1974) noticed the great resemblance of *Eospirifer profusus* Rubel, 1970, from the upper Llandoveryan of Estonia with *M. marklini*. The species determined by Rubel (1970, Pl. 35, Figs 12–18) as *Eospirifer radiatus*, also from the upper Llandoveryan of Estonia, has the typical micro-ornament of the genus. Therefore, the occurrence of *Myriospirifer* in the Silurian of the Baltic region seems well established. Carter et al. (1994) synonymized *Acutilineolus* Amsden, 1978, from the Silurian (Wenlockian) of Oklahoma (USA) with *Myriospirifer*. However, in our opinion the finer micro-ornament of *Acutilineolus* with capillae that increase both by implantation and branching (Amsden – Barrick 1988) indicate that this genus represents a different eospiriferine branch typical of the Laurentian region.

Myriospirifer has not been found in latest Silurian age strata for reasons difficult to ascertain, but it occurs again in Gondwana at least from the earlier Devonian onwards with *M. myriophila* Havlíček, 1978, from the Lochkovian and Pragian of central Bohemia, and *M. ceneratiensis*

Gourvenec, 1989a and *Myriospirifer* sp. (Gourvenec 1989b) of the Pragian of the Armorican Massif (Fig. 1). Gourvenec (1989a) included the species *Spirifer davousti* Verneuil, 1850, from the Pragian of the Armorican Massif, in *Eospirifer*, but its micro-ornament with bifurcating, flattened capillae larger than interspaces (Gourvenec 1989a, b) is characteristic of *Myriospirifer*. Bublichenko (1967) and Kaplun (1967) cited respectively *Eospirifer togatus insidiosus* and *E. togatus togatus*, from the Lochkovian of Kazakhstan, but these forms have to our knowledge neither been described nor figured and their generic assignment remains doubtful.

The climax of the genus is recorded in the Emsian. During this time *Myriospirifer* was widespread both in Gondwana and Baltica, reaching even as far as Siberia (Fig. 1). By the latter part of the Early Devonian, the genus can be found throughout much of the Old World Realm, but is notably absent from cratonic faunas of both western and Arctic North America (Cordilleran Region of the Old World Realm), as well as from the Eastern Americas and Malvinokaffric realms.

The number of *Myriospirifer* species that lived in such a vast region during the Early Devonian is unknown. In Gondwana there occur *M. insidiosus* (Barrande, 1879),

