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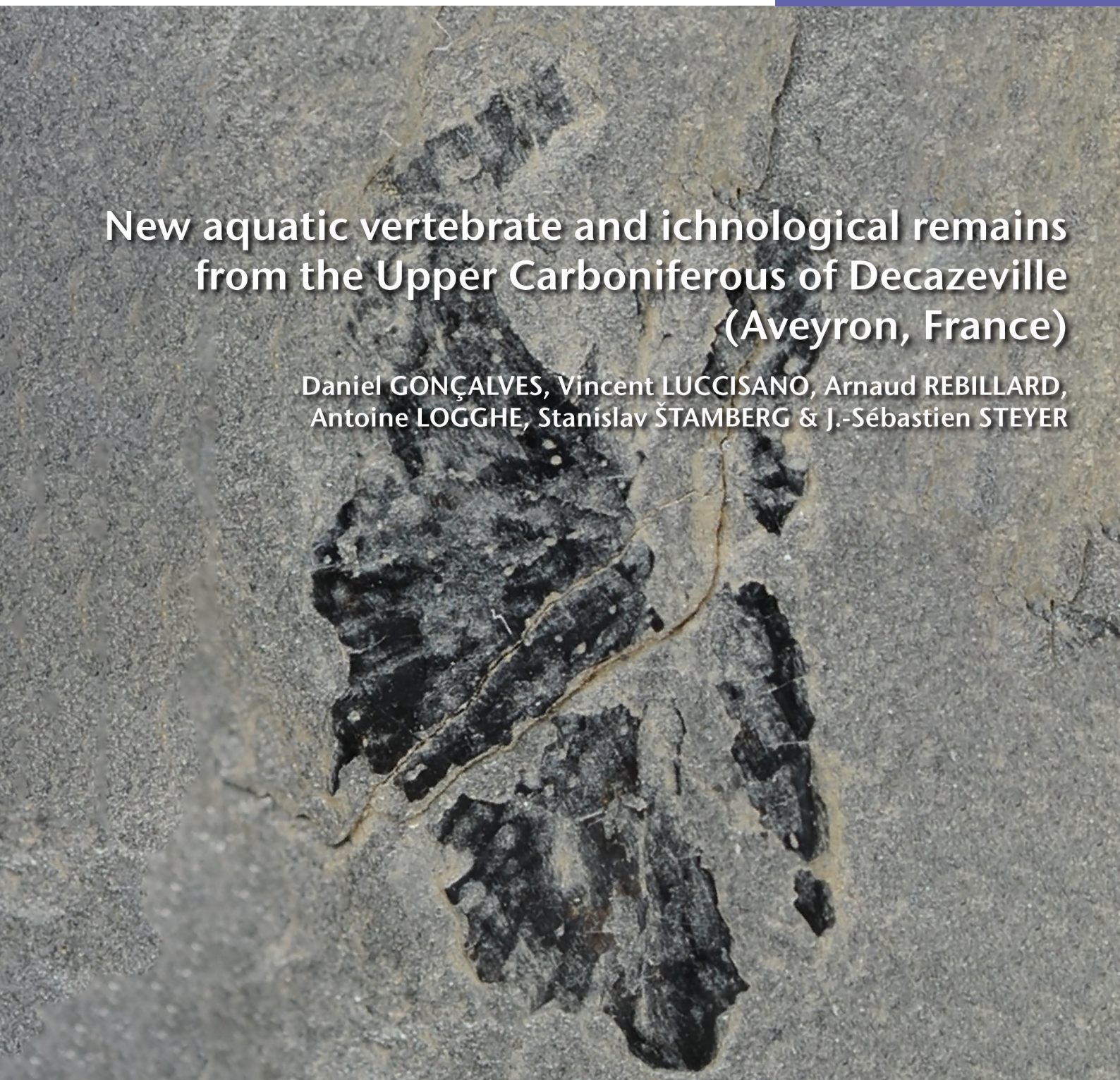

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# New aquatic vertebrate and ichnological remains from the Upper Carboniferous of Decazeville (Aveyron, France): implications for the paleofauna of the French Variscan basins

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**ABSTRACT**
The Decazeville Basin (Aveyron, France) is an Upper Carboniferous intra-Variscan basin of the southern part of the French Massif Central. Its geology and paleontological content (fauna and flora) have been the subject of regular studies before and during its coal mining activities, but unfortunately not since they ceased: no fossil from the Decazeville Basin has been described over the past 50 years. Recent fieldwork at the La Découverte locality led to the rediscovery of a vertebrate-rich deposit in the Bourran Formation, of which we describe new material here. This material consists of numerous specimens including new skeletal remains of the xenacanthiform *Orthacanthus* sp. and the acrolepid cf. *Progyrolepis,* two taxa never before reported in the Decazeville Basin. We also describe here the first coprolites from the Decazeville Basin, likely produced by *Orthacanthus*. The nature and taphonomy of these finds highlight the hypothesis that the depositional environment of the La Découverte locality was an anoxic freshwater lake, acting as the discharge zone of a powerful river. These discoveries confirm the similarity of the Decazeville fauna to the other intra-Variscan basins of the French Massif Central, although a few endemic forms such as the aeduellid *Decazella vetteri* (Heyler, 1964) are reported. The new ichthyofauna list provided here constitutes a solid basis for future comparisons with other Upper Carboniferous basins.

**KEY WORDS**
Decazeville Basin,
French Massif Central,
Actinopterygii,
Decazella,
Xenacanthiformes,
*Orthacanthus*,
Acanthodii,
Coprolites.

**RÉSUMÉ**
*Nouveaux restes de vertébrés aquatiques et ichnologiques dans le Carbonifère Supérieur de Decazeville (Aveyron, France) : implications sur les paléofaunes des bassins varisques français.*
Le bassin de Decazeville (Aveyron, France) est un bassin intra-varisque du Carbonifère supérieur de la partie méridionale du Massif central. Sa géologie et son contenu paléontologique (faune et flore) ont fait l'objet d'études régulières avant et pendant l'exploitation minière du charbon, mais malheureusement pas après son arrêt : aucun fossile du bassin de Decazeville n'a été décrit au cours de ces 50 dernières années. Cependant, des fouilles récentes à la localité de La Découverte ont permis de redécouvrir un gisement riche en vertébrés dans la Formation de Bourran, et de décrire ici du nouveau matériel. Ce matériel consiste en de nombreux spécimens, dont de nouveaux restes squelettiques du xénacanthiforme *Orthacanthus* sp. et de l'acrolépidé cf. *Progyrolepis*, deux taxons jamais rapportés dans le bassin de Decazeville jusqu'à présent. De plus, nous décrivons ici les premiers coprolites du bassin de Decazeville, probablement produits par *Orthacanthus*. La nature et la taphonomie de ces découvertes appuient l'hypothèse selon laquelle l'environnement de dépôt du site de La Découverte était un lac d'eau douce anoxique, faisant office de zone de déversement d'un cours d'eau puissant. Ces découvertes confirment la similitude de cette paléofaune avec celles des autres bassins intra-varisques du Massif Central, même si quelques formes endémiques comme l'aeduellidé *Decazella vetteri* (Heyler, 1964) y sont présentes. La nouvelle liste ichtyofaunique fournie ici constitue une base solide de comparaisons futures avec d'autres bassins du Carbonifère Supérieur.

**MOTS CLÉS**
Bassin de Decazeville,
Massif Central,
Actinopterygii,
Decazella,
Xenacanthiformes,
*Orthacanthus*,
Acanthodii,
Coprolites.

## INTRODUCTION

The French Massif Central partly consists of late-Variscan intramontane sedimentary basins, formed in limnic environments in the axial zone of the Gondwanan margin of the Variscan Belt during the Upper Carboniferous and the Upper Permian (Fig. 1B; e.g. Pruvost 1947; Dolle 1985; Faure & Becq-Giraudon 1993; Fauré 2022; Aretz *et al.* 2023). These Permo-Carboniferous ("Stephanian and Autunian") basins are mostly known for their rich paleofauna and flora (e.g. Doubinger 1956; Heyler 1969; Steyer *et al.* 1997, 2000; Gand & Durand 2006; Charbonnier *et al.* 2008). Indeed, numerous fossil deposits have been discovered and continue to be discovered in the basins of Montceau-les-Mines (e.g. Rolfe *et al.* 1982; Heyler & Poplin 1988; Perrier & Charbonnier 2014), Commentry (e.g. Blot 1966; Heyler 2000), Autun (e.g. Heyler 1969; Luccisano *et al.* 2021, 2022), Bourbon-l'Archambault (e.g. Heyler 1969; Heyler & Poplin 1990; Poplin 1999; Steyer *et al.* 2000, 2012; Štamberg 2018; Luccisano *et al.* 2022), Rodez (e.g. Sigogneau-Russell & Russell 1974; Bourges *et al.* 1986; Reisz *et al.* 2011), Najac (Delsahut 1981; Fauré & Delsahut 2024), Saint-Affrique (e.g. Gand *et al.* 1996; Moreau *et al.* 2024), Graissessac-Lodève (e.g. Heyler 1977; Martín-Closas & Galtier 2005; Werneburg *et al.* 2022), L'Argentière (Poplin *et al.* 1998), Brive (e.g. Heyler 1969; Štamberg & Steyer 2021), Figeac (Vetter 1968), Carmaux (e.g. Doubinger & Vetter 1959; Dion *et al.* 1979; Heyler 2000) and Réalmont (Delsahut 1981; Fauré 2022).

The Decazeville Basin (Fig. 1B) is one of these fossil-rich "Stephanian basins". Before the advent of open-pit mining in the city of Decazeville, this basin was known as the Aubin Basin (e.g. Daubrée 1872). Its Upper Carboniferous fauna is mainly known from the Bourran Formation and includes lamellibranch bivalves, insects, trigonotarbids, xenacanthiform chondrichthyans, acanthodians, aeduellids, amblypterid and temnospondys (Petrunkevitch 1955; Heyler 1964, 1969; Vetter 1968; Steyer *et al.* 1997). The Bourran Formation outcrops notably in the former open-pit mine of La Découverte (also

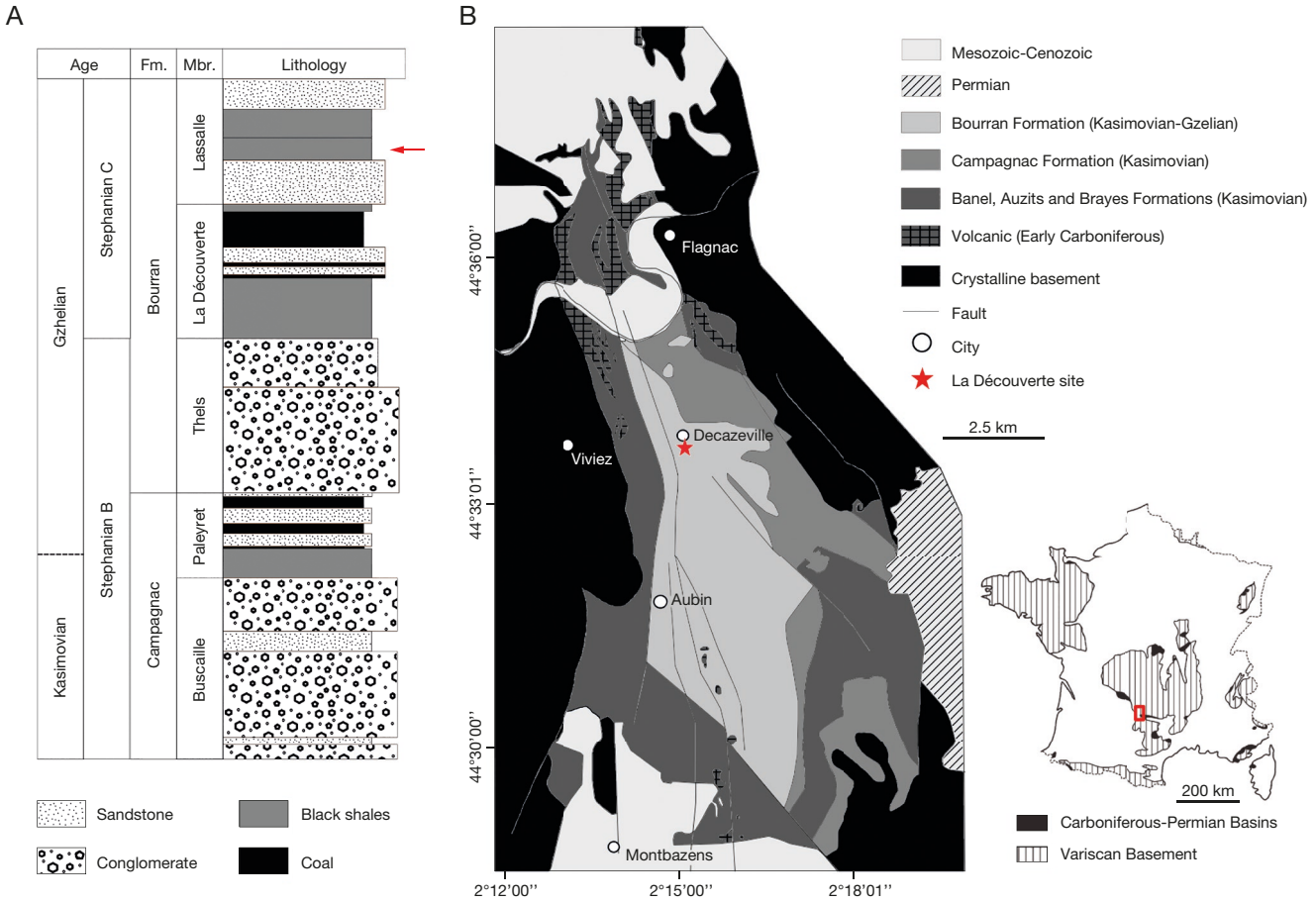


FIG. 1. — Geological context: **A**, simplified stratigraphy of the upper part of the Decazeville Basin (modified from Vetter 1968; Christophoul *et al.* 2019), the **red arrow** points the ANLD (see text for explainations) in the Lassalle Member ("*niveau 270*" in Vetter 1968); **B**, location of the Decazeville Basin in the French Massif central (map from Gand & Durand 2006), simplified geology of the Decazeville Basin and location of the La Découverte locality (modified from Vetter 1968; Basile 2006). Abbreviations: **Fm.**, Formation; **Mbr.**, Member.

locally as "*Découverte de Lassalle*" or "*Grande Découverte*"), located in Decazeville (Aveyron, France) (Heyler 1964, 1969, 2000; Vetter 1968; Pertus & Herranz 2007). Most of the other outcrops of this formation have disappeared or became inaccessible since the closure of the mines (e.g. Vetter 1968; Mazars 1999; Pertus & Herranz 2008; Guiollard 2020, for the history of the researches).

The flora of La Découverte is very well known and consist of *Calamites* Brongniart, 1828, *Annularia* Stenrberg, 1821, *Pecopteris* Brongniart, 1822, *Sphenopteris* Brongniart, 1822, *Callipteridium* Weiss, 1870, *Asterophyllites* Brongniart, 1822, *Linopteris* Presl, 1838, *Odontopteris* Brongniart, 1822, and *Walchia* Stenrberg, 1825 (e.g. Bergeron 1888; Bergeron *et al.* 1900; Bergounioux & Doubinger 1943; Doubinger 1951, 1956, 1957, 1958, 1964; Doubinger & Vetter 1953; Piérart 1957; Vetter 1968). The first mentions of vertebrates in the Decazeville Basin were made by Daubrée (1872), Bergeron (1885, 1889) and Sauvage (1893) but these come from La Découverte de Lavaysse locality, another open-pit mine at Combes (Bourran Formation, Aveyron, France). The vertebrates of La Découverte, described later, consists of chondrichthyans (*Expleuracanthus* sp.), acanthodians (*Acanthodes* sp.), aeduellids (*Aeduella blainvillei* (Agassiz, 1833) and *Decazella vetteri* (Heyler, 1964)) and amblypterids (*Paramblypterus* sp.) (Heyler 1964, 1969; Vetter 1968; Blieck *et al.* 1999). Concerning the "protostomians", it contains also the bivalve *Anthracomya prolifera* Waterlot,1935, the insects *Orthomylacris* sp. and *Phylloblatta* sp. and some annelid traces (Vetter 1968). This fauna comes almost exclusively from the Lassalle Member (Vetter 1968).

