

LOST AND FOUND *MACHAERACANTHUS* SPINES FROM THE LOWER DEVONIAN OF WESTERN FRANCE

Épines de Machaeracanthus (spécimens perdus et nouveaux) *du Dévonien inférieur de l'ouest de la France*

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Abstract. – Despite *Machaeracanthus* spines being first recorded and described from western France in the mid-nineteenth century, since then they have only rarely been documented from this region. Here we describe specimens from several localities of Pragian age, in particular those from Saint-Germain-le-Fouilloux which were first figured by Bézier in the early twentieth century. Although the spines are relatively rare, we have recognized two morphotypes, one with a characteristic feature of robust ribbing on the convex edged keel and the other with the same type of ribbing on the concave edged wing. As this feature distinguishes them from other *Machaeracanthus* species, we erect a new species *Machaeracanthus bezieri* nov. sp., which we have also identified in the Pragian of the Czech Republic and Germany.

Résumé. – Bien que des épines de *Machaeracanthus* ait été mentionnées et décrites dans l'ouest de la France au milieu du XIX^e siècle, elles n'ont été que rarement documentées depuis dans cette région. Nous décrivons ici des spécimens de plusieurs localités du Pragien, en particulier de Saint-Germain-le-Fouilloux, qui ont été figurés pour la première fois par Bézier au début du XX^e siècle. Bien que les épines soient relativement rares, nous avons reconnu deux morphotypes : le premier est caractérisé par une nervure robuste sur la quille externe convexe, le second possède le même type de nervures mais sur l'aile concave. Comme cette caractéristique les distingue des autres espèces de *Machaeracanthus*, nous érigeons une nouvelle espèce *Machaeracanthus bezieri* nov. sp., que nous avons également identifiée dans le Pragien de République tchèque et d'Allemagne.

Mots-clés. – Devonian, Pragian, *Machaeracanthus*, *Acanthodii*, Armorican Massif.
Key words. – Dévonien, Pragien, *Machaeracanthus*, *Acanthodii*, Massif armoricain.

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I. — INTRODUCTION

Vertebrates are very rare in the Lower Devonian of western France. The first specimens to be recorded from mid-Palaeozoic deposits in the region were *Machaeracanthus* spines, assigned to two species and described briefly by Rouault (1858). According to Burrow *et al.* (2010, p. 59): “*Machaerius archiaci* Rouault, 1858 and *Machaerius larteti* Rouault, 1858 were erected the year after Newberry's first description, for small fragments of spines from the Lower Devonian of northwestern France. Unfortunately, these were poorly described, not figured, and have been lost, so Zidek (1981) in his review of *Machaeracanthus* spp. listed them as nomina vana.” In fact the fragments, based on their width (Bézier, 1913, table), were from quite large spines. Their provenance is unclear, as Rouault (1858) only recorded that they were from western France. According to a letter written by M. de Verneuil to M. d'Archiac in 1858 (Anonymous, 1858), Rouault's locality was reported to be Saint-Léonard in north

Sarthe department (= Saint-Léonard-des-Bois). However, on investigation (Tromelin in Guillier, 1971) the only rocks found in this area were Ordovician. Tromelin in Guillier (1871) and Tromelin & Lebesconte (1876) recorded that Rouault's specimens were from Les Courtoisiers, near Brûlon, Sarthe, but gave no proof for this assertion. All other *Machaeracanthus* spines reported from western France (Mayenne, Maine-et-Loire, Manche, Sarthe departments; Fig. 1A) have been considered to belong to *Machaeracanthus bohemicus* (Barrande, 1872), or *Machaeracanthus* cf. *bohemicus* (Bézier, 1913). (Bézier [1913] listed the genus as *Ctenacanthus* as originally designated by Barrande [1872], not *Machaeracanthus*, even though Kayser [1883] had long since reassigned the species to the latter genus). The description given by Rouault (1858) for his genus *Machaerius* comprises generic characters of *Machaeracanthus* Newberry, 1857 and specific characters of *M. bohemicus*. Unfortunately the spines described by Rouault (1858) have still not been found.