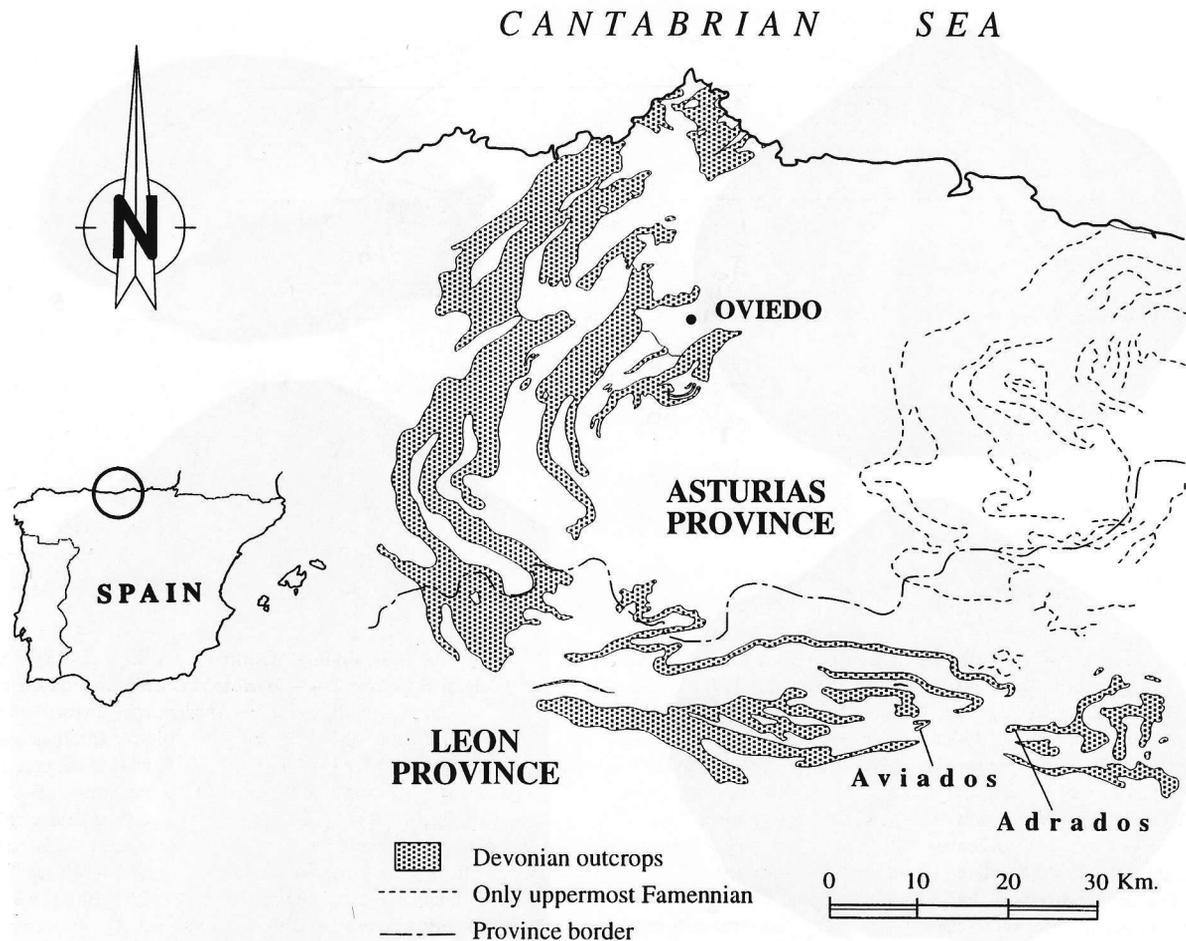


Fig. 2 Geographical situation of the Cantabrian localities where *Myriospirifer crassus* sp. nov. occurs.

in Bohemia, and *M. crassus* sp. nov., in northern Spain. Other references to *Eospirifer togatus* and *E. togatus insidiosus*, far from Bohemia, would at least partially correspond to *Myriospirifer* species (*Myriospirifer* sp. 1, *M.* sp. 2, *M.* ? sp. 3) that evolved in the Carnic Alps (Scupin 1906, Heritsch – Wolsegger 1935), Morocco (Drot 1964), and New Zealand (Shirley 1938) (Fig. 1). *Spirifer togatoides* Paeckelmann, 1925, from the Emsian of the Bosphorus could also belong in *Myriospirifer*.

As indicated above, in Emsian time the genus returns to Baltica, represented by *Myriospirifer* sp. (Havlíček – Mergl 1990), from Moravia, *M.* ? *subsINUATUS* (Roemer, 1855), and *M.* sp. 4 (= *Spirifer togatus* sensu Kayser, 1878) of the Harz Mountains (Germany), *M.* ? *KARMANOVI* (Khodalevich, 1951) of the Polar Urals, and *M.* sp. 5 (= *Eospirifer* aff. *togatus insidiosus* sensu Sapelnikov – Mizens 1985) from central western Urals. Finally, it even reached Siberia, with *M. breasei* sp. nov. from the Farewell terrane (most likely a rifted part of Siberia) of south-western Alaska, *M.* sp. 6 [= *Eospirifer (Eospirifer)* aff. *secans* sensu Kulkov, in Alekseeva et al. 1970] and *M. kolymensis* nom. nud. (Rzhonsnitskaya in Nikolaev – Rzhonsnitskaya 1967) from Kolyma (Fig. 1). The forms

determined by Nalivkin (1930) as *Eospirifer davousti* from Turkestan, could represent an extension of *Myriospirifer* into the paleocontinent of Kazakhstan, but its identification requires further study.

Even if the paleogeographical range of *Myriospirifer* is not completely known, it shows some very curious features. The initial spreading throughout the Baltic and Bohemian regions as well as the widespread Devonian migration can be ascribed mainly to dispersive phenomena that were favored during the Silurian for the projecting position of Perunica (Havlíček 1999, Havlíček et al. 1994) and during the Emsian by the narrowing of the Rheic Ocean (Scotese – McKerrow 1990) (Fig. 1). Nevertheless, the occurrence of *Myriospirifer breasei* sp. nov. in south-central Alaska is rather a vicariance effect corresponding to the interesting paleobiogeographic process described by McKenna (1973) as the “Beached Viking Funeral Ship”. In effect, as indicated above, *M. breasei* occurs in an accreted terrane (Farewell terrane), that was originally part of the Siberian paleocontinent (Blodgett – Boucot 1999), subsequently rifted after Devonian time, and accreted to the western margin of North America (southern Alaska) in the latter part of the Mesozoic.

