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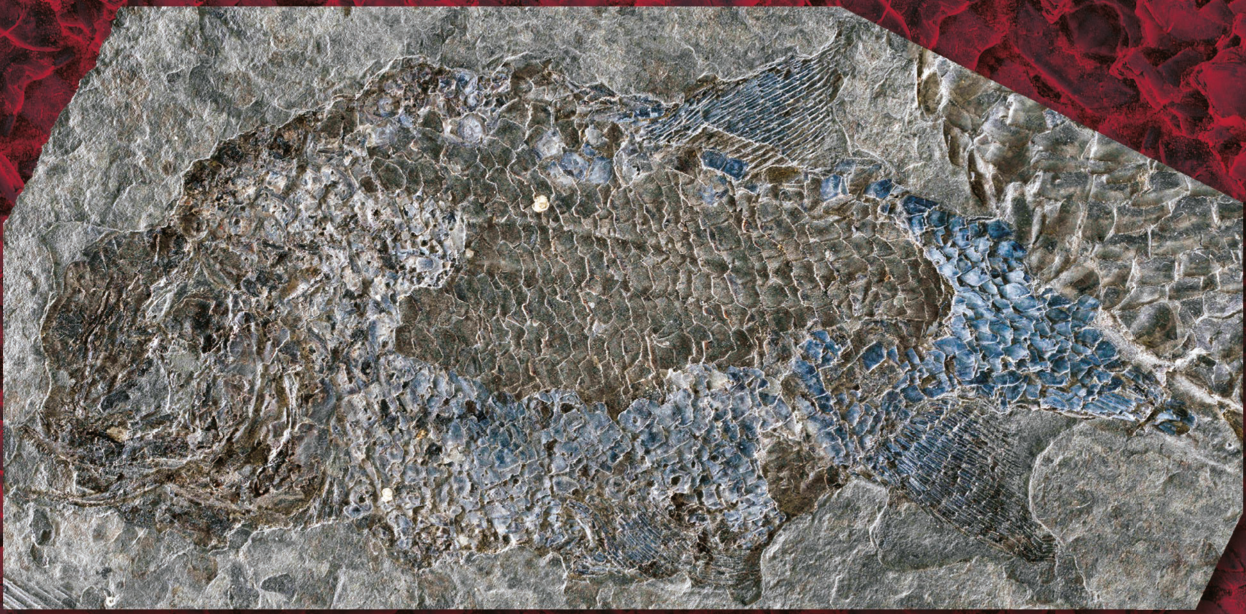
Daniel GONÇALVES



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Paleontological content of the Stephano-Permian basins from the Armorican Massif (France): review, actinopterygian taxonomy, paleobiogeography and correlations

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ABSTRACT

The Armorican Massif (France) is located in the western part of the Variscan Belt, in which few Stephano-Permian sedimentary basins are known. These basins have been poorly documented over time, and their fauna remains poorly understood. These basins are the Carentan, Saint-Pierre-la-Cour, Finistère, Doué-la-Fontaine and Sillon Houiller Vendéen basins. This study synthesises the available sedimentary and palaeontological data in order to relate these Stephano-Permian basins to other Variscan basins. New specimens of *Aeduella blainvillei* (Agassiz, 1833) are described from the Saint-Pierre-la-Cour Basin, extending the distribution range of this taxon and suggesting two distinct modes of repartition among Aeduellidae actinopterygians. The revision of the faunal occurrences in the Carentan and Saint-Pierre-la-Cour basins allows to establish the distribution of taxa across the Variscan Belt, in particular the key taxa *Pseudestheria* Raymond, 1946 and *Anthraconaia* Trueman & Weir, 1946. The application of regional dating based on paleoflora makes it possible to correlate the basins of the Armorican Massif with other Variscan basins. Updating the chronology and palaeobiogeography in these basins of the Armorican Massif shed light on the state of art in one of the westernmost areas of the Variscan Belt and enable future comparisons with other Variscan massifs.

KEY WORDS
Variscan Belt,
stratigraphy,
Anthraconaia,
Pseudestheria,
Aeduella,
faunal distribution.

RÉSUMÉ

Contenu paléontologique des bassins stéphano-permiens du Massif Armoricain (France): révision, taxonomie des actinoptérygiens, paléobiogéographie et corrélations.

Le Massif Armoricain (France) se trouve à l'ouest de la chaîne varisque, dans lequel quelques bassins sédimentaires stéphano-permiens sont connus. Toutefois, ces bassins ont été très peu documentés au cours du temps, et leur faune reste méconnue. Ces bassins sont ceux de Carentan, Saint-Pierre-la-Cour, Finistère, Doué-la-Fontaine et du Sillon Houiller Vendéen. Cette étude synthétise les données sédimentaires et paléontologiques disponibles, afin de pouvoir mettre ces bassins stéphano-permiens en relation avec les autres bassins varisques. De nouveaux spécimens d'*Aeduella blainvillei* (Agassiz, 1833) sont décrits en provenance du bassin de Saint-Pierre-la-Cour, et permettent d'augmenter l'aire de répartition de ce taxon, et de considérer deux modes de répartition distincts chez les actinoptérygiens aeduellidés. La révision des occurrences fauniques des bassins de Carentan et Saint-Pierre-la-Cour permet de déterminer la distribution des taxons à travers la chaîne varisque, notamment les taxons clés *Pseudestheria* Raymond, 1946 et *Anthraconaia* Trueman & Weir, 1946. L'application de la datation régionale basée sur la paléoflore permet de corréler les bassins du Massif Armoricain avec les autres bassins varisques. La mise à jour de la datation et de la paléobiogéographie dans ces bassins du Massif Armoricain met en lumière l'état des connaissances dans l'une des zones les plus à l'ouest de la chaîne varisque, permettant sa comparaison avec les autres massifs varisques.

MOTS CLÉS
Chaîne varisque,
stratigraphie,
Anthraconaia,
Pseudestheria,
Aeduella,
distribution faunique.

INTRODUCTION

The Variscan Belt is a mountain range in the middle of Pangaea, which results from Devonian to Carboniferous subductions and terrane accretion followed by a major Carboniferous collision between Gondwana and Laurussia (Matte 1986; Matte 2001; Stampfli *et al.* 2013; Edel *et al.* 2018; Machek *et al.* 2022; Schulmann *et al.* 2022; Martínez Catalán *et al.* 2024). These events led to the thickening of the continental crust (Matte 1991, 2001; Franke 1992; Stampfli *et al.* 2002), followed by heating of orogenic roots and gravitational instability of the thickened lithosphere during the late orogenic processes (Rey *et al.* 2001; Jadamec *et al.* 2007). The unstable continental lithosphere was subjected to gravitational collapse and a compressional regime was replaced by transverse extension, manifested in large number of intrusions of granitoids at deep levels and the formation of sedimentary basins at the surface during the latest Carboniferous and early Permian (Malavieille *et al.* 1990; Pešek 1994; Mazur & Kryza 1996; Rodríguez-Méndez *et al.* 2016; Bárta *et al.* 2021). These Permo-Carboniferous sedimentary basins were formed in the internal zones of the European part of the Variscan Belt in response to its gravitational collapse, in an extensional and/or on strike-slip tectonic context (Echtler & Malavieille 1990; Mattauer & Matte 1998; Lapierre *et al.* 2008; Schäfer 2011; Bárta *et al.* 2021; Aretz *et al.* 2023). Their filling is made of siliciclastic, volcano-detritic and continental carbonaceous sedimentation, with cinerites and ash levels, depicting alluvial fans, fluvial and lake environments with volcanic activities (e.g., Vetter 1968; Delsahut 1981; Châteauneuf & Farjanel 1989; Debriette 1992; Opluštil & Pešek 1998; Schäfer 2011; Aretz *et al.* 2023).

Permo-Carboniferous basins outcrops in almost all massifs resulting from the Variscan orogeny in Europe, from Iberia to Ural (Fig. 1A, B; e.g., Aretz *et al.* 2023; Knight *et al.* 2023). These basins are most often referred to as "Stephano-Permian basins" (e.g., Echtler & Malavieille 1990; Carmignani *et al.* 1994; Beccaletto *et al.* 2015; Rodríguez-Méndez *et al.* 2014), as the vast majority have been dated using floral assemblages with the regional continental subdivisions of the Stephanian, Autunian and Saxonian (e.g., Grand'Eury 1877; Jongmans & Pruvost 1950; Doubinger & Vetter 1985; Doubinger *et al.* 1995). These regional stages were widely used until radiochronological dating, but remain in use in the basins where such dating is absent (e.g., Šimůnek & Zajíc 2021; Börjesson *et al.* 2024; Gonçalves *et al.* 2025). The floristic assemblages, which served as the basis for dividing the Stephanian into sub-stages A, B and C, are linked to variations in depositional environments in space and time (e.g., Martín-Closas & Galtier 2005). The use of these sub-stages and their correlation between basins must therefore be treated with caution (e.g., Pellenard *et al.* 2017; Nelson & Lucas 2021; Knight *et al.* 2023; Mercuzot *et al.* 2023). Currently, the Stephanian extends from 308 to 300 Ma (late Moscovian-middle Gzhelian; Aretz *et al.* 2020), while the Autunian begins at 300 Ma and its top is more uncertain, ranging from 288 to 275 Ma (middle Gzhelian-Artinskian to Kungurian; Henderson *et al.* 2020). At this time, the paleoelevation of the Variscan Belt was estimated to be 3.4 ± 0.7 km (Dusséaux *et al.* 2021), but this result has been challenged recently (Rossignol *et al.* 2025). Indeed, the wide distribution of some temnospondyl and bivalve taxa indicates migrations across the Variscan Belt, which would have been possible with a lower palaeoelevation or within a fragmented belt (Rossignol *et al.* 2025; Ballèvre 2025).

In France, numerous Variscan massifs include intramontane Stephano-Permian basins: the Ardennes (part of the Rhenish Massif), Vosges, Armorican, Mont-Blanc, Aiguilles-Rouges, Belledonne, Pelvoux, Argentera, French Massif Central, Mouthoumet and Pyrénées (Fig. 1B; e.g., Fernandez *et al.* 2002; Lombardo *et al.* 2011; Skrzypek *et al.* 2014; Ballèvre *et al.* 2018; Aretz *et al.* 2023). At the surface, the Stephano-Permian basins are best documented in the French Massif Central (e.g., Delsahut 1981; Doubinger & Vetter 1985; Châteauneuf & Farjanel 1989), and few are known in other massifs (e.g., Boulay 1879; Dhellemmes 1954; Pelhate 1994; Saillol *et al.* 2019; Aretz *et al.* 2023): these latters have been under-investigated as for their paleontological content because of much less intensive mining activites and poorer outcrop conditions (e.g., Mulot 1975; Gonçalves *et al.* 2026d). Contrary to the fossils of these "secondary" basins, those of the French Massif Central have been studied continuously since the 19th century, with well-documented diversity and palaeobiogeography (e.g., Blainville 1818; Agassiz 1833; Sauvage 1893; Heyler 1969; Poplin & Heyler 1994; Steyer *et al.* 2000, 2012; Luccisano *et al.* 2022; Gonçalves & Luccisano 2025a, b; Gonçalves *et al.* 2026a, b, c). The faunas of these "secondary" massifs are often limited to mentions of fish scales in geological map notes, or brief studies on bivalves, arthropods and ostracods dating back a hundred years (e.g., Péneau 1930; Ginsburg *et al.* 1980; Le Gall *et al.* 2011).

The Armorican Massif (Fig. 1C) does not make exception to this lack of research: its Stephano-Permian basins are poorly understood and often incompletely listed (e.g., Doubinger & Vetter 1985: Aretz *et al.* 2023). The fauna of this massif remains largely unknown, and limited to a few occurrences that have been overlooked in recent studies (e.g., Vieillard 1872; Picquenard 1924; Pruvost 1925; Bigot & Pruvost 1925; Péneau 1930). The objective of this study is to summarise the Stephano-Permian basins of the Armorican massif, with a review of faunal occurrences. Vertebrate specimens forgotten in museum collections are also described here for the first time, thereby expanding our knowledge on the faunas. This enables the inclusion of the Armorican Massif in a broader study of the Variscan mountain range in relation to the evolution of the Stephanian-Permian basins and under a palaeobiogeographical context.

MATERIAL AND METHODS

Nomenclature terminology

In this article, regional stages are regularly used instead of international stages, because of the lack of absolute dating in the Armorican basins. The datation of these basins is based on

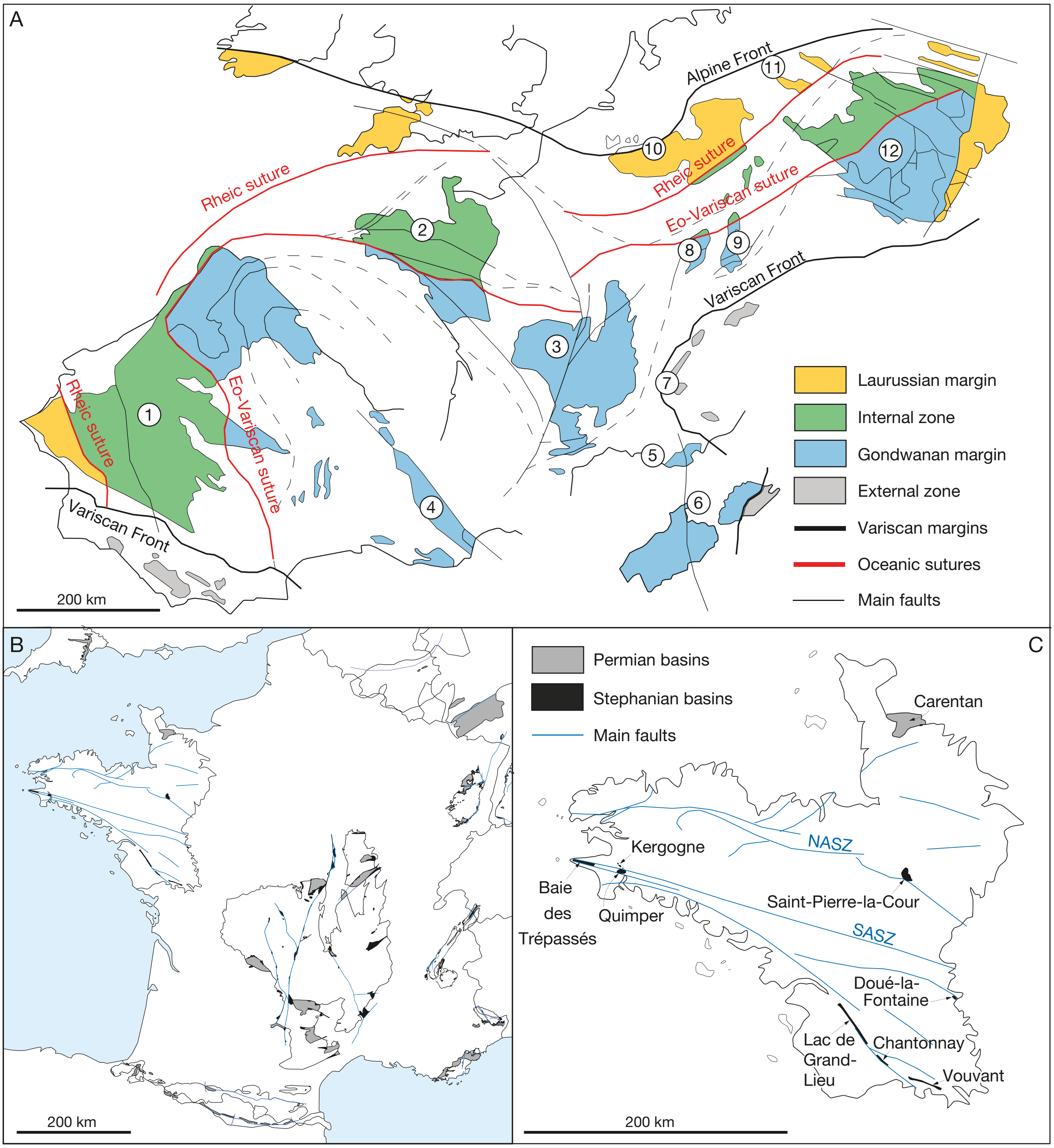

FIG. 1. — **A**, Structural map of Variscan orogenic zones in Europe, showing the Variscan massifs in Europe (modified after Aretz *et al.* 2023; Gonçalves *et al.* 2026d and references therein). Numbers: **1**, Iberia; **2**, Armorican Massif; **3**, French Massif Central; **4**, Pyrénées Massif; **5**, Maures-Tanneron Massif; **6**, Corsica and Sardinia; **7**, Alps and Argentera Massif; **8**, Vosges Massif; **9**, Schwartzwald Massif; **10**, Rhenish Massif; **11**, Harz Massif; **12**, Bohemian Massif; **B**, map of France showing the Stephano-Permian basins within the Variscan massifs (modified after Vetter 1968; Aretz *et al.* 2023); **C**, map of Armorican Massif showing the Stephano-Permian basins (modified after Pelhate 1994). Abbreviations: **NASZ**, North Armorican Shear Zone; **SASZ**, South Armorican Shear Zone. Map by D. Gonçalves.

the flora, which uses the regional European stages: Namurian, Westphalian, Stephanian, and Autunian (e.g., Doubinger & Vetter 1985). These stages are difficult to correlate with international stages (e.g., Knight *et al.* 2023). Therefore, the already suspected diachronism of the Autunian and Stephanian subdivisions (e.g. Becq-Giraudon *et al.* 1995; Knight & Wagner 2014), documented at regional scale (Opluštil *et al.* 2022) could also occur at a local geographical scale (Mercuzot *et al.* 2023), and here we follow the most recent correlation proposed by Aretz *et al.* (2020) and Henderson *et al.* (2020).