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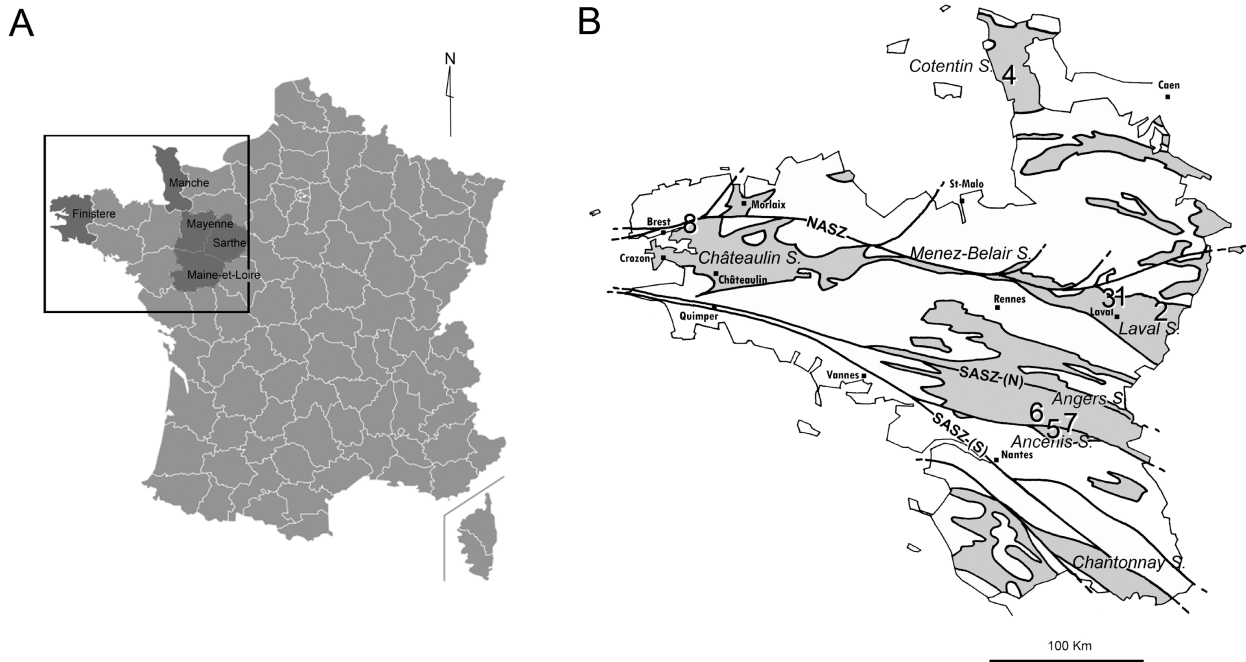


Fig. 1. — Map of localities. **A**, France showing departments where *Machaeracanthus* spines have been reported. **B**, Palaeozoic synclinoria of the Massif Armoricain (after Wright *et al.*, 2016, fig. 1B: S, synclinorium [shaded grey]; NASZ = North Armoricain Shear Zone; SASZ = South Armoricain Shear Zone), showing *Machaeracanthus* localities: 1, La Roussière quarry, Saint-Germain-le-Fouilloux, Mayenne; 2, Les Courtoisiers quarry, Brûlon, Sarthe; 3, St-Roch, Changé, Mayenne; 4, Néhou, Manche; 5, Chaudefonds, Maine-et-Loire; 6, Vern-d'Anjou, Maine-et-Loire; 7, Saint-Barthélemy-d'Anjou, Maine-et-Loire; 8, Plougastel-Daoulas, Pointe de l'Armorique, Finistère.

Fig. 1. — Localisation des gisements. **A**, Départements français ayant livré des épines de *Machaeracanthus*. **B**, Synclinaux paléozoïques du Massif Armoricain (d'après Wright *et al.*, 2016, fig. 1B: S, synclinorium [gris foncé]; NASZ = Zone de cisaillement nord-armoricain; SASZ = Zone de cisaillement sud-armoricain), avec indications des gisements: 1, carrière de La Roussière, Saint-Germain-le-Fouilloux, Mayenne; 2, carrière Les Courtoisiers, Brûlon, Sarthe; 3, St-Roch, Changé, Mayenne; 4, Néhou, Manche; 5, Chaudefonds, Maine-et-Loire; 6, Vern-d'Anjou, Maine-et-Loire; 7, Saint-Barthélemy-d'Anjou, Maine-et-Loire; 8, Plougastel-Daoulas, Pointe de l'Armorique, Finistère.