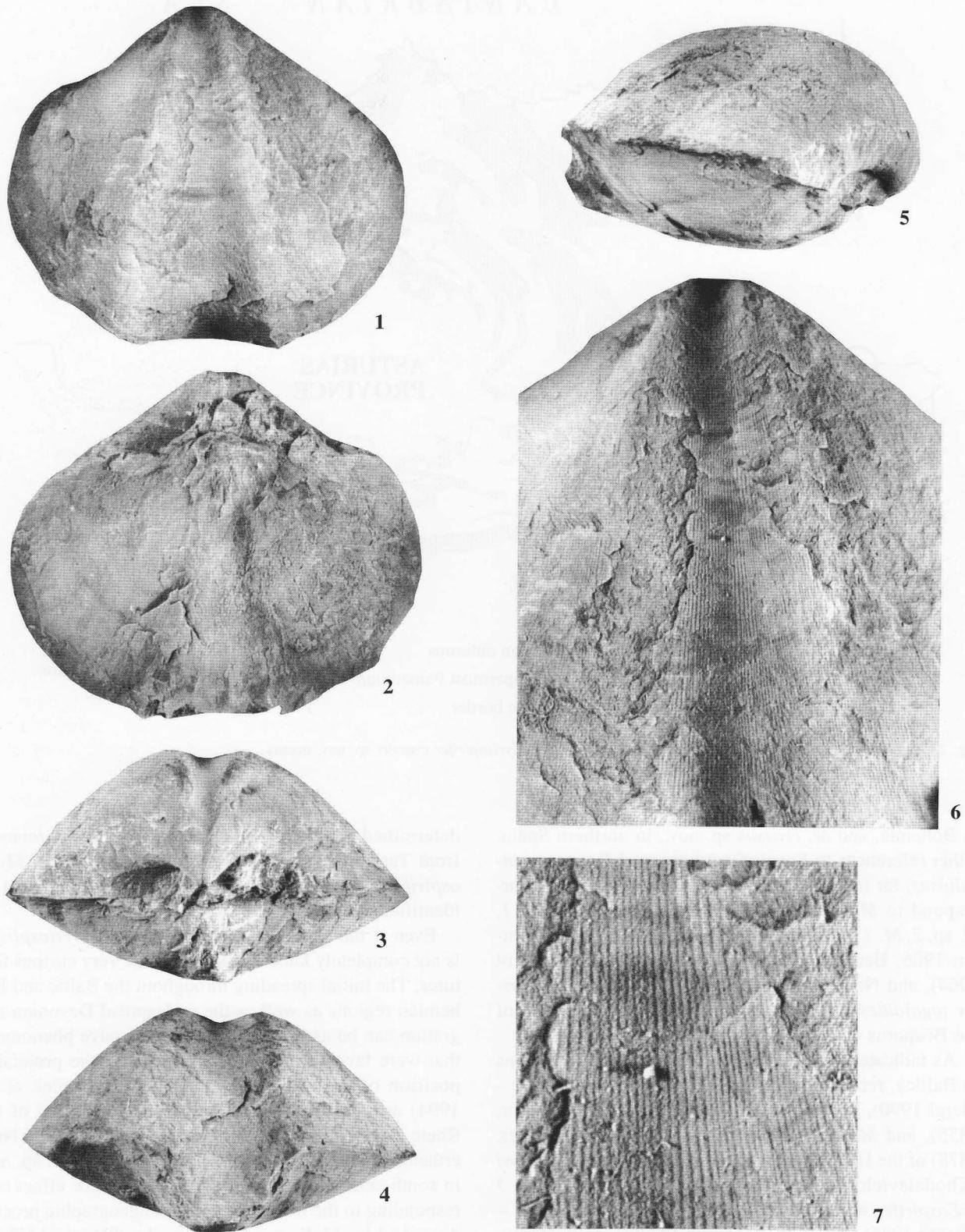


Fig. 3 *Myriospirifer breasei* sp. nov. 1-5 - Holotype UAM 2569. Ventral, dorsal, posterior, anterior, and lateral views (1.5x). Unnamed late Emsian limestone unit, Shellabarger Pass, Talkeetna C-6 quadrangle, south-central Alaska; 6-7 - Same specimen: 6 - Enlarged view of ventral valve under low lights to show fine micro-ornamentation, (3x). Further enlargement of previous view showing micro-ornamentation, (8x).

Systematic paleontology

Suborder Spiriferidina Waagen, 1883
 Superfamily Cyrtioidea Fredericks, 1924
 Family Cyrtiidae Fredericks, 1924
 Subfamily Eospiriferinae Schuchert in Schuchert
 and LeVene, 1929

Genus *Myriospirifer* Havlíček, 1978

Type species: *Myriospirifer myriofila* Havlíček, 1978

Myriospirifer breasei sp. nov.