Underground mining at La Découverte ended in 1966 (Wolff 1972) and the operations definitively ceased in 2001 (Charbonnages de France 2001; Guiollard 2020), hampering severely the discovery of new fossil specimens. Since then, no new paleontological material has been described from the site. Recent studies on La Découverte focused on geology (Tabeaud 1984; Bellenguez & Revel 1986; Bellenguez 1987; Ligouis 1988; Ligouis & Doubinger 1991; Bruguier *et al.* 1998; Basile 2006; Lapierre *et al.* 2008; Christophoul *et al.* 2019).

In order to update our knowledge on the fauna from Decazeville, systematical excavations were carried out at La Découverte by one of us (DG) from 2019 to 2023. These fieldworks led to the discovery of new fossil specimens described here: these specimens allow to discuss the palaeodiversity, the palaeoenvironment and the palaeobiogeography of the European intra-mountainous aquatic faunas from the late Carboniferous of the Variscan Belt.

## GEOLOGICAL CONTEXT

The Decazeville Basin lies in the southern Massif Central (Fig. 1B; Aveyron, France) and is filled with volcanic, volcanoclastic and silico-clastic sediments, representing the Decazeville Group (Vetter 1968; Ligouis 1988; Ligouis & Doubinger 1991; Basile 2006). The filling of the base of the Decazeville Basin is, based on rhyolites and dacites, of Visean age (332 ± 2 Ma, Bruguier *et al.* 1998). The Decazeville Group is made up of six formations, called "*assises*" by Vetter (1968) in French mining terminology: the Brayes Formation, the Volcanic Complex, the Auzits Formation, the Banel Formation, the Campagnac Formation and the Bourran Formation. These formations, of Carboniferous age, are correlated with the Kasimovian-Gzhelian international units (Vetter 1968; Wagner 2017; Aretz *et al.* 2020). They show a granodecreasing trend: the base is conglomeratic while the top is made of alternating clay-silt/coal veins (Vetter 1968). From base to top, the Brayes, Auzits, Banel and Campagnac formations are Stephanian B, which corresponds to the Upper Kasimovian (Wagner 2017) or the Lower-Middle Gzhelian (Aretz *et al.* 2020: 824, fig. 23.5). Following the correlations proposed between the regional and international stages, an Upper Kasimovian-Lower Gzhelian age is estimated for these formations. Above, the Bourran formation is Stephanian B (Upper Kasimovian-Lower Gzhelian) at its base (Thels Member) and Stephanian C (Gzhelian) at its top (La Découverte and Lassalle Members) (Vetter 1968; Christophoul *et al.* 2019). According to Wagner (2017), the Stephanian C corresponds to the Lower Gzhelian, but following Aretz *et al.* (2020), it corresponds to the Middle Gzhelian. In any case, the La Découverte and Lassalle members are firmly established as dating from the Lower-Middle Gzhelian. Vetter (1968) defines an additional "Volcanic Complex" formation whose stratigraphic position is difficult to specify (Thiébaud & Vetter 1956; Vetter 1968): it may constitute a volcanic equivalent of the Stephanian B (Upper Kasimovian-Lower Gzhelian) formations (Christophoul *et al.* 2019).

In terms of depositional environments, the coarse silico-clastic series correspond to alluvial and fluvial fan environments. The finer series, on the other hand, correspond to floodplain and lacustrine deposits (Ligouis 1988; Christophoul *et al.* 2019).

The Bourran Formation (Fig. 1A), of around 550 meters thick, is divided into three members: the Thels Member, La Découverte Member and the Lassalle Member (respectively called "*Poudingues de base*", "*Série de couches*" and "*Série de Lassalle*" in Vetter 1968: 246) (see also Vetter 1980; Christophoul *et al.* 2019). This formation is intersected by three layers of tonsteins 2-3 cm thick: two at the base of the La Découverte Member (Tonsteins H and I) and one in the middle of the Lassalle Member (Tonstein Henri) (Vetter 1968). The Thels Member is 200 meters thick and consists of conglomerates. The La Découverte Member is 170 meters thick and consists of a succession of black argillites (also called "*schistes bitumineux*" [bituminous shales], in Vetter 1968: 247), sandstones and coals. The top of this member is a large coal layer, known as the "*Grande Couche de Bourran*" (Stevenson 1911; Vetter 1968; Ligouis 1988). This layer is covered by a 2-3 meters thick bed of black argillites, containing vertebrate remains (Vetter 1968; Ligouis 1988). This outcrop was accessible when the open-pit mine was in operation, but is now covered by a lake (in reality, it is an upwelling of the aquifer uncovered by mining activity, preserved as part of the rehabilitation of the site; see Cojean *et al.* 2005) and vegetation. The Lassalle Member is also composed of a succession of black argillites and sandstones, some of which also contain vertebrate remains (Vetter 1968). The Lassalle Member is itself divided into three sub-units (Horizons IV, V and VI in Vetter 1968: 264): the "*Grès de La Découverte*" at the base, consisting of sandstones 80-100 m thick, the "*Schistes gris-bleuté*" in the middle, consisting of black argillites 80-90 m thick, and the "*Grès de Buffet*" at the top, consisting of sandstones 40 m thick (Vetter 1968: 264). Three vertebrate levels (called "s*chistes bitumineux à écailles de poissons*" [bituminous shales with fish scales] in Vetter 1968: 264) of the Lassalle Member outcrop at the La Découverte locality and come from the "*Schistes gris-bleuté*" (Horizon V; Vetter 1968: 264) and the "*Grès de Buffet*" (Horizon VI; Vetter 1968: 265). The first level is a 5-6 m thick bed of black argillites at the "*niveau 270*" of the Horizon V (Vetter 1968: 265), at the middle of the Lassalle Member and below the Tonstein Henri. This layer is referred here as "Argilites Noires de La Découverte" (ANLD) in this study. The second level lies also in the middle of the Lassalle Member in the Horizon V, but above the Tonstein Henri, and is 2-3 m thick (Vetter 1968: 265). The last level is a 4 m thick bed of black argillites between two beds of sandstone, at almost the top of La Découverte site, in the Horizon VI (Vetter 1968: 265). Almost all of the vertebrate specimens described by Heyler (1964, 1969) and Vetter (1968) as well as the insects mentioned by Vetter (1968) were found in the black argillites at the "*niveau 270*" of this Horizon V, in what we refer to here as the ANLD (Vetter 1968).

At the La Découverte locality, the mine workings exposed around 200 meters of the Bourran Formation, representing the top of La Découverte Member and a great part of the Lassalle Member (Vetter 1968, 1980). In this locality, the ANLD correspond to carbon-rich lacustrine deposits, indicating a partially anoxic depositional environment (Ligouis 1988). The presence of numerous macroscopic plants, mostly in the form of debris (mainly pecopterids), indicates significant allochthonous contributions of plant matter (Vetter 1968; Ligouis 1988). This layer appears to correspond to a river discharge zone with calm depositional conditions (Ligouis 1988). The ANLD layer corresponds to lacustrine deposits with fairly low oxygenation levels at the bottom of the water column (Ligouis 1988).

## MATERIAL AND METHODS

All of the studied specimens were found between 2019 and 2023 in the ANLD on the west side of the La Découverte former open-pit coal mine (GPS coordinates available to qualified researchers), during excavations carried out by one of us (DG). This material is currently housed at the


Fig. 2. — Partially preserved tooth (MHNT.PAL.2023.9.1) referred to *Orthacanthus* sp. in: **A**, labial; **B**, lateral; **C**, and oral views. Scale bars: 5 mm.

Muséum d'Histoire Naturelle de Toulouse, France (MHNT). Because of the vegetation and the cover of the site, but also the stepped architecture of the former mine, only the lower part of the ANLD is currently accessible. However, some of the ANLD material is detached from the outcrop by weather conditions, enabling it to be harvested on the ground. This harvesting method enabled the specimens to be uncovered without damaging the site, which remain stratigraphically well-controlled (see below).

For the historical specimens used as comparative material, a table which summarises the changes of inventory numbers and taxonomic identifications in the literature is given in Appendix 1.

Specimens were examined, measured with a calliper, and photographed using a Nikon D700 camera in different lighting conditions, including natural light and a pair of LED lamps.

Here we follow the nomenclature of Schneider (1985, 1986) to describe Xenacanthiformes tooth, Štamberg (2007, 2018) to describe actinopterygians and Hunt & Lucas (2012) to describe coprolites.

Institutional abbreviations

| | |
|---|---|
| HBA | Houillères du Bassin d'Aquitaine; |
| MRGPV | Musée Régional de Géologie Pierre Vetter, Decazeville; |
| MHNG | Muséum d'Histoire Naturelle de Gaillac; |
| MHNT | Muséum d'Histoire Naturelle de Toulouse; |
| ML | Musée Labenche, Brive; |
| MNHN | Muséum national d'Histoire naturelle, Paris. |

## SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Order XENACANTHIFORMES Berg, 1937
Family Diplodoselachidae Dick, 1981
Genus *Orthacanthus* Agassiz, 1843

*Orthacanthus* sp.
(Fig. 2)

Material. — A partially preserved isolated tooth (MHNT.PAL.2023.9.1 [Fig. 2]).

Description

The tooth only preserves one of the two lateral cusps, the base of the medial cusp and a part of the basal tubercle. It has a preserved height of 12 mm from the base to the apex of the complete lateral cusp. The incomplete nature of the tooth makes it impossible to determine its orientation. The surface of the preserved cusps is smooth. The lateral cusp is slightly compressed labio-lingually and has a slightly curved dagger shape, with a slightly blunt apex. Serrations are present on both external cutting edges of the lateral cusp, with a denticle density of four denticles per mm. According to the basal diameter of the median cusp, its total high, when preserved, should not exceed a third of that of the lateral cusps. As the base of the tooth is broken, we are unable to determine the exact morphology of the basal tubercle.

Comparisons

A tricuspid tooth morphology is characteristic of Xenacanthiformes (e.g. Ginter *et al.* 2010). The genera *Orthacanthus* and *Lebachacanthus* Soler-Gijon, 1997 are characterised by labio-lingually compressed lanceolate lateral cusps and a reduced median cusp (Ginter *et al.* 2010). In *Lebachacanthus*, the lateral cusps of the side teeth are straight and pointed (Ginter *et al.* 2010), whereas in *Orthacanthus*, they have a blunt apex and a tendency to be slightly curved (Hampe 2003). MHNT.PAL.2023.9.1 corresponds to an *Orthacanthus* tooth in terms of its blunt apex and the curvature of its lateral cusp. Unfortunately, it is too incomplete to be specifically identified, and is therefore referred here to *Orthacanthus* sp.

Sub-class ACANTHODII Owen, 1846,
*sensu* Coates *et al.*, 2018
Order ACANTHODIFORMES Berg, 1940
Family Acanthodidae Huxley, 1861

Acanthodidae indet.
(Fig. 3)

Material. — Eight partially preserved fin spines (MHNT.PAL.2023.9.31 [Fig. 3A]; MHNT.PAL.2023.9.32, MHNT.

PAL.2023.9.33 [Fig. 3B]; MHNT.PAL.2023.9.34 [Fig. 3C]; MHNT.PAL.2023.9.35 [Fig. 3D]; MHNT.PAL.2023.9.36, MHNT.PAL.2023.9.37 and MHNT.PAL.2023.9.51)

Description

These spines are all slightly curved, more or less pointed at their distal end (see below) and have a smooth surface. All have a groove along their lateral sides and none bear denticles. Their sizes and morphologies vary slightly in terms of total length, curvature, shape of the apex and width of the entire spine. Two morphotypes can be distinguished: the first, with specimens MHNT.PAL.2023.9.31, MHNT.PAL.2023.9.32, MHNT.PAL.2023.9.33, MHNT.PAL.2023.9.36, MHNT.PAL.2023.9.37 and MHNT.PAL.2023.9.51 corresponds to large spines with a total length above 30 mm, a width of 3 to 5 mm along the entire length, and a rather rounded distal end. The second morphotype, with specimens MHNT.PAL.2023.9.34 and MHNT.PAL.2023.9.35, corresponds to smaller and finer spines with a total length below 10 mm, a width of less than 1 mm and a pointed distal end.

Comparisons

The spines herein described are long, slender, slightly curved and grooved on each lateral side, making them attributable to the Acanthodidae (e.g. Beznosov 2009). Isolated acanthodian fin spines found in the Carboniferous basins of France have traditionally been referred to the genus *Acanthodes* (e.g. Heyler 1969). However, acanthodid fin spines are generally devoid of diagnostic features at the generic level (e.g. Zidek 1976). The presence of different morphotypes may correspond to variations between pectoral, anal and dorsal fin spines, although these are poorly known in acanthodids. Despite their number, the acanthodian fin spines from La Découverte remain isolated and, in the absence of more complete associated skeletal remains, they cannot be assigned to a more precise taxon. Pending more discovery, we hereby refer these specimens to the open nomenclature Acanthodidae indet.

Class ACTINOPTERYGII Cope, 1887,
*sensu* Goodrich, 1930
Family Acrolepidae Aldinger, 1937
Genus *Progyrolepis* Fritsch, 1895

cf. *Progyrolepis*
(Fig. 4)

Material. — An isolated fulcral scale (MHNT.PAL.2023.9.52 [Fig. 4]).

Description

The scale is isolated and lacks the most posterior part. It is 11 mm long and 5 mm wide as preserved. The scale is triangular in shape, with sculpted ridges running anteroposteriorly. A longitudinal groove runs through the middle of the scale, tapering off towards the anterior end.

Comparisons

Among the ichthyofauna of the Carboniferous-Permian basins of France, the morphology of MHNT.PAL.2023.9.52 most closely resembles the fulcral scales of *Progyrolepis* (e.g. Štamberg 2016a, 2018). The ridge scales of *Progyrolepis* have indeed a triangular shape with ornamentation consisting of prominent ridges arranged anteroposteriorly (Poplin 1999; Štamberg 2018). MHNT.PAL.2023.9.52 does not resemble aeduellid nor amblypterid fulcral scales, which lack highly visible ornamentation (e.g. Dietze 1999; Poplin & Dutheil 2005). Ultimately, MHNT.PAL.2023.9.52 resembles the fulcral scales of *Progyrolepis*, with several identical specimens already reported from the Carboniferous-Permian of the Massif Central (e.g. Štamberg 2018: 268, fig. 22I; Štamberg & Steyer 2021: 159; fig. 10B). The preservation of MHNT.PAL.2023.9.52 does not allow a more precise systematic attribution, so we refer this specimen to cf. *Progyrolepis*.

Family Aeduellidae Romer, 1945,
*sensu* Štamberg, 2007
Genus *Decazella* Heyler, 1967a

*Decazella vetteri* (Heyler, 1964)
(Figs 5; 6)

*Aeduella* – Heyler 1964: 6-14 – Vetter 1968: 154.

*Decazella* Heyler, 1967a: 87 – Heyler 1969: 175-185. – Poplin & Dutheil 2005: 20.

Material. — A postrostral associated with an operculum (MHNT.PAL.2023.9.14 [Fig. 5A, B, G, H]), an isolated parietal (MHNT.PAL.2023.9.30 [Fig. 5E, F]) and an isolated suboperculum (MHNT.PAL.2023.9.18 [Fig. 5I, J]).