We follow the nomenclatures of Schultze *et al.* (2021) to describe the actinopterygian skull and body, with the modifications of Gonçalves *et al.* (2026b) to describe aeduellid skull bones, and Štamberg (2020) to describe the actinopterygian tooth morphology. The measurements follow those of Gonçalves & Luccisano (2025b: fig. S1) and are available in Appendices 1 and 2.

As in several recent articles dealing with the palaeobiogeography of the Stephano-Permian basins of the Variscan Belt (e.g., Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026a, b, c, d), we here assign each VIB to the geological entity that constitutes the sedimentary source of the materials filling these basins (e.g., the Ronchamp-Giromagny Basin within the Vosges Massif; the Thuringian Forest Basin within the Bohemian Massif).

We follow Raymond (1946) and recent studies (e.g., Zajíc 2014; Opluštil *et al.* 2016) in assigning the 'conchostracan' '*Estheria*' *tenella* to the genus *Pseudestheria*. This decision stems from the homonymy between *Estheria* Rüppell *in* Strauss-Dürkheim, 1837 and *Estheria* Robineau-Desvoidy, 1830 (see Raymond 1946). A majority of authors mistakenly used the name '*Estheria*' to refer to species of Permo-Carboniferous conchostracans (e.g., Feys 1960; Delsahut 1981; Châteauneuf & Farjanel 1989). Some authors have assigned '*E.*' *tenella* to other genera, with the following combinations: *Paleestheria tenella* (Warth 1963), *Cyzicus* (*Lioestheria*) *tenella* (Boy 1976), *Euestheria tenella* (Feys & Langiaux 1980; Wagner 1985), and *Megasitum tenellum* (Kozur & Sittig 1981).

Here we follow Trueman & Weir (1946), using the name *Anthraconaia* Trueman & Weir, 1946 instead of *Anthracomya* Salter, 1861, as the latter is a junior homonym of *Anthracomya* Rondani, 1856. Many authors used the name *Anthracomya* to refer to species of Permo-Carboniferous bivalves (e.g., Vetter 1968; Châteauneuf & Farjanel 1989; Essamoud & Courel 1998; Elliott 2016), thus creating a confusion between these two names.

Institutional abbreviations

IGR	Institut de Géologie de Rennes, Rennes;
MHNL	Muséum d'Histoire naturelle de Lille, Lille;
ML	Musée de Laval, Laval;
MNHN	Muséum national d'Histoire naturelle, Paris;
SU	Sorbonne Université, Paris;
UCO	Université catholique de l'Ouest, Angers;
UNISTRA	Université de Strasbourg, Strasbourg.

RESULTS

Armorican Massif basins review

Carentan Basin (Fig. 2)

Geological context. This Permo-Carboniferous basin, formerly known as the Littry Basin, is the easternmost exposure of the Armorican Massif before the Variscan basement overlapping with the Mesozoic sediments of the Paris-London Basin (L'Homér & Pareyn 1989). It measures maximum 40 km east-west and 20 km north-south (L'Homér & Pareyn 1989). It is well known thanks to several boreholes which allow to precise its stratigraphy (Vieillard 1872; Bigot & Pruvost 1925; L'Homér & Pareyn 1989). Near the base, the Littry Formation consists of an alternation of conglomerates, sandstones, shales and coal, intercalated by several lava flows (Vieillard 1872; Pareyn 1954; L'Homér & Pareyn 1989). At the western part of the basin, the Autunian formations lays unconformably on the basalmost Plessis Formation, which is a series of folded siliciclastic series (L'Homér & Pareyn 1989). The coal-bearing Plessis and Littry formations were perceived as belonging to separate basins during mining exploration (e.g., Vieillard 1872; Pareyn 1954; Coquel *et al.* 1969). Above, the Inférieure Formation consists of a succession of reddish conglomerates, sandstones and shales. Then the Saint-Martin-de-Blagny Formation is an alternance of shales, few sandstones, limestones, black limestones, basalt flows and ash levels. Above, the Intermédiaire, Cartigny-l'Epinay and Saint-Jean-de-Daye formations are made up with reddish conglomerates, sandstones, siltstones, argilites, ash levels and basalt flows (Vieillard 1872; L'Homér & Pareyn 1989). The uppermost Saint-Jean-de-Daye Formation is covered slightly unconformably by Triassic marls (L'Homér & Pareyn 1989).

The Inférieure, Intermédiaire and Saint-Jean-de-Daye formations correspond to strong seasonal depositional environments, supported by the presence of raindrops, carbonate nodules and silcrete (L'Homér & Pareyn 1989). The Cartigny-l'Epinay Formation corresponds to more erosive and energetic fluviatile deposits (L'Homér & Pareyn 1989). Finally, the Saint-Martin-de-Blagny Formation records calm lacustrine deposits, with algal mats at the bottom of a shallow water column whose presence is inferred from alternating layers of carbonate and darker laminations (L'Homér & Pareyn 1989). The top of this formation is a thick succession of limestones, suggesting a phase of biostasis (L'Homér & Pareyn 1989), i.e. deposit of carbonaceous mud following the chemical dissolution of soils by dense vegetation cover (e.g., Erhart 1951; Gachon 1957; Garbeva *et al.* 2011).

Flora and datation. The flora of the basal Plessis Formation was studied by Lemoigne (1968), who attributed it a Westphalian B-C age. This age was confirmed by unpublished palynological data (L'Homér & Pareyn 1989).

Vieillard (1872) studied the flora of the Littry Formation and mentioned the presence of *Annularia* sp., *Pecopteris arborescens* (Schlotheim, 1820), *P. polymorpha* Brongniart, 1834a, *Alethopteris serlii* (Brongniart, 1828a), *Dicopteris brongniarti* (sic), *Sphenophyllum erosum* Lindley & Hutton, 1831, *Calamites dubius* Artis, 1825, *C. cruciatus* Sternberg, 1825, *C. suckowii* Brongniart, 1828c, and *C. arenaceus* Jäger, 1827. Among these taxa, *S. erosum* is considered as a synonym of *S. cuneifolium* (Sternberg, 1921) by Zeiller (1879), and '*Dicopteris brongniarti*' is a *nomen nudum*, probably a typographical error. Bigot & Pruvost (1925) described the lithology and the palaeontological content of the Port-Ribet borehole, including the presence of *Pecopteris arborescens* in black shales at the top of the Saint-Martin-de-Blagny Formation.

Coquel *et al.* (1969) studied the palynology of the Littry Formation, from the Bernesq mine, represented by 62 species, distributed in 31 genera. Based on the abundance of these

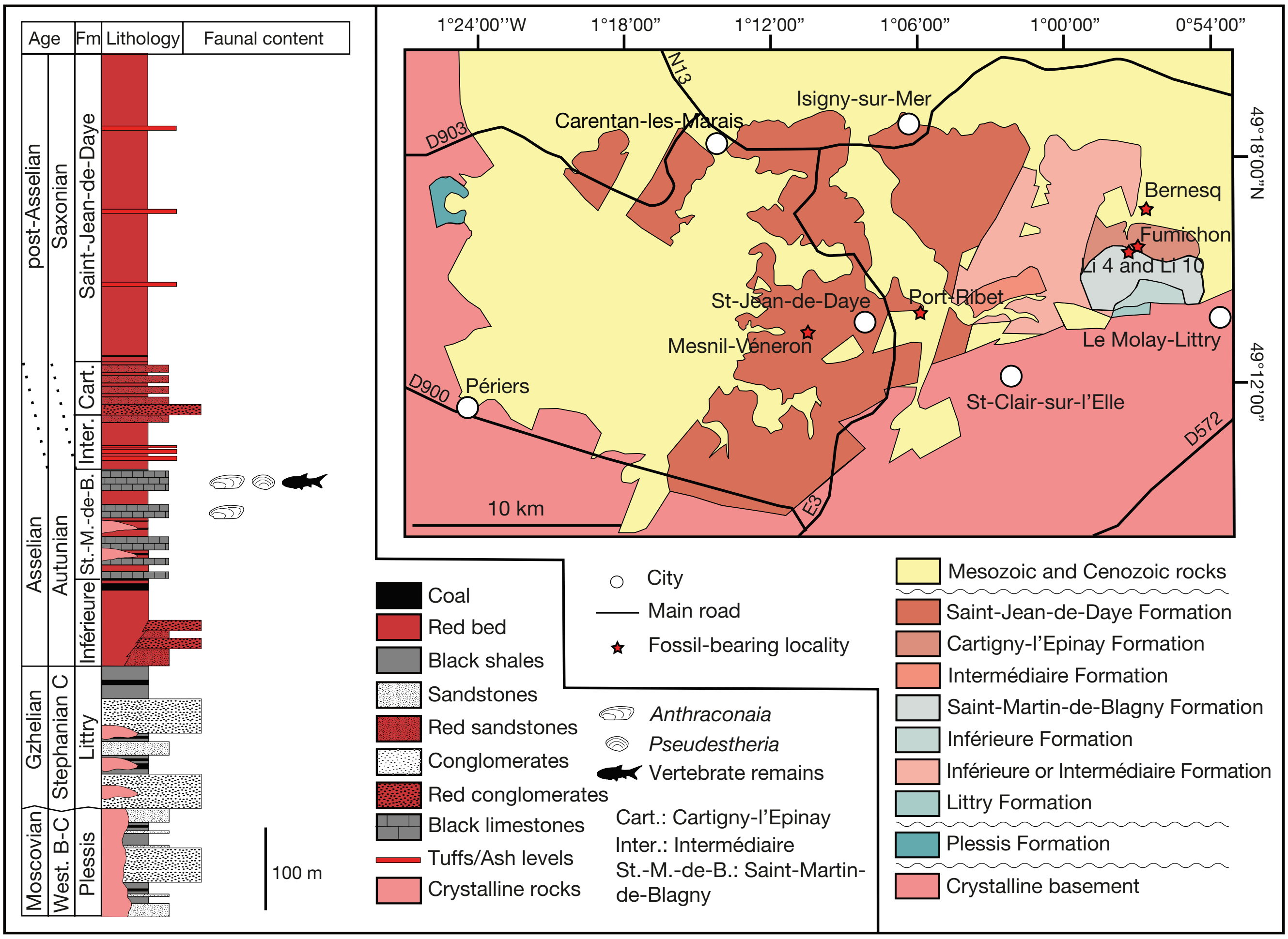

FIG. 2. — Geological map and stratigraphy of the Carentan Basin (modified after L'Homér & Pareyn 1989). Schema and map by D. Gonçalves.

taxa, Liabeuf *et al.* (1967) suggested that this formation is in the palynological zone II of the Upper Carboniferous, i.e. Stephanian C. This is consistent with the macrofloral assemblage (Coquel *et al.* 1969; Doubinger & Vetter 1985). At least, in the formations above the Littry Formation, L'Homér & Pareyn (1989) mentioned an Autunian microflora with *Dissaccites* Cookson, 1947 and *Cordaitina* Samoilovitch, 1953, but without precising where. They also noted the absence of fossils in the Saint-Jean-de-Daye Formation, and tentatively attributed it to a Saxonian age, on the basis of facies correlation.

Fauna. Pareyn (1954) mentioned *Pseudestheria tenella* in black shales from the Littry Formation.

Vieillard (1872) reported the discovery, in 1857, of actinopterygians during the digging of the 'Fumichon n°2' well. They come from black shales intercalated in limestones and are briefly described as "heterocercal fish, with pyritized scales, almost square on the body, diamond-shaped on the tail, appearing to belong to the genera *Palæoniscus* (sic) or *Amblypterus*" (Vieillard 1872: 249). Given the precise lithology of the 'Fumichon n°2' well, these black shales belong to the upper part of the Saint-Martin-de-Blagny Formation. These actinopterygians were not found in museum collections and are most likely lost. The description of Vieillard (1872) is very brief and can refer to any early-diverging actinopterygian (e.g., Schultze *et al.* 2021), which does not allow a more precise attribution. For these reasons, I consider them as belonging to Actinopterygii indet.

In their description of the fossils from the Port-Ribet borehole, Bigot & Pruvost (1925) described black shales at the top of the Saint-Martin-de-Blagny Formation with an abundance of *Pseudestheria tenella* (Bronn, 1850), associated with spines that they attributed to *Acanthodes* sp. Bigot & Pruvost (1925) also described the presence of *Anthraconaia carbonaria* (Bronn, 1829) in a limestone bed and in several black shales at the top of the Saint-Martin-de-Blagny Formation. *P. tenella* and *Anthraconaia* sp. were also discovered in black shales of the Saint-Martin-de-Blagny Formation in the Mesnil-Vénéron borehole (Bigot & Pruvost 1925). Based on this fauna, an early Autunian age was attributed to this formation (Bigot & Pruvost 1925; L'Homér & Pareyn 1989). Unfortunately, the core samples were stored in the collections of the Caen Museum, and destroyed during the Second World War (Bigot 1945).

The spines of *Acanthodes* sp. are described as curved, without any other distinguishing features (Bigot & Pruvost 1925: 37). The absence of diagnostic features at the generic level does

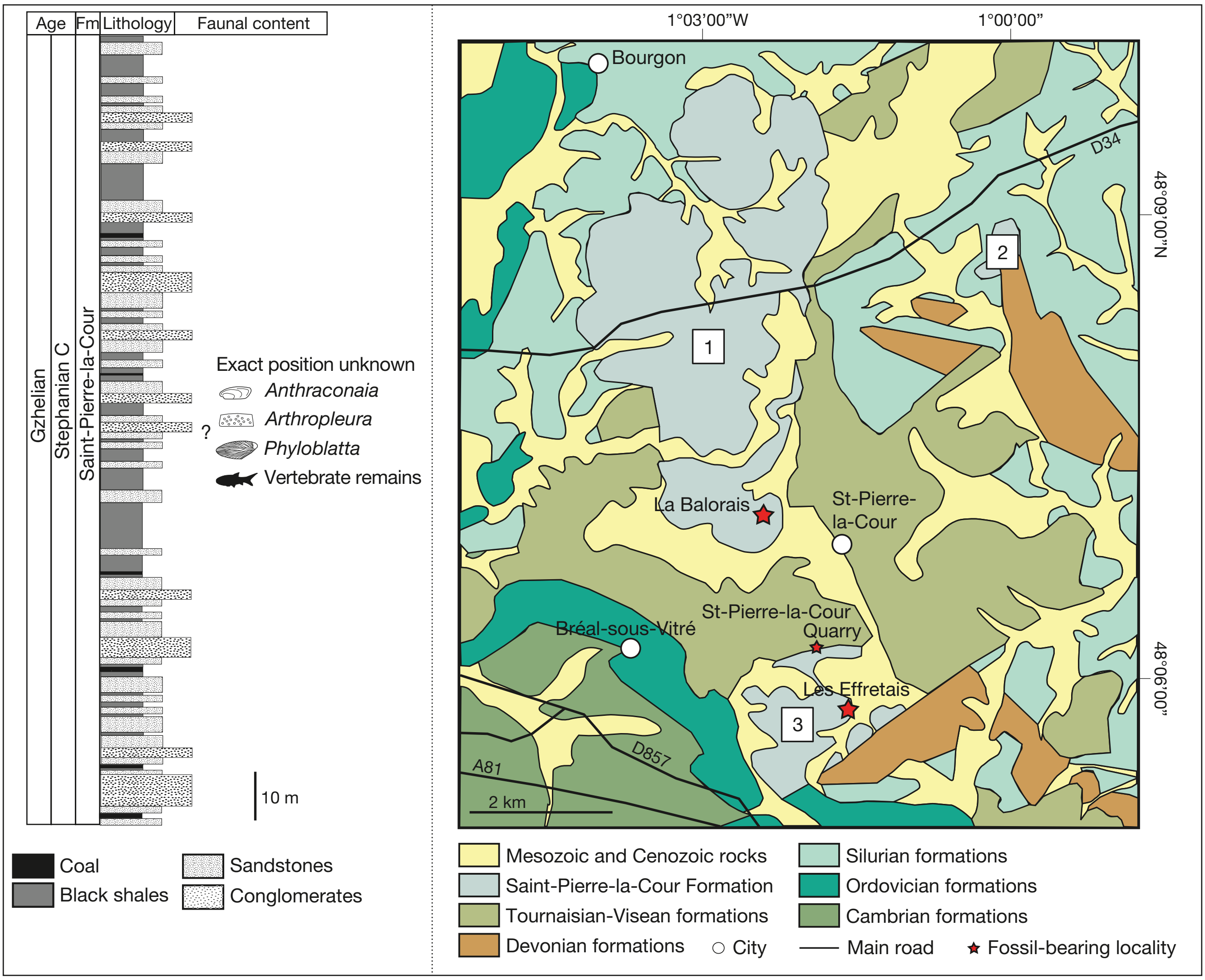

FIG. 3. — Geological map and stratigraphy of the Saint-Pierre-la-Cour Basin (modified after Étienne & Limasset 1979; Le Gall *et al.* 2011). Numbers: **1**, La Balorais sub-basin; **2**, Launay-Villiers sub-basin; **3**, Germandières sub-basin. Schema and map by D. Gonçalves.

not allow assigning these spines to *Acanthodes*, especially since this genus is not the only acanthodid known in the Permo-Carboniferous basins of Europe (Heidtke 2003, 2011). I therefore consider these remains described by Bigot & Pruvost (1925) as belonging to Acanthodidae indet.