Figs 3.1–3.7, 4, 5

v. 1999 *Myriospirifer* sp. nov. aff. *Myriospirifer myriofila*; Blodgett – Boucot, p. 213–214, Pl. 1, Figs 1a–g.

Etymology: For Phil F. Brease, U. S. National Park Service geologist at Denali National Park, Alaska, who ably assisted one of us (Blodgett) during late July, 1996 in the collection of this species.

Type locality and type horizon: An interval corresponding to 13.4 m to 15.8 m above the base of a measured section in unnamed limestone unit exposed in the Shellabarger Pass area, Talkeetna C-6 quadrangle, south-central Alaska (see Blodgett – Boucot 1999, p. 212 for a more detailed locality description). This unit is of late Emsian age (*serotinus* zone) and corresponds locally to the basalmost part of the Mystic subterranean (or sequence) of the Farewell terrane (Blodgett 1998, Blodgett – Boucot 1999).

Material: A single articulated specimen (Figs 3.1–3.7), UAM 2569, was collected from the type locality by Bruce Reed of the USGS in 1975 and was previously illustrated in Blodgett – Boucot (1999, Pl. 1, Figs 1a–g). It is here designated the holotype. Subsequently, Blodgett in 1996 gathered a much larger collection of this species from a detailed measured section made that year of type locality exposure, including a total of 97 articulated specimens and 35 ventral valves (see Blodgett – Boucot 1999, p. 213, for a detailed bed by bed occurrence). Another illustrated specimen (Fig. 4), UAM 2588, represents a partially calcined articulated specimen prepared to show the ventral interior, and was collected from an interval 13.7–14.0 m (45–46 ft) above the base of the measured section. Another articulated specimen (Fig. 5), UAM 2590, was sectioned to demonstrate internal features of this species. It collected from talus derived from beds at or slightly above 13.4 m (44 ft) above the base of the measured section.

Diagnosis: Relatively large species of *Myriospirifer* with rounded outline and strongly convex, deep and elongate ventral valve.

Description: Relatively large shell for genus, attaining a width of up to 50 mm. Shell outline transversely rounded; greatest width slightly posterior to mid-length of the ventral valve. Ventral interarea low, weakly incurved. Cardinal margin straight, up to 80–85 % of maximum shell width. Ventral umbo strongly and evenly curved. Ventral valve strongly convex, whereas the dorsal valve is moderately convex with depth about 60 % of the ventral valve. Shell surface smooth totally lacking plications. Ventral sulcus moderately rounded and extending the entire length of the valve. Dorsal fold moderately and evenly convex. Micro-ornament composed of numerous, closely spaced, broad, flattened capillae separated by much narrower, grooved interspaces. Ventral interior with prominent vascular markings composed of

numerous, raised, radially disposed narrow ridges (Fig. 4). Shell and internal structures markedly thickened posteriorly. Deltidium, small, subapical. Dental plates sulcus-bounding, long, extending more than 1/3 of shell length. Ventral flanges short, ventromedially directed, relatively long; ventral adminicula nearly parallel to one another. Cardinal teeth strong, fitted into large ventral cavities, the latter strongly raised with respect to shell floor. Crural plates vertical, short and very fine, slightly divergent distally. Ventral and dorsal umbonal cavities well developed. Dimensions of holotype specimen (UAM 2569), the largest shell in collection: shell width: 50.6 mm; shell thickness: 25.3 mm; ventral valve length: 37.3 mm; dorsal valve length: 31.7 mm.

Discussion: *Myriospirifer breasei* sp. nov. most closely resembles the type species, *M. myriofila* Havlíček, from the Koneprusy Limestone (Pragian) of the Czech Republic, notably in its relatively large size, but differs in having a less transverse, more rounded shell outline, in having a more prominent, more elongate ventral valve, and in having a relatively narrower ventral sulcus and dorsal fold. The Alaskan species differs from *M. insidiosus* (Barrande) from the Suchomasty Limestone (Emsian) of the Czech Republic in being much larger in size and in having a relatively much more inflated ventral valve. It differs from *Spirifer (Theodossia) karmanovi* Khodalevich, 1951 from Emsian/Eifelian boundary beds in the Urals, placed questionably in *Myriospirifer* by Sapelnikov et al. 1987, in being relatively larger, in having a markedly more convex ventral valve, a more rounded outline, and a deeper sulcus. It differs also from *M. ceneratiensis* Gourvenec, 1989a, from the Pragian of Brittany, in attaining greater size, and having a relatively broader ventral sulcus, and a ventral valve which is markedly more convex in posterior view. The Alaskan species compares