Description

Specimen MHNT.PAL.2023.9.14 shows an association of two bones, each other distant from 13 mm. The first bone (Fig. 5A, B) has a rectangular to pentagonal shape, with a straight posterior edge and a rounded anterior edge. It is 17 mm long and 9 mm wide (length/width ratio 1.9). Its right lateral edge and anterior edge are damaged and difficult to distinguish. A strong ornamentation of elongated ridges is visible on the lateral face of the posterior edge, and diminishes towards the anterior edge. Although the anterior part of this bone is damaged, several flat tubercles can be distinguished. We identified this bone as a postrostral. The second bone (Fig. 5G, H) is an operculum, which is well recognizable by its shape and large size (8 mm long and 17 mm high). It is almost complete, only its dorsal end was destroyed during its delicate extraction. This operculum, with a 180° bending angle, has a straight anterior and ventral edge and a slightly rounded dorsal and posterior edge, giving it a very rectangular appearance. The ratio between the width of the ventral part and the width of the dorsal part of this operculum cannot be measured

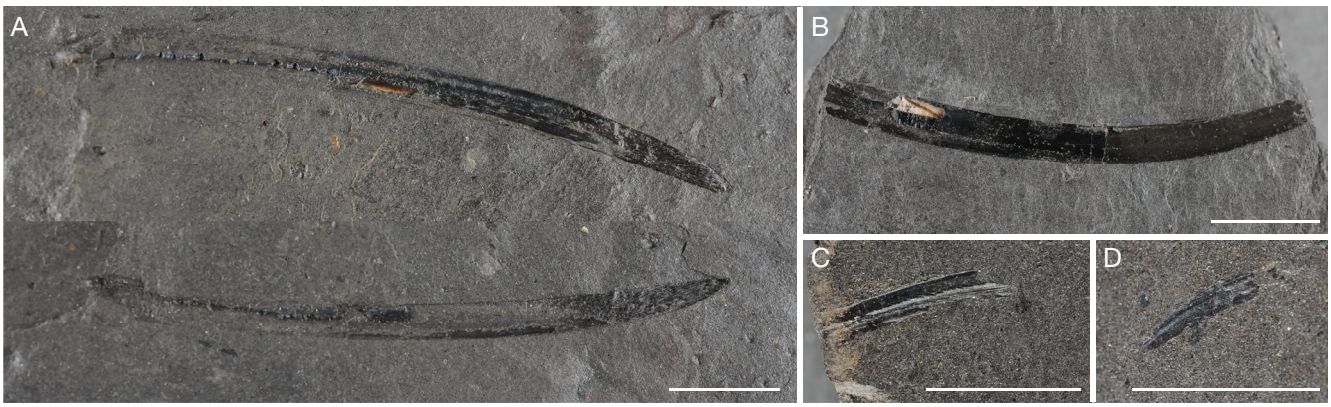


Fig. 3. — Fin spines of Acanthodidae indet.: **A**, MHNT.PAL.2023.9.31 (specimen above and counter-part below); **B**, MHNT.PAL.2023.9.33; **C**, MHNT.PAL.2023.9.34; **D**, MHNT.PAL.2023.9.35. Scale bars: A, B, 1 cm; C, D, 5 mm.

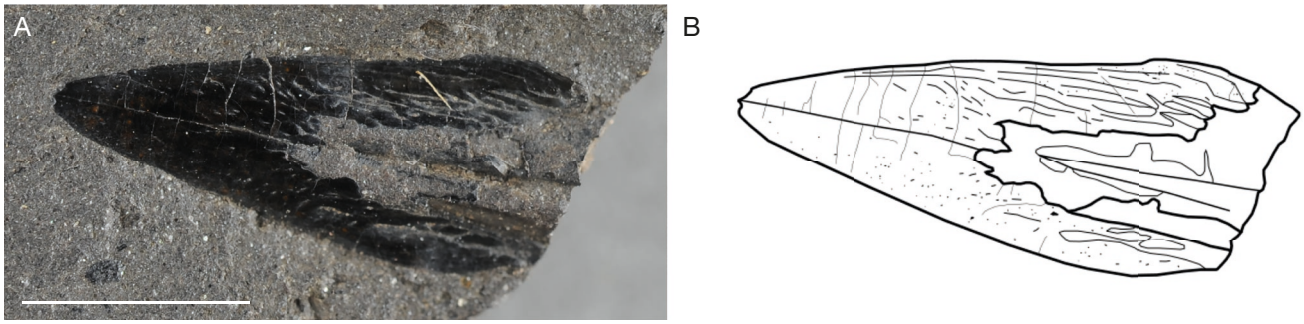


Fig. 4. — Isolated fulcral scale MHNT.PAL.2023.9.52 referred to cf. *Progyrolepis* Fritsch, 1895: **A**, photograph; **B**, interpretative drawing. Scale bar: 5 mm.

with confidence due to the slight incompleteness of the postero-ventral part of the bone. It is ornamented with ridges parallel to the edges of the bone (growth lines), but no flat tubercles are visible. Even if these operculum and postrostral of MHNT.PAL.2023.9.14 are both attributed to *Decazella vetteri* (see below), it is difficult to know whether they belong to the same individual or not, because they are disarticulated.

MHNT.PAL.2023.9.30 (Fig. 5E, F) is a slightly oblong bone, measuring 10 mm long and 6.5 mm wide (length/width ratio 1.5). Only the posterior part of the bone is preserved, the anterior part being discernible only as a counterpart. Its anterior and posterior edges are straight, while its lateral edges are slightly concave. The bone is slightly ornamented with rounded to oval pores on its lateral surface. Two pit lines are present, but it is not possible to determine whether they join or not, as the bone is not complete enough. These pit lines form a V oriented towards the left lateral edge of the bone. The morphology and presence of pit lines in MHNT.PAL.2023.9.30 allow us to identify it as a parietal.

MHNT.PAL.2023.9.18 (Fig. 5I, J) is clearly a subopercu-lum, as shown by its ornamentation of small flat tubercles on its lateral surface, its large size (12 mm long and 8 mm high) and its shape. One half of the bone is fully preserved, the other half appearing as a counter part. It is parallelogram-shaped, with opposite sides perfectly parallel and the same size. It is therefore impossible to determine its orientation in the anterior-posterior direction.

### Comparisons

The postrostral of MHNT.PAL.2023.9.14 is a large bone, ornamented with elongated ridges on its posterior part and flat tubercles on its anterior part, with a roughly pentagonal shape and rounded edges. These features enable us to assign it to Aeduellidae (e.g. Heyler 1969; Poplin & Dutheil 2005). MHNT.PAL.2023.9.14 is extremely similar to the postrostral of MNHN.DEC.32 (Fig. 5C, D; Heyler 1969: 183, 184, fig. 135) assigned to *Decazella vetteri* by Heyler (1969). These two specimens share very similar dimensions and morphology, notably with the straight posterior margin and the anterior margin forming a rounded median tip. The straight posterior margin distinguishes MNHN.DEC.32 and MHNT.PAL.2023.9.14 from *Aeduella blainvillei*, *Bourbonnella hirsuta* Štamberg, 2007, *B. jocelynae* Mickle, 2011 and *Neslovicella* spp. (e.g. Heyler 1969; Štamberg 2007, 2010; Mickle 2011). MNHN.DEC.32 and MHNT.PAL.2023.9.14 are very similar to the postrostral of *Westollia crassa* (Pohlig, 1892), with the exception of the posterior end, for which the character is ambiguous (either straight or slightly wavy) (Štamberg 2024). The postrostral of other Aeduellidae is poorly known or unknown, but Heyler (1969)

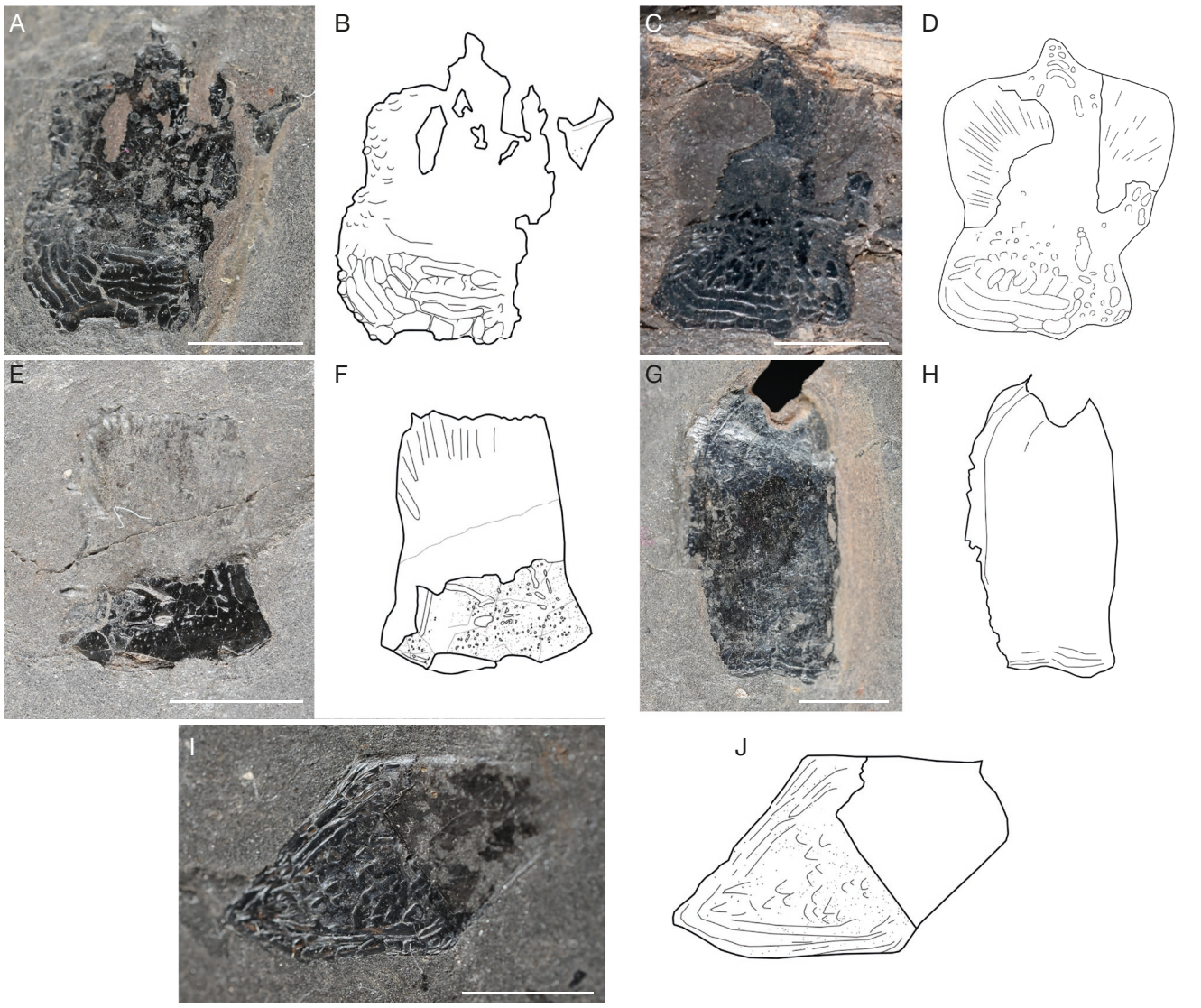


FIG. 5. — Cranial elements of *Decazella vetteri* (Heyler, 1964). Newly discovered (**A**, **B**, **E**-**J**) and comparative (**C**, **D**) specimens: **A**, **B**, rostro-postrostral MHNT.PAL.2023.9.14; **C**, **D**, postrostral MNHN.DEC.32; **E**, **F**, parietal MHNT.PAL.2023.9.30; **G**, **H**, operculum MHNT.PAL.2023.9.14; **I**, **J**, suboperculum MHNT.PAL.2023.9.18. A, C, E, G, I, photographs; B, D, F, H, J, interpretative drawings. Credits: D is reproduced after Heyler (1969: 183, 184, fig. 135). Scale bars: 5 mm.

hypothesised that the posterior edge of the postrostral of *Decazella vetteri* should be straight, based on the shape of its frontal. It is therefore entirely possible to assign MHNT.PAL.2023.9.14 to *Decazella vetteri*.

The parietal MHNT.PAL.2023.9.30 has a short rectangular shape and shows two pit lines forming a V-shaped pattern, allowing us to assign it to Aeduellidae (e.g. Heyler 1969; Poplin & Dutheil 2005). The anterior margin of MHNT.PAL.2023.9.30 is straight, unlike *Neslovicella* spp., *Bourbonnella hirsuta* and *Aeduella blainvillei*, which have V-shaped anterior margins (Heyler 1969; Poplin & Dutheil 2005; Štamberg 2007, 2010). *Decazella vetteri*, *Amelangia ornata* Štamberg & Werneburg, 2023, *Westollia crassa, Bourbonnella fourrieri* Poplin, 2001, *B. guilloti* Heyler, 1967a, *B. jocelynae* and *B. sottyi* (Anonymous, 1972) have straight anterior and posterior edges (Heyler 1969; Poplin & Dutheil 2005; Mickle 2011; Štamberg & Werneburg 2023; Štamberg 2024). MHNT.PAL.2023.9.30 can be distinguished from the parietal of *A. ornata* because in the latter, the parietal is pentagonal with a V-shaped contact with the dermopterotic (Štamberg & Werneburg 2023). The parietals of *W. crassa*, *B. fourrieri*, *B. guilloti*, *B. jocelynae* and *B. sottyi* are similar to those of *D. vetteri*. However, MHNT.PAL.2023.9.3 is closer to the morphology of *D. vetteri* parietals, for example that of holotype MNHN.DEC.25 (Fig. 6; Heyler 1969: 176, fig.121, pl. XLIII, fig. 2).

The operculum of MHNT.PAL.2023.9.14 can be assigned to the Aeduellidae clade based on its large size, rectangular shape and ornamentation (e.g. Heyler 1969; Štamberg 2018). It is twice as high as long, which distinguishes it from the operculum of *Puertollanichthys ritchiei* Forey & Young, 1985, proportionally shorter (Forey & Young 1985).

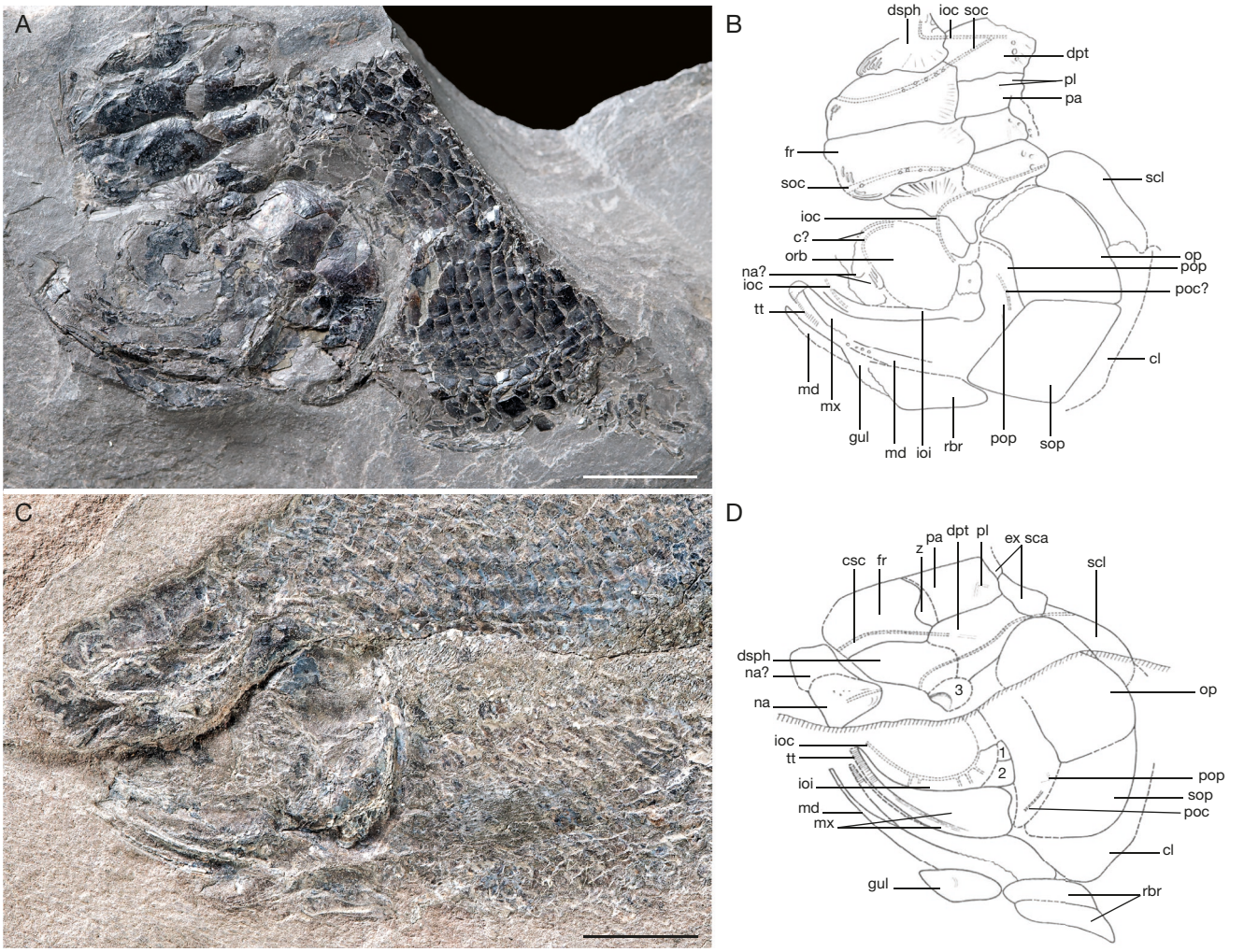


Fig. 6. — *Decazella vetteri* from the Decazeville Basin: **A**, **B**, holotype MNHN.DEC.25; **C**, **D**, referred specimen MNHN.DEC.24. A, C, photographs; B, D, interpretative drawings reproduced after Heyler (1969: 176, 178, figs 121, 122). Abbreviations: **c?**, canal?; **cl**, cleithrum; **dpt**, dermopterotic; **dsph**, dermosphenotic; **ex sca**, extrascapular; **fr**, frontal; **gul**, lateral gular; **ioi**, inferior infraorbital; **ioc**, infraorbital canal; **md**, mandible; **mx**, maxilla; **na**, nasal *sensu lato*; **op**, operculum; **orb**, orbit; **pa**, parietal; **pl**, pit line; **poc**, preoperculum canal; **pop**, preoperculum; **rbr**, branchiostegal ray; **scl**, supracleithrum; **so**, supraorbital; **soc**, supraorbital canal; **sop**, suboperculum; **tt**, tubular teeth; **z**, overlap zone; **1**, **2**, suborbital; **3**, spiracular. Scale bars: 10 mm.