Bigot & Pruvost (1925) described teeth of the xenacanthiform *Diplodus* sp. from the same black shales. They noted on these teeth two diverging sinuous crowns, with a third, smaller, at their point of separation (Bigot & Pruvost 1925: 38). Unfortunately this description is too sketchy to revise the attribution to *Diplodus* Agassiz, 1833-1843, which is no longer a valid genus and distributed among several genera of xenacanthiformes (e.g., Dick 1981; Ginter *et al.* 2010). I therefore attribute these teeth to Xencanthiformes indet.

Finally, Aubry (1982: 41, 43) mentions the presence of invertebrate burrows in the Saint-Martin-de-Blagny Formation, in boreholes Li 4 and Li 10 drilled to the south of the hamlets of La Montagne and Cropey.

Saint-Pierre-la-Cour Basin (Fig. 3)

Geological context. The Saint-Pierre-la-Cour Basin is divided in three sub-basins: the Germandières sub-basin (2.3 km²), the Launay-Villiers sub-basin (1 km²) and the La Balorais sub-basin (10 km²) (Vetter 1957; Étienne & Limasset 1979; Le Gall *et al.* 2011). These sub-basins are separed by Dinantian limestones (Oehlert 1882; Milon & Dangeard 1920; Étienne & Limasset 1979). The basin strata lay unconformably on the underlying Dinantian, Silurian and Ordovician formations (Vetter 1957; Le Gall *et al.* 2011). Its fill is composed of alternating conglomerates, sandstones and shales containing more or less coal (Dufrénoy & Élie de Beaumont 1841; Burat 1867; Dorlhac 1881; Milon & Dangeard 1920; Vetter 1957; Étienne & Limasset 1979). This group rests on a basal conglomerate (Vetter 1957; Étienne & Limasset 1979). The Saint-Pierre-la-Cour Basin outcrops are mainly located at the Saint-Pierre-la-Cour quarry (Le Gall *et al.* 2011).

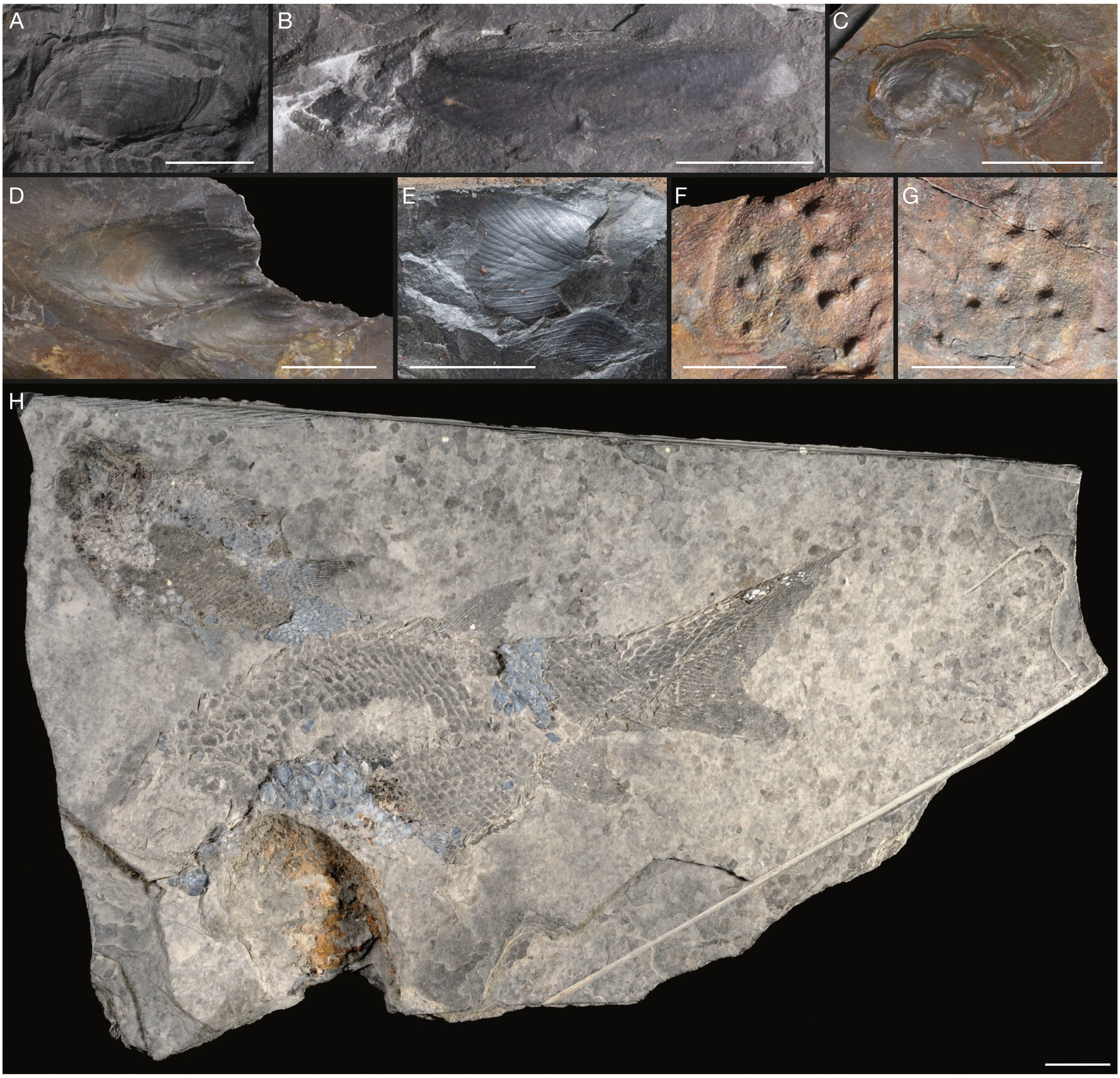

Fig. 4. — Saint-Pierre-la-Cour Basin paleofauna: **A**-**D**, valves of *Anthracomya prolifera* (Waterlot, 1934) from the Stephanian C of La Balorais; **A**, IGR.111183; **B**, IGR.111185; **C**, IGR.111188; **D**, IGR.111186; **E**, ML-PAL-28764, counterpart of the holotype of *Phyloblatta girardi* Péneau, 1930 from the Stephanian C of La Balorais mine; **F**, **G**, IGR.111279, part and counterpart of a partial syntergite of *Arthropleura* sp. from the Stephanian C of La Balorais mine; **H**, ML-PAL-0451, slab containing two specimens of *Aeduella blainvillei* (Agassiz, 1833) and a spiralled coprolite from the Stephanian C of Les Effretais. Scale bars: 1 cm. Photos: A-G, IGR; H, ML (modified by D. Gonçalves).

Flora and datation. Unlike the majority of the Stephanian basins in the Armorican Massif, the flora of the Saint-Pierre-la-Cour Basin has been the subject of several detailed studies (Brongniart 1828b; Schimper 1869; Crié 1879; Grand'Eury 1877; Zeiller 1879; Oehlert 1882, 1912; Carpentier 1920; Picquenard 1920c; Vetter 1957). Vetter (1957) reviewed 54 species and assigned a Stephanian C age to this basin, on the basis of the presence of *Pecopteris monyi* Zeiller, 1888, *Neuropteris planchardi* Zeiller, 1888, *Odontopteris minor* Brongniart, 1832a, *Sphenophyllum angustifolium* Germar, 1845 and *S. thoni* Mahr, 1868.

Fauna (Fig. 4). The first faunal elements from the Saint-Pierre-la-Cour Basin are the bivalves *Naiadites* sp. mentioned in black shales from the La Balorais mine (Oehlert 1882; Milon & Dangeard 1920). Pruvost (1925) described three of these specimens and attributed them to *Anthraconaia calcifera* (Hind, 1899), whereas Waterlot (1934) revised and reattributed all the specimens to *A. prolifera* (Waterlot, 1934). The exact number and current location of specimens described by Oehlert (1882) and by Milon & Dangeard (1920) are unknown, and some specimens may be lost. The collections of the Institut de Géologie de Rennes (IGR) contain four specimens of

A. prolifera discovered by Yves Milon during excursions to La Balorais in 1919-1920 (Fig. 4A-D; IGR.111182/111183, IGR.111185, IGR.111186 and IGR.111188). Among them, IGR.111185 was studied but not figured by Pruvost (1925).

Picquenard (1922) reported a left fragment of *Arthropleura* Jordan *in* Jordan & von Meyer, 1854 syntergite (IGR.111279; Fig. 4F-G) found during an excursion at La Balorais. This fragment was studied by Van Straelen (1923), who confirmed its attribution to *Arthropleura* sp., noting a similarity in ornamentation with *A. britannica* Andrée, 1910 but unique narrow articular surface and smooth posterior edge. The use of ornamentation alone as a diagnostic feature in *Arthropleura* does not allow for the identification of species, but only of morphotypes (Lhéritier *et al.* 2024). Consequently, IGR.111279 cannot be attributed to a specific species, but shows similarities with the morphotypes *A. armata* Jordan *in* Jordan & von Meyer, 1854 and *A. britannica* (e.g., Van Straelen 1923). I therefore follow Van Straelen (1923) who attributed the syntergite IGR.111279 to *Arthropleura* sp.

A species of cockroach from the Saint-Pierre-la-Cour Basin was described by Péneau (1930) under the name *Phyloblatta girardi* Péneau, 1930. Its holotype (UCO 76.593 and ML-PAL-28764; Fig. 4E) is a forewing found by Abbé Girard in a black shale from the La Balorais mine. Since, as *P. girardi* has been mentioned only (e.g., Vetter 1957; Le Gall *et al.* 2011) but never redescribed, its status requires revision. This revision is necessary because the diagnosis of the genus *Phyloblatta* Handlirsch, 1906 has been largely modified since Péneau (1930), and many species of *Phyloblatta* have been described or revised (e.g., Vršanský 2003; Anisyutkin 2007; Béthoux *et al.* 2011; Belahmira *et al.* 2019). Pelhate (1994) refers to a *Protoblattopteris* in this basin, but this name is a *nomen nudum* and it probably alludes to *Phyloblatta girardi*.

“Fish” and “freshwater crustaceans” were reported by Le Gall *et al.* (2011: 82), without details on the remains found and their taxonomic classification. Racheboeuf & Crasquin (2012) reported *Paramblypterus* cf. *decorus* associated with a supposed tetracorallian *Caninia* from Les Effretais (Fig. 4H). These specimens are described below (see Systematic paleontology). The supposed tetracorallian they identified is in fact a spiralled coprolite with inclusions of smooth scales of aeduellids (Fig. 4H). Based on its large size and spiralled architecture, this coprolite was likely produced by a large carnivorous non-tetrapod vertebrate (e.g., McAllister 1987; Argyriou *et al.* 2016).

Finistère basins (Fig. 5)

They are located between several faults in metamorphic and magmatic units of the northwestern Armorican Massif (e.g., Pelhate 1994; Ballèvre *et al.* 2013). These faults belong to the South Armorican Shear Zone (SASZ; Ballèvre *et al.* 2009). The Baie des Trépassés Basin lies at the western end of this fault system, while the Quimper, Kergogne, Gourléo and Gouesnac’h basins lie further east (Fig. 1C; e.g., Picquenard 1920d; Mulot 1975; Pelhate 1994). These very narrow basins rest directly on the basement (Mulot 1975).

Baie des Trépassés Basin (Fig. 5C)

Geological context. This basin is a strip of 18 km long and less than 500 m wide. It is also known as the Plogoff-Pont-Croix Basin (Picquenard 1918, 1920b), or the Cléden-Cap-Sizun Basin (Picquenard 1921), or the Cap Sizun Basin (e.g., Pelhate 1994). It is wedged between two E-W faults of the SASZ (Mulot 1975). It consists of a conglomeratic base whose clasts have a local source, followed by alternances of sandstones and black shales, with a few coal seams (Mulot 1975; Plaine 1981; Barrière *et al.* 1985). The rare outcrops do not allow to define the thickness nor the stratigraphic section of this basin (Plaine 1981). The only poor data we have on this basin come from the mines undertaken between 1759 and 1918 at Lamboban, Pont-Yan, Lescléden, Kerloc’h and Kergaradec for the main ones (Picquenard 1920d; Mulot 1975).

Flora and datation. The flora was compiled by Picquenard (1920b, c, d, 1924) and Hanmer (1977) who listed portions of *Calamites cisti* Brongniart, 1828c, *Neuropteris cordata* Brongniart, 1830, *Dicranophyllum gallicum* Grand’Eury, 1877 and undetermined pteridopsids from brown-grey sandstones of the Lamboban and Kerloc’h mine slag heaps (Picquenard 1920b, c, d, 1924). In various black shales, Picquenard (1920b, d) also reported *Aphlebia* cf. *fasciculata* and *Poacordaites* sp. from the Kerloc’h mine slag heap; *Cordaicarpus orbicularis* Newberry, 1873 from an outcrop near Saint-Tugdual; and *Annularia radiata* (Brongniart, 1822), *Calamites cisti*, *Ca. suckowii* and *Cordaites* sp. from the Lescléden mine. He also listed *Calamites dubius* in the basin but without precising the locality (Picquenard 1918, 1920d). Hanmer (1977) reported *Odontopteris* (*Mixoneura*) *peyerimhoffi* Bertrand, 1930, *Callipteridium* cf. *jongmansi*, *Pecopteris* sp. and *Annularia cordata* in the basin. The name *Annularia cordata* is a typographical error, however, and corresponds to either *Neuropteris cordata* or *Annularia radiata* previously reported by Picquenard (1920b, c, d, 1924).

Picquenard (1920d, 1924) considered the whole flora as typical of the Stephanian, then representing an intermediate age between the older Quimper and the younger Kergogne basins. The stratigraphic revision of this flora (e.g. Vetter 1968; Doubinger & Vetter 1985) and the discoveries of Hanmer (1977) led Plaine (1981) to precise a Stephanian B age to this Baie des Trépassés Basin.

Fauna. The presence of animal remains in the Baie des Trépassés Basin is uncertain. In sandstones from the Lamboban mine slag heap, Picquenard (1924) reported oblong, shiny charcoal moulds of 5 by 8 mm, without visible details, but which may be seeds or valves of *‘Estheria’* (synonym of *Pseudestheria*).

Quimper Basin (Fig. 5A, E)

Geological context. The Quimper Basin measures 6km by 1km and is WNW-ESE trending, bounded by faults parallel to the SASZ (Béchennec *et al.* 1999). It is filled by granodecreasing detrital series with rapidly changing facies, with heterometric conglomerates at the base, covered by sandstones, grey-green siltstones and bituminous shales (Fuchs 1953; Mulot 1975;

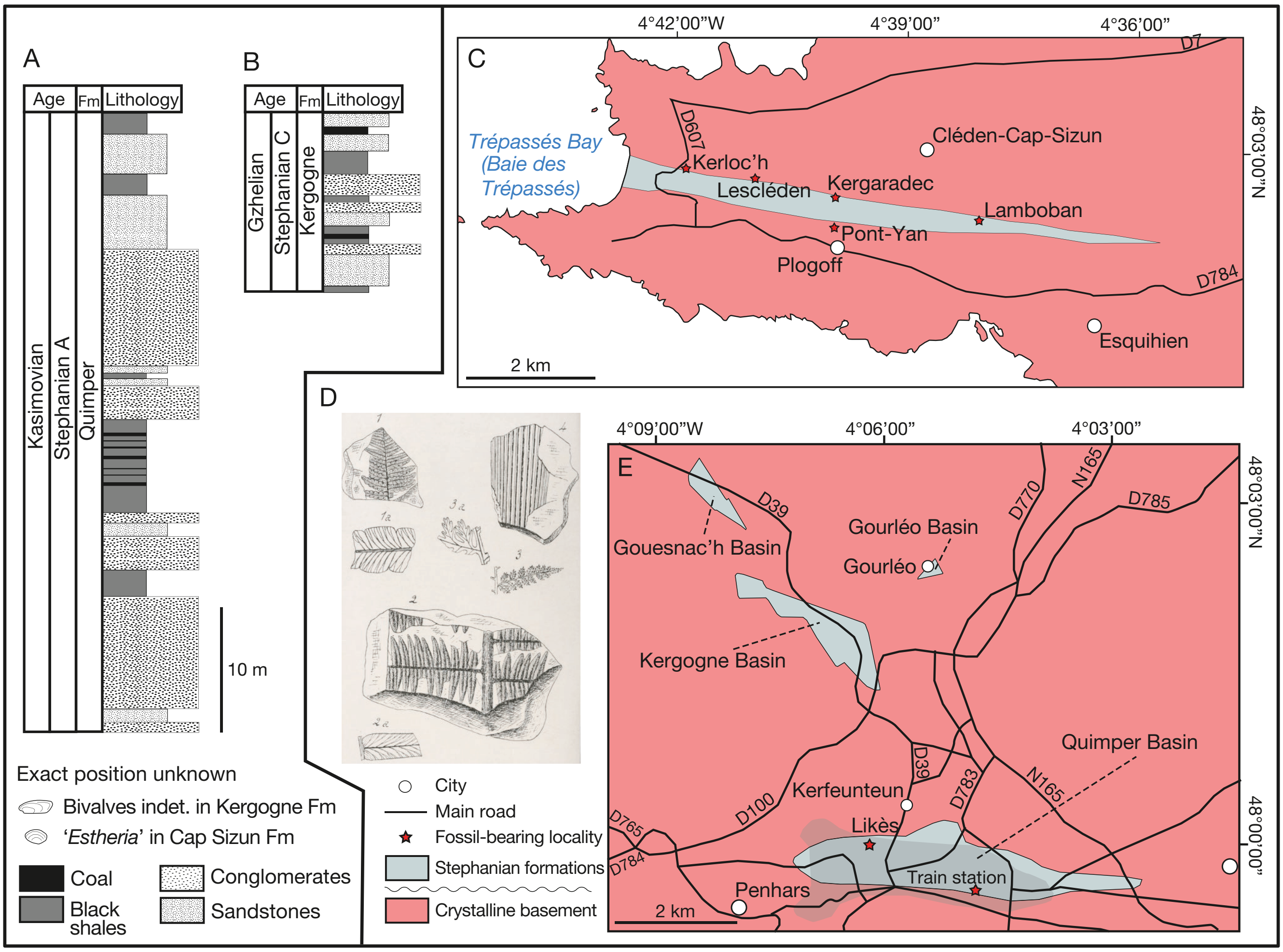

FIG. 5. — Geological maps and stratigraphy of the Finistère basins: **A**, stratigraphic section of the Prat ar Rouz mine shaft, Quimper Basin (modified after Mulot 1975); **B**, stratigraphic section of the Turmoch mine shaft, Kergogne Basin (modified after Mulot 1975); **C**, geological map of the Baie des Trépassés Basin (modified after Mulot 1975; Plaine 1981; Barrière *et al.* 1985); **D**, plate from Picquenard (1921) showing the paleoflora of the Kergogne Basin. Numbers: **1**, *Odontopteris ctenoclada* Picquenard, 1921; **2**, *Alethopteris costei* (Zeiller, 1906); **3**, *Sphenopteris matheti* Zeiller, 1888; **4**, *Titanophyllum* sp.; **E**, geological map of the Quimper region, showing the Quimper, Kergogne, Gourléo and Gouesnac'h basins (modified after Béchennec *et al.* 1999). Schemas and maps by D. Gonçalves.