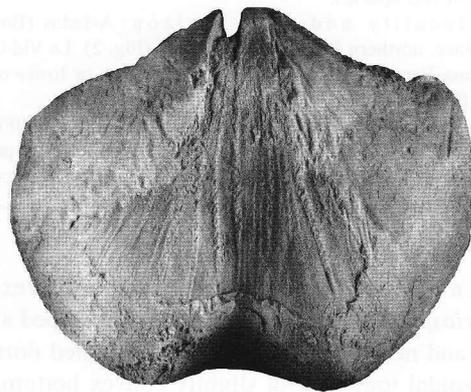


Fig. 4 *Myriospirifer breasei* sp. nov., UAM 2588. An articulated specimen which has been partially calcined to show vascular markings on ventral valve, (1.5x). Collected from an interval 13.7–14.0 m (45–46 ft) above the base of of a measured section in an unnamed late Emsian limestone unit, Shellabarger Pass, Talkeetna C-6 quadrangle, south-central Alaska.

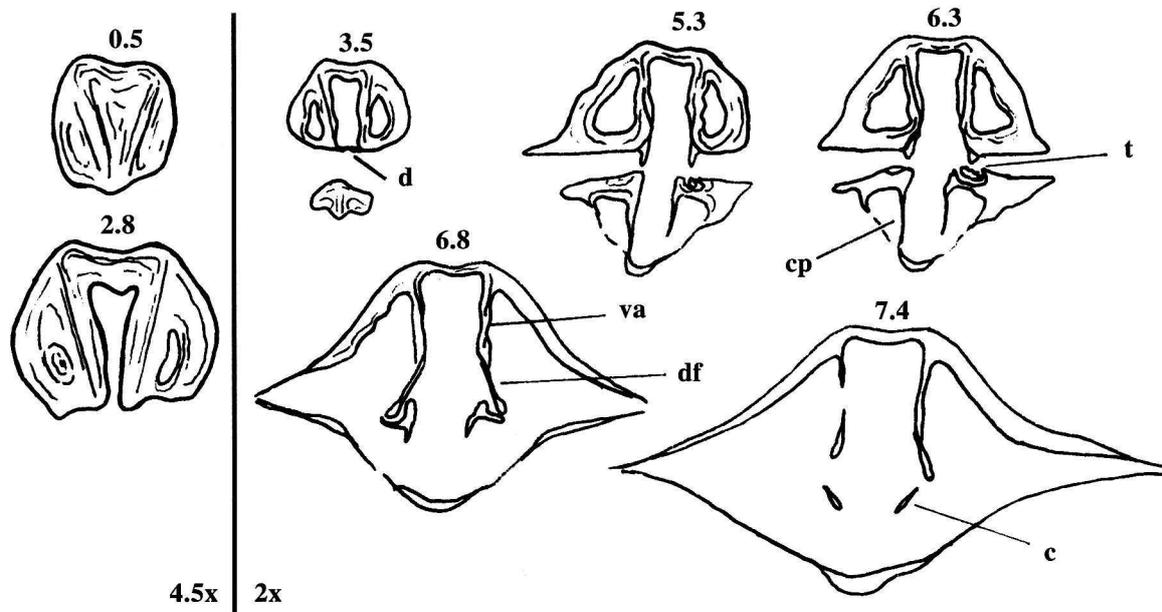


Fig. 5 *Myriospirifer breasei* sp. nov. Serial sections of UAM 2590. An articulated specimen collected from talus derived from beds at or slightly above 13.4 m (44 ft) above the base of measured section in an unnamed late Emsian limestone unit, Shellabarger Pass, Talkeetna C-6 quadrangle, south-central Alaska. Number above each section refers to distance from the ventral apex of the ventral valve. Abbreviations: c – crus; cp – crural plate; d – deltidium; df – dental flange; t – cardinal tooth; va – ventral adminiculum.

very closely to *Eospirifer (Havlicekia) pseudosecans kolymensis* Rzhonsnitskaya in Nikolaev – Rzhonsnitskaya (1967, Pl. 3, Figs 5a–c) from the Vecherinsk horizon in the Kolyma region of northeast Siberia. The latter species has never been formally described, and thus remains a nomen nudum. The Alaskan species differs from it in having a much more prominently incurved ventral umbo.

Myriospirifer crassus sp. nov.