It can also be distinguished from the operculum of *Amelangia ornata*, which has a very characteristic ornamentation with pointed tubercles, the apex of which is oriented posteriorly (Štamberg & Werneburg 2023). It differs from *Platysella* spp. in which the ventral edge of the operculum has a medial hump (Heyler & Poplin 1983). The straight and horizontal ventral margin of MHNT.PAL.2023.9.14 and its 180° bending angle are highly characteristic: indeed, the operculums of *Bourbonnella* spp., *Neslovicella* spp., *Spinarichthys dispersus* (Fritsch, 1895), *Westollia crassa* and *Aeduella blainvillei* have oblique ventral margins and/or a bending angle between 140° and 160° (Heyler 1969; Poplin 2001; Štamberg 1986, 2007, 2010, 2018, 2024). The straight and horizontal ventral margin of MHNT.PAL.2023.9.14 is present only in the operculum of *Decazella vetteri* (Fig. 6; Heyler 1969; Poplin & Dutheil 2005). Note that among the isolated operculums from the Decazeville Basin attributed to Aeduellidae indet. by Heyler (1969), none have an horizontal ventral margin like MHNT.PAL.2023.9.14. The operculums of *D. vetteri* show some variation in their bending angle, amounting to 170° in MNHN.DEC.24 but 140° in the holotype MNHN.DEC.25 (Fig. 6; Heyler 1969: 176, 178, figs 121, 122, pl. XLIII, fig. 2 and pl. XLIV, fig. 5). The 180° bending angle of MHNT.PAL.2023.9.14 may therefore fall within the range of intraspecific variation of this character in *D. vetteri* (which could be between 140° and 180°). We therefore refer the operculum of MHNT.PAL.2023.9.14 to *Decazella vetteri*.

The suboperculum MHNT.PAL.2023.9.18 has a morphology characteristic of Aeduellidae, with a trapezoidal to rectangular shape (e.g. Poplin & Dutheil 2005). Among Aeduellidae, only *Decazella vetteri* (Fig. 6) and *Amelangia ornata* have a parallelogram-shaped suboperculum with a straight suture to the operculum (Heyler 1969; Poplin & Dutheil 2005; Štamberg & Werneburg 2023). However, the suboperculum of *A. ornata* has very characteristic ornamentation with pointed

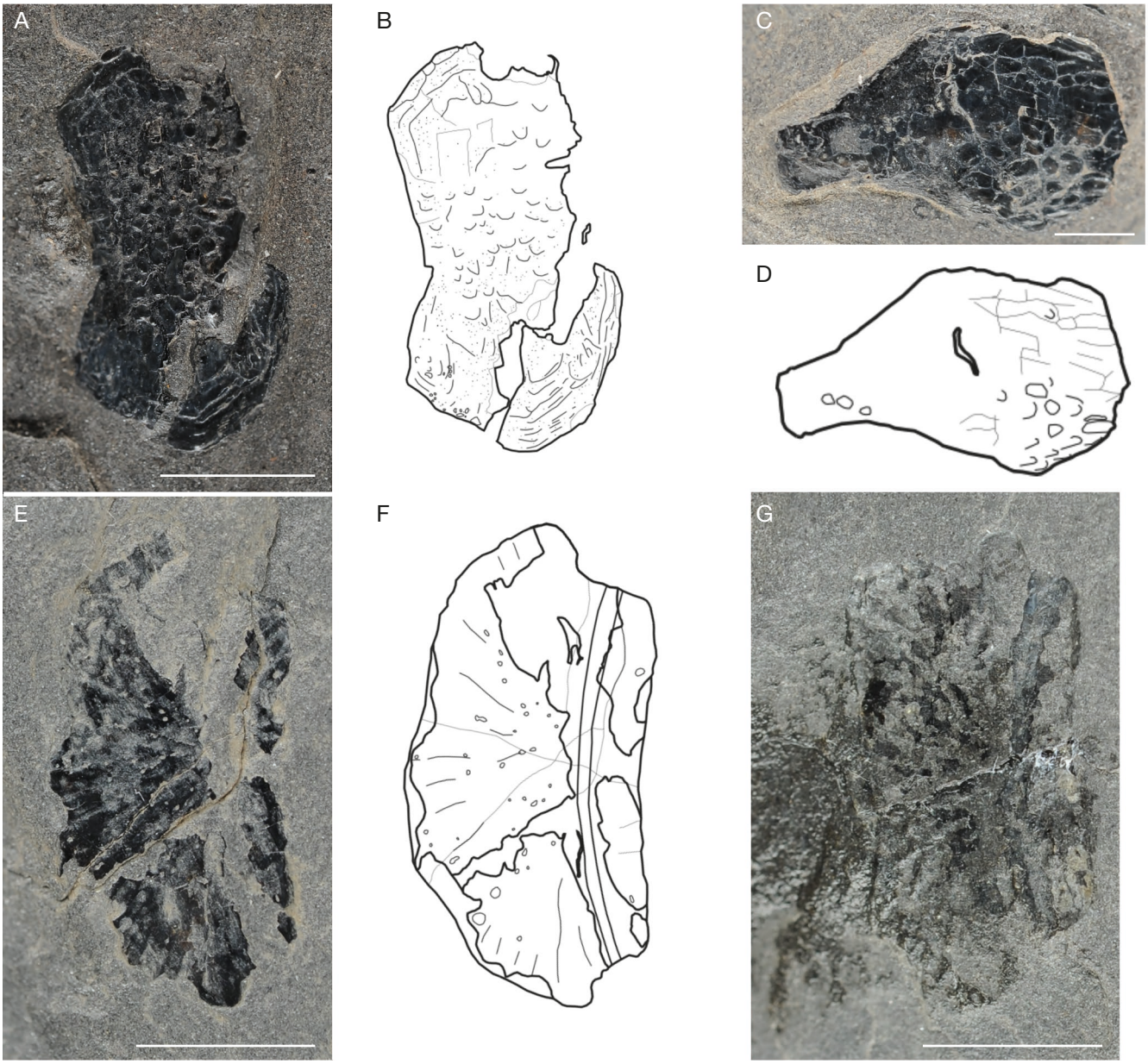


Fig. 7. — Specimens referred to *Aeduella* sp.: **A**, **B**, postrostral MHNT.PAL.2023.9.19; **C**, **D**, medial gular MHNT.PAL.2023.9.12; **E**-**G**, frontal MHNT.PAL.2023.30.3. A, C, E, photographs; B, D, interpretative drawings; G, photograph (reversed) of the specimen counter-part. Scale bars: A, B, E-G, 5 mm; C, D, 2 mm.

tubercles, with the apex oriented posteriorly (Štamberg & Werneburg 2023). This specimen is therefore attributable to *Decazella vetteri* due to its parallelogram shape and lack of characteristic ornamentation.

## Genus *Aeduella* Westoll, 1937

### *Aeduella* sp.
(Figs 7; 8)

Material. — An isolated postrostral (MHNT.PAL.2023.9.19 [Fig. 7A, B]), an isolated frontal (MHNT.PAL.2023.30.3 [Fig. 7E-G]), an isolated operculum (MHNT.PAL.2023.9.21 [Fig. 8A, B]), a suboperculum associated with articulated scales (MHNT.PAL.2023.9.11 [Fig. 8G, H]), an isolated suboperculum (MHNT.PAL.2023.9.10 [Fig. 8E, F]) and a suboperculum associated with a medial gular (MHNT.PAL.2023.9.12 [Fig. 8C, D; 7C, D]).

Description

MHNT.PAL.2023.9.19 (Fig. 7A, B) have a symetric hexagonal shape, with a rounded anterior and posterior edge. It is 15 mm long and 8 mm wide (length/width ratio 2.1), and both its left lateral and posterior edges are damaged. A deformation of the matrix cuts the bone in half and distorts its relief. An ornamentation of flat tubercles is visible on the lateral surface at the posterior edge, reducing towards the anterior edge. No sensory canal or pit lines are visible. This bone is identified here as a postrostral.

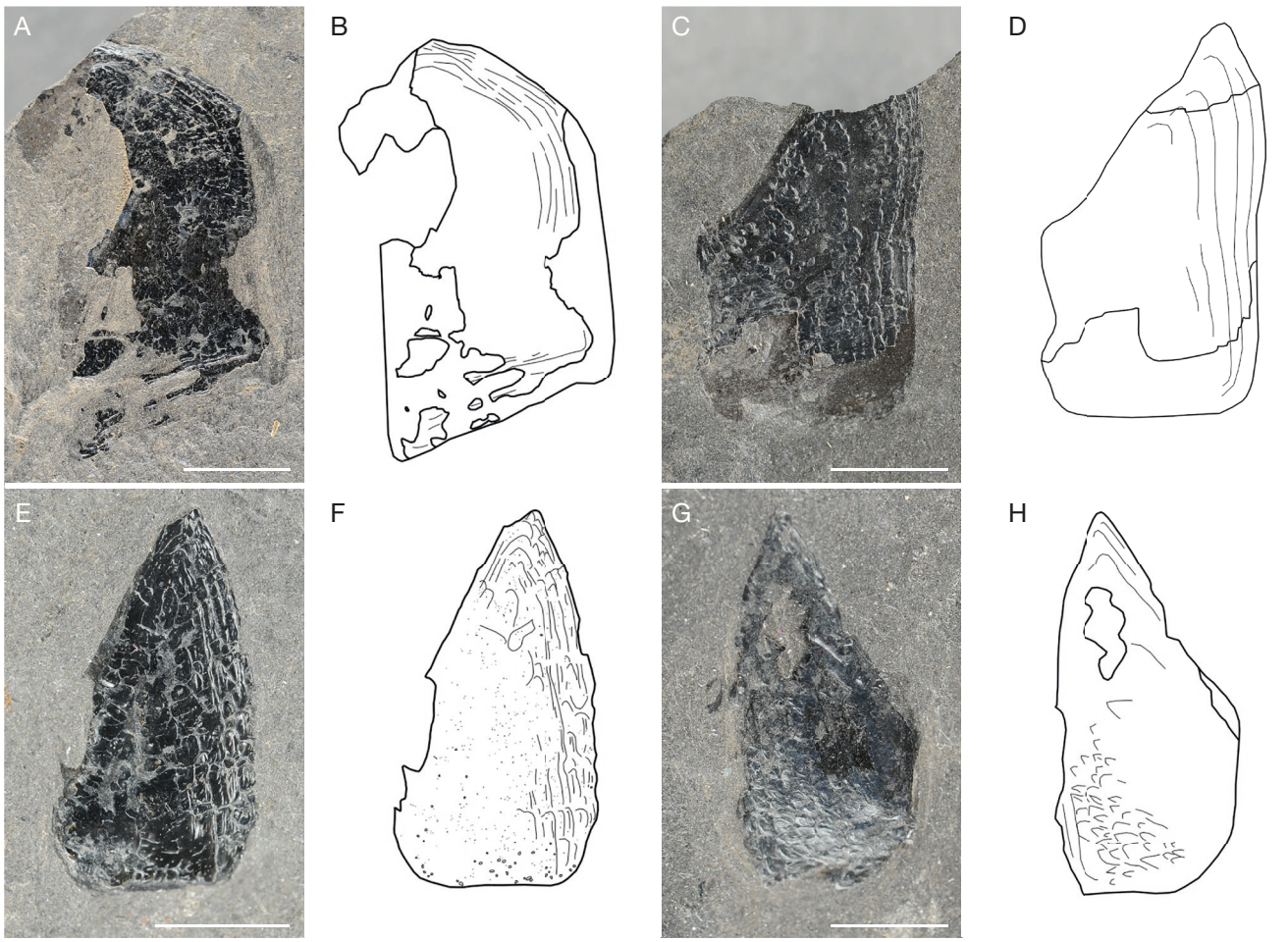


FIG. 8. — Specimens referred to *Aeduella* sp.: **A**, **B**, operculum MHNT.PAL.2023.9.21; **C**, **D**, suboperculum MHNT.PAL.2023.9.12; **E**, **F**, suboperculum MHNT.PAL.2023.9.10; **G**, **H**, suboperculum MHNT.PAL.2023.9.11. A, C, E, G, photographs; B, D, F, H, interpretative drawings; D is also based on the couterpart not figured here. Scale bars: 5 mm.

MHNT.PAL.2023.30.3 (Fig. 7E-G) is an elongated rectangular bone, identified here as a frontal. It is preserved in part and counter-part and measures 13 mm long by 6 mm wide (length/width ratio 2.2). It has V-shaped anterior and posterior margins and has an ornamentation made by light ridges. The supraorbital canal is well marked and runs along the lateral margin of the frontal, making a slight curve.

MHNT.PAL.2023.9.21 (Fig. 8A, B) is an operculum measuring 10 mm long and 20 mm high, with a bending angle of 151°. The ratio between the width of the ventral part and the width of the dorsal part is 0.9. Its bone structure is partially preserved, but its shape is well visible thanks to its imprint on the matrix, with the exception of its dorsal end: this shape is rectangular, with a straight anterior edge, the dorsal and posterior edges rounded dorsally and the ventral edge oblique posterodorsally. It is ornamented with ridges parallel to the bone margins (growth lines) and light, flat tubercles all along its lateral surface.

MHNT.PAL.2023.9.10 (7.5 mm long, anterior part 6 mm high and posterior part 14 mm high; Fig. 8E, F), MHNT.PAL.2023.9.11 (8.2 mm long, anterior part 7 mm high and posterior part 16 mm high; Fig. 8G, H) and MHNT.PAL.2023.9.12 (10 mm long, anterior part 7 mm high and posterior part 16 mm high; Fig. 8C, D) correspond to suboperculum bones as evidenced by their trapezoidal shape, their ornamentation of small flat tubercles on their lateral surface, and their relatively large sizes. MHNT.PAL.2023.9.10 and MHNT.PAL.2023.9.11 are complete, whereas the dorsal end of MHNT.PAL.2023.9.12 is missing but visible on the bone counterpart. The ratio between the depth along the anterior margin and the depth along the posterior margin is 2.3 for these three subopercula. These subopercula described here have a distinctly concave, sloping dorsal margin, while the anterior, posterior and ventral margins are straight.

The suboperculum MHNT.PAL.2023.9.12 is associated with a bone 13 mm further away, identified here as a medial gular (Fig. 7C, D). Its anterior and posterior ends are missing and the lateral margins are damaged, but it measures 9 mm long and 5.5 mm wide as preserved. It is elongated anteroposteriorly, with a slender anterior part and an enlarging medial part. A slightly V-shaped pit line is present in the centre of the gular and the bone is ornamented with flat tubercles over its entire lateral surface.

Comparisons

The postrostral MHNT.PAL.2023.9.19 is a large bone, ornamented with tubercles on the lateral face of its posterior part, with a hexagonal shape and rounded edges. These features allow it to be attributed to the Aeduellidae. With its pointed anterior and posterior margins, MHNT.PAL.2023.9.19 is similar to *Aeduella blainvillei*, *Bourbonnella hirsuta* and *Neslovicella* spp. (e.g. Heyler 1969; Štamberg 2007, 2010). Of these taxa, the hexagonal shape and anterior reduction of the ornamentation of MHNT.PAL.2023.9.19 are identical to the postrostral of *Aeduella blainvillei* (Heyler 1969; Štamberg 2018). Even if the latter is described as pentagonal by Heyler (1969), it has a hexagonal shape (e.g. Heyler 1969: figs 46, 55, 76). These characters suggest that MHNT.PAL.2023.9.19 belongs to *Aeduella blainvillei*, but based on its isolated nature, we prefer cautiously refer it to *Aeduella* sp. only, pending more complete material from the Decazeville Basin.