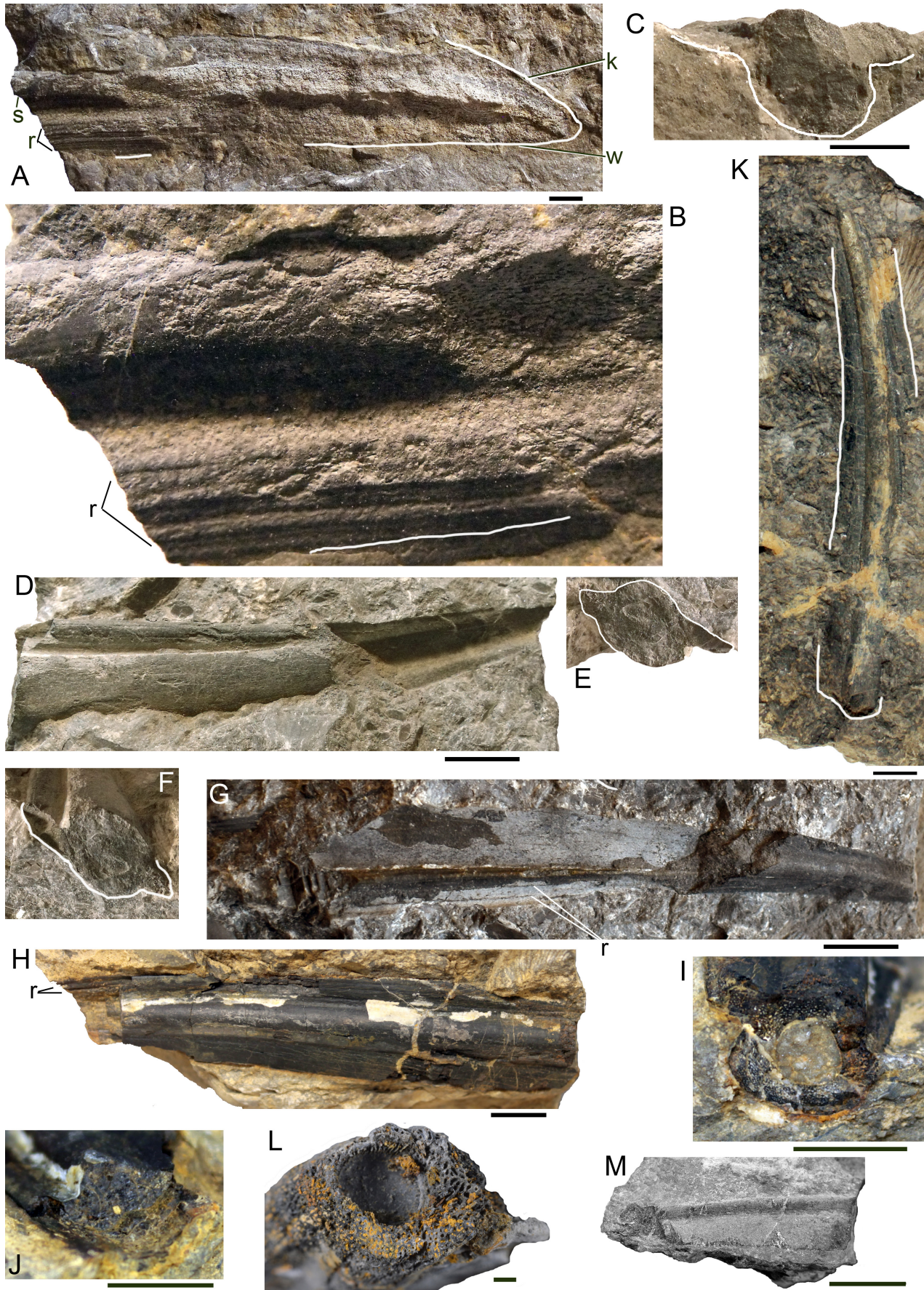
As well as spines, scales assigned to *Machaeracanthus* sp. have also been recorded in western France. Goujet (1976, 1980) described and figured scales from the Saint-Cénére and l'Armorique formations respectively. Botella *et al.* (2012) referred the scales from the Saint-Cénére Formation that Goujet (1976) originally assigned to *Machaeracanthus* sp. to a new species *M. goujeti*, based on their similarity in morphology and

stratigraphic occurrence (Lochkovian-Pragian) with the type material of this species from Celtiberia, Spain.

Bézier (1913) published the only detailed description, including photographs, of two *Machaeracanthus* spines from western France. His specimens, collected at Saint-Germain-le-Fouilloux and originally described as "*Ctenacanthus* cf. *bohemicus*", were until recently, like those of Rouault,

Fig. 2. — *Machaeracanthus bezieri* nov. sp. from La Roussière quarry, Saint-Germain-le-Fouilloux (A-J, ?K), and *Machaeracanthus* sp. (L, M) from Changé, Mayenne and Angers, Maine-et-Loire respectively. **A–C**, holotype spine IGR 132670 (collected by de Vaucenay, figured by Bézier, 1913), morphotype one: **A**, whole specimen, lacking proximal end; **B**, magnified view of ridged wing; **C**, end-on view of natural cross section (outlined). **D–F**, paratype spine IGR 132671a, part (collected in 1914), morphotype one: **D**, whole specimen, lacking proximal end; **E**, end-on view of natural cross section (outlined), exposed side down; **F**, end-on view of natural cross section, exposed side up. **G**, paratype IGR 132671b, counterpart. **H–J**, paratype spine ML-PAL-03006, morphotype two, lacking distal and proximal ends (Oehlert Coll.): **H**, whole specimen, proximal to right; **I**, proximal end view; **J**, distal end view. **K**, spine ML-PAL-29822, morphotype two, nearly whole length preserved, proximal end to top, distal part of ridged keel exposed. **L**, spine fragment IGR 144560, from Changé, showing internal surface of pulp cavity. **M**, spine fragment UCO-71929 from Saint-Barthélemy-d'Anjou. Abbreviations: k, keel; r, ridge; s, shaft; w, wing. Scale bar = 1 cm in A–K, M, 1 mm in L.