Béchennec *et al.* 1999). Tuff, tuffite and coal layers are also present in the upper part of the basin (Mulot 1975; Béchennec *et al.* 1999). Yet, here again, the stratigraphy is limited to completed mines, as most of the basin is covered by the town of Quimper (Fuchs 1953; Mulot 1975). Most of the palaeontological discoveries were made during works around the train station and the Likès neighbourhood (Fuchs 1953; Mulot 1975). Pelhate (1957) described sandstone pseudonodules in shales, interpreted as loadcasts and suggesting that the deposital environment of the Quimper Basin was a lake edge. Large mudflow type waste dumps are also described from this basin (Pelhate 1957).

Flora and datation. Rivière (1838) was the first to mention the flora of the Quimper Basin, as determined by Brongniart (pers. comm. *in* Rivière, 1838), with *Pecopteris cyathea* (Schlotheim, 1820)*, P. arborescens*, lepidodendrales, and indeterminate ferns. Picquenard (1920a, 1920c) also listed the flora of the Quimper Basin on the basis of museum collections and personal discoveries, yet without detailing his findings. He reported *Calamites suckowii*, *C. cisti*, *Asterophyllites tenuifolius* (Sternberg, 1825), *Sphenophyllum* cf. *myriophyllum*, *Pecopteris arborescens*, *P. cyathea*, *P. hemitelioides* Brongniart, 1834b, *P. polymorpha*, *P. unita* Brongniart, 1836, *P. dentata* var. *delicatula* Brongniart, 1836, *Alethopteris serli* Brongniart, 1836, *Sphenopteris obtusiloba* Brongniart, 1829, *Neuropteris* sp., *Cordaites borassifolius* (Sternberg, 1821), *Dicranophyllum* cf. *striatum*, and *Doleropteris* cf. *gigantea*. Abrard (1948) and Fuchs (1953) added the occurences of *Al. densifolia*, *Archaeopteris virleti*, *Annularia radiata*, *Calamites schreibersi*, *Stigmaria* sp., *Sigillaria* sp., and *Equisetum* sp. There are several inconsistencies concerning these latter taxa: the name *Alethopteris densifolia* does not exist and may be a typographical error for *Pecopteris densifolia* (Göppert, 1864) (Zeiller 1890: 58); *Archaeopteris virleti* does not exist either, but may be a typographical error for *Lesleya virletii* (Brongniart, 1828b); *Calamites schreibersi* is also an unknown name in the literature.

The presence of *As. tenuifolius*, *Al. serli* and *S. obtusiloba* was regarded as characteristic of the top of the Westphalian and the base of the Stephanian by Picquenard (1920a), leading him to consider the Quimper Basin as being from the beginning of the Stephanian (i.e., Stephanian A). This ambiguity of the flora has led some authors to categorize the Quimper Basin as Westphalian C (e.g., Rolet 1984), while others have confirmed its position at the base of the Stephanian (e.g., Mulot 1975; Pelhate 1994; Béchennec *et al.* 1999).

Fauna. No animal remains have been discovered in the Quimper Basin.

Kergogne Basin (Fig. 5B, D-E)

Geological context. This 3.5 km x 650 m basin is oriented NW-SE, and filled by silicoclastic sediments (Picquenard 1921; Mulot 1975): these sediments are alternated conglomerates, sandstones, siltstones and black shales, with some layers of coal (Picquenard 1921; Mulot 1975; Béchennec *et al.* 1999). As with the other Finistère Basins, only a small part of the basin is known, due to the poor outcrop and the shallow depth of the exploitations during the 19th century (Mulot 1975). Rivière (1838) was the first to study the Kergogne Basin, assuming a local origin of its detrital rocks based on the identical composition between the detrital materials and those of the basin basement Rivière (1838: 47). The granulometric analysis of Pelhate (1960) confirmed this local nature and hypothetized a torrential regime with large volumes of sediments deposited in a lake.

Flora and datation (Fig. 5D). Virlet (1832) mentionned *Cannophyllites virletii* Brongniart, 1828b in the Kergogne Basin, as confirmed by Picquenard (1920c) under the name *Megalopteris virletii* (Brongniart, 1828b). Grand'Eury (1877) and Picquenard (1920a, 1920c, 1921) listed the following flora from non-specified localities: *Calamites cisti*, *Annularia stellata* (Schlotheim, 1820), *Pecopteris arborescens*, *P. cyathea*, *P. candollei* Brongniart, 1834a, *P. daubreei* Zeiller, 1888, *P. lepidorachis* Brongniart, 1834b, *P. densifolia*, *P. polymorpha*, *P. dentata*, *P. biotii* Brongniart, 1836, *Ptychopteris benoiti* Zeiller, 1888, *Pecopteridium pluckeneti* (Schlotheim, 1820), *Callipteridium costei* (Zeiller, 1906), *C. pteridium* (Schlotheim, 1920), *C.* cf. *gigas*, *Alethopteris grandini* Brongniart, 1832b, *Neuropteris* cf. *cordata*, *N. heterophylla* Brongniart, 1822, *Odontopteris minor*, *O. ctenoclada* Picquenard, 1921, *Sphenopteris matheti* Zeiller, 1888, *Linopteris germari* (Giebel, 1857), *Cordaites principalis* (Germar, 1848), *Co. lingulatus* Grand'Eury, 1877, *Co.* sp., *Poacordaites linearis* Grand'Eury, 1877, *Titanophyllum grandeuryi* Renault, 1890 and *Dicranophyllum* sp. Picquenard (1924) added the occurences of *Pecopteris hemitelioides* and *Odontopteris lingulata* (Göppert, 1846), while Mulot (1975) reported the presence of *Pecopteris aspidioides* Sternberg, 1825.

Spores found in black shales of the Kergogne Basin were listed by Pelhate (1960): *Triletes* (*Laevigati*) sp., *Leiotriletes* sp. and *Laevigatosporites* sp.

Picquenard (1920a, 1921) considered this flora as belonging to the '*étage des calamodendrées*', an old floral subdivision corresponding to the Stephanian C (Doubinger & Vetter 1985). The spores described by Pelhate (1960) are not characteristic of a stage and do not help to precise the datation. Although the floral assemblage of the Kergogne Basin is characteristic of the Stephanian C (Pelhate 1960, 1994; Mulot 1975; Béchennec *et al.* 1999), Rolet (1984) considered this basin as Westphalo-Stephanian without discussion. As this exception is not justified in the literature, I consider Rolet's (1984) dating to be erroneous.

Fauna. Picquenard (1921) reported a single valve of a mollusc from an unknown locality. He described growth lines and noted similarities with *Mytilus edulis* Linnaeus, 1758 (Blue mussel). These brief details did not allow to precise the affinities of this indeterminate bivalve.

Gouesnac'h and Gourléo basins (Fig. 5E)

Geological context. These very small basins consist only of conglomerates (Béchennec *et al.* 1999). The Gourléo and Gouesnac'h basins are triangular, maesuring 450 × 450 × 200 m and 1400 × 1400 × 400 m respectively (Béchennec *et al.* 1999). Their relationship with the nearby Quimper and Kergogne basins has not been determined, and no outcrops exist as their existence is based on indirect evidences.

Fauna, flora and datation. No fossil remains have been discovered in the conglomerates of the Gouesnac'h and Gourléo basins. They were dated to the Stephanian by Béchennec *et al.* (1999), based on similarities with conglomerates in neighbouring basins of Quimper and Kergogne.

Doué-la-Fontaine Basin (Fig. 6A)

Geological context. Virlet (1832) firstly reported this small (2.6 km×0.3 km), rectangular Stephanian basin at the eastern end of the Basse Loire Basin. This basin rests unconformably on the Namurian layers of the Basse Loire Basin, and is made up of alternating conglomerates, sandstones and black shales, with two lenticular layers of coal (Virlet 1832; Bureau 1910; Alcaydé *et al.* 1970; Étienne & Limasset 1979). This basin was previously known as the Minière Basin (Virlet 1832; Bureau 1910; Alcaydé *et al.* 1970). The main old outcrops are the mine shafts Minière, Argent Perdu and Beauregard.

Flora and datation. Brongniart (1828b) reported *Cannophyllites virletii* from the black shales, a name recombined as *Lesleya virletii* by Alcaydé *et al.* (1970). Brongniart (1828a) also reported *Pecopteris cyathea*, *P. hemitelioides*, *P. candollei* and *Neuropteris planchardi*. He did not precise the location which is likely the Minière mine shaft, as it is the only area of the basin that has been mined where fossils have been collected (Bureau 1910; Alcaydé *et al.* 1970). This flora gives a Stephanian age to the Doué-la-Fontaine Basin (Bureau 1910; Alcaydé *et al.* 1970; Étienne & Limasset 1979), but the absence of species characteristic of a Stephanian stage prevents any precision in the dating (see Doubinger & Vetter 1985).

Fauna. No animal remains have been discovered in the Doué-la-Fontaine Basin.

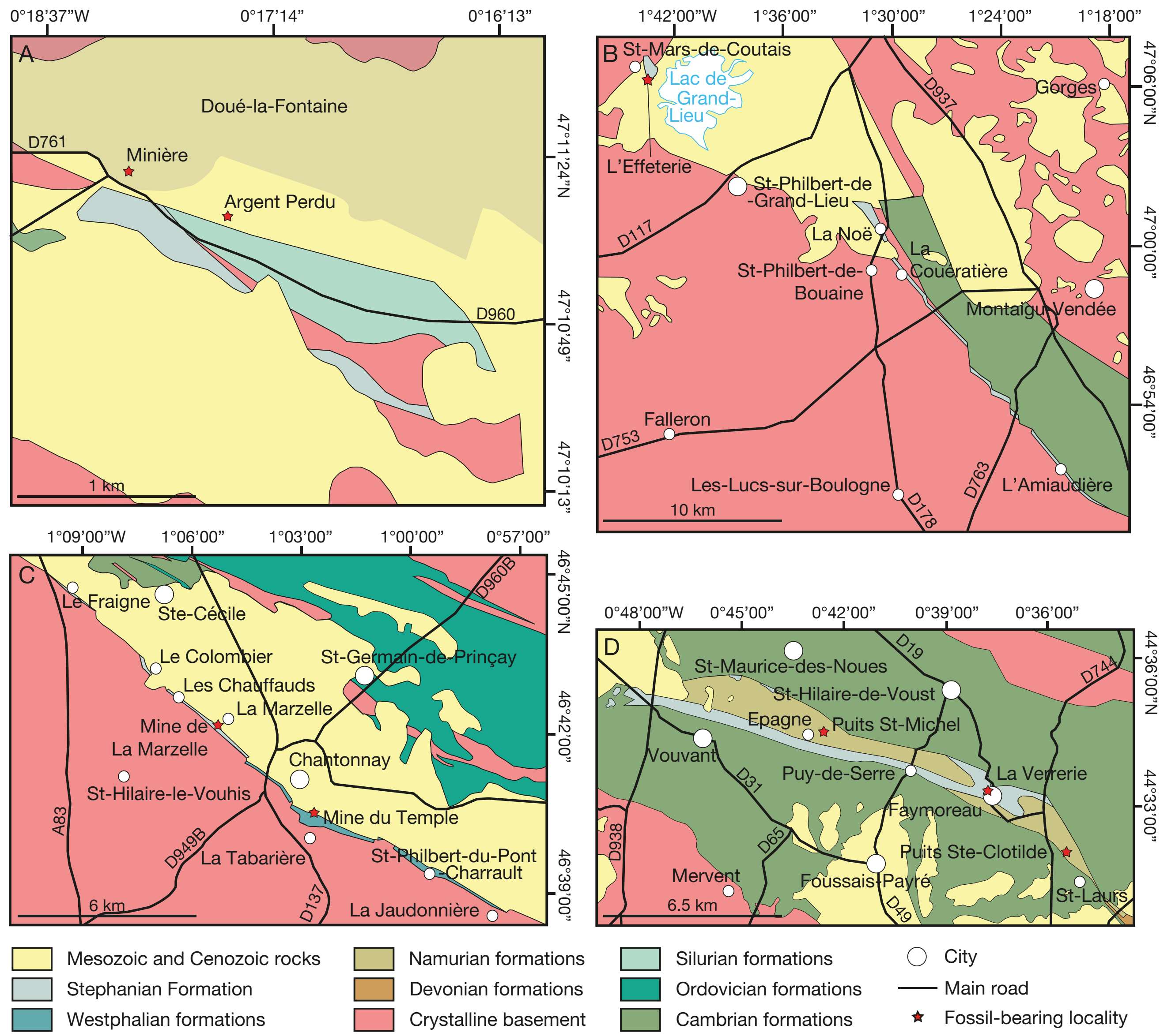

FIG. 6. — Geological maps and stratigraphy of the Doué-la-Fontaine and Sillon Houiller Vendéen basins: **A**, Doué-la-Fontaine Basin (modified after Alcaydé *et al.* 1970); **B**, Lac de Grand-Lieu Basin (modified after Ters & Greber 1982; Wyns *et al.* 1989; Lahondère *et al.* 2009); **C**, Chantonnay Basin (modified after Wyns *et al.* 1988, 1989); **D**, Vouvant Basin (modified after Bouton 1990; Bouton & Branger 2007). Maps by D. Gonçalves.

SILLON HOUILLER VENDÉEN BASINS (Fig. 6B-D)

The Sillon Houiller Vendéen Basins are three basins bordered by faults oriented NW-SE, and wedged between metamorphic rocks and sometimes covered by Mesozoic and Cenozoic sediments (e.g., Bureau 1910; Étienne & Limasset 1979; Wyns *et al.* 1988, 1989). These are not basins *sensu stricto*, but rather a succession of lenses over more than 100 kilometers with three distincts sets (e.g., Pelhate 1994).

Lac de Grand-Lieu Basin (Fig. 6B)

Geological settings. This basin is a succession of lenses over 40km along the Sillon Houiller Vendéen on a NW-SE axis, intersected by NNE-SSO oriented faults (Étienne & Limasset 1979; Lahondère *et al.* 2009). These lenses are, from North to South, located around Saint-Mars-de-Coutais, La Noë, La Couératière, Malabrit, La Giraudière, La Marière, Le Bois Châtelier, La Mitennière, L'Amiaudière, and La Brossette (Bureau 1910; Ters & Greber 1982; Wyns *et al.* 1989; Lahondère *et al.* 2009). Most of the deposits are conglomerates and sandstones sometimes intercalated with black shales and few coal seams (Ters & Greber 1982; Lahondère *et al.* 2009). Hidden by a thick Pliocene cover, outcrops are extremely rare, and knowledge of the basin is limited to a few roadsides and mine shafts at L'Effeterie (Saint-Mars-de-Coutais vicinity): the Puits A, B and C (Ters & Greber 1982). The thickness of the layers and their base are not known, and knowledge of the succession of layers is limited to mine shafts (Péneau 1921; Ters & Greber 1982).

Flora and datation. From the 'Puits B' mine shaft (L'Effeterie), Péneau (1921) reported *Pecopteris (Dactylotheca) dentanta* var. *plumosa, P. (Candolliana) hemitelioides, P. arborescens, P. cyathea*, *P. simoni* Zeiller, 1888, *P. affinis* Brongniart, 1834a, *Alethopteris serlii, Annularia stellata, Asterophyllites equisetiformis* (Schlotheim, 1820) and *Cordaites principalis*. This flora is typical of the Stephanian (Doubinger & Vetter 1985), with the exception of *Al. serlii* which is more characteristic of the Westphalian but its identification is equivocal (Péneau 1921; Ters & Greber 1982). Absence of species characteristic of a Stephanian stage prevents any precision in the dating (Ters & Greber 1982).

Fauna. No animal remains have been discovered in the Lac de Grand-Lieu Basin.

Chantonnay Basin (Fig. 6C)

Geological context. This basin is a succession of two lenses over 15km along the Sillon Houiller Vendéen on a NW-SE axis, intersected by NNE-SSO oriented faults (Wyns *et al.* 1988, 1989). The first is located near Le Fraigne, and the second is between La Marzelle and Saint-Philibert-du-Pont-Charrault (Wyns *et al.* 1988, 1989). The basin filling is made up of conglomerates, sandstones with few black shales and coal seams (Wyns *et al.* 1988, 1989). These rocks rarely outcrop and are very altered, which limits knowledge of the basin to the mine shafts (Wyns *et al.* 1988, 1989). The two main mine shafts are located at La Marzelle (Mine de La Marzelle) and Chantonnay (Mine du Temple) (Fournel 1836; Mathieu 1937; Étienne & Limasset 1979).