The frontal MHNT.PAL.2023.30.3 can be confidently assigned to Aeduellidae due to the presence of the supraorbital canal running close to the lateral edge of the bone (Poplin & Dutheil 2005). The V-shaped margins of MHNT.PAL.2023.30.3 are only found on *Neslovicella* spp., *Bourbonnella hirsuta* and *Aeduella blainvillei* (Heyler 1969; Poplin & Dutheil 2005; Štamberg 2007, 2010). MHNT.PAL.2023.30.3 differs from *B. hirsuta* and *Neslovicella* spp. in its elongated shape, whereas the frontals of *Neslovicella* spp. and *B. hirsuta* are broad and short (Štamberg 2007, 2010). The *B. jocelynae* frontal has also a V-shaped posterior margin, but is too poorly preserved for further comparison (Mickle 2011). In contrast, the frontals of *Aeduella blainvillei* are elongated and very similar to MHNT.PAL.2023.30.3. These characters suggest that MHNT.PAL.2023.30.3 belongs to *Aeduella blainvillei*, but, again, its isolated nature push us to refer it cautiously to *Aeduella* sp. only.

The operculum MHNT.PAL.2023.9.21 can be assigned to Aeduellidae on the basis of its large size, rectangular global shape and ornamentation (e.g. Heyler 1969; Štamberg 2018). With its posterodorsally oblique ventral margin and 151° bending angle, MHNT.PAL.2023.9.21 falls within the morphological variation of operculums of *Bourbonnella* spp., *Neslovicella* spp., *Spinarichthys dispersus*, *Westollia crassa* and *Aeduella blainvillei* (Heyler 1969; Poplin 2001; Štamberg 1986, 2007, 2010, 2018, 2024). *Aeduella* and *Decazella* are the only Aeduellidae currently reported from the Bourran Formation, which suggests that MHNT.PAL.2023.9.21 can be attributed to *Aeduella* sp.

The suboperculums MHNT.PAL.2023.9.10-12 are attributable to Aeduellidae due to their trapezoidal shape and ornamentation (e.g. Poplin & Dutheil 2005). The trapezoidal shape and the presence of a distinctly concave, sloping dorsal margin are characteristic of *Aeduella blainvillei* and *Westollia crassa* (e.g. Štamberg 2018, 2024). Among the Aeduellidae specimens with a preserved suboperculum already described from the Bourran Formation, some of them have an identical shape to those described here and were attributed to *Aeduella* sp. by Heyler (1969: 183, fig. 132, pl. XLIV, fig. 6 [see Fig. 8L]). It is very likely that MHNT.PAL.2023.9.10-12 belong to the same taxon. The characteristics of MHNT.PAL.2023.9.10-12 allow them to be assigned to the genus *Aeduella*, but their isolated nature suggests caution about specific attribution. We therefore refer them here to *Aeduella* sp.

The medial gular of MHNT.PAL.2023.9.12 is attributable to Aeduellidae on the basis of its ornamentation and presence of a distinct pit line (e.g. Heyler 1969; Štamberg 2018). In most Aeduellidae, the medial gulars are poorly known because they are either masked by other skull bones in articulated specimens, or not preserved as isolated bones in disarticulated specimens (e.g. Heyler 1969; Heyler & Poplin 1983; Štamberg 2007). Among the Aeduellidae, *Aeduella blainvillei* is the only known taxon in which the median gular has a sharply tapered anterior end and an enlarged posterior part (Štamberg 2018). Although the median gular of *Decazella vetteri* is unknown, the difference between the median gular of *A. blainvillei* and that of other aeduellids suggests that this morphology is diagnostic of the species (e.g. Heyler 1969; Štamberg 2018, 2024; Štamberg & Werneburg 2023). The characters of this specimen and its isolated nature therefore allow us to assign it to *Aeduella* sp.. This attribution is consistent with that of the associated suboperculum on MHNT.PAL.2023.9.12, and could possibly suggest that they belong to the same individual.

## Family Aeduellidae Romer, 1945, *sensu* Štamberg, 2007

### Aeduellidae indet.
(Figs 9-11)

Material. — An isolated anterior supraorbital (MHNT.PAL.2023.9.3 [Fig. 9A, B]), an isolated maxilla (MHNT.PAL.2023.9.5 [Fig. 9E, H]), (MHNT.PAL.2023.30.1a and MHNT.PAL.2023.30.1b [respectively Fig. 9F, I, G, J]), an isolated dentary (MHNT.PAL.2023.30.4 [Fig. 9C, D]), two isolated operculums (MHNT.PAL.2023.9.17 [Fig. 10C, E]; MHNT.PAL.2023.9.22 [Fig. 10A, B]), six isolated cleithra (MHNT.PAL.2023.9.13 [Fig. 10I-K]; MHNT.PAL.2023.9.15 [Fig. 10G, H]; MHNT.PAL.2023.9.23, MHNT.PAL.2023.9.27, MHNT.PAL.2023.9.28 and MHNT.PAL.2023.30.2), four isolated supracleithra (MHNT.PAL.2023.9.7, MHNT.PAL.2023.9.8 [Fig. 10N, O]; MHNT.PAL.2023.9.9 [Fig. 10L, M]; MHNT.PAL.2023.9.16 [Fig. 10P, Q]), two isolated indeterminate cranial bones (MHNT.PAL.2023.9.4 [Fig. 10D, F]; and MHNT.PAL.2023.9.38), an isolated ridge scale (MHNT.PAL.2023.9.6 [Fig. 11D]), articulated scales (MHNT.PAL.2023.9.20 [Fig. 11A]; MHNT.PAL.2023.9.24 [Fig. 11B]; MHNT.PAL.2023.9.25) and isolated scales (MHNT.PAL.2023.9.26; Fig. 11C]; MHNT.PAL.2023.9.42).

Description

MHNT.PAL.2023.9.3 (Fig. 9A, B) is an oblong bone, measuring 4.5 mm by 1.5 mm. It is strongly ornamented with dorsoventrally elongated ridges and interpreted here as the anterior supraorbital. Its shape is ovoid-to-L-shaped, with rounded edges and a wider dorsal region.

MHNT.PAL.2023.9.5 (Fig. 9E, H) is clearly identifiable as a maxilla, while MHNT.PAL.2023.30.1 has two associated maxillae (Fig. 9F-I, G-J). The maxilla MHNT.PAL.2023.9.5 is 21 mm long, 10 mm wide posteriorly (length/width

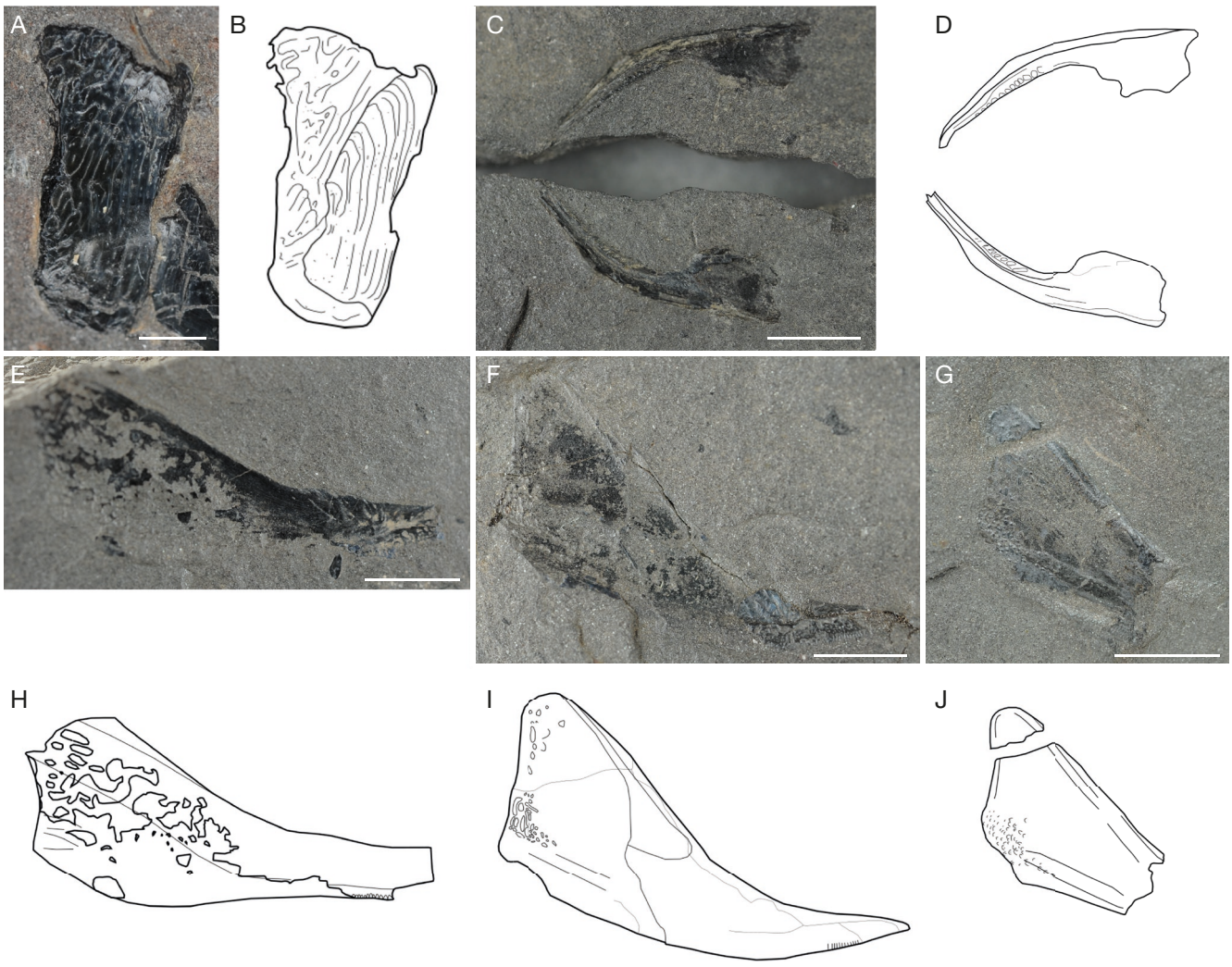


Fig. 9. — Specimens referred to Aeduellidae indet.: **A**, **B**, anterior supraorbital (see text) MHNT.PAL.2023.9.3; **C**, **D**, dentary MHNT.PAL.2023.30.4 (part and counterpart); **E**, **H**, maxilla MHNT.PAL.2023.9.5; **F**, **G**, **I**, **J**, associated maxillae MHNT.PAL.2023.30.1a (**F**, **I**) and MHNT.PAL.2023.30.1b (**G**, **J**). A, C, E-G, photographs; B, D, H-J, interpretative drawings. Scale bars: A, B, 2 mm; C-J, 5 mm.

ratio 2.1) and 5 mm wide anteriorly. The bone is missing in some areas, but is visible as a counterprart on the matrix, and the postero-dorsal part and the anterior tip of the bone are missing. Tubular teeth are only preserved in the most anterior region of the ventral margin of the maxilla. No flat tubercle ornamentation is visible on MHNT.PAL.2023.9.5, but it is distinguishable on its counterpart. In MHNT.PAL.2023.30.1, the two associated maxillae are 36 mm apart. The more complete of the two (MHNT.PAL.2023.30.1a) is fully preserved and measures 25 mm long by 10 mm wide posteriorly (length/width ratio of 2.5) and 3 mm wide anteriorly. The second maxilla MHNT.PAL.2023.30.1b preserves only its posterior part and measures 20 mm wide posteriorly. Tubular teeth are only visible on MHNT.PAL.2023.30.1a but the ornamentation, composed of flat tubercles, is visible on the lateral face of the posterior part of both MHNT.PAL.2023.30.1a and MHNT.PAL.2023.30.1b. The identical dimensions and morphology of these maxillae MHNT.PAL.2023.30.1a and MHNT.PAL.2023.30.1b suggest they belong to the same individual.

MHNT.PAL.2023.30.4 (Fig. 9C, D) is a dentary preserved in part and counterpart, its anterior end is missing. It measures 13 mm long, 6 mm wide posteriorly (length/width ratio of 2.1) and 1.3 mm wide anteriorly, is curved and presents a longitudinal mandibular canal as well as mandibular pores appearing as alveolar cavities. The posterior part is enlarged and rectangular and form the dentary plate.

MHNT.PAL.2023.9.17 (Fig. 10C, D) and MHNT.PAL.2023.9.22 (Fig. 10A, B) are both partial operculums: MHNT.PAL.2023.9.17 is rounded as preserved, of 14 mm of diameter, and slightly ornamented by ridges, which are parallel to the bone edges (growth lines), and flat tubercles on its lateral surface. MHNT.PAL.2023.9.22 is rectangular as preserved, of 20 mm of anterior margin, and strongly ornamented by wrinkles parallel to the bone edges (growth lines) and flat tubercles on its lateral surface, along the growth lines.

MHNT.PAL.2023.9.4 (Fig. 10E, F) is an partial indeterminate cranial bone, ornamented with several ridges parallel to its edges (growth lines) and visible on its lateral surface. Only a portion is preserved, measuring 7 mm long and 5 mm

wide. Its incomplete nature prevents further identification. The shape of the ornamentation is similar to that of a postrostral bone, but the bone is too incomplete to confirm this.

MHNT.PAL.2023.9.38 is also a partial indeterminate cranial bone, ornamented with several ridges that follow its curvature. Its preserved portion is ovoid, of 7 mm long and 3 mm wide. Its incomplete nature renders its identification impossible.

MHNT.PAL.2023.9.13 (14 mm long and 27 mm high [Fig. 10I-K]), MHNT.PAL.2023.9.15 (13 mm long and 26 mm high [Fig. 10G, H]), MHNT.PAL.2023.9.23 (4.5 mm long and 10 mm high), MHNT.PAL.2023.9.27 (2.3 mm long and 4.5 mm high), MHNT.PAL.2023.9.28 (5 mm long and 9 mm high) and MHNT.PAL.2023.30.2 (13 mm long and 25 mm high) are all identifiable as cleithra. They are ovoid in shape with a very pronounced relief, and have a large ridge that runs dorsoventrally and separates them into two branches (lateral and ventral). The lateral branch of these cleithra is elliptical and ornamented with marked ridges and a dorsally extending process and a concave anterior edge. The ventral branch is much narrower, has a concave edge and forms a ventrally extending process. MHNT.PAL.2023.9.13, MHNT.PAL.2023.9.23 and MHNT.PAL.2023.30.2 are preserved as parts and counterparts. The dorsal process of the lateral branch of MHNT.PAL.2023.9.15 is partly missing. MHNT.PAL.2023.9.27 and MHNT.PAL.2023.9.28 are complete.

MHNT.PAL.2023.9.8 (15 mm high and 4 mm long, length/width ratio 3.75 [Fig. 10L, M]), MHNT.PAL.2023.9.9 (11 mm high and 4 mm long, incomplete [Fig. 10N, O]) and MHNT.PAL.2023.9.16 (18 mm wide and 5 mm high, length/width ratio 3.6 [Fig. 10P, Q]) are elliptical, dorsoventrally elongated bones, and all with a sensory canal passing through the first dorsal quarter of the bone. They are identified here as supracleithra and the sensory canal as the lateral canal. The supracleithrum process is clearly visible on all specimens except MHNT.PAL.2023.9.7 which is not complete: this process forms a small dorsal projection. MHNT.PAL.2023.9.7 (10 mm high and 5 mm wide) preserves only its ventral half, but its shape and ornamentation are also characteristic of a supracleithrum. MHNT.PAL.2023.9.8 and MHNT.PAL.2023.9.9, preserved laterally, are ornamented with longitudinal ridges and a few flattened tubercles on their lateral surface. MHNT.PAL.2023.9.9 is also preserved by its dorsal half. MHNT.PAL.2023.9.16, preserved in medial view, presentmedially by two strong crests (crista anterior and crista posterior). The crista anterior starts from the lateral canal, runs ventrally and ends along the anterior margin of the bone. The crista posterior also starts from the lateral canal and ends at the last quarter of the posterior margin of the bone.