Fig. 2. — *Machaeracanthus bezieri* nov. sp. de la carrière de La Roussière, Saint-Germain-le-Fouilloux (A-J, ?K) et *Machaeracanthus* sp., respectivement, de Changé en Mayenne et d'Angers dans le Maine-et-Loire (L, M). **A–C**, holotype IGR 132670, épine collectée par Vaucenay, figurée par Bézier (1913), morphotype 1: **A**, spécimen subcomplet, sans la terminaison proximale; **B**, zoom sur les sillons du bord concave interne (« ridged wing »); **C**, coupe naturelle avec tracé du contour. **D–F**, épine IGR 132671a, paratype (collecté en 1914), morphotype 1: **D**, spécimen subcomplet, sans la terminaison proximale; **E**, coupe naturelle avec tracé du contour de l'extrémité proximale, spécimen renversé. **F**, coupe naturelle de l'extrémité distale, à l'endroit. **G**, IGR 132671b, paratype, contrepartie. **H–J**, paratype ML-PAL-03006, terminaisons proximale et distale manquantes (coll. Oehlert), morphotype 2: **H**, spécimen complet, extrémité proximale à droite; **I**, vue de l'extrémité proximale; **J**, vue de l'extrémité distale. **K**, ML-PAL-29822, longueur presque entièrement préservée, extrémité proximale en haut, partie distale avec quille portant des sillons visibles, morphotype 2. **L**, fragment d'épine de Changé IGR 144560, montrant la surface interne de la cavité pulpaire. **M**, UCO-71929, fragment d'épine de Saint-Barthélemy-d'Anjou. Abréviations: k, expansion latérale externe (quille); r, ride; s, « tige » centrale; w, expansion latérale interne. Barre d'échelle = 1 cm pour A–K, M, 1 mm pour L.



considered to be lost. DG (technical curator in the Rennes University Geological Museum collections) located the specimens in his institute's collections in 2015: two were donated by G. de Vaucenay (IGR 132670 and IGR 132671), part and counterpart, and there is another spine (IGR 10869) from the Musée de Rennes collection. As such specimens are so rare, we consider it appropriate to refigure them and reassess their taxonomic affinity.

II. — GEOLOGICAL SETTING

Several localities in the Laval Synclinorium in the eastern part of the Massif Armoricain of western France (Fig. 1B), including Saint-Germain-le-Fouilloux village about 8 km N of Laval, Mayenne department, have been famous since Oehlert's work in the late 19th century on invertebrate fossils from the region (e.g. Oehlert, 1884). The La Roussière quarry at Saint-Germain-le-Fouilloux (Fig. 1B, locality 1) is the type locality for many Lower Devonian (Pragian) fossils. The quarry exposes the shales and limestones of the middle part of the Early Devonian Saint-Cénére Formation (Frýda *et al.*, 2008). According to Bézier (1913), other *Machaeracanthus* localities in the Laval Synclinorium are les Courtoisières, Sarthe (Fig. 1B, locality 2), and Saint-Roch quarry, Changé, Mayenne (Fig. 1B, locality 3). These are in Pragian strata of the Saint-Cénére Formation. *Machaeracanthus* spine localities in western France also include Néhou, Manche department (Fig. 1B, locality 4), presumably in the Pragian Nehou Formation of the Cotentin region (for stratigraphy see Morzadec *et al.*, 1988). Another locality listed by Bézier (1913) is near Angers, Maine-et-Loire department (Fig. 1B, localities 5-7), in the 'Calcaire d'Angers' of the Angers Synclinorium. It is unclear if the 'Calcaire' denoted was the Angers Limestone (Pragian-Emsian) or the Vern Limestone (Pragian), the latter being the regional stratigraphic equivalent of the Saint-Cénére Formation. However, Péneau (1935) recorded that *Machaeracanthus* spines are found in the Vern Limestone. Le Maître (1934) also recorded *Machaeracanthus* spines from the Valet quarry in Chaudfond (= Chaudfond-sur-Layon village) in the 'Calcaires de Chaudfond' of Maine-et-Loire.

As well as these records of spines, *Machaeracanthus* sp. scales were collected and described from Saint-Cénére, Mayenne in the Saint-Cénére Formation (Goujet, 1976; Fig. 1B, near locality 3), and from la Pointe de l'Armorique, Finistère, in the L'Armorique Formation (lower Pragian), Châteaulin Synclinorium (Goujet, 1980; Fig. 1B, locality 8).

III. — SYSTEMATIC DESCRIPTION

†Class ACANTHODII OWEN, 1846

Order indet.