Figs 6.1–6.6, 7.1–7.7, 8

Etymology: Crassus (Latin), in reference to the large, fat appearance of this species.

Type locality and type horizon: Aviados (Boñar, Leon province, northern Spain). Locality I-67 (Fig. 2), La Vid Group (La Pedrosa Formation), uppermost lower Emsian or lower upper Emsian (Fig. 2).

Material: Holotype DPO 33014 and 6 Paratypes, DPO 33015–33020 (Figs 6.1–6.6, 7.1–7.4) from type locality and type horizon. One articulated, deformed specimen, DPO 38057 (Figs 7.5–7.7) from Adrados (Leon, northern Spain), La Vid Group (La Pedrosa Formation, Emsian).

Diagnosis: A very large and thick, biconvex species of *Myriospirifer*. Faint ventral sulcus developed along the umbo and near front commissure. Flattened dorsal fold. Trapezoidal tongue with slightly convex bottom. Large extra-sinal, short dental plates.

Description: Very large (length up to 55 mm, width up to 74 mm), thick (thickness up to 47 mm), biconvex (thickness up to 90 % of length) shell. Shell outline transversely rounded (length up to 74 % of width); greatest width near the mid-length of the shell. Cardinal margin straight, up to 81 % of maximum shell width.

Ventral interarea relatively low, weakly curved, cateniform, differentiated in two dissimilar ornamented regions. The more external region (ventral palintrope, sensu Krans 1969), is vaguely separated by rounded edges from the rest of the valve and shows the same capillate ornamentation as the valve exterior. In the region adjoining the delthyrium (interarea sensu stricto; see Krans 1969) occur very fine transverse and longitudinal striae. The longitudinal striae are not strictly normal to the hinge, but slightly diagonal to it. Both regions of the ventral interarea are separated by narrow, straight furrows that diverge anteriorly from the delthyrium apex. Delthyrium relatively small with well developed, vertical, deltidial plates that join below the ventral beak in a convex apical deltidium. Inflated ventral umbo with beak strongly curved over the interarea.

Dorsal interarea concave, lower than the ventral interarea. Dorsal palintrope lacking. Dorsal beak strongly curved, concealing the nothothyrium.

Ventral sulcus extending from the umbo, faintly marked, narrow and very shallow, up to 33 % of the shell width anteriorly. Bottom of ventral sulcus concave near umbo and faintly convex near anterior commissure. Dorsal fold extending from umbo, faintly rounded to flattened, bounded near the apex by narrow, longitudinal furrows that disappear anteriorly. Tongue trapezoidal, high, dorsally to posterodorsally turned. Uniplicate anterior commissure. Non-ribbed, evenly convex flanks forming along the commissure in anterior and posterior views an angle close to 90°.

The available small collection of *M. crassus* sp. nov. is mainly composed of very weathered or decorticated