MHNT.PAL.2023.9.6 (Fig. 11D) is an isolated hexagonal to oval ridge scale (6.5 mm wide by 10 mm long) covered with a thin layer of ganoine. It has no serrations and its ornamentation consists of light growth lines and marked ridges. A marked ridge runs longitudinally across its middle, dividing it into two regions (left and right) of equal size. MHNT.PAL.2023.9.20 (Fig. 11A) comprises five articulated scales, with four scales located in the same horizontal row and one straddling the second and third scales in this row. These scales are rhombic and also covered with a thin layer of ganoine. They have no serrations and their ornamentation consists of light growth lines. MHNT.PAL.2023.9.24 (Fig. 11B) comprises two articulated scales on the same vertical row. They are semi-rectangular in shape and also covered with a thin layer of ganoine. They have slight serrations on their posterior edge (nine on the dorsalmost scale and eight on the ventralmost scale) and their ornamentation consists of light growth lines. MHNT.PAL.2023.9.25 includes two disarticulated scales, fragments of scales and the impression of four articulated scales in the same vertical row. These scales are semi-rectangular in shape and covered with a thin layer of ganoine. They have light serrations on their posterior edge and their ornamentation also consists of slight growth lines. One scale shows a peg process. MHNT.PAL.2023.9.26 (Fig. 11C) comprises a rectangular isolated scale covered with a thin layer of ganoine. Its dorsal part is missing but this scale shows eleven serrations on its posterior margin and its ornamentation consists of light growth lines. At least, MHNT.PAL.2023.9.42 is an isolated rhombic scale covered with a thin layer of ganoine. It has no serrations and its ornamentation consists of light growth lines.

### Comparisons

The anterior supraorbital MHNT.PAL.2023.9.3 is ornamented with parallel ridges and ovoid-to-L-shaped: these features allow it to be assigned to Aeduellidae (Heyler 1969; Poplin & Dutheil 2005). This anterior supraorbital is not fused with a nasal, whereas other known aeduellid specimens show nasals fused to the anterior supraorbital: this variation in the fusion of the bones has already been observed within the Aeduellidae by Heyler (1969) and Štamberg (2007, 2018, 2024). The fusion of the nasal bone with the anterior supraorbital bone forms a bone which is sometimes referred to as the nasal *sensu lato* (Heyler 1969). The ovoid shape and ornamentation of MHNT.PAL.2023.9.3 are key features which are found in *Aeduella blainvillei* (Štamberg 2018). However, the nasal region of *Decazella vetteri*, which remains poorly described, could also correspond to the morphology observed in MHNT.PAL.2023.9.3 (Heyler 1969). Pending a more precise description of the nasal region of *D. vetteri*, we prefer staying prudent and referring MHNT.PAL.2023.9.3 to Aeduellidae indet.

The three maxillae MHNT.PAL.2023.9.5 and MHNT.PAL.2023.30.1a-b are very similar in morphology and proportions, suggesting the same taxon. They are attributable to Aeduellidae on the basis of their low triangular shape, their widen posterior region, and their ornamentation with flat tubercles and their tubular teeth (Heyler 1969; Poplin & Dutheil 2005). Within the Aeduellidae, characters can be used to distinguish the maxillae: the absence of a prominent posteroventral angle and a length/width ratio between 2.1 and 2.5 in MHNT.PAL.2023.9.5 and MHNT.PAL.2023.31.1a, MHNT.PAL.2023.31.1b, however, suggest that they are related to *Bourbonnella* spp., *Neslovicella* spp., *Decazella vetteri*, *Amelangia ornata*, *Westollia crassa* or *Aeduella blainvillei* (Heyler 1969; Štamberg 2007, 2010, 2018, 2024;

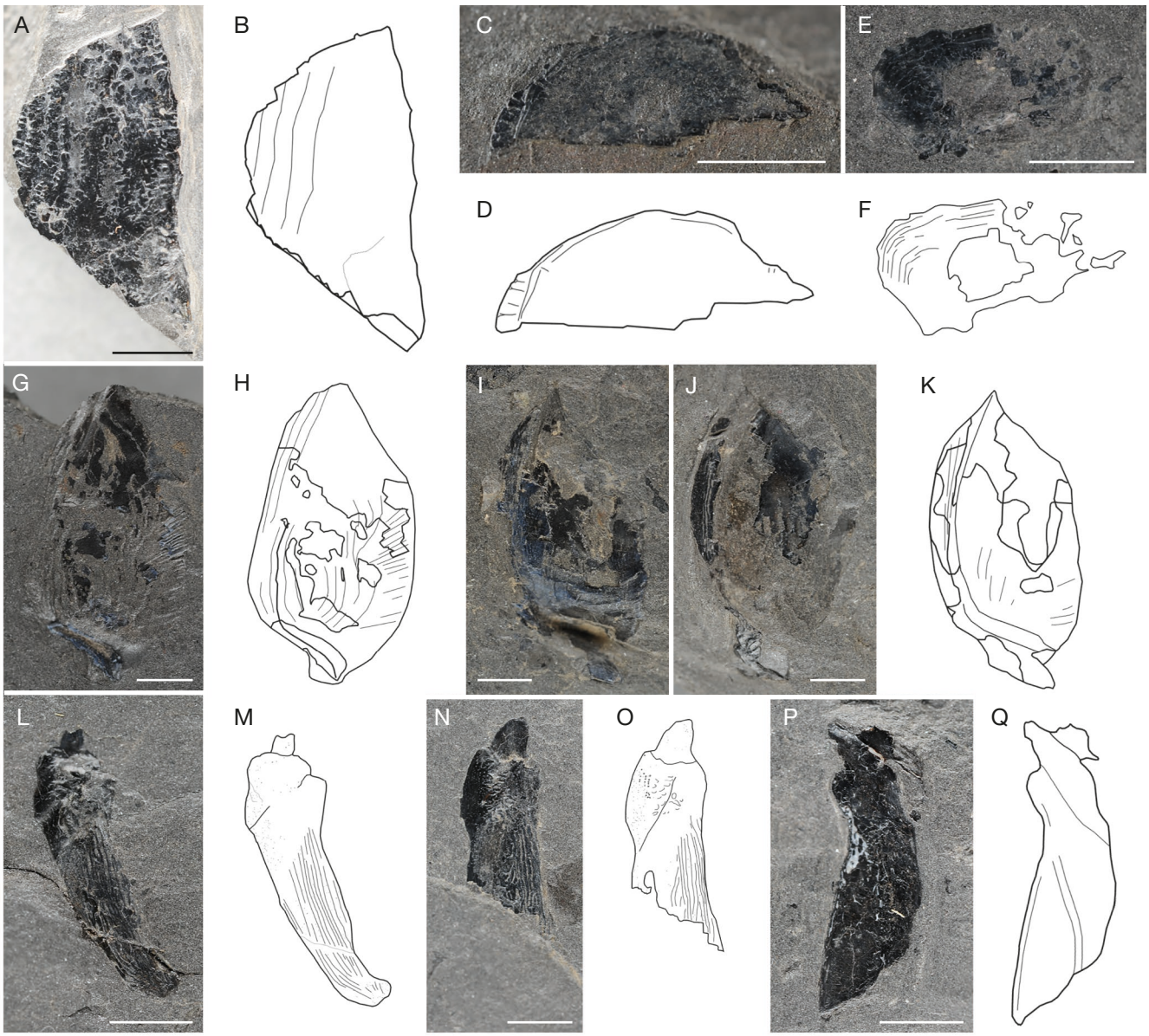


FIG. 10. — Specimens referred to Aeduellidae indet.: **A**, **B**, partial operculum MHNT.PAL.2023.9.22; **C**, **D**, partial operculum MHNT.PAL.2023.9.17; **E**, **F**, indeterminated skull bone MHNT.PAL.2023.9.4; **G**, **H**, cleithrum MHNT.PAL.2023.9.15; **I**-**K**, cleithrum MHNT.PAL.2023.9.13; **L**, **I**, supracleithrum MHNT.PAL.2023.9.8; **N**, **O**, supracleithrum MHNT.PAL.2023.9.9; **P**, **Q**, supracleithrum MHNT.PAL.2023.9.16). I is reversed. A, C, E, G, I-J, L, N, O, photographs; B, D, F, H, K, M, O, Q, interpretative drawings. Scale bars: 5 mm.

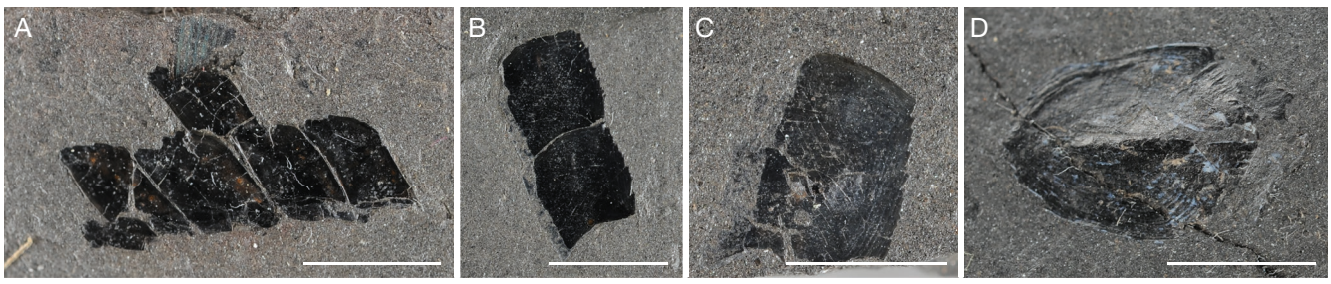


FIG. 11. — Scales referred to Aeduellidae indet.: **A**, articulated scales MHNT.PAL.2023.9.20; **B**, articulated scales MHNT.PAL.2023.9.24; **C**, isolated scale MHNT.PAL.2023.9.26; **D**, isolated ridge scale MHNT.PAL.2023.9.6. A-D, photographs. Scale bars: 5 mm.

Štamberg & Werneburg 2023). As it is impossible to assign MHNT.PAL.2023.9.5 and MHNT.PAL.2023.31.1a, MHNT.PAL.2023.31.1b to any of these taxa in particular, we prefer referring them to Aeduellidae indet.

The dentary MHNT.PAL.2023.30.4 does not preserve any tubular teeth that would allow to assign it confidently to Aeduellidae (Poplin & Dutheil 2005). However, its general curvature, its gracile morphology, the shape of the dentary plate and the presence of a mandibular canal support an attribution within Aeduellidae (Heyler 1969; Poplin & Dutheil 2005). As with the maxillae described above, there are distinct dentaries within the Aeduellidae: the dentary plate of MHNT.PAL.2023.30.4 resembles that of *Bourbonnella* spp., *Neslovicella* spp., *Decazella vetteri*, *Amelangia ornata, Westollia crassa* or *Aeduella blainvillei* (Heyler 1969; Štamberg 2007, 2010, 2018, 2024; Štamberg & Werneburg 2023). Once again, as it is impossible to choose here, we refer MHNT.PAL.2023.30.4 to Aeduellidae indet.

The operculums MHNT.PAL.2023.9.22 and MHNT.PAL.2023.9.17 are attributed to Aeduellidae on the basis of their typical ornamentation, size and shape (e.g. Poplin & Dutheil 2005). This is consistent with the multiple presence of Aeduellidae remains in the La Découverte locality (Vetter 1968; Heyler 1969, 2000; this study). Due to the partial nature of MHNT.PAL.2023.9.17 and MHNT.PAL.2023.9.22, it is impossible to compare them with the operculums of known Aeduellidae, including those from the Bourran Formation. Consequently, we refer them to Aeduellidae indet.

The indeterminate cranial bones MHNT.PAL.2023.9.4 and MHNT.PAL.2023.9.38 are attributed to Aeduellidae on the basis of their ornamentation and, to a lesser degree, of the great abundance of various remains of this family in the Bourran Formation (Heyler 1969; Poplin & Dutheil 2005). Their shape and ornamentation rule out their identification as scapular bones, but it is difficult to assign them to a particular series of cranial bones MHNT.PAL.2023.9.4 ornamentation is similar with the postrostrals of *Decazella vetteri* (Fig. 5A-D), but its very partial nature calls for caution in its identification. Moreover, considering the preservation state of MHNT.PAL.2023.9.4 and MHNT.PAL.2023.9.38, it is preferable to assign them to Aeduellidae indet.

The cleithra MHNT.PAL.2023.9.13, MHNT.PAL.2023.9.15, MHNT.PAL.2023.9.23, MHNT.PAL.2023.9.27, MHNT.PAL.2023.9.28 and MHNT.PAL.2023.30.2 can be assigned to Aeduellidae on the basis of their ovoid shape, ornamentation and morphology of their two branches (lateral and ventral) (Heyler 1969; Štamberg 2007, 2010, 2018). Their ovoid and elongated shape and their both dorsal and ventral processes resemble those of the cleithra of *Neslovicella* spp., *Aeduella blainvillei*, *Bourbonnella* spp., *Decazella vetteri, Westollia crassa* and *Amelangia ornata* (Heyler 1969; Poplin 2001; Poplin & Dutheil 2005; Štamberg 2007, 2010, 2018, 2024; Štamberg & Werneburg 2023). Given the similarity between cleithra of different Aeduellidae, it is preferable to refer MHNT.PAL.2023.9.13, MHNT.PAL.2023.9.15, MHNT.PAL.2023.9.23, MHNT.PAL.2023.9.27, MHNT.PAL.2023.9.28 and MHNT.PAL.2023.30.2 to Aeduellidae indet. MHNT.PAL.2023.9.23, MHNT.PAL.2023.9.27 and MHNT.PAL.2023.9.28 are smaller, rounder, less ornamented and with less relief than MHNT.PAL.2023.9.13, MHNT.PAL.2023.9.15 and MHNT.PAL.2023.30.2. These differences in morphology and size suggest that MHNT.PAL.2023.9.23, MHNT.PAL.2023.9.27 and MHNT.PAL.2023.9.28 are juvenile individuals.

The supracleithra MHNT.PAL.2023.9.7, MHNT.PAL.2023.9.8, MHNT.PAL.2023.9.9 and MHNT.PAL.2023.9.16 can be assigned to Aeduellidae on the basis of their ornamentation, the presence of the lateral canal, their proportions as well as the cristae observed on MHNT.PAL.2023.9.16 (Heyler 1969; Štamberg 2007, 2010, 2018). The morphology of the supracleithrum differs only slightly between the different Aeduellidae species. The arrangement of the anterior and posterior cristae of MHNT.PAL.2023.9.16 are identical to what observed in *Neslovicella rzehaki* and *Aeduella blainvillei* (Štamberg 2007, 2018). However, these data are missing for most other Aeduellidae for which the supracleithrum is not known in medial view. MHNT.PAL.2023.9.7, MHNT.PAL.2023.9.8 and MHNT.PAL.2023.9.9 show ornamentation found in all Aeduellidae, including previously described specimens of *Decazella vetteri* from the Bourran Formation (e.g. MNHN.DEC.24 and MNHN.DEC.30, Heyler 1969: figs 122, 123). Given the similarity between the supracleithra of different Aeduellidae, it is preferable to refer MHNT.PAL.2023.9.8, MHNT.PAL.2023.9.9 and MHNT.PAL.2023.9.16 to Aeduellidae indet.