Family MACHAERACANTHIDAE BURROW & YOUNG, 2005

Genus *Machaeracanthus* NEWBERRY, 1857

Type species. *Machaeracanthus peracutus* Newberry, 1857.

Machaeracanthus bezieri nov. sp.

(Figs. 2A-K, 3A-F)

Synonymy.

? 1858 *Machaerius Larteti* Rouault. p. 102

? 1858 *Machaerius Archiaci* Rouault. p. 103

? 1858 *Machaerius*. Anonymous, p. 370

? 1868 *Machaerius Larteti et Archiaci*. D'Archiac, p. 32

in part 1872 *Ctenacanthus bohemicus* Barrande. p. 641, pl. 28 figs. 8-10, 16, 20, 24

1878 *Ctenacanthus bohemicus* Barr. Kayser, p. 4, pl. 35 figs. 12, 12a, 12b

? 1879 *Ctenacanthus bohemicus*, Barr. Oehlert & Davoust, p. 699

1883 *Machaeracanthus*. Kayser, pl. 4 fig. 2

1889 *Ctenacanthus bohemicus*. Barrois, p. 333

? 1890 *Ctenacanthus bohemicus*, Barr. Oehlert, p. 755

1913 *Ctenacanthus* cf. *bohemicus* Barr., "probably *Ctenacanthus bohemicus* Barr.". Bézier, p. 67, plate figs. 1-2

1924 *Machaerius Larteti*. Havel, p. 16

1928 *Machaeracanthus* cf. *bohemicus* (BARRANDE). Péneau, p. 132-133

1933 *Machaeracanthus bohemicus*. Schmidt, p. 240, fig. 6a

1934 *Machaeracanthus bohemicus* BARRANDE. Le Maître, p. 106, pl. 17 fig. 8

1935 *Machaeracanthus* cf. *bohemicus* (BARRANDE). Péneau, p. 43-44

1953 *Machaeracanthus* cf. *bohemicus*. Pillet, p. 16

1959 *Machaeracanthus* sp. n. Gross, p. 30

? 1976 *Machaeracanthus* sp. Goujet, p. 313, fig. 54 A-E, pl. 61 figs. 3-17, pl. 63 fig. 1a,b

in part 1979 *M. bohemicus* (Barrande) 1872A. Denison, p. 52

? 1979 *Machaeracanthus* sp. Morzadec *et al.*, p. 187

? 1980 *Machaeracanthus* sp. Goujet, p. 311, pl. 42 figs. 1-5

? *in part* 1993 *Machaeracanthus* Goujet, p. 28

in part 2010 *Machaeracanthus bohemicus*. Burrow *et al.* p. 76, fig. 8

? *in part* 2012 *Machaeracanthus goujeti* Botella *et al.*, p. 765

Type material. (All from Saint-Germain-le-Fouilloux) Holotype IGR 132670; Paratypes IGR 132671a,b part and counterpart, and ML-PAL-03006.

Etymology. Acknowledging Toussaint Bézier for his important contributions as curator of the Natural History Museum of Rennes, and his contribution to the study of *Machaeracanthus* remains from France.

Material examined. From Saint-Germain-le-Fouilloux: type specimens: holotype IGR 132670 (Fig. 2A–C), paratype 132671a,b (Fig. 2D–G) in the Rennes University Geological Museum collection (IGR 132670 collected by de Vaucenay possibly in 1909; IGR 132671 collected in 1914); paratype spine ML-PAL-03006 Fig. 2H–J), Collection Oehlert, Laval Museum. From an unrecorded locality (matrix indicates Saint-Germain-le-Fouilloux): ML-PAL-29822 (Fig. 2K), Collection Oehlert, Laval Museum.

Type horizon. Saint-Cénére Formation (Pragian).

Type locality. La Roussière quarry, Saint-Germain-le-Fouilloux, Mayenne.

Geographical and stratigraphic distribution. Western

France: Saint-Cénére Formation (Pragian); western Germany: Taunus Quartzite (Pragian); Czech Republic: Dvorce-prokop Formation (Pragian).

Diagnosis. *Machaeracanthus* species with adult spines c. 16 cm long and a length to maximum width ratio c. 6:1; smooth surfaced central shaft with semicircular cross sections of different diameters above and below the plane of the side expansions; inner lateral expansion (wing) and outer lateral expansion (keel) of similar widths; one morphotype has wing with one surface convex (side to side) bearing thin longitudinal ridges, other surface smooth, and keel with both surfaces smooth and flat; second morphotype with: keel with one surface convex and bearing thin longitudinal ridges, and wing with both surfaces smooth and flat.