Flora and datation. Picquenard (1918, 1920e, 1923) listed the flora of the Mine du Temple which he considered first to be Stephanian (Picquenard 1918), but later as transitional between the Westphalian and the Stephanian (Picquenard 1920e, 1923). However, Mathieu (1937) interpreted this assemblage as being solely Westphalian. Mathieu (1937) highlighted the presence of two distinct floral assemblages in the Chantonnay Basin: a Stephanian assemblage at Mine de La Marzelle and a Westphalian assemblage at Mine du Temple, thus explaining the ambiguity of previous results that had mixed these two flora. He listed the following taxa from Mine de La Marzelle: *Alethopteris grandini*, *Callipteridium ovatum* (Brongniart, 1828a), *C. pteridium*, *Pecopteris integra* (Andrae *in* Germar, 1849), and *P. daubreei*. A palynological study of samples from the Mine de La Marzelle only found spores of *Crassispora* sp. (Wyns *et al.* 1989). Although typically Stephanian, the paleoflora of Mine de La Marzelle does not contain any index species that could specify its dating. Previous studies have failed to determine the boundary between the Stephanian and Westphalian parts of the Chantonnay Basin, which does not allow us to know if they are in conformable contact or not (Mathieu 1937; Wyns *et al.* 1989). Mathieu (1937) distinguished the Stephanian La Marzelle Formation and the Westphalian Chantonnay Formation. It is likely that the Stephanian part is located to the north of the basin and the Westphalian part to the south, based on geographical distribution of these formations.

Fauna. No animal remains have been discovered in the Chantonnay Basin.

Vouvant Basin (Fig. 6D)

Geological context. This basin is a thin strip over around 13km along the Sillon Houiller Vendéen on a WNW-ESE axis, from Vouvant to Faymoreau (e.g., Mathieu 1937; Bouton & Branger 2007). Unlike the other basins of the Sillon Houiller Vendéen, the Vouvant Basin has been the subject of a detailed geological study (Bouton 1990). The base of the infill, called the Saint-Laurs Formation, consists of conglomerates and sandstones showing a granodecreasing trend, with some intercalations of coal (Bouton 1990). The La Verrerie Formation rests unconformably above (Bouton 1990): its base is a very coarse conglomerate, followed by alternating black shales and coal seams, then by alternating sandstones and conglomerates (Mathieu 1937; Bouton 1990). The alternating black shales and coal seams are called Faisceau de la Verrerie, and the alternating sandstones and conglomerates above belong to the Puy-de-Serre Member (Bouton 1990). The detrital deposits of the Vouvant Basin are interpreted as alluvial fans with a proximal sediment source, which becomes somewhat more distal at the top of the basin (Bouton 1990; Bouton & Branger 2007).

Flora and datation. The macroflora of the Saint-Laurs Formation is known from old mine shafts and museum collections and was listed by Mathieu (1937). Mathieu (1937) listed also the macroflora from the La Verrerie Formation, mainly from La Verrerie and the Puits Saint-Michel near Epagne. It comprises *Odontopteris reichi* Gutbier, 1835, *Sigillaria candollii* Brongniart, 1828a, *S. rugosa* Brongniart, 1828a, *S. tessellata* Brongniart, 1828a, *S. scutellata* Brongniart, 1822, *S. davreuxii* Brongniart, 1828a, *S. elliptica* Brongniart, 1824, *Pecopteris arborescens*, *P. dentata*, *P. abbreviata* Brongniart, 1828a, *P. unita*, *Neuropteris planchardi* and *Callipteridium pteridium*. Palynological analysis of the Puy-de-Serre Member conglomerates yielded the association of *Laevigatosporites vulgaris* (Ibrahim *in* Potonie *et al.*, 1932) and *Florinites* Schopf *et al.* 1944, *Convolutispora* Hoffmeister *et al.* 1955, *Lycospora* Schopf *et al.* 1944, *Calamospora* Schopf *et al.* 1944, and *Raistrickia* Schopf *et al.* 1944 (Bouton & Branger 2007).

The flora of the Saint-Laurs Formation is typical from the Namurian, while the flora of the La Verrerie Formation corresponds to a Stephanian age (Mathieu 1937; Bouton 1990). Unfortunately, the absence of taxa specific to a stage of the Stephanian prevents any more precise dating (see Doubinger & Vetter 1985). The palynofloral assemblage confirms the Stephanian age of the La Verrerie Formation (Bouton & Branger 2007).

Fauna. No animal remains have been found in the Stephanian of the La Verrerie Formation. A freshwater conchostracean, *Leaia tricarinata* var. *minina* Meek & Worthen, 1868, was reported by Mathieu (1937) from the Sainte-Clotilde spoil heap, from the Namurian Saint-Laurs Formation.

SYSTEMATIC PALAEONTOLOGY

The material examined here corresponds to all vertebrate specimens from the Stephano-Permian basins of the Armorican Massif available for study, following a survey of museum collections. Other vertebrate specimens previously reported in the literature are now lost or destroyed (Bigot 1945).

Class ACTINOPTERYGII Cope, 1887
sensu Goodrich (1930)
Order AEDUELLIFORMES Heyler 1967
sensu Gonçalves *et al.* (2026b)
Family AEDUELLIDAE Romer, 1945
sensu Gonçalves *et al.* (2026b)

Genus *Aeduella* Westoll, 1937
sensu Gonçalves & Luccisano (2025b)

TYPE SPECIES. — *Palaeoniscum blainvillei* Agassiz, 1833 by monotypy.

Aeduella blainvillei (Agassiz, 1833)
sensu Gonçalves & Luccisano (2025b)
(Figs 4H; 7; 8)

Palaeoniscum blainvillei Agassiz, 1833: 4, 48-55, pl. V, figs 1-7.

Paramblypterus cf. *decorus* – Racheboeuf & Crasquin 2012: 230, fig. 158.

Aeduella blainvillei – Gonçalves & Luccisano 2025b: 17-26 (last diagnosis).

TYPE MATERIAL. — **Lectotype**. **France** • 1 specimen (almost complete skeleton); Saône-et-Loire, Dracy-Saint-Loup, Muse; Muse Formation, Grès et Schistes de Muse Member, Muse OSB; Early Asselian, 298.57 ± 0.16 Ma; UNISTRA[UNISTRA.2013.0.133]. **Paralectotypes**. **France** • 6 specimens (complete to subcomplete skeletons); Saône-et-Loire, Dracy-Saint-Loup, Muse; Muse Formation, Grès et Schistes de Muse Member, Muse OSB; Early Asselian, 298.57 ± 0.16 Ma; MNHN[MNHN.F.AUT25, AUT676, AUT704], SU[SU.PAL.2017.0.1.16], UNISTRA[UNISTRA.2013.0.135, UNISTRA.2013.0.136].

LECTOTYPE. — An almost complete skeleton (UNISTRA.2013.0.133).

PARALECTOTYPES. — Six complete to subcomplete skeletons (MNHN.F.AUT25, AUT676, AUT704, SU.PAL.2017.0.1.16, UNISTRA.2013.0.135, UNISTRA.2013.0.136), following Brignon (2019).

TYPE LOCALITY AND HORIZON. — Muse, Dracy-Saint-Loup, Saône-et-Loire, France (Muse Formation, Grès et Schistes de Muse Member, Muse OSB). Early Asselian, 298.57 ± 0.16 Ma (Pellenard *et al.* 2017; Mercuzot *et al.* 2023).

NEWLY REFERRED SPECIMENS. — Two complete skeletons in a single slab (ML-PAL-0451; Figs 4H; 7; 8).

NEW LOCALITY AND HORIZON. — Les Effretais (precise layer unknown, Saint-Pierre-la-Cour Formation, Saint-Pierre-la-Cour Basin). Stephanian C regional substage (Vetter 1957), early to middle Gzhelian (Aretz *et al.* 2020).

REMARKS
This slab was donated to the Musée de Laval by Louis Saminn (1816-1887), former director of the coal mines at Saint-Pierre-la-Cour. It may have been discovered during the mining of Les Effretais mine, which was in operation during the second half of the 19th century (e.g., Étienne & Limasset 1979).

COMPARATIVE DESCRIPTION
General body shape
The ML-PAL-0451 slab contains two specimens; ML-PAL-0451a of 13.2 cm in body length and its posterior-ventral skull covered by a coprolite; and ML-PAL-0451b (5.7 cm preserved body length) with almost all its caudal fin covered by ML-PAL-0451a (Fig. 4H, 7A, B). Complete ossification of the skull bones, short lepidotrichia articles, and deep body indicate that both specimens are skeletally mature (Growth Stage 3, following Gonçalves & Luccisano 2025b). The size and body length/depth ratio (3.2) of ML-PAL-0451a are typical of derived aeduellids, such as *Aeduella blainvillei*, *Bourbonnella fourrieri* Poplin, 2001, *B. guilloti* Heyler, 1967, *B. hirsuta* Štamberg, 2007, *Decazella vetteri* Heyler, 1967, *Neslovicella rzehaki* Štamberg, 2007, and *Westollia crassa* (Pohlig, 1892) (Heyler 1969; Poplin 2001; Štamberg 2007, 2024; Gonçalves & Luccisano 2025b).

Rostral region
The rostral region of ML-PAL-0451a is poorly preserved and absent in ML-PAL-0451b. A possible fragment of the ventral part of the rostral and a preorbital are present in ML-PAL-0451a.

The V-shape of the ventral edge of the rostral of ML-PAL-0451a is found in other aeduellids (Fig. 8A, B) (e.g. Heyler 1969; Štamberg 2007, 2010, 2018, 2024; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2025, 2026c).

The preorbital of ML-PAL-0451a is ornamented with long dorsoventral ridges, a characteristic unique to Aeduellidae but invariable within the family (Fig. 8A, B; e.g., Heyler 1969; Heyler & Poplin 1983; Štamberg 2007, 2010, 2018, 2024; Gonçalves & Luccisano 2025b).

Skull roof
The skull roof of ML-PAL-0451a is well preserved in its posterior region, and the bones sutures are not preserved in ML-PAL-0451b.

The parietal is elongated with straight lateral and medial margins and sigmoid posterior margins (Fig. 8A, B). This morphology is the most common among aeduellids (e.g., Heyler 1969; Štamberg 2007; Gonçalves & Luccisano 2025b), but differs from the broad parietal of *Westollia crassa* and *Puertollanichthys ritchiei* Forey & Young, 1985 and from the parietal with lobed interparietal suture in Otovice aeduellid (Forey & Young 1985; Štamberg 2021, 2024).

The postparietal of ML-PAL-0451a and ML-PAL-0451b is rectangular (length/width ratio of 2.1) with straight lateral, medial and posterior margins (Fig. 8). Its anterior margin is oblique, like that of some specimens of *Aeduella blainvillei*, *Bourbonnella guilloti* and *B. hirsuta* (Fig. 8A, B; Heyler 1969; Štamberg

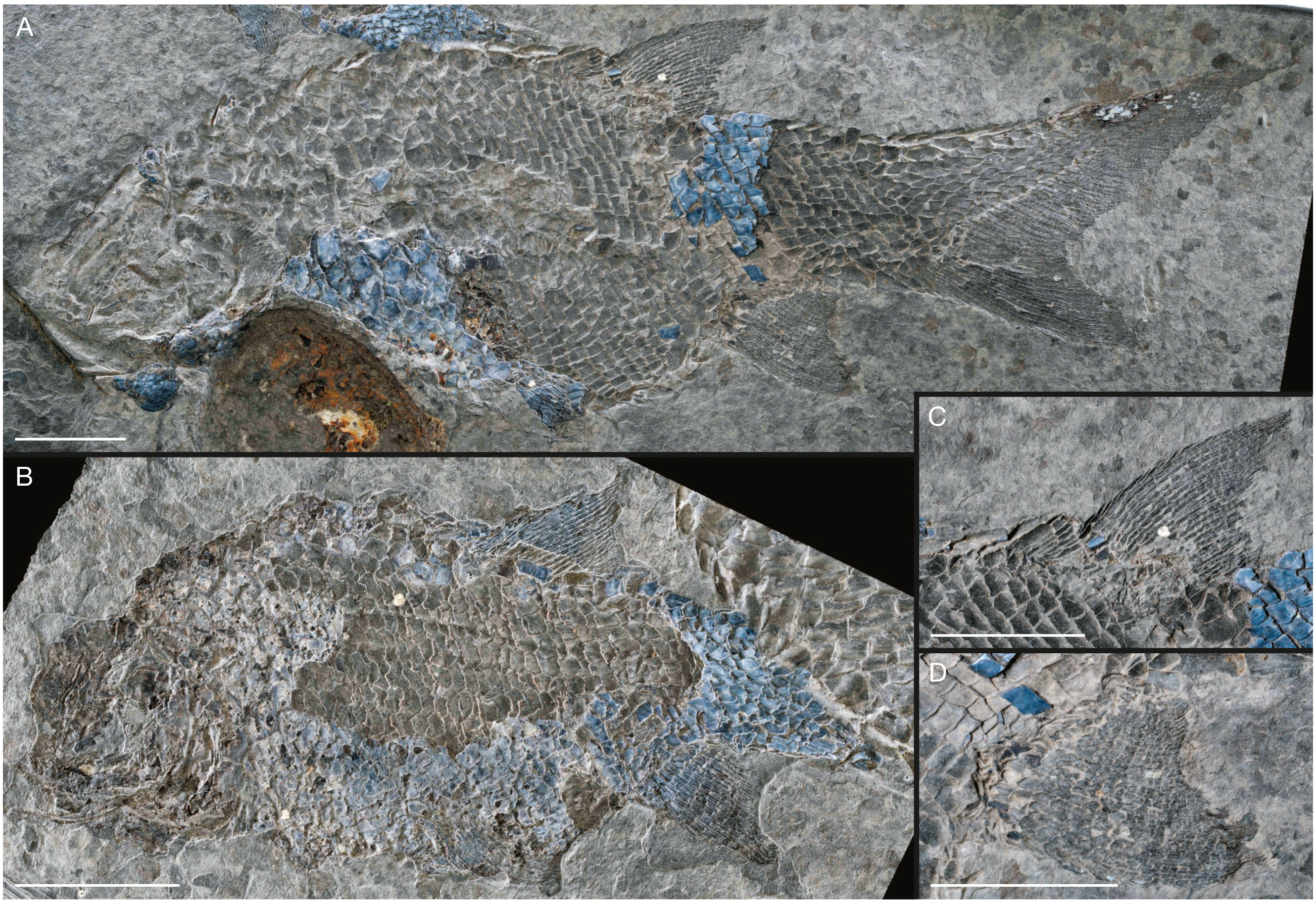

Fig. 7. — *Aeduella blainvillei* (Agassiz, 1833) from the Stephanian C of Les Effretais, Saint-Pierre-la-Cour Basin: **A**, ML-PAL-0451a; **B**, ML-PAL-0451b, reverted; **C**, detail of the dorsal fin of ML-PAL-0451a; **D**, detail of the anal fin of ML-PAL-0451a. Scale bars: 1 cm. Photos: ML, modified by D. Gonçalves.

2007, 2018). It differs from the postparietal with a V-shaped ventral margin of *Amelangia ornata* Štamberg & Werneburg, 2023 and *Platysella lallyi* Heyler & Poplin, 1983 (Heyler & Poplin 1983; Štamberg & Werneburg 2023). The postparietals of ML-PAL-0451a and ML-PAL-0451b have only two and one pit lines, respectively. The presence of two pit lines, the medial and posterior ones, is a diagnostic character of Aeduellidae (e.g., Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b). The absence of the posterior pit line in ML-PAL-0451b is also observed in certain specimens of aeduellids and constitutes an intraspecific variation (Fig. 8C, D; e.g., Heyler 1969).

The triangular intertemporo-dermosphenotic of ML-PAL-0451a is similar to that of other aeduellids (Fig. 8A, B; e.g., Heyler 1969; Štamberg 2007, 2010, 2024; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b, c), except that of '*Neslovicella*' *elongata* Štamberg, 2010, which is more crescent-shaped (Štamberg 2010). The anterior part of the intertemporo-dermosphenotic is not preserved in ML-PAL-0451a, and this bone is not distinct in ML-PAL-0451b.

The supratemporal is complete in ML-PAL-0451a but its margins are not distinct in ML-PAL-0451b (Fig. 8). It is rectangular (length/width ratio of 2.0), with straight medial, lateral and posterior margins, and a V-shaped anterior margin. The supratemporal pit line is present in ML-PAL-0451a, and common among aeduellids (Fig. 8A, B; e.g., Heyler 1969; Gonçalves & Luccisano 2025b). The supratemporal of ML-PAL-0451a is distinct from the supratemporal with M-shaped anterior margin of *Decazella vetteri* (Gonçalves & Luccisano 2025b), and similar to the supratemporal of other aeduellids (e.g., Heyler 1969; Forey & Young 1985; Štamberg 2007, 2010, 2024; Štamberg & Werneburg 2023; Gonçalves *et al.* 2026b, c).

The extrascapulars are preserved in ML-PAL-0451a and indistinct in ML-PAL-0451b. They are arranged in a mediolateral band, with at least three extrascapulars in each side: one medial and two lateral extrascapulars (Fig. 8A, B). *Aeduella blainvillei* is the only aeduellid to possess six or more extrascapulars (Heyler 1969). The most common arrangement in aeduellids is the presence of four extrascapulars (Heyler 1969; Štamberg 2007, 2010, 2024; Gonçalves *et al.* 2026c).