The scales MHNT.PAL.2023.9.20, MHNT.PAL.2023.9.24, MHNT.PAL.2023.9.25, MHNT.PAL.2023.9.26 and MHNT.PAL.2023.9.42 can be assigned to Aeduellidae on the basis of their rectangular to rhombic shape, thin ganoine layer and peg and socket articulation when present (e.g. Heyler 1969; Yankevich & Minich 1998; Štamberg 2007, 2018). The ridge scale MHNT.PAL.2023.9.6 can be assigned to Aeduellidae on the basis of its hexagonal to oval shape, its thin ganoid layer and the presence of a marked median longitudinal ridge (e.g. Heyler 1969; Štamberg 2007, 2018). This attribution is consistent with the multiple presence of Aeduellidae remains in the La Découverte locality (Vetter 1968; Heyler 1969, 2000; this study). In Aeduellidae, the shape and ornamentation of the scales vary greatly depending on their position on the body and the individual age of the specimens (e.g. Štamberg 2007, 2018). The flank scales through which the lateral sensory canals pass are the largest scales, rectangular in shape, and with a posterior margin showing marked serrations (e.g. Štamberg 2007). Flank scales in the anterior region are rectangular in shape, with marked serrations on their posterior margin (e.g. Štamberg 2007). The isolated scale MHNT.PAL.2023.9.26 is rectangular with serrations, which may correspond to a scale in the anterior part of the flanks or to a scale through which the lateral canal passes. These serrations become less and less distinct, and the shape of the scales becomes rhombic towards the posterior, ventral and dorsal regions (e.g. Štamberg 2007). The scales MHNT.PAL.2023.9.24 and MHNT.PAL.2023.9.25 have a semi-rectangular shape with small serrations, corresponding to an

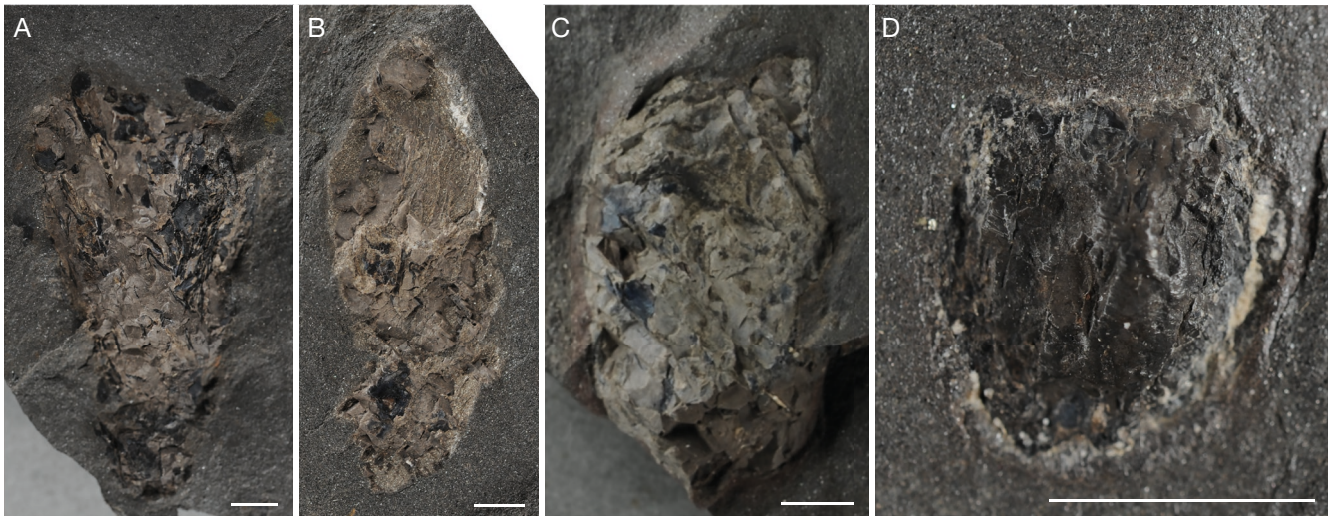


Fig. 12. — Coprolites of Morphotype 1 (**A**-**C**) and 2 (**D**): **A**, MHNT.PAL.2023.9.54; **B**, MHNT.PAL.2023.9.57; **C**, MHNT.PAL.2023.9.53); **D**, MHNT.PAL.2023.9.56. Scale bars: 5 mm.

intermediate morphology between the scales of the anterior region and those of the extremities of the posterior, ventral or dorsal regions. The scales MHNT.PAL.2023.9.20 and MHNT.PAL.2023.9.42 are rhombic and devoid of serrations, corresponding to scales at the ends of the posterior, ventral or dorsal regions. Due to their position anterior to the dorsal fin, they are rarely distinct on articulated specimens (e.g. Heyler 1969). The scales of Aeduellidae are particularly well known, but do not allow to distinguish taxa (e.g. Štamberg 2007, 2018). Similarly, the ridge scales of Aeduellidae are still poorly documented and currently do not allow more precise attributions (Heyler 1969; Štamberg 2007, 2018). The scales described here cannot be attributed to one of the two Aeduellidae known from the Bourran Formation (*Aeduella* and *Decazella*) (Heyler 1969). We therefore refer MHNT.PAL.2023.9.6, MHNT.PAL.2023.9.20, MHNT.PAL.2023.9.24, MHNT.PAL.2023.9.25, MHNT.PAL.2023.9.26 and MHNT.PAL.2023.9.42 to Aeduellidae indet.

## ICHNOTAXONOMY

The coprolites from the ANLD described here can be classified into two morphotypes.

### Morphotype 1
### (Fig. 12A-C)

Material. — Five specimens (MHNT.PAL.2023.9.53 [Fig. 12C]; MHNT.PAL.2023.9.54 [Fig. 12A]; MHNT.PAL.2023.9.55, MHNT.PAL.2023.9.57 [Fig. 12B]; MHNT.PAL.2023.9.58).

#### Description

The specimens of this morphotype have an ovoid shape that tapers at one end. Size does not exceed 65 mm in length and 20 mm in width. The coprolites are brown to light gray in color, with an irregular, fragmented surface. This fragmentation does not permit the observation of a potential external morphology, such as a spiral pattern. These coprolites contain inclusions of small bone fragments and numerous small scales. These scales belong to Aeduellidae based one their rectangular to rhombic shape, their possible slight serrations on the posterior margin, and their ornamentation composed of light growth lines. Within the coprolites, they are preserved either in relatively dense localized patches in which they are more or less oriented (Fig. 12A, B), or they are more regularly spread as regular cluster in the whole volume of the coprolites (Fig. 12 C). These scales are identical to those found isolated or articulated on the La Découverte Member described above. The bone fragments observed on the surface cannot be determined due to their fragmentary and altered condition.

#### Comparisons

Among the coprolite morphotypes described by Hunt & Lucas (2012), Morphotype 1 herein described is close to Morphotypes F2, F3 and F4 in its ovoid shape (Hunt & Lucas 2012). However, Morphotype 1 cannot be assigned to one of these morphotypes as its preservation does not allow to see whether it is spiraled or not. This is a key feature as amphipolar spirality characterizes Morphoptype F2 while microscopic heteropolar spirality characterizes Morphotype F3 and macroscopic heteropolar spirality characterizes Morphotype F4 (Hunt & Lucas 2012).

According to the nomenclature of Hunt & Lucas (2012), Morphotype F2 includes the ichnogenera *Hyronocoprus* Hunt, Lucas & Spielmann, 2005a, *Kalocoprus* Hunt, Lucas, Spielmann, Cantrell & Suazo, 2012, *Elacacoprus* Hunt, Lucas, Spielmann, Cantrell, Suazo & Lerner, 2012 and *Iuloeidocoprus* Hunt, Lucas & Spielmann, 2012a (Hunt *et al.* 2005a, 2012b, c, d), Morphotype F3 includes *Heteropolacoprus* Hunt, Lucas & Lockley, 1998, *Saurocoprus* Hunt, Lucas, Spielmann & Lerner, 2007, *Strabelocoprus* Hunt, Lucas &

Spielmann, 2012b, *Malericoprus* Hunt, Lucas, Spielmann & Lerner, 2007 and *Megaheteropolacopros* Hunt, Lucas & Spielmann, 2005b (Hunt *et al.* 1998, 2005b, 2007, 2012b; Hunt & Lucas 2012), and Morphotype F4 includes *Liassocoprus* Hunt, Lucas, Spielmann & Lerner, 2007, *Crassocoprus* Hunt, Lucas, Spielmann, Cantrell, Suazo & Lerner, 2012 and *Speiracoprus* Hunt, Lucas, Spielmann, Cantrell, Suazo & Lerner, 2012 (Hunt *et al.* 2007, 2012d). In their review of Carboniferous and Permian coprolites, Hunt & Lucas (2013) mention very few European specimens. However, coprolites corresponding or likely to correspond to Morphotype F4 have been described from the Carboniferous-Permian basins of Autun (France), Montceau-les-Mines (France), Puertollano (Spain) and Krkonoše-Piedmont (Czech Republic) (Renault 1900; Poplin 1994; Štamberg *et al.* 2016; Mercuzot *et al.* 2022; Soler-Gijón & Ruiz 2023). Some of these coprolites have inclusions of actinopterygian scales and bone fragments (e.g. Poplin 1994; Štamberg *et al.* 2016). Krzykawski *et al.* (2014) described a coprolite from the Upper Carboniferous of Poland with inclusions of vertebrate bony elements and whose external structure is too poorly preserved to distinguish potential spirality. This coprolite is very similar to Morphotype 1 and presents the same identification problems. It has been cautiously attributed to a large actinopterygian (Krzykawski *et al.* 2014), but it cannot be ruled out that it may also have been produced by a chondrichthyan.

The poor preservation of Morphotype 1 specimens makes identification difficult, but it seems to correspond more to either Morphotype F2, Morphotype F3 or Morphotype F4. Both morphotypes have been identified as having been produced in the vast majority of cases by chondrichthyans (e.g. Hunt & Lucas 2012; Hunt *et al.* 1998; 2005a, b, 2012b, c, d). Furthermore, coprolites found in the Permo-Carboniferous basins of Europe belong almost exclusively to Morphotype F4. Taken together, these data point to a close relationship between the Morphotype 1 described here and the Morphotype F4 of Hunt & Lucas (2012). Morphotype 1 could therefore potentially have been produced by a large chondrichthyan. Given our current knowledge of the fauna of the Bourran Formation, *Orthacanthus* seem a likely candidate.

### Morphotype 2
### (Fig. 12D)

Material. — One specimen (MHNT.PAL.2023.9.56 [Fig. 12D]).

#### Description
The only specimen of this morphotype is subspherical in shape, with a smooth surface. It measures 8.5 mm in diameter and is dark gray to black in color, with a thin whitish layer surrounding it. The specimen contains few small bone fragments and small scales in the form of inclusions, separated from each other. The scales can be attributed to Aeduellidae indet. Based on their rectangular to rhombic shape, their light to absent serrations on their posterior margin, and their ornamentation composed of light growth lines. These scales are identical to those found isolated or articulated on the La Découverte Member described above. The bone fragments observed on the surface cannot be determined due to their fragmentary and altered state.

#### Comparisons
Of the coprolite morphotypes described by Hunt & Lucas (2012), Morphotype 2 described here is close to Morphotype C1 in its subspherical shape and relatively small size, but differs in age and nature of inclusions (Hunt & Lucas 2012).

The white layer covering MHNT.PAL.2023.9.56 probably represents phosphate deposits resulting from the digestion of organic bone matter (e.g. Mercuzot *et al.* 2022). The presence of Aeduellidae scales, together with the depositional environment and fauna present in the Bourran Formation, suggests that the producer of Morphotype 2 was a carnivorous aquatic vertebrate. Morphotype 2 could have been produced by a small aquatic vertebrate, perhaps a xenacanth or a carnivorous actinopterygian (e.g. *Progyrolepis*).

## DISCUSSION

### The aquatic fauna and trophic relationships at the La Découverte locality
These new discoveries allow to reconstruct the trophic relationships of the aquatic fauna from the Bourran Formation of the Decazeville Basin. Derived edentulous acanthodids are microphagous predators that feed on zooplankton, e.g. Conchostracea, Ostracoda (e.g. Burrow 2021). Aeduellids and amblypterids are actinopterygians with specialised tubular dentition, mainly feeding on aquatic invertebrates such as conchostraceans (e.g. Dietze 2001; Štamberg 2020). The snout of the amblypterids is proportionally shorter than that of aeduellids, their suspensorium is inclined anteriorly, and the posterior part of the jaw of the amblypterids is deeper than in aeduellids, suggesting the presence of more powerful muscles (e.g. Štamberg 2013). The other major distinction between the dentition of aeduellids and amblypterids lies in the fact that aeduellids have only one row of teeth per jaw (Štamberg 2020). Based on their different jaw morphology and tooth arrangement, the niche partitioning between these two families may be based on prey size or robustness, with amblypterids being more able to capture large, robust prey. Within the Aeduellidae, the distinctions between the feeding ecologies of *Decazella* and *Aeduella* are very thin. Their jaws and dimensions being virtually identical, the nature of the niche partition between *Decazella* and *Aeduella* is currently unknown but it is likely that these two taxa had very similar feeding ecologies. The acrolepid *Progyrolepis* is a carnivorous actinopterygian, capable of hunting acanthodians, actinopterygians, small chondrichthyans and even small tetrapods. (e.g. Štamberg 1991, 2020). Finally, the xenacanth *Orthacanthus* was the apex predator of the food web in the Bourran Formation ecosystem, since it is described as a large predator, capable of

feeding on acanthodians, aeduellids, amblyperids, acrolepids, smaller xenacanths and tetrapods (e.g. Soler-Gijón 1995; Kriwet *et al.* 2008; Luccisano *et al.* 2022, 2023).

The newly found coprolites confirm some predator-prey relationships in this environment. The producers of Morphotype 1 and 2 are most likely xenacanths and the presence of numerous bone fragments and scales of aeduellids inside the coprolites confirms their consumption of small fishes: these abundant coprolites from the La Découverte locality show that large xenacanths hunted Aeduellidae (*Decazella* and *Aeduella*). Yet a more detailed examination of a larger sample of coprolites using chemical and 3D methdolologies could reveal more complex trophic relationships.

### Depositional environment at the La Découverte locality

The fossilisation conditions and fossil content of the ANLD in the Lassalle Member document the depositional environment of this layer. The high number of disarticulated specimens at La Découverte suggests high-energy transport, but their excellent state of preservation contrasts with this hypothesis. The presence of plant debris, e.g. *Pecopteris*, *Asterophyllites*, *Calamites*, supports the fact that material transport has occured (Vetter 1968; Ligouis 1988). However, the large accumulations of fossils and the granulometry of the sediment suggest that the depositional environment was relatively calm (Vetter 1968; Christophoul *et al.* 2019). This combination suggests that the La Découverte locality was a calm outlet of a high-energy river. The high carbon content of the black argillites of the Lassalle Member (e.g. Vetter 1968) is indicative of an anoxic environment. The abundant fauna discovered in Lassalle Member suggests that the water column was not entirely anoxic. The water column was probably subject to oxygen partitioning, with oxygen-poor levels at the surface and anoxic levels at depth. The calm nature of the water would have prevented the proper circulation of oxygen, leading to anoxic conditions at depth. This hypothesis could be coherent with the possible adaptation of xenacanths to low-oxygenised waters (Compagno 1990).

The previous work of Ligouis (1988) about the depositional environments in the Decazeville Basin indicates that the environment of the ANLD was a lacustrine-type environment. The presence of Xenacanthiformes, Acanthodidae, Acrolepidae and Aeduellidae in the Bourran Formation is a faunal association typical of a Permo-Carboniferous aquatic environment. Following Schultze (2009), this assemblage occurred in both freshwater and marine environments. Although possible marine influences are discussed in the late-Variscan intra-mountainous basins (e.g. Schultze 2009; Olive *et al.* 2012; Steyer *et al.* 2012; Fischer *et al.* 2013; Luccisano *et al.* 2023), no clear marine influence has been proposed for the Decazeville Basin (e.g. Vetter 1968; Ligouis 1988; Christophoul *et al.* 2019). Our new discoveries, together with the previously described faunal elements of the Bourran Formation and the taphonomy of all these specimens, support the hypothesis of Ligouis (1988) that the ANLD correspond to a calm freshwater environment.

### Vertebrate fauna diversity

Our findings in the Lassalle Member of the Bourran Formation have highlighted a large number of actinopterygian and acanthodian specimens, as well as chondrichthyan remains and a few coprolites. These discoveries also allow to revisit previous works carried out in the Decazeville Basin (Heyler 1964, 1969, 2000; Vetter 1968). Xenacanthiformes is the only group of chondrichthyans present in the Decazeville Basin, and their specimens are rare. The presence of Xenacanthiformes in the Decazeville Basin was previously documented by the mention of undescribed small teeth and the description of a cephalic spine (MNHN.DEC.57) attributed to *Expleuracanthus* sp. (Vetter 1968; Heyler 1969). As *Expleuracanthus* is not a valid taxon (e.g. Ginter *et al.* 2010; Luccisano *et al.* 2021), the morphology of MNHN.DEC.57, which has a small size (80 mm) and two rows of lateral denticles, suggests that this spine belongs to the genus *Triodus*. However, a detailed description of this specimen is beyond the scope of this study. The presence of the Xenacanthiformes in the Decazeville Basin is confirmed here, with the addition of the presence of a larger taxon: *Orthacanthus*. Acanthodidae are common in the Decazeville Basin, but only represented by isolated spines, often associated with isolated Aeduellidae scales. Acrolepidae, on the other hand, are much rarer but here described for the first time in the Decazeville Basin, with the potential occurrence of *Progyrolepis*. The Aeduellidae remains are by far the most abundant ones in the Decazeville Basin, with a relatively equal proportion between *Decazella* and *Aeduella*. Their bones are always disarticulated and very rarely associated, with the exception of a few scales. The presence of the genus *Aeduella*, hypothesised by Heyler (1969), is therefore confirmed here, although more complete material and revision of the historical specimens is needed to precise a specific assignment. Finally, coprolites likely produced by *Orthacanthus* are very abundant.