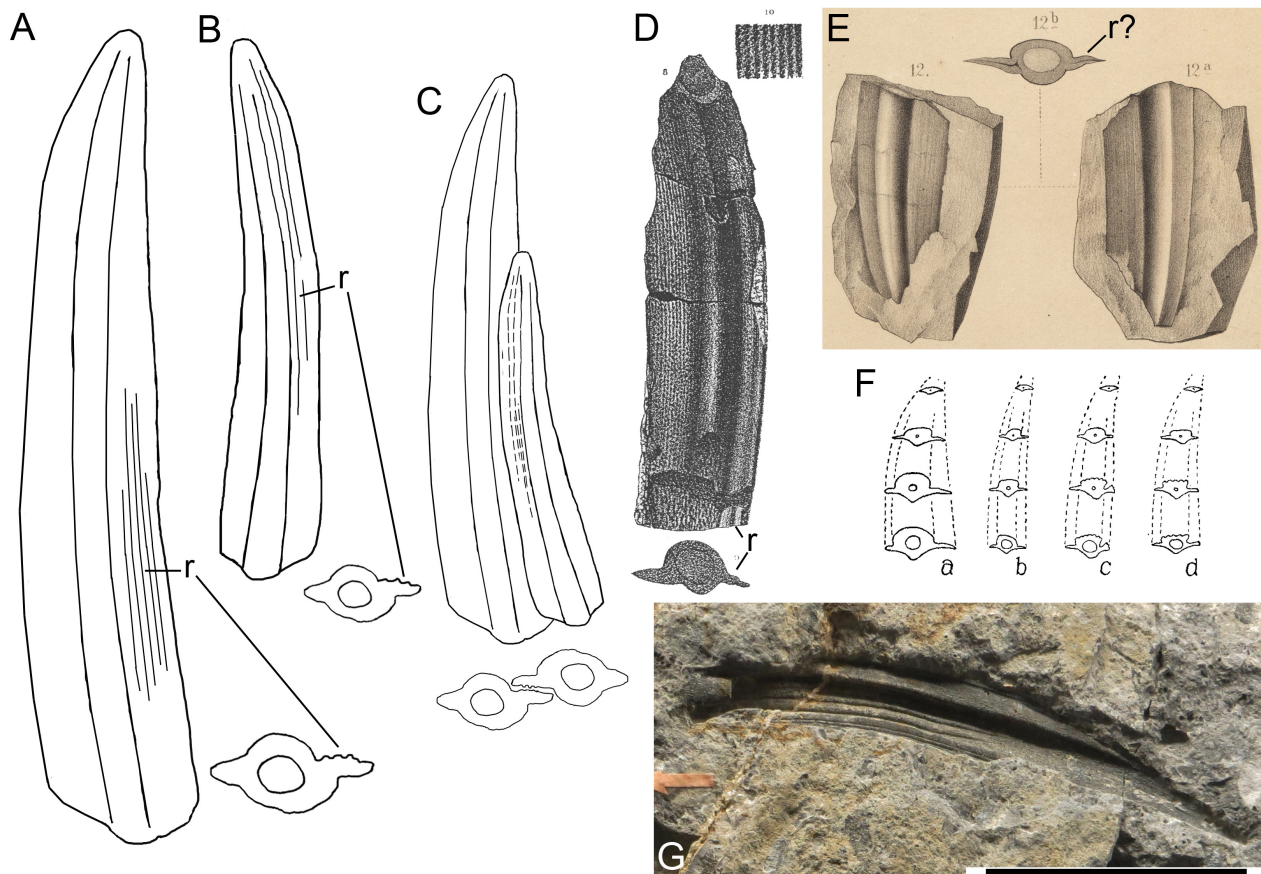


Fig. 3. — Pragian *Machaeracanthus* from Europe. A–C, *Machaeracanthus bezieri* nov. sp., reconstructions of ornamented surfaces and cross-sections of A, morphotype one spine; B, morphotype two spine; C, reconstruction of a pair of interlocking morphotype one and two spines. D–F, *Machaeracanthus bezieri* nov. sp. spines previously referred to *M. bohemicus*: D, Dvorce-prokop Formation, Czech Republic: Barrande, 1872, pl. 28, figs. 8–10. E, Taunus Quartzite, Harz Mts, Germany: Kayser, 1878, pl. 35, figs. 12, 12a, 12b. F, Taunus Quartzite, Harz Mts, Germany: Schmidt, 1933, fig. 6a–d (a, captioned as *Machaeracanthus bohemicus*, is here considered to be *M. bezieri* nov. sp.). G, *Machaeracanthus kayseri* Kegel, 1913, specimen MUWI Galladé 56.9.29 from the Taunus Quartzite, Stephanshausen, Grauer Stein, impression of lower surface of spine, Natural History Museum, Wiesbaden (Image by Ghedoghedo [(Own work -) [CC BY-SA 4.0 (<http://creativecommons.org/licenses/by-sa/4.0/>))], via Wikimedia Commons: https://upload.wikimedia.org/wikipedia/commons/0/05/Machaeracanthus_kayseri.jpg). Abbreviation: r, ridge. Scale bar = 10 cm.