The course of the sensory canals is not visible in ML-PAL-0451a and poorly defined in ML-PAL-0451b: its supraorbital canal runs along the lateral margin of the parietal in (Fig. 8C, D). The presence of a pit line in the supratemporal of ML-PAL-0451a indicates a supraorbital canal course from the parietal to the supratemporal (Fig. 8A, B). This is characteristic of aeduellids (Heyler 1969; Štamberg 2007; Gonçalves & Luccisano 2025b).

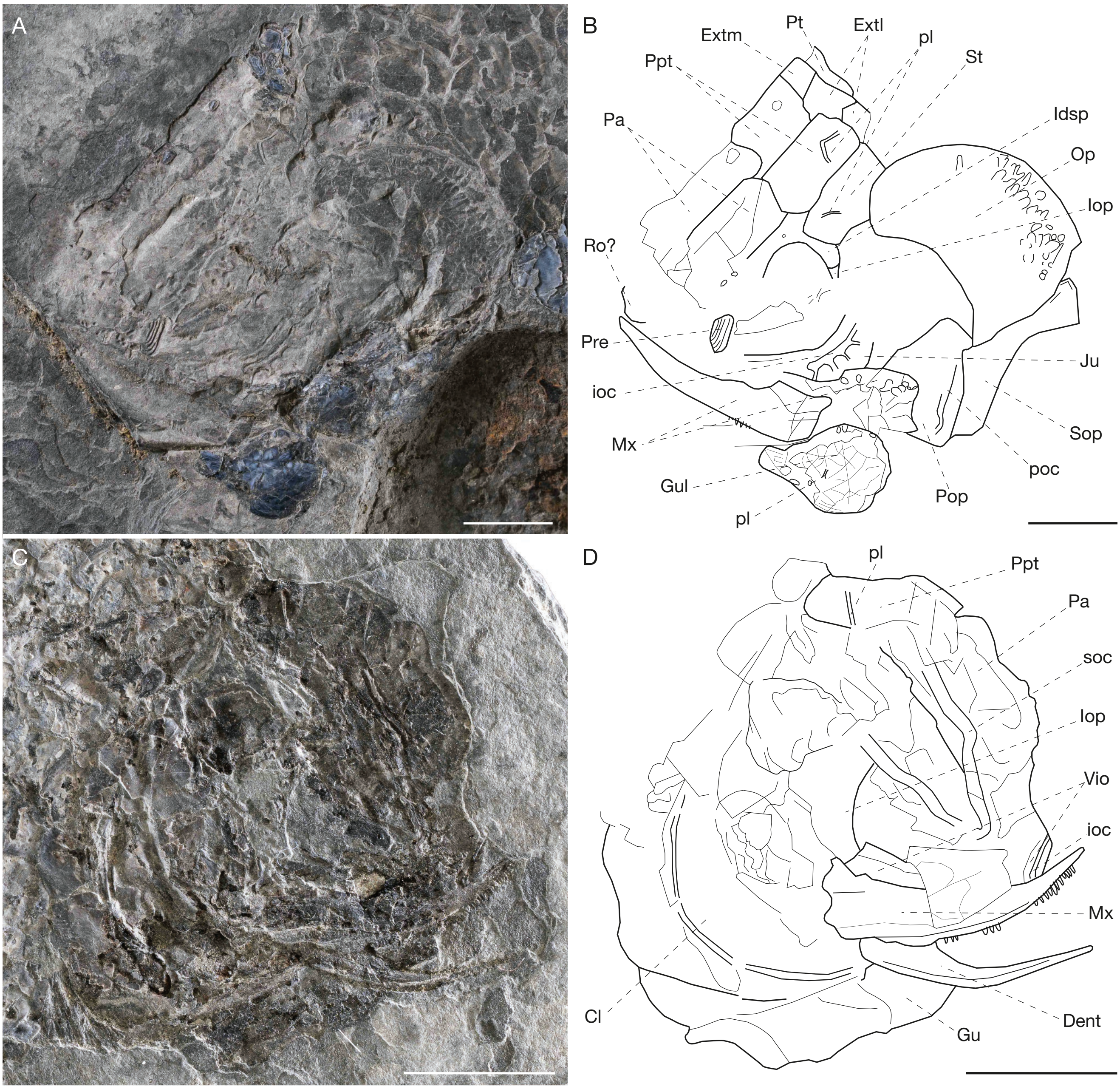

Fig. 8. — Skulls of *Aeduella blainvillei* (Agassiz, 1833) from the Stephanian C of Les Effretais, Saint-Pierre-la-Cour Basin: **A**, **B**, ML-PAL-0451a; **C**, **D**, ML-PAL-0451b, reverted; **A**, **C**, photographs; **B**, **D**, interpretative drawings. Abbreviations: **Cl**, cleithrum; **Dent**, dentalosplenial; **Extl**, lateral extrascapular; **Extm**, medial extrascapular; **Gu**, gular; **Gul**, lateral gular; **Idsp**, intertemporo-dermosphenotic; **ioc**, infraorbital canal; **Iop**, infraorbital posterior; **Ju**, jugal; **Mx**, maxilla; **Op**, operculum; **Pa**, parietal; **pl**, pit line; **poc**, preopercular canal; **Pop**, preoperculum; **Pre**, preorbital; **Ppt**, postparietal; **Pt**, posttemporal; **Ro**, rostral; **soc**, supraborbital canal; **Sop**, suboperculum; **St**, supratemporal; **Vio**, ventral infraorbital. Scale bars: 5 mm. Photos: ML, modified by D. Gonçalves; drawings by D. Gonçalves.

Circumorbital series

The circumorbital bones of ML-PAL-0451a-b are poorly preserved: fragments of ventral infraorbitals are present in ML-PAL-0451b while the dorsalmost posterior infraorbital and the jugal of ML-PAL-0451a are present. Therefore, the number of ventral infraorbitals and posterior infraorbitals cannot be counted and compared with aeduellids.

The ventral infraorbitals are narrow, rectangular elongated antero-posteriorly, and without ornamentation (Fig. 8C, D). The infraorbital canal runs along the ventral infraorbitals margins.

The jugal is L-shaped and unornamented, but its margins are not preserved in ML-PAL-0451a, making unclear its exact shape and relationships with the posteriormost ventral infraorbital and ventralmost posterior infraorbital (Fig. 8A, B). The infraorbital canal runs along the middle of the jugal, following the bone curvature. Numerous branches of this canal are regularly positioned, starting from the main infraorbital canal branch to the posterior and ventral margins of the jugal. While the ambiguous shape of the jugal of ML-PAL-0451a does not allow comparisons, its sensory canal disposition is characteristic: *Aeduella blainvillei* is the only aeduellid with numerous branches of the infraorbital canal regularly positioned, starting from the main infraorbital canal branch to the posterior and the ventral margin of the jugal (Heyler 1969).

Cheek bones

The cheek bones of ML-PAL-0451b are indistinct, and the preoperculum is the only preserved cheek bone in ML-PAL-0451a.

The preoperculum of ML-PAL-0451a reach around the fifth of the operculum depth, as in *Aeduella blainvillei*, *Amelangia ornata*, *B. hirsuta*, *Franchessella pohlcremeri* Gonçalves, Lemaître, Štamberg, Logghe, Rebillard, Pouillon, Fernandez & Steyer, 2026 and *Neslovicella* spp. (Fig. 8A, B; Heyler 1969; Štamberg 2007, 2010, 2018; Štamberg & Werneburg 2023; Gonçalves & Luccisano 2025b). The preopercular canal runs dorso-ventrally along the posterior margin of the preoperculum. The preoperculum of ML-PAL-0451a has a bending angle of 156° and an inclination of 52°. This inclination is low because aeduellids usually have an inclination of around 80°, but not uncommon (e.g., Štamberg 2010; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b).

Jaws

The jaw bones are the best preserved skull elements in ML-PAL-0451b and poorly preserved in ML-PAL-0451a. Their maxilla is triangular, with a curved ventral margin and tubular teeth (Fig. 8). This morphology is a synapomorphy of Aeduellidae (Heyler 1969; Štamberg 2007; Gonçalves *et al.* 2026b). The complete maxilla of ML-PAL-0451b has a length/height ratio of 3.0 (Fig. 8C, D). Most of the specimens of *A. blainvillei* have maxillae with length/height ratio of 3.0-3.5, as in *Amelangia ornata, Platysella* spp. and *Stephaniella melanocephala* Gonçalves, Pouzadoux & Luccisano, 2026 (Heyler 1969; Heyler & Poplin 1983; Štamberg 2018; Štamberg & Werneburg 2023; Gonçalves *et al.* 2026c).

A dentalosplenial is preserved in ML-PAL-0451b, but its posterior part is overlapped by the maxilla (Fig. 8C, D). It is elongated antero-posteriorly, with the ventral margin curved, as in other aeduellids (e.g., Heyler 1969; Štamberg 2007, 2010, 2024; Gonçalves & Luccisano 2025b).

Opercular series

The opercular bones of ML-PAL-0451b are poorly defined. In ML-PAL-0451a, they are incompletely preserved – the branchiostegal rays and the medial gular are not preserved – and bear ornamentation made of flat tubercles. This ornamentation is identical compared to other aeduellids, excepted with *Amelangia ornata* which bears pointed tubercles (Štamberg & Werneburg 2023).

The operculum of ML-PAL-0451a is slightly elevated (depth/length of 1.6) with a rounded dorsal margin, an oblique ventral margin, and a bending angle of 126° (Fig. 8A, B). This morphology is common among aeduellids (e.g., Heyler 1969; Heyler & Poplin 1983; Štamberg 1986, 2007, 2010, 2018, 2024; Gonçalves *et al.* 2026c).

The suboperculum of ML-PAL-0451a is trapezoidal, with a larger posterior margin: the posterior margin/anterior margin depth ratio is 1.8 (Fig. 8A, B). The suboperculum is lower than the operculum, with an operculum/suboperculum depth ratio of 1.5. Among aeduellids, *Aeduella blainvillei*, Otovice taxon, *Puertollanichthys ritchiei*, *Stephaniella melanocephala*, *Spinarichthys dispersus* (Fritsch, 1895) and *Westollia crassa* also possess trapezoidal subopercula with conspicuously sloping dorsal margin (e.g., Heyler 1969; Štamberg 2007, 2018, 2021, 2024; Gonçalves & Luccisano 2025a, 2025b; Gonçalves *et al.* 2026c). The posterior margin/anterior margin depth ratio of 1.8 of ML-PAL-0451a falls within the range of that of *A. blainvillei*, Otovice taxon, *P. ritchiei* and *W. crassa* (Heyler 1969; Štamberg 2018, 2021, 2024; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026c).

The lateral gular of ML-PAL-0451a is ovoid and slightly rhombic, narrowing anteriorly at the middle of the anterior margin (Fig. 8A, B). This morphology is unique to *Aeduella blainvillei* (Heyler 1969; Štamberg 2018; Gonçalves *et al.* 2025; Gonçalves & Luccisano 2025b). Gular elements of ML-PAL-0451b are preserved but indistinct (Fig. 8C, D).

Pectoral girdle

The pectoral girdle of ML-PAL-0451a is not preserved, and poorly defined in ML-PAL-0451b, the posttemporal being very incomplete and the cleithrum being the only bone with well-defined outlines

This cleithrum is ovoid and has a large ridge that runs dorso-ventrally and separates into the lateral and ventral branches (Fig. 8C, D). This morphology is shared by all aeduellids (e.g., Heyler 1969; Štamberg 2007, 2010, 2024; Štamberg & Werneburg 2023; Gonçalves & Luccisano 2025b).

Fins

Like almost all aeduellids, the fins of ML-PAL-0451a and ML-PAL-0451b are composed of lepidotrichia with sigmoidal sutures, which divide dichotomously (Fig. 7; e.g., Heyler 1969; Heyler & Poplin 1983; Forey & Young 1985; Štamberg 1986, 2007, 2010, 2024; Poplin & Dutheil, 2005). The pectoral fins are not preserved in ML-PAL-0451a and ML-PAL-0451b, and a large portion of the caudal fin of ML-PAL-0451b is overlapped by the body of ML-PAL-0451a. Dorsal and anal fin bases of ML-PAL-0451a are located on a field of minute scales (Fig. 7C, D). These minute scales are not observable in ML-PAL-0451b, but this absence may be linked to the poor preservation.

The pelvic fins are triangular, with a leading edge length/base ratio of 1.6-1.8 and around 22 lepidotrichia (Fig. 7A, B). It is located on 4 scale rows in the middle of the body, between the pectoral and anal fins.

The anal fin is triangular with a leading edge length/base ratio of 1.0-1.3 (Fig. 7A, B, D). The anal fin has 20 lepidotrichia and its base sits on 9 scale rows. The base of the anal fin is located just after the posterior end of the base of the dorsal fin. The dorsal fin is also triangular, with a length/base ratio of 1.0-1.5 and is composed of 26 to 28 lepidotrichia (Fig. 7A-C). Its base sits on 10-11 scale rows and is located in the middle of the body length.

The paired and unpaired fins shape and size of ML-PAL-0451a and ML-PAL-0451b are similar to those of the other aeduellids (e.g., Heyler 1969; Heyler & Poplin 1983; Poplin 2001; Štamberg 2007, 2024; Štamberg & Werneburg 2023; Gonçalves & Luccisano 2025b).

The caudal fin of ML-PAL-0451a is large (caudal fin/body length ratio of 3.1) and heterocercal, with a dorsal lobe/ventral lobe length ratio of 1.5 (Fig. 7A). It differs from the caudal fin of *Decazella vetteri*, *Bourbonnella hirsuta* and '*Neslovicella' elongata* in which the ventral lobe is almost as elongated as the dorsal lobe (Štamberg 2007, 2010; Gonçalves & Luccisano 2025b). The ventral lobe of the caudal fin of ML-PAL-0451a has 12 lepidotrichia and its dorsal lobe 44 preserved lepidotrichia, the dorsalmost lepidotrichia being missing. Its caudal inversion is gradual as in *Aeduella blainvillei*, *Franchessella pohlcremeri*, *Platysella lallyi* and *P. descusi* Heyler & Poplin, 1983 (e.g., Heyler 1969, 2002; Heyler & Poplin 1983; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b).

Squamation

The body of ML-PAL-0451a and ML-PAL-0451b is covered with large, rhombic smooth scales (Fig. 7A, B). The lateral sensory canal crosses the body through its middle and extends into the caudal inversion. The posterior edge of the posterior flank scales is straight. The posterior margin of the scales is always broken in the anterior flank scales. Presence or absence of serration on these scales cannot be therefore assessed. The squamation of ML-PAL-0451a and ML-PAL-0451b is identical to that of most of the aeduellids, being different from the ornamented scales of *Franchessella pohlcremeri* (Gonçalves *et al.* 2026b). The scale count of ML-PAL-0451a is:

$$\frac{23}{8 \quad 23 \quad 34}\ 38$$

The scale count of ML-PAL-0451b is:

$$\frac{21}{8 \quad 21 \quad 34}\ ?$$

These scale counts are within the range of *Aeduella blainvillei*, *Decazella vetteri, Neslovicella rzehaki*, and *Stephaniella melanocephala* (Heyler 1969; Štamberg 2007; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026c). The number of scales rows at the anal fin base is higher than in *Puertollanichthys ritchiei*, and that at the dorsal fin base is lower than in *Platysella lallyi* (Heyler & Poplin 1983; Forey & Young 1985). The scale counts of ML-PAL-0451a and ML-PAL-0451b are higher than in *Platysella descusi* (Heyler & Poplin 1983), and lower than in *Amelangia ornata*, *Bourbonnella* spp., *Franchessella pohlcremeri*, *Platysella poplinae* and *Westollia crassa* (Heyler 1969, 2002; Poplin 2001; Štamberg 2007, 2024; Štamberg & Werneburg 2023; Gonçalves *et al.* 2026b).

Ridge scales are poorly preserved in ML-PAL-0451a and ML-PAL-0451b. Few are present in front of the dorsal fin base, and two large scutes are located before the ventral lobe of the caudal fin (Fig. 7A, B). The dorsal lobe of the caudal fin is protected by numerous fulcral scales. These specialized scales of ML-PAL-0451a and ML-PAL-0451b are typical of aeduellids (e.g., Heyler 1969; Poplin 2001; Štamberg 2007, 2024; Gonçalves & Luccisano 2025b)

DISCUSSION

Aeduella stratigraphic and geographic record

Aeduella is the aeduellid genus with the widest stratigraphic and geographical distribution. It has been described from France, Switzerland, Germany and the Czech Republic (e.g. Heyler 1967, 1969; Blieck *et al.* 1999; Poplin & Dutheil 2005; Henderson *et al.* 2023). However, this wide distribution is partly due to the use of characters that were previously thought to be unique to *A. blainvillei* (e.g. trapezoidal suboperculum), but which are now known to occur in many aeduellids (Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b, c). The distribution of *Aeduella*, reviewed in the light of these recent studies, is summarised Figure 9.