### Palaeobiogeography of the intra-mountainous vertebrate aquatic fauna

The palaeofauna recovered in the Decazeville Basin shows strong links with the faunas of other basins in the French Massif Central (Table 1; Fig. 13), but also with other basins of the Variscan Belt in Europe (e.g. Spain, Germany, Czech Republic, Sardinia) or in the United States (Forey & Young 1985; Gottfried 1987; Štamberg 2007, 2016b; Fischer *et al.* 2010; Mickle 2011; Štamberg & Werneburg 2023). Our new discoveries, together with the specimens previously described in the Bourran Formation, allow to compare the ichthyofaunas of the various Permo-Carboniferous basins from the French Massif Central.

Based on the work of Vetter (1968), Heyler (1969, 2000) and Blieck *et al.* (1999) as well as the present work, we have summarised the faunal diversity of vertebrates in the Decazeville Basin. To estimate this diversity, we have taken into account the number of individuals per family. These figures are also completed by the results of excavations carried out at the La Découverte locality by DG and examination

TABLE 1. — Permo-Carboniferous ichthyofauna from the French Massif Central. Preliminary total counts of individuals by families (**rows**) and basins (**columns**) based on literature (Vetter 1968; Heyler 1969, 2000; Blieck *et al.* 1999; Štamberg & Steyer 2021), collection studies and excavations. Abbreviations: **C**, Carboniferous; **P**, Permian.

| Family/Basins | Decazeville (C) | Montceau-les-Mines (C) | Commentry (C) | Carmaux (C) |
|---|---|---|---|---|
| Chondrichthyes Sphenacanthidae | 0 | 0 | 0 | 0 |
| Chondrichthyes Xenacanthiformes (e.g., *Orthacanthus*, *Triodus*) | 3 | 3 | 14 | 0 |
| Chondrichthyes Hybodontidae (*Lissodus*) | 0 | 0 | 0 | 0 |
| Acanthodii Acanthodidae indet. | 40 | 43 | 0 | 0 |
| Actinopterygi Acrolepidae (*Progyrolepis*) | 1 | 0 | 0 | 0 |
| Actinopterygi Aeduellidae (e.g., *Aeduella*, *Decazella*, *Bourbonella*) | 80 | 4 | 0 | 1 |
| Actinopterygi Amblypteridae (*Paramblypterus*) | 20 | 3 | 125 | 0 |
| Actinopterygi Pygopteridae (*Usclasichthys*, *Briveichthys*) | 0 | 0 | 0 | 0 |
| Actinopterygi Igornichthyidae (*Igornella*, *Commentrya*, *Igornichthys*) | 0 | 2 | 47 | 0 |
| Actinopterygi Elonichthyidae (*Blanzychthys*, *Elonichthys*) | 0 | 12 | 0 | 0 |
| Actinopterygi Haplolepidae (*Blanzyhaplolepis*) | 0 | 1 | 0 | 0 |
| Actinopterygi Charleuxiidae (*Charleuxia*) | 0 | 2 | 0 | 0 |
| Dipnoi (*Megapleuron*, *Sagenodus*) | 0 | 1 | 0 | 0 |
| Agnatha (*Myxineidus*) | 0 | 3 | 0 | 0 |
| Total | 144 | 74 | 186 | 1 |

| Family/Basins (C, Carboniferous; P, Permian) | Brive (P) | Autun (P) | Bourbon-L'Archambault (P) | Lodève (P) | L'Argentière (P) |
|---|---|---|---|---|---|
| Chondrichthyes Sphenacanthidae | 1 | 0 | 0 | 0 | 0 |
| Chondrichthyes Xenacanthiformes (e.g., *Orthacanthus*, *Triodus*) | 0 | 120 | 50 | 10 | 0 |
| Chondrichthyes Hybodontidae (*Lissodus*) | 0 | 0 | 5 | 0 | 0 |
| Acanthodii Acanthodidae indet. | 63 | 50 | 300 | 15 | 0 |
| Actinopterygi Acrolepidae (*Progyrolepis*) | 40 | 0 | 300 | 0 | 0 |
| Actinopterygi Aeduellidae (e.g., *Aeduella*, *Decazella*, *Bourbonella*) | 1 | 500 | 200 | 0 | 0 |
| Actinopterygi Amblypteridae (*Paramblypterus*) | 0 | 500 | 20 | 0 | 1 |
| Actinopterygi Pygopteridae (*Usclasichthys*, *Briveichthys*) | 4 | 0 | 0 | 11 | 0 |
| Actinopterygi Igornichthyidae (*Igornella*, *Commentrya*, *Igornichthys*) | 0 | 5 | 0 | 0 | 0 |
| Actinopterygi Elonichthyidae (*Blanzychthys*, *Elonichthys*) | 0 | 0 | 0 | 0 | 0 |
| Actinopterygi Haplolepidae (*Blanzyhaplolepis*) | 0 | 0 | 0 | 0 | 0 |
| Actinopterygi Charleuxiidae (*Charleuxia*) | 0 | 4 | 0 | 0 | 0 |
| Dipnoi (*Megapleuron*, *Sagenodus*) | 0 | 1 | 0 | 0 | 0 |
| Agnatha (*Myxineidus*) | 0 | 0 | 0 | 0 | 0 |
| Total | 109 | 1180 | 875 | 36 | 1 |

of museum collections of MRGPV (Decazeville), ML (Brive) and MNHN (Paris). For the others French Massif Central basins, we have taken up the data set of Štamberg & Steyer (2021), to which we have added the data collected from the Carmaux Basin (Heyler 2000), Commentry Basin (Blot 1966; Heyler 2000) and from Montceau-les-Mines (Heyler 1964, 1969, 1980, 2000; Heyler & Poplin 1983, 1988, 1994; Langiaux 1984; Poplin & Heyler 1987; Poplin 1997; Poplin *et al.* 2001; Olive *et al.* 2012; Germain *et al.* 2014; Štamberg 2016b). We have also added data for several families (Elonichthyidae, Igornichthyidae, Haplolepidae and Charleuxiidae) not mentioned by Štamberg & Steyer (2021), on the basis of Heyler (1969, 2000), Poplin (1997) and Štamberg (2016b). It should be noted that for the Commentry and Montceau-les-Mines basins, this is a preliminary table, based also on unpublished catalogues of the MNHN (Paris) and inventory of the MHNG (Gaillac). For the Commentry Basin, there is no mention of acanthodians or aeduellids, but this is probably a bias in identification and cataloguing. It should also be noted that *Commentrya* Sauvage, 1888 specimens are considered to be *Paramblypterus* specimens in the catalogue of the Commentry collections. *Commentrya* is retained here as a valid taxon (e.g. Štamberg 2016b). For the Montceau-les-Mines Basin, the data for acanthodians are estimates of the specimens present in the collections, and the data for amblypterids is most certainly underestimated through incomplete consultation of the collections. To obtain a more complete picture, a detailed review of the collections of several museums is required, which is out of the scope of the present study. We have obtained an updated table (Table 1) and map (Fig. 13) of Štamberg & Steyer (2021) dealing with the palaeobiogeography of the intra-mountainous aquatic vertebrates from the French Massif Central.

The results of this comparison show that the Decazeville Basin does not reach the faunal richness of well-studied basins such as Autun and Bourbon-L'Archambault basins, but that it does present a hitherto underestimated interest, following the example of the Brive basin (Štamberg & Steyer 2021). The Decazeville Basin shares common groups with the other basins (Aeduellidae and Acanthodidae) or slightly rarer ones (Amblypteridae, Acrolepidae and Xenacanthiformes), including the presence of an endemic taxon: *Decazella vetteri*. However, it should be noted that pygopterids are absent from the Decazeville Basin, whereas they are common in other basins in the south of the French Massif Central. Focusing

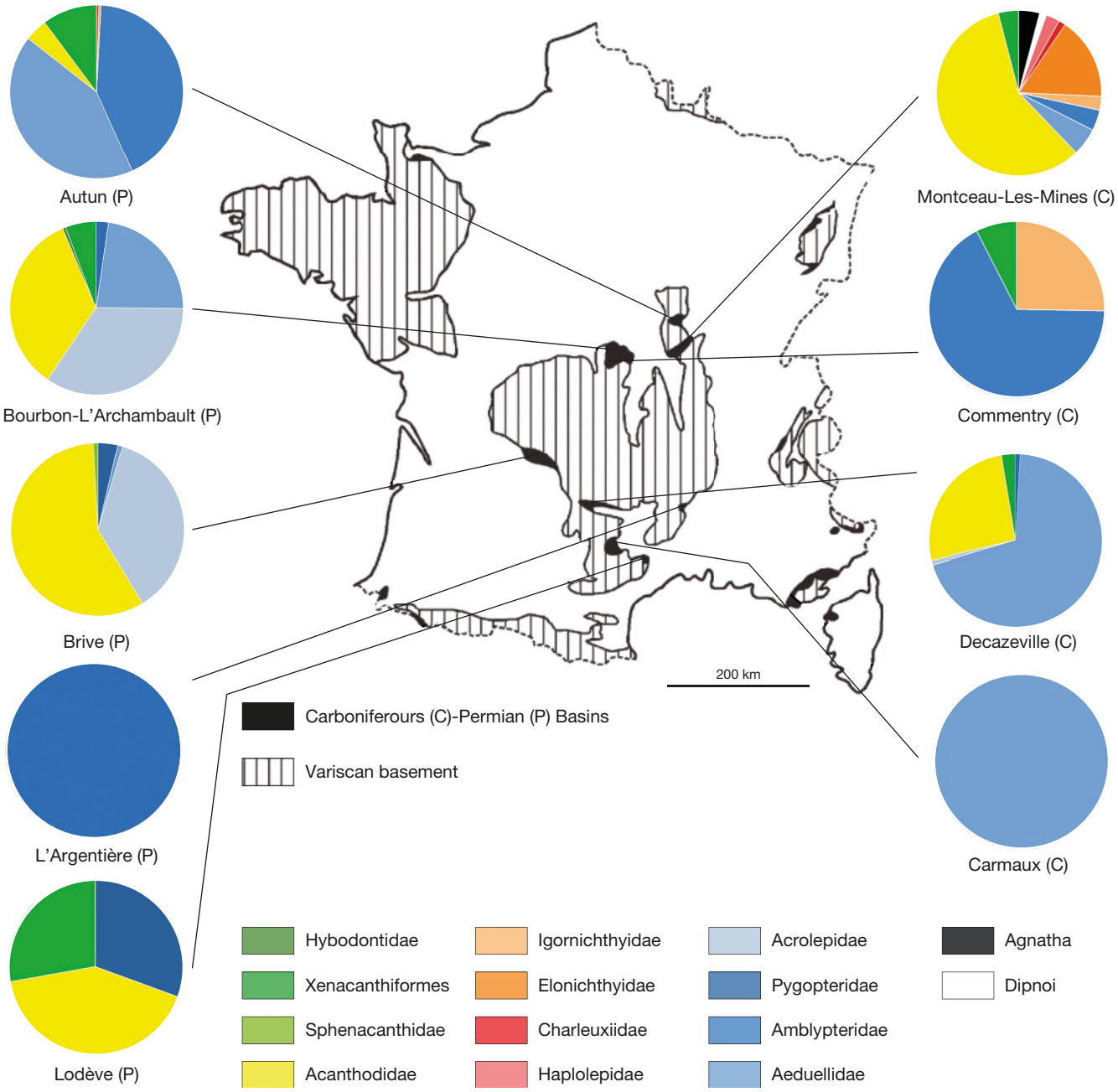


Fig. 13. — Permo-Carboniferous ichthyofauna of the French Massif Central. Data come from Table 1 and Štamberg & Steyer (2021). Map modified from Gand & Durand (2006).

on Carboniferous basins, the preliminary results of these comparisons show major faunistic differences, since the igornichthyids, haplolepids, charleuxiids and elonichthyids are absent from the Decazeville Basin and the acrolepids are only present in Decazeville Basin. However, it is possible that *Charleuxia* Heyler, 1967b is a synonym of *Paramblypterus* Sauvage, 1888 (Štamberg 2020), which would make Charleuxiidae synonymous with Amblypteridae and reduce the number of distinct families to three. The Montceau-les-Mines and Decazeville basins share an abundance of acanthodians and a relative rarity of xenacanths. However, while aeduellids outnumbers amblypterids in Decazeville, this proportion is unknown in Montceau-les-Mines where data is missing. Finally, the absence of dipnoi and agnatha at Decazeville cannot be discussed, given the great rarity of remains from these groups in the French basins. The data for the Commentry Basin are very incomplete but also suggest an abundance of Igornichthyidae shared with the Montceau-les-Mines Basin. Amblypterids appear to be in the majority, unlike in the Decazeville Basin. Finally, xenacanths are once again common here, as in Decazeville and Montceau-les-Mines basins. The data for the Carmaux Basin are too poor to be discussed, but confirm the wide distribution of aeduellidae in the Carboniferous basins. The Carboniferous ichthyofaunas

of Montceau-les-Mines and Commentry basins appear to be closer to the Permian ichthyofauna of the Autun Basin than the Carboniferous ichthyofauna of the Decazeville Basin. The Carboniferous ichthyofauna of the Decazeville Basin appears to be similar to that of the Permian ichthyofaunas, without having any great similarities with any particular basin. However, these similarities may be a bias in taxonomic identification, particularly for several little-known groups (charleuxiids, igornichthyids, haplolepids, elonichthyiids...). More data is needed to distinguish the endemic from the provincial or cosmopolitan faunal elements in the Permo-Carboniferous basins of the French Massif Central.

Our discoveries allow to update the faunal composition of the Decazeville Basin, which is already relatively complete compared with that of Carmaux or Montceau-les-Mines. Yet further fieldworks and collection studies are of course needed to better document the evolution of the aquatic fauna in Europe through the Carboniferous-Permian transition.

## CONCLUSIONS

A new ichthyofauna and coprofauna from the Gzhelian (Carboniferous) of the Decazeville Basin are herein described. We report here an isolated tooth that constitutes the first occurrence of the Xenacanthiformes *Orthacanthus* in the Decazeville Basin. We also report an isolated fulcral scale that may correspond to the first record of the Acrolepidae *Progyrolepis* in the Decazeville Basin. We also describe new disarticulated specimens of Acanthodidae and Aeduellidae, some of which can be attributed to the genera *Aeduella* and *Decazella*. Finally, we describe two coprolite morphotypes that may have been produced by Xenacanthiformes. Based on our findings, we interpret the depositional environment of the Bourran Formation as a calm and anoxic freshwater environment, potentially a lake, where disarticulated skeletal elements and coprolites were discharged from a river. The vertebrate fauna shows a trophic organisation typical of other late Variscan intra-mountain basins in Europe. This fauna is similar to that of other Permo-Carboniferous basins in the Massif Central, notably Brive, Autun and Bourbon-l'Archambault. The Decazeville Basin stands out, however, for its endemic aeduellid species: *Decazella vetteri*. Several clades present in these basins are absent from the Decazeville Basin (e.g. Pygopteridae). This basin differs also from the only other sufficiently documented Carboniferous basin, the Montceau-les-Mines Basin, by the presence of Acrolepidae and the absence of Igornichthyidae, Haplolepidae, Charleuxiidae and Elonichthyidae. These differences may be excavation and identification artefacts, endemism, or genuine provincialism. In the absence of data certainty, these conclusions must be treated with caution. To answer this paleobiogeographic question, new excavations and a re-examination of the historical specimens are required. Nevertheless, this new ichthyofauna list provides a solid basis for comparison with other Upper Carboniferous basins.

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## APPENDIX

APPENDIX 1. — List of historical specimens of vertebrates from the Decazeville Basin mentionned in this article, with their previous and current inventory numbers.

| HBA number | New number | Identification | Vetter (1968) | Heyler (1969) | This article |
|---|---|---|---|---|---|
| HBA 3004 | MNHN.DEC.24 | Almost complete skeleton | *Aeduella vetteri* | *Decazella vetteri* | *Decazella vetteri* |
| HBA 3005 | MNHN.DEC.25 | Anterior portion of skeleton | *Aeduella vetteri* (holotype) | *Decazella vetteri* (holotype) | *Decazella vetteri* |
| HBA 3010 | MNHN.DEC.30 | Anterior portion of skeleton | *Aeduella vetteri* | *Decazella vetteri* | *Decazella vetteri* |
| HBA 3012 | MNHN.DEC.32 | Skull elements and scales | – | *Decazella vetteri* | *Decazella vetteri* |
| HBA 3104 | MNHN.DEC.57 | Spine | *Pleuracanthus* cf. *frossardi* | *Expleuracanthus* sp. | Xenacanthidae indet. (*Triodus*?) |