Fig. 3. — *Machaeracanthus* du Praguén d'Europe. A–C, *Machaeracanthus bezieri* nov. sp., reconstitution des surfaces ornementées et coupes transversales de A, épine du morphotype 1 ; B, épine du morphotype 2 ; C, reconstitution d'une paire d'épines (morphotype 1 et 2) en connexion ; D, Formation de Dvorce-prokop, République tchèque: Barrande, 1872, pl. 28, figs. 8–10. E, Quartzites du Taunus, Montagnes du Harz, Allemagne: Kayser, 1878, pl. 35, figs. 12, 12a, 12b. F, Quartzites du Taunus, Montagnes du Harz, Allemagne: Schmidt, 1933, fig. 6a–d (a, figuré comme *Machaeracanthus bohemicus*, ici attribué à *M. bezieri* nov. sp.). G, *Machaeracanthus kayseri* Kegel, 1913, spécimen MUWI Galladé 56.9.29 des Quartzites du Taunus, Stephanshausen, Grauer Stein, impression de la surface inférieure de l'épine, Muséum d'Histoire naturelle de Wiesbaden (Image de Ghedoghedo [Own work - CC BY-SA 4.0 (<http://creativecommons.org/licenses/by-sa/4.0/>))], via Wikimedia Commons: https://upload.wikimedia.org/wikipedia/commons/0/05/Machaeracanthus_kayseri.jpg). Abbreviation: r, ride. Barre d'échelle = 10 cm.

Remarks. Bézier (1913) did not describe the morphology of the spines from Saint-Germain-le-Fouilloux, he merely referred to Barrande's (1872) original description and plates of *Machaeracanthus bohemicus*, Rouault's (1858) descriptions of *Machaerius larteti* and *M. archiaci*, and Oehlert & Davoust's (1879) description of *Ctenacanthus* cf. *bohemicus*, noting that these descriptions fitted the Saint-Germain-le-Fouilloux spines as well.

Description. The Saint-Germain-le-Fouilloux spine IGR 132670 (Fig. 2A-C), nominated as the holotype, lacks the proximal end, and is 13 cm long and 2.5 cm at its widest. As exposed by the natural cross-section terminating the specimen, the central shaft has a semicircular upper and lower profile. The surfaces of the central shaft and the keel show no ornament (although very little of the shaft surface is preserved intact), whereas the wing has a convex exposed surface with longitudinal ridges and grooves (six visible near the fractured end). Paratype IGR 132671a (Fig. 2D-F) is the distal half of a spine, lacking the tip, 7 cm long and 2 cm at its widest, with a cross-sectional profile similar to that of IGR 132670. The exposed surface is smooth, including the wing, although the surface appears abraded with possible traces of longitudinal grooves on the slightly convex wing. The counterpart IGR 132671b preserves the distal end of the spine that is missing in the part, and shows impressions of longitudinal ridging on the wing (Fig. 2G: r). The two specimens IGR 132670 and 132671 are morphotype one spines.

Two of the morphotype two spine forms are identified. Paratype spine ML-PAL-03006 (Fig. 2H-J) is 10 cm long, lacking the distal and proximal ends. On this spine, a short impression of the side originally buried in the matrix (at the proximal end of the preserved spine fragment) shows that the keel on this spine has longitudinal ridges (Fig. 2H: r). ML-PAL-29822 (Fig. 2K) is 12 cm long and almost complete, only missing the distal tip. The keel is partly preserved on the distal half of the spine, and is ornamented with at least three longitudinal ridges. The exposed surfaces of the wing and shaft are smooth.

Discussion and comparison. It seems probable that surfaces exposed in the two type specimens IGR 132670 and 132671a are the upper and lower surfaces (although we cannot confidently nominate which is which), as the narrowest and shallowest side of the shaft is exposed in IGR 132670 and the widest and deepest in IGR 132671a. If this is the case, it is also probable that only one or other of the upper and lower surfaces of the wing or keel is ridged. We thus recognize two morphotypes (Fig. 3A, B), one with a ridged wing (IGR 132670, 132671) and the other with a ridged keel (ML-PAL-03006, 29822). We propose that the two morphotypes were contiguous in life, as a pair of spines articulating via the ridging on the wing and keel respectively (Fig. 3C). It is not possible to distinguish the upper and lower (i.e. dorsal and ventral, in life) surfaces, as neither surface of the central shaft is worn smoother than the other (cf. Burrow *et al.* 2010, for a discussion of this feature in other species).