Among the major Variscan massifs, *Aeduella blainvillei* was thus already known to exist in the French Massif Central and the Rhenish Massif (e.g., Heyler 1969, 1991, 2000; Blieck *et al.* 1999; Štamberg 2018; Gonçalves & Luccisano 2025b). This new occurrence at Les Effretais extends its distribution to the Armorican Massif. Material undoubtedly attributable to *Aeduella blainvillei* comes from the late Gzhelian-Asselian of France and Germany, with specimens described from the Saar-Nahe (Niederkirchen, Meisenheim Formation), Autun (Lally and Muse, Muse Formation; Millery and Les Télots, Millery Formation), Bourbon-l'Archambault (Buxières-les-Mines, Buxières Formation), Decazeville (La Découverte, Bourran Formation), and Saint-Pierre-la-Cour (Les Effretais, Saint-Pierre-la-Cour Formation) basins (Heyler 1969, 1991, 2000; Heyler & Pacaud 1978; Blieck *et al.* 1999; Štamberg 2018; Gonçalves & Luccisano 2025a, b; this study). Two distinct patterns of repartition can be identified among aeduellids: either endemism or large-scale distribution. Thus, *A. blainvillei* has a wide distribution area within the Variscan Belt, being present in the Armorican Massif, the French Massif Central and the Rhenish Massif. *Westollia crassa* is relatively widely distributed, occurring in both the Rhenish Massif and the Bohemian Massif (Štamberg 2024; Gonçalves & Luccisano 2025b). The genus *Bourbonnella* is also relatively widespread, occurring in both the French Massif Central and the Bohemian Massif, but each species is endemic to a small region (Heyler 1969; Poplin 2001; Štamberg 2007). Finally, the other aeduellids appear to be limited to a single Variscan massif, and often to a single Stephano-Permian basin (e.g., Heyler & Poplin 1983; Forey & Young 1985; Štamberg 1986, 2007, 2010; Heyler 2000; Štamberg & Werneburg 2023; Gonçalves & Luccisano 2025b).

Specimens from the Blanzy-Montceau (Montceau Formation) and Brive basins (Saint-Antoine Limestones Formation) have been attributed to *Aeduella* cf. *blainvillei* but the material is too incomplete to confirm this attribution (Heyler 2000; Poplin 2001; Štamberg & Steyer 2021). The presence of several aeduellids in the French Massif Central, particularly certain taxa with similar morphology such as *Decazella vetteri* and *Stephaniella melanocephala* (Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026c), calls for caution. More specimens from the Brive Basin and a detailed description of those from the Blanzy-Montceau Basin are required and pending such results, I prefer

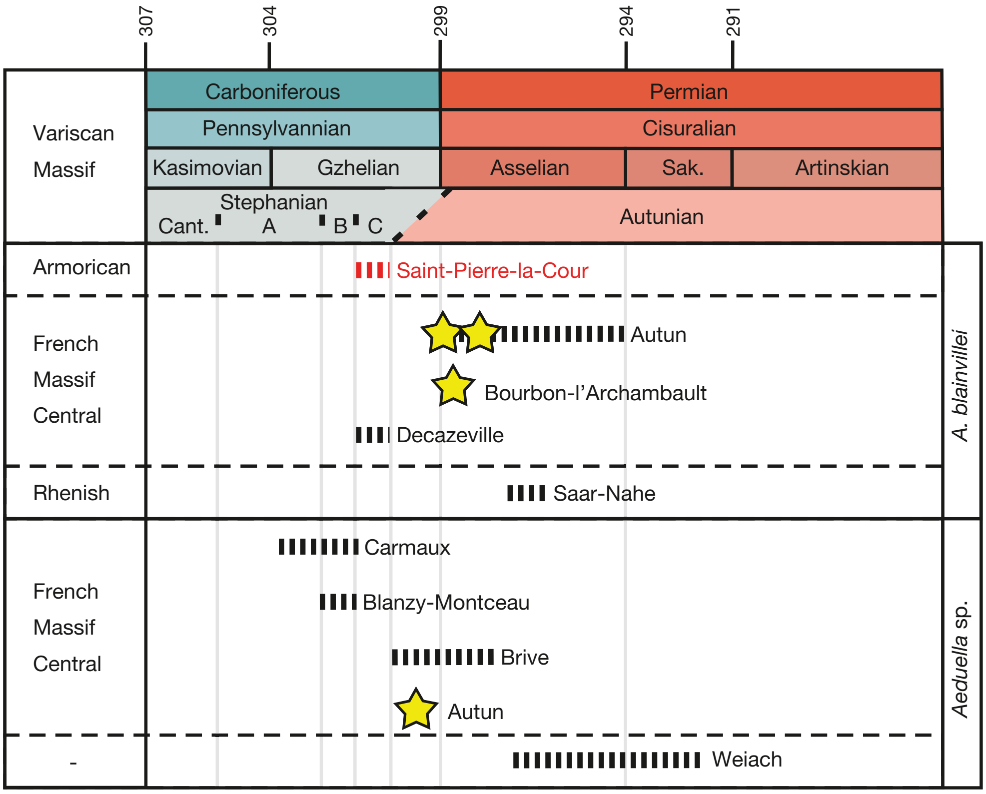

Fig. 9. — Temporal and geographical distribution of *Aeduella* Westoll, 1937: **Dotted lines** indicate biostratigraphic dating based on macroflora (with new occurrence reported here in **red**), and **yellow stars** indicate radiochronological age. Datations based on Pellenard *et al.* (2017) (Autun Basin, Igornay, Lally, Muse, Millery and Les Télots OSBs); Mercuzot *et al.* (2023) (Bourbon-l'Archambault Basin, Buxières-les-Mines); Feys (1976) and Štamberg & Steyer (2021) (Brive Basin, road D1089 at Brive); Delsahut (1981) (Carmaux Basin, exact locality unknown); Vetter (1968) and Gonçalves & Luccisano (2025b) (Decazeville Basin, La Découverte); Heyler (2000) (Blanzy-Montceau Basin, exact locality unknown); Boy & Schindler (2012) (Saar-Nahe Basin, Niederkirchen M6-N); Vetter (1957) (Saint-Pierre-la-Cour Basin, Les Effretais); and Ajuaba *et al.* (2023) (Weiach borehole). Chronostratigraphic scale, including European regional stratigraphy, follow Aretz *et al.* (2020) for the Carboniferous and Henderson *et al.* (2020) for the Permian. Abbreviations: **Cant**, Cantabrian; **Sak**, Sakmarian. Schema by D. Gonçalves.

to assign them to *Aeduella* sp. Erni (1940) described fragmentary postcranial specimens found at a depth of 381.30 m in the Wintersingen borehole (Switzerland), which he attributed to *A. blainvillei*. However, these remains are too fragmentary to allow identification beyond Actinopterygii indet. Blieck *et al.* (1999) listed the presence of *A. blainvillei* in the Autunian of Ruprechtice (MHNL 41003 and MHNL 41006; Broumov Formation, Intra-Sudetic Basin, Czech Republic) and Saint-Wendel (MHNL 41004; Lebach Group, Saar-Nahe Basin, Germany). First-hand examination of these specimens indicates that they are amblypterid specimens, with a rectangular maxillary plate, tubular teeth and seven to nine branchiostegal rays. Based on their provenance and characters (i.e. a length/depth ratio of the maxillary plate close to 1.0), MHNL 41003 and MHNL 41006 are probably specimens of *Paramblypterus vratislaviensis* (Štamberg 2021).

Aeduella sp. has been described from the Autun (Igornay Formation), Carmaux (Carmaux Formation), Saar-Nahe (Meisenheim and Wadern formations), Krkonoše-Piedmont (Prosečné Formation) and Weiach (Weiach Formation) basins (Heyler 1969, 2000; Bürgin 1990; Štamberg 2002, 2006, 2013a; Poplin & Dutheil 2005). The material from Igornay and Carmaux needs a revision to precise its identification (Heyler 1969, 2000). That of Weiach slightly differs from *A. blainvillei* in its smaller number of scale rows and its fins located on a smaller number of scale rows (Bürgin 1990). It is possible that this is a morphological variability of *A. blainvillei*, but more material is needed to determine this.

Aeduella sp. material from the Saar-Nahe Basin is mainly represented by undescribed specimens listed in Brauckmann *et al.* (2007). It comprises occurrences from the Geisberg (M5-G) and Rehborn banks (M8-R) in the Meisenheim Formation, which are listed here as Aeduellidae indet., in the absence of further evidence and considering the numerous aeduellid diagnoses revisions posterior to this study (e.g., Štamberg 2007, 2024; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2026b, c). The other records listed by Brauckmann *et al.* (2007) are *Aeduella* sp. RK, *Aeduella* sp. NK and *Aeduella* sp. SO, which were discussed in a brief, unpublished and unfinished report (Boy 2004; Boy & Spahn [unpublished] in Brauckmann *et al.* 2007). *Aeduella* sp. RK corresponds to a specimen originally described by Uhl (1997) and now assigned to *Westollia crassa* (Gonçalves & Luccisano 2025b). *Aeduella* sp. NK (also called *Aeduella niederkircheniana* in Boy [2004], which is a *nomen nudum*) corresponds to the occurrences of *Aeduella blainvillei* from Niederkirchen (Meisenheim Formation) (Boy 2004; Brauckmann *et al.* 2007), for which there is currently no evidence to distinguish them from *A. blainvillei* from other basins. Finally, *Aeduella* sp. SO

TABLE 1. — List of occurrences of *Pseudestheria tenella* (Bronn, 1850) and *Anthracomya prolifera* (Waterlot, 1934) in Europe.

Taxon	Variscan Region	Basin	Formation	Regional Age	References
Pseudestheria tenella	Armorican Massif	Carentan	Littry	Stephanian C	Pareyn 1954
			Saint-Martin-de-Blagny	Autunian	Bigot & Pruvost 1925
	Bohemian Massif	Krkonoše-Piedmont	Vrchlabí	Autunian	Zajíc 2014
		Intra-Sudetic	Chvaleč	Autunian	Opluštil *et al.* 2016
		Kladno-Rakovník	Kladno	Westphalian B	Pruvost 1922
	French Massif Central	L'Argentière	La Lande	Autunian	Poplin *et al.* 1998
		Autun	Millery	Autunian	Bigot & Pruvost 1925
			Muse	Autunian	Châteauneuf *et al.* 1980
		Bert	Mandins	Autunian	Feys 1960
		Blanzy-Montceau	Bariolée or Grise	Autunian	Feys 1960
		Brive	Saint-Antoine Limestones	Autunian	Feys 1976
		Decize-La Machine	Grey Autunian	Autunian	Bigot & Pruvost 1925; Feys 1960
		Rodez	Série II	Autunian	Vetter 1968; Fuchs & Becq-Giraudon 1989
		Vallée du Cérou	Bosc de Soulié	Autunian	Delsahut 1981
	Iberia	Pálmaces de Jadraque	Pálmaces de Jadraque	Autunian	Sopeña *et al.* 1977
		Puertollano	Puertollano	Stephanian C	Wagner 1985
	Rhenish Massif	Saar-Nahe	Meisenheim	Autunian	Bronn 1850; Pruvost 1911
Anthraconaia prolifera	Armorican Massif	Saint-Pierre-la-Cour	Saint-Pierre-la-Cour	Stephanian C	Pruvost 1925
	Belledonne Massif	La Mure	La Mure	Stephanian A	Haudour & Sarrot-Reynauld de Cresseneuil 1956
	Bohemian Massif	Intra-Sudetic	Ludwikowice	Stephanian C	Birkenmajer *et al.* 1968
	French Massif Central	Alès	Saint-Jean-de-Valériscle	Stephanian A	Pruvost 1925; Waterlot 1934
		Autun	Igornay	Stephanian C	Bigot & Pruvost 1925
		Decazeville	Bourran	Stephanian C	Vetter 1968
	Harz Massif	Saale	Gorenzen	Stephanian A	Eagar 1984, 1987; Gebhardt & Hiete 2013
	Iberia	Ciñera-Matallana	Cascajo	Stephanian B	Wagner & Artieda 1970
	Rhenish Massif	Saar-Nahe	Göttelborn	Stephanian A	Waterlot 1934; Eagar 1984, 1987

is based on isolated bones, including an unfigured triangular maxilla, from the Saxonian stage of the Wadern Formation (Boy 2004; Brauckmann *et al.* 2007). The proportions of the maxilla cannot be verified, and in the absence of associated diagnostic features, these remains can only be assigned to Aeduellidae indet.

Aeduella sp. from the Saar-Nahe basin was also mentioned by Poplin & Dutheil (2005) citing Boy (1987), yet the latter did not mention *Aeduella* but "Aeduelliden" (Boy 1987: 41). Blieck *et al.* (1999) reported two specimens of *Aeduella* sp. from the Saar-Nahe Basin, without specifying their exact provenance. These specimens are preserved in nodules identical to those from Lebach and have the same characteristics as *Amblypterus latus* (triangular maxillary plate, identical opercular region, same scale count), which is known from these nodules (Dietze 2000; Štamberg 2013b). I consider the specimens mentioned by Blieck *et al.* (1999) to belong to *Am. latus*. Finally, the material from the Prosečné Formation described as *Aeduella* sp. by Štamberg (2002, 2013a) belongs to a taxon with a wide parietal, a deep maxilla (length/depth ratio of 2.3), a trapezoidal suboperculum, and smooth and non-serrated scales. This combination of characters does not correspond to *A. blainvillei*, which has a low maxilla, but is close to *Westollia crassa* (Štamberg 2024). Pending further discoveries, I prefer to refer this material as to Aeduellidae indet.

Occurrences of *Pseudestheria tenella* and *Anthraconaia* spp. in Europe

Pseudestheria tenella is a freshwater 'conchostracan' known in the Westphalian B to the Autunian of Europe (Table 1). It is also the only 'conchostracan' from the Stephano-Permian of the Armorican Massif, more precisely from the Littry and Saint-Jean-de-Blagny formations of the Carentan Basin (Bigot & Pruvost 1925; Pareyn 1954). *P. tenella* is used as a stratigraphic indicator for the Autunian (Feys 1960, 1976; Poplin *et al.* 1998), and sometimes even for the early Autunian (Delsahut 1981; Opluštil *et al.* 2016). This questions the attribution of older remains from the Westphalian Kladno Formation and from the Stephanian Littry and Puertollano formations, which could belong to one or more other taxa. Another possibility is that *P. tenella* has a wider stratigraphic distribution. The taxonomic history of *P. tenella* is complex (see Nomenclature above) and the lack of diagnostic characters limits its identification: *P. tenella* is rather a morphotype than a biological species (Feys 1960; Kozur & Sittig 1981). It is therefore difficult to use it as a reliable marker of dispersal events, but its presence in a many European Autunian basins (Table 1) suggests a connection between them.

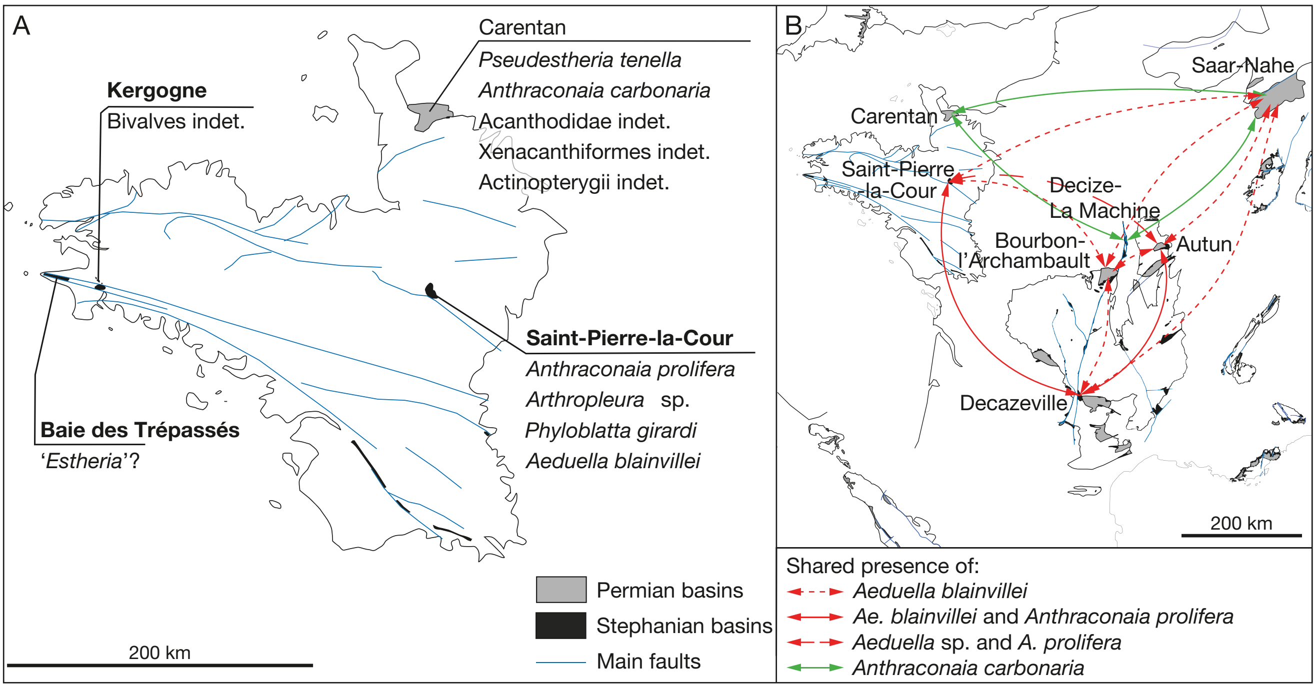

Fig. 10. — Faunal distribution during the Carboniferous-Permian transition in the Armorican Massif: **A**, distribution within the Armorican Massif (map modified from Pelhate 1994); **B**, armorican faunas compared with those of north-western Variscan basins (paleomap modified from Fig. 1A, B). Maps by D. Gonçalves.