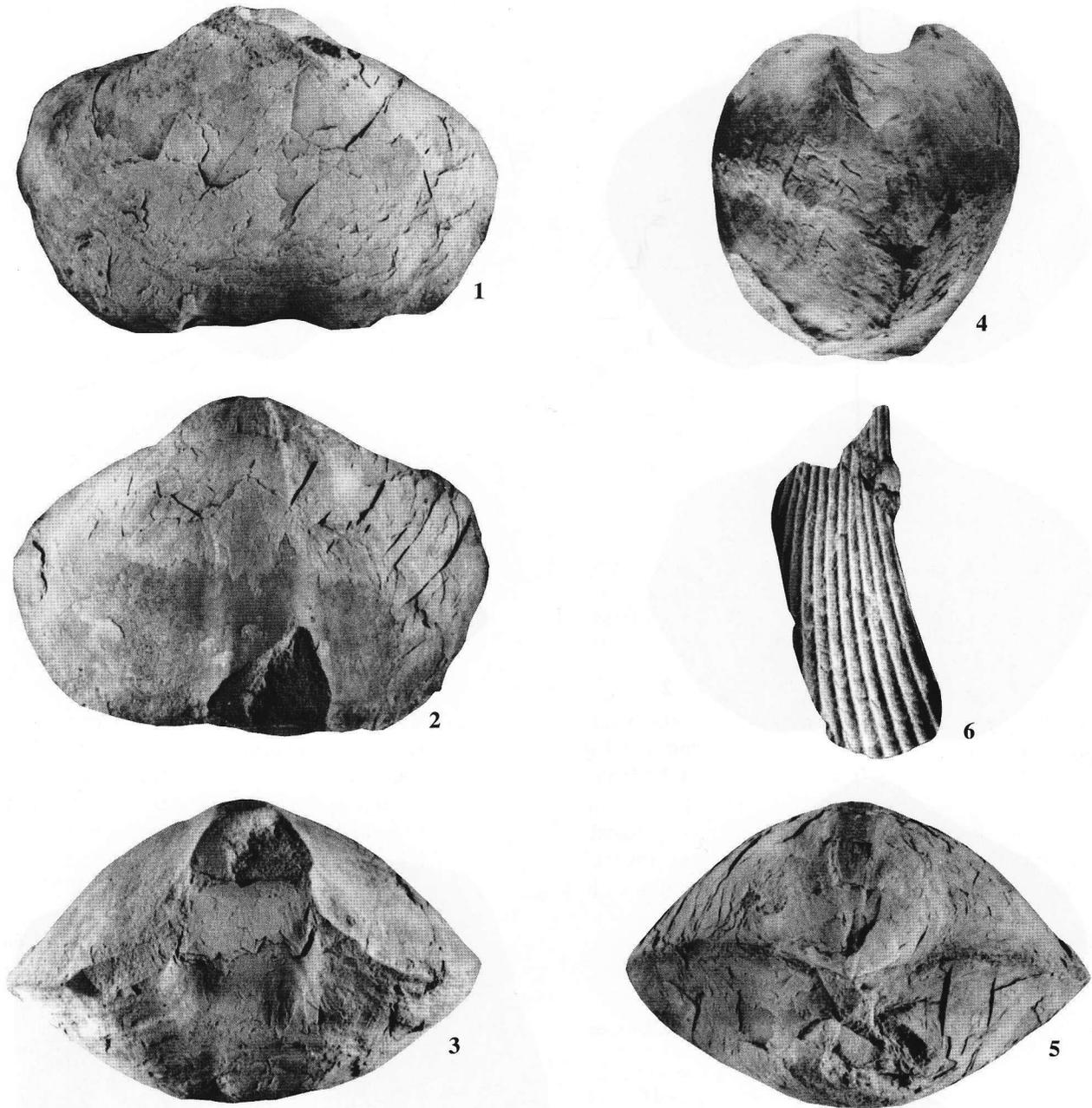


Fig. 6 *Myriospirifer crassus* sp. nov. 1–5 – Holotype DPO 33014. Ventral, dorsal, anterior, lateral and posterior views (1x). Aviados (northern Spain), locality I-67, La Pedrosa Formation, uppermost lower Emsian or lowermost upper Emsian; 6 – enlarged fragment of ventral valve showing typical micro-ornamentation of *Myriospirifer*. Paratype DPO 33018 (3x).

specimens in which growth lamellae or rugellae are not visible. In parts of some shells a clear micro-ornament composed by numerous, closely spaced, broad, flattened capillae separated by much narrower, sharp, grooved interspaces is developed (Figs 6.6, 7.7); the number of capillae increases by bifurcation (up to 3–4 capillae per 1 mm).

Dental plates short, strong, largely extra-sinal. Crural plates short, but thick. Laterally directed coiled brachidium with up to 12 coils in the spiralium.

Discussion: The non-ribbed macro- and capillate micro-ornament (see Gourvenec 1989b) and some of the internal structures justify the generic assignment of this species. However there are small discrepancies that are not for the moment considered strong enough to propose a new genus, but could perhaps be indicative of paleogeographic differentiation. For example, all figured *Myriospirifer* and *Eospirifer* species (even the most developed as *M. breasei* sp. nov. described above) have the dorsal fold bounded by narrow, more or less sharp furrows,