Bézier (1913) provided a table comparing the lengths and widths of the Czech Republic and western France spines, which showed that the dimensions of the latter compared closely with those of *Machaeracanthus bohemicus*. The Armorican spines resemble most closely some of the Pragian syntype spines assigned to *M. bohemicus* (e.g. Barrande, 1872, pl. 28, figs. 8–10, 16, 20, 24; Burrow *et al.*, 2010, fig. 8B; Fig. 3D here) rather than the Emsian lectotype and syntype spines of *M. bohemicus* (Barrande, 1872, pl. 28, figs. 4, 6). The Armorican and Pragian Bohemian spines have one convex, longitudinally ridged surface on either the inner (concave edged) wing or the outer (convex edged) keel. This feature is also visible on other Pragian spines previously assigned to *M. bohemicus* from the Taunus Quartzite,

Germany (Kayser, 1878, pl. 35, figs. 12, 12a, 12b; Fig. 3E here; Schmidt, 1933, fig. 6a; Fig. 3F here). This feature is not found in any other *Machaeracanthus* species, including *M. goujeti*, which is distinguished from other species in having adult spines with narrow equal width keel and wing, and a wide shaft with dense longitudinal striations on the upper surface on one of the two morphotypes. The other *Machaeracanthus* species from the Taunus Quartzite, *M. kayseri* Kegel, 1913, is easily distinguishable from *M. bezierei* nov. sp. by the robust sharp-crested longitudinal ribbing (Kegel, 1913) on the lower surface of the axial shaft (Fig. 3G).

As noted by Burrow *et al.* (2010, p. 77), “the stratigraphic range of material in the National Museum in Prague which has been assigned to *M. bohemicus* is Lochkovian to Eifelian”, and several authors (Perner, 1918; Gross, 1959; Burrow *et al.*, 2010) have indicated that there is more than one species in the Barrandian sequence. Based on our observations of the spines from western France described here and Barrande's material, we have assigned the Pragian examples with the distinctive longitudinal ridges on the wing or keel, from France, the Czech Republic, and Germany, to the new species *M. bezierei*.

Machaeracanthus sp.
(Fig. 2 L-M)

Material examined. From Saint-Germain-le-Fouilloux: spine fragment IGR 10869. From Changé: one spine fragment IGR 144560 (Fig. 2L) found by DG during the construction of the railroad (LGV) in 2014. From Vern-d'Anjou (now Erdre-en-Anjou): spine fragment UCO-71631, Collection Davy, Université Catholique de l'Ouest, Angers. From Saint-Malo Quarry, Saint-Barthélemy-d'Anjou near Angers: spine fragment UCO-71929 (Fig. 2M), Collection Jouitteau, Université Catholique de l'Ouest, Angers.

Description. Specimen IGR 10869 (not figured) from Saint-Germain-le-Fouilloux is probably the proximal end of a spine with the wider side of the shaft exposed, but it is very poorly preserved with only a small area of hard tissue present. The spine fragment from Changé (Fig. 2L; IGR 144560) is very poorly preserved; it retains the characteristic cross-sectional shape of *Machaeracanthus*, but shows no specific characters. The surface of the hollow central pulp cavity shows narrow parallel ridges near the fracture surface; these are probably exposed vascular canals of the osteodentine. The specimens from Angers (UCO-71629, 71631; Fig. 2M) are short midspine fragments which are poorly preserved. They do not show evidence of ridging on the side expansions (wing, keel), possibly because these are on the sides buried in the matrix. They are thus only assigned to *Machaeracanthus* sp. rather than to *M. bezierei*.

IV. — TAXONOMIC DISCUSSION

Unfortunately we have been unable to examine the well preserved *Machaeracanthus* spine from Sablé-sur-Sarthe mentioned by Goujet (1993) and Janvier (1996), which should be in the collection of the Muséum National d'Histoire Naturelle, Paris, as it appears to have been misplaced and no images of it are available.

It is possible that the new species *M. bezierei* is synonymous with Rouault's (1858) species, but as his original descriptions make no mention of the distinguishing feature we recognize in *M. bezierei* nov. sp., and his specimens were not figured and are still lost, *M. larteti* and *M. archiaci* must remain *nomina vana*. We question whether the scales from western France, originally assigned by Goujet (1976, 1980) to *Machaeracanthus* sp., can

reliably be assigned to *M. goujeti* as proposed by Botella *et al.* (2012) given that we have not seen spines like those of the latter species from western France. Although it is only known from limited material, the Pragian *M. bezieri* nov. sp. is characterised by the distinctive longitudinal ridging on the inner wing or outer keel of the spines, a feature that is not present on the type material of any other *Machaeracanthus* species. For this reason, we feel justified in assigning both the morphotypes showing complementary ridging on wing and keel to the same biological species rather than to two form species, despite not finding them as associated pairs. All of the type specimens are, however, from the same quarry. It now seems highly likely that most, if not all, *Machaeracanthus* fish had paired pairs of spines, as two morphotypes have now been identified in *M. hunsrueckianum*, *M. longaevus*, *M. peracutus*, *M. sulcatus*, and *M. polonicus*

(Burrow *et al.* 2010; Burrow & Srek, 2017). The geographical distribution of *M. bezieri* includes France, Germany and the Czech Republic.

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