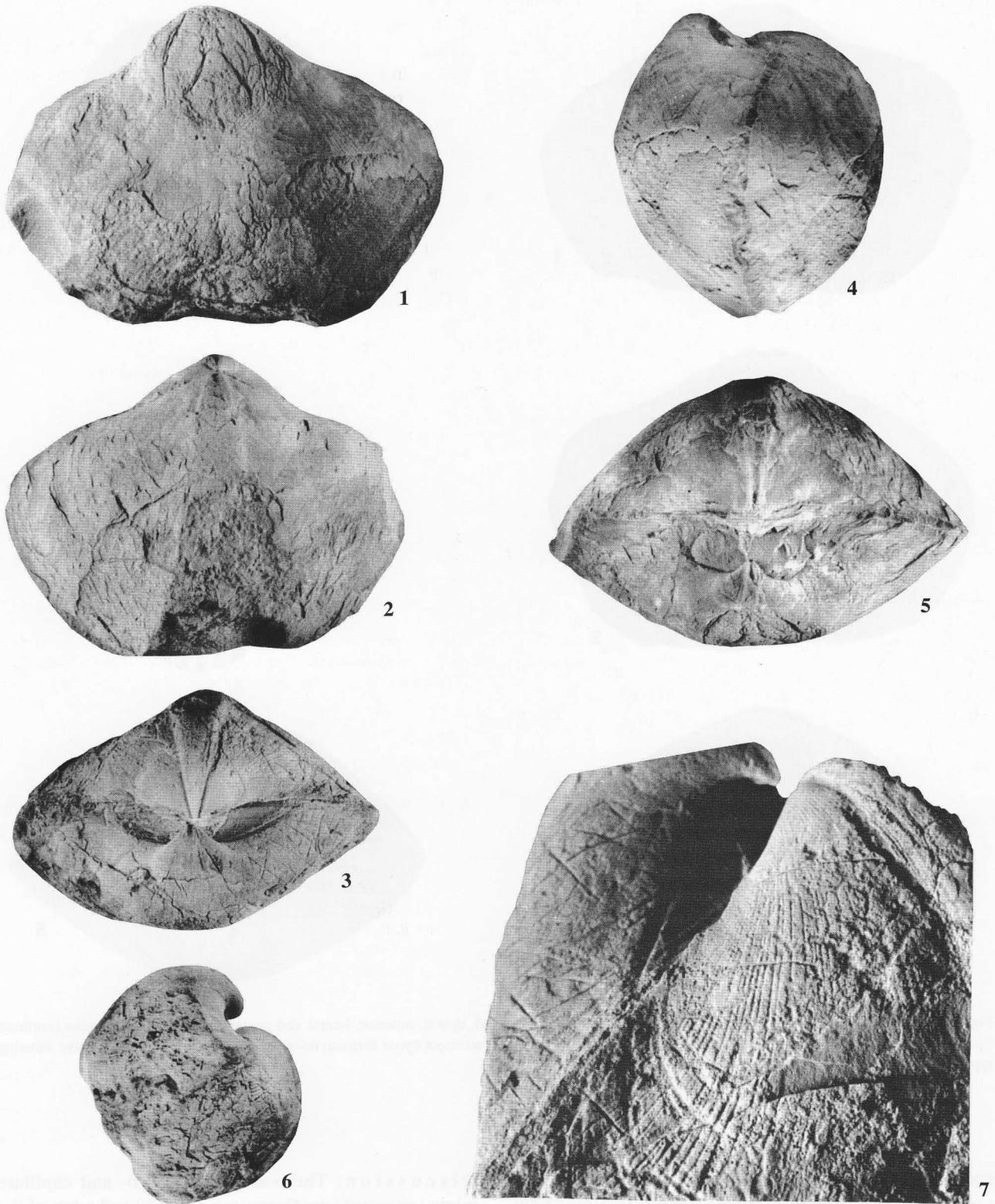


Fig. 7 *Myriospirifer crassus* sp. nov. 1-4 - Paratype DPO 33016. Ventral, dorsal, posterior and lateral views. (1x); 5-6 - Posterior and lateral views of an deformed specimen, DPO 38057. Adrados (Leon, northern Spain), La Pedrosa Formation, Emsian, (1x); 7 - Same specimen. Oblique dorsal view showing typical *Myriospirifer* micro-ornamentation (3x).

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Nové druhy rodu *Myriospirifer* (Brachiopoda, Eospiriferinae) se spodního devonu (svrchní ems) z Aljašky a severního Španělska a paleogeografické rozšíření rodu *Myriospirifer*

V práci je analyzováno paleogeografické rozšíření eospiriferního rodu *Myriospirifer* v siluru a devonu. Rod se objevuje poprvé ve spodním siluru jižního prostoru paleokontinentu Baltiky a odtud se rozšiřuje podél obou okrajů rheického oceánu. V devonu se stává široce rozšířeným na Gondwaně a Baltice a zasahuje až na Sibirii. Ve spodním devonu se rod vyskytoval na většině území provincie Starého světa, avšak chybí v kratonních faunách arktické severní Ameriky (kordillerská oblast provincie Starého světa) a ve východoamerické a malvinokaffrické provincii. Popsány jsou dva nové druhy emského stáří: *M. breasei* sp. nov. z Aljašky a *M. crassus* sp. nov. ze severního Španělska. Druh *M. breasei* sp. nov. se v prostoru současné Aljašky ocitl přenesením na akrečním terranu, který byl odtržen od Sibirie a připojen k severoamerickému kontinentu v průběhu mladšího mesozoika.