Anthraconaia is currently the only non-marine bivalve from the Stephano-Permian of the Armorican Massif, with *A. prolifera* in the Saint-Pierre-la-Cour Basin and *A. carbonaria* in the Carentan Basin (Pruvost 1925; Bigot & Pruvost 1925). It is an almost cosmopolitan genus with a complex taxonomic history (see Nomenclature above), known from the Westphalian to the Autunian of Africa, America, Europe and Asia (e.g., Trueman & Weir 1946; Babin 1985; Eagar & Belt 2003; Díaz-Saravia 2009; Silantiev & Carter 2015; Pereira & Correia 2025). *A. prolifera* is a typical Stephanian species with a wide geographical distribution, present in most European Variscan massifs (Table 1), the Northern Appalachian Basin (USA; Eagar & Belt 2003), the shale horizons of Béchar-Kenadza (Algeria; Deleau 1945) and Morocco (Waterlot 1934). The presence of *A. prolifera* in the Stephanian C of the Saint-Pierre-la-Cour Basin is one of its last occurrences, and it suggests a synchronous distribution event linking the Decazeville, Autun, Saint-Pierre-la-Cour and Intra-Sudetic basins. *A. carbonaria* was firstly described in the early Autunian of the Kusel Group, Saar-Nahe Basin (Bronn 1829; Goldfuss 1834; Waterlot 1934). Its presence also in the Autunian of the Carentan Basin is its second occurrence outside the Kusel Group, in addition with its occurrence in the Decize-La Machine Basin (French Massif Central) (Bigot & Pruvost 1925; Roger *et al.* 2010). *A. carbonaria* was formerly mentioned in the Collio (Italy) and Najac (France) basins and the Wanneperveen I borehole (Netherlands) (Jongmans & van der Heide 1953; Berruti 1970; Delsahut 1981), but these attributions have been re-evaluated (Van Amerom 1972; Ronchi & Santi 2003; Fauré & Delsahut 2024). Specimens from Russia have also been assigned to *A. carbonaria* (placing it within the genera *Anthracosia* or *Carbonicola*), (e.g., Netchaev 1894: 301, 302 and references therein; Venukov 1895), but their descriptions are very generic, rendering them indeterminate and in need of revision. The presence of *A. carbonaria* in the Carentan and Saar-Nahe basins alone suggests a connection between these basins.

Biogeography of the Stephano-Permian faunas from the Armorican Massif

The flora and fauna of the Armorican Massif are very fragmentary (Fig. 10A), which can be explained by the predominantly coarse depositional environments and limited mining activity. The Stephanian basins of the Armorican Massif were almost all filled in a short period of time, mainly by coarse elements of proximal origin, during mudflows and collapsing events (Pelhate 1957, 1960, 1994; Rolet 1984). The remains of bivalves and estherids are rare and disarticulated with the valves always isolated (e.g., Péneau 1921; Picquenard 1918, 1921, 1924; Mathieu 1937). This mode of preservation indicates transport and therefore an allochthonous origin of these fossils, but the proximal origin of the debris flows suggests a relatively close origin for the organic remains. The absence of stable lacustrine phases in these basins explains the absence of thick coal layers (e.g., Tabor & Poulsen 2008; Zouicha *et al.* 2025), but also probably that of vertebrates in most of the basins (i.e. Finistère, Doué-la-Fontaine, Sillon Houiller Vendéen). Compared to the French Massif Central basins, this relative lack of coal in the Armorican basins is the reason for the low level of mining activity, which has limited the paleontological discoveries (e.g., Bureau 1910;

Mulot 1975; Étienne & Limasset 1979; Bouton 1990). The only exception is the Saint-Pierre-la-Cour basin, where more complete plants, articulated bivalves, arthropods, a coprolite likely produced by a tetrapod, and actinopterygians have been discovered (Pruvost 1925; Bigot & Pruvost 1925; Péneau 1930; Vetter 1957; this study). These discoveries suggest a calmer depositional environment in this basin, at least during part of its history.

The fauna of the Saint-Pierre-la-Cour Formation in the Saint-Pierre-la-Cour Basin consists of *Anthraconaia prolifera*, *Arthropleura* sp., *Phyloblatta girardi*, *Aeduella blainvillei*, undetermined actinopterygians, and a putative tetrapod according to the coprolite record (Van Straelen 1923; Pruvost 1925; Péneau 1930; this study). The aquatic and semi-aquatic fauna is most closely related to the fauna of the Bourran Formation of the Decazeville Basin, which also includes *A. prolifera* and *Ae. blainvillei* (Vetter 1968; Heyler 1969; Gonçalves & Luccisano 2025b; Gonçalves *et al.* 2025). The ichthyofauna of the Igornay Formation of the Autun Basin is also similar, with the shared presence of *A. prolifera* and *Aeduella* sp. (Bigot & Pruvost 1925; Heyler 1969, 2000). These faunas are all from the Stephanian C-early Autunian of the French Massif Central (Vetter 1957, 1968; Pellenard *et al.* 2017), suggesting a strong synchronous aquatic connection between these three basins (Fig. 10B). *Phyloblatta* is known from the Moscovian-Capitanian of America, Europe, Asia and Africa (e.g. Belahmira *et al.* 2019), while *Arthropleura* is known from the Visean-Asselian of Europe and North America (e.g. Moreau *et al.* 2021). *Arthropleura* occurrences in the European Stephanian-Permian are limited to Puertollano, Ciñera-Matallana, Saint-Pierre-la-Cour, Commentry, Autun, Blanzy-Montceau, Saint-Étienne, Graissessac-Lodève, Saale and Saar-Nahe basins (see Moreau *et al.* 2021 and references therein). In addition to the Saint-Pierre-la-Cour Basin, only the Commentry, Saint-Étienne, Saale and Saar-Nahe basins also share the presence of *Phyloblatta* (e.g., Waterlot 1934; Laurentiaux 1950; Schneider 1978; Béthoux *et al.* 2011). Although these arthropod of Saint-Pierre-la-Cour are fragmentary and deserves a re-examination, they seem to be linked with certain basins of the French Massif Central, the Rhenish and the Harz massifs.

The fauna of the Saint-Martin-de-Blagny Formation of the Carentan Basin, composed of *Anthraconaia carbonaria*, *Pseudestheria tenella*, actinopterygians, acanthodians and xenacanthiformes (Vieillard 1872; Bigot & Pruvost 1925; this study), is typically lacustrine and resembles those from the Permo-Carboniferous French Massif Central basins (e.g., Heyler 1969, 1996, 2000; Heyler & Poplin 1990, 1994; Steyer *et al.* 2000; Štamberg & Steyer 2021; Gonçalves *et al.* 2025), and others from Europe (e.g., Bigot & Pruvost 1925; Freytet *et al.* 2002; Schindler 2005; Opluštil *et al.* 2013a, 2013b; Soler-Gijón & Ruiz 2023). The combined presence of *P. tenella* with this vertebrate fauna is indeed similar to that found in the Autun, Brive, Bourbon-l'Archambault, Saar-Nahe and Krkonoše-Piedmont basins (Bigot & Pruvost 1925; Boy 1976; Heyler 1969, 2000; Opluštil *et al.* 2016; Štamberg & Steyer 2021). The lack of precise identification of the vertebrate remains does not allow for a more accurate connection between the Carentan Basin and these other Variscan basins, but the presence of *Anthraconaia carbonaria* indicates a strong connection with the Saar-Nahe and Decize-La Machine basins (Fig. 10B; Bigot & Pruvost 1925).

Correlations with other Stephano-Permian basins of the Variscan Belt

The Stephano-Permian basins of the Armorican Massif are mostly unconformably overlying Namurian-Westphalian deposits (Carentan, Saint-Pierre-la-Cour, Doué-la-Fontaine, and Sillon Houiller Vendéen basins), and more rarely on the basement (Finistère basins). This trend is not observed in other well-studied French Variscan massifs such as the French Pyrénées, the Vosges and the French Massif Central. There, older Carboniferous basins are rarer and only the Stephano-Permian basins of Decize-La Machine and Decazeville lie unconformably on these kind of rocks. At Decize-La Machine, the base of the Stephanian B overlies the Westphalian Girodons Formation (e.g., Châteauneuf & Farjanel 1989). At Decazeville, the base of the Stephanian B basin overlies the Visean Volcanic Complex, with the Brayes Formation located between volcanic layers of this Volcanic Complex (Vetter 1968; Bruguier *et al.* 1998). It should be noted that the flora of this Brayes Formation suggests a Stephanian age (Vetter 1968), which questions the age of the Volcanic Complex as noted by Basile (2006). The dating of the Volcanic Complex in the Decazeville Basin may therefore have been affected by the presence of inherited zircons, and further study is required to resolve the inconsistencies between the palaeobotanical and radiometric dating data. These differences in the basement for the Stephano-Permian basins in the Armorican Massif can be explained by its more external position in the Variscan Belt in relation to the French Massif Central (e.g., Matte 2001; Ballèvre *et al.* 2009). It was affected earlier by the extensive orogenic phase with the formation of basins during the early Carboniferous (i.e., Châteaulin, Laval and Ancennis Basins) (e.g., Pelhate 1994). In the French Massif Central, which was located more centrally within the Variscan Belt, the basins were mainly filled during the Stephano-Autunian (e.g., Aretz *et al.* 2023). While the rare Stephano-Permian basins of the Armorican Massif were often formed near existing basins, those of the Massif Central were mostly formed directly on the basement.

The Doué-la-Fontaine and Sillon Houiller Vendéen basins are poorly exploited and do not outcrop largely. This could explain why fossils have not been discovered there. The relationship between these basins and the others of the Armorican Massif and, more generally the Variscan Belt, is therefore impossible to determine. The Finistère basins are equally poorly exposed, but they have been more extensively exploited and studied (e.g., Picquenard 1918, 1920b, 1921, 1924). Floral datation attempts have been

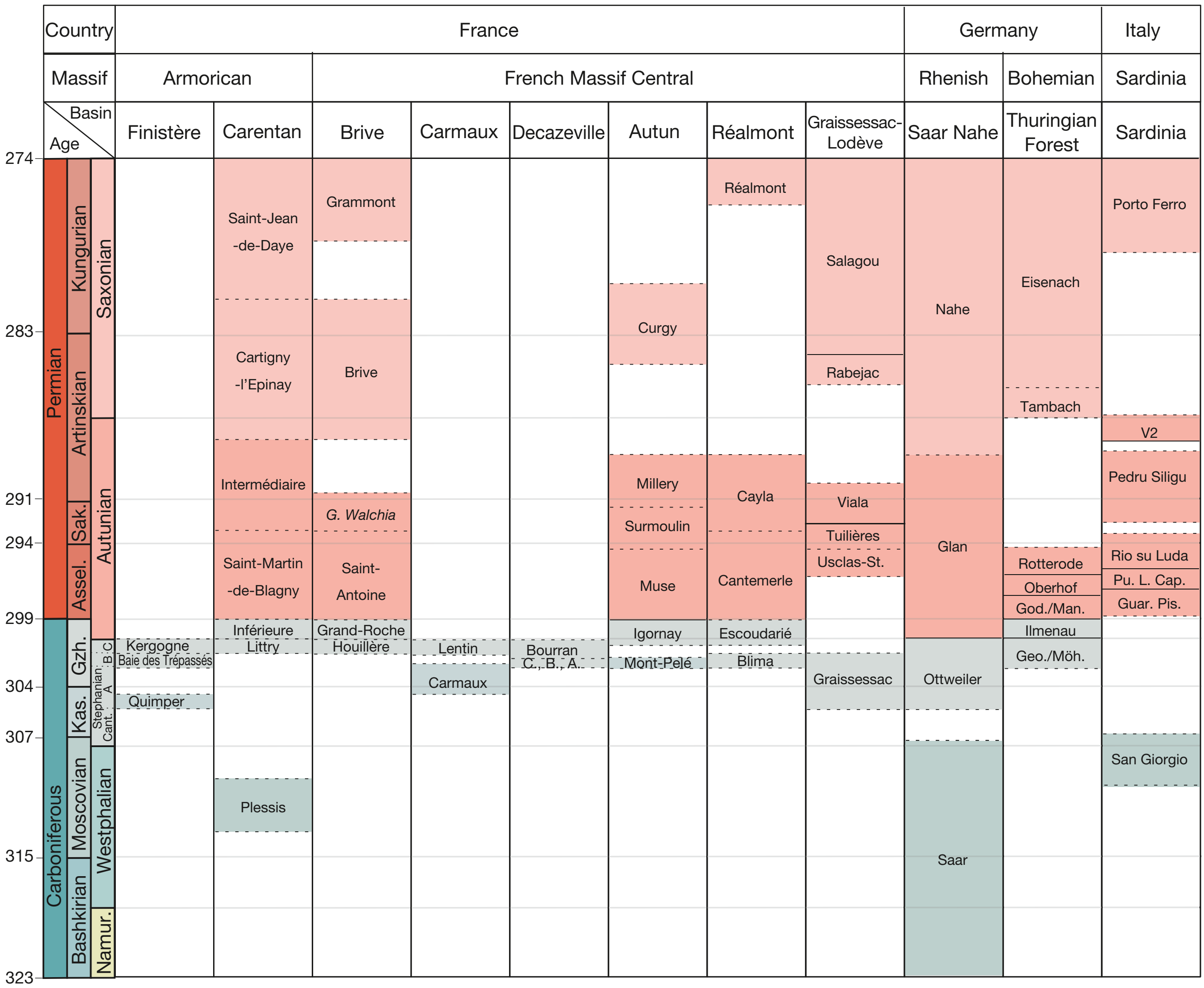

FIG. 11. — Temporal correlation of the Armorican Permo-Carboniferous basins with others of western Europe, based on available biostratigraphic and radioisotopic age constraints (modified from Feys, 1976; Delsahut 1981; Mercuzot *et al.* 2023). Abbreviations: **C.**, **B.**, **A.**, Campagnac, Banel and Auzits formations; **Geo./Möh.**, Georgenthal and Möhrenbach formations; **God./Man.**, Goldlauter and Manebach formations; **Guar. Pis.**, Guardia Pisano Formation; **Pu. L. Cap.**, Punta Lu Caparoni; **Usclas-St.**, Usclas-St-Privat Formation. Schema by D. Gonçalves.

made but are discussed below (see Nomenclature above). In the Saint-Pierre-la-Cour and Carentan basins, floras are also well known but no absolute age has been proposed. Floral comparisons allow regional correlations between Armorican Massif basins and more global ones with other Variscan basins (Fig. 11; e.g., Doubinger & Vetter 1985; Nádaskay *et al.* 2025).

The coarse azoic levels of the Stephanian A of the Quimper Basin are equivalent to those known in France, such as the lower part of the Alès Basin, the lower Carmaux Formation (Carmaux Basin), the Fagairolles, Croix de Mounis and Pabau (Graissessac-Lodève Basin, Graissessac sub-basin), the Rive-de-Gier (Saint-Étienne Basin), Saint-Perdoux (Figeac Basin), and La Mure (La Mure Basin) formations (e.g., Louis 1954; Haudour & Sarrot-Reynauld de Cresseneuil 1956; Vetter 1968; Delsahut 1981; Doubinger & Vetter 1985). On a larger Variscan scale, these levels can be correlated with the Gorenzen Formation (Saale Basin), and the Göttelborn and Dilsburg formations (Saar-Nahe Basin) (e.g., Gebhardt & Hiete 2013; Izart *et al.* 2025). Among these formations, only those in the Saar-Nahe Basin have been radiometrically dated with the T00 tonstein between the Dilsburg and Göttelborn formations, for which an age of 304.49 ± 0.12 Ma has been obtained (Izart *et al.* 2025). This age is consistent with the 305 to 302 Ma age indicated for the Stephanian A in Aretz *et al.* (2020), but also with the 304.9 to 303.5 Ma age proposed in Knight *et al.* (2023).

The Stephanian B of the Baie des Trépassés Basin has many coeval formations in France, from the Massif Central to the small Brassac Basin; they are the top of the Alès Basin, the Mont-Pelé (Autun Basin), Campagnac, Banel and Auzits (Decazeville Basin), Figeac (Figeac Basin), upper Carmaux (Carmaux Basin), Houillère (Graissessac sub-basin, Graissessac-Lodève Basin), Blima (Réalmont Basin), Puech

Mignon (Laguépie Basin), Loubezac (Najac Basin), Saint-Étienne (Saint-Étienne Basin), and the Blanzy and Carrières (Blanzy-Montceau Basin) formations (e.g., Vetter 1968; Delsahut 1981; Doubinger & Vetter 1985; Pellenard *et al.* 2017; Mercuzot *et al.* 2023). Elsewhere in France, these Stephanian B layers correlate with deposits in the Ségure and Durban basins (Mouthoumet Massif), and the Plan de la Tour and Reyran basins (Maures-Tanneron Massif) (e.g., Doubinger & Vetter 1985; Saillol *et al.* 2019). In the other Variscan regions, the Týnec and Slaný Formations of the Bohemian Massif, the Heusweiler (Saar-Nahe Basin), Rothenburg (Saale Basin) and Cascajo (Ciñera-Matallana Basin) formations are equivalent (e.g., Wagner & Artieda 1970; Gebhardt & Hiete 2013; Izart *et al.* 2025; Nádaskay *et al.* 2025). Few radiometric datations have been proposed for the Stephanian B and some are debated: the Graissessac Formation has been dated to two contradictory ages: 295.3 ± 4.8 Ma (Bruguier *et al.* 2003) and 304.07 ± 0.07 (Michel *et al.* 2015). The tonstein of the Týnec Formation is dated to 303.73 ± 0.13 Ma, while the tonsteins of Mšec and Kounov in the Slaný Formation are dated to 302.47 ± 0.08 Ma and 301.50 ± 0.11 Ma, respectively (Opluštil *et al.* 2016). On the international chronostratigraphic scale, the regional sub-stage of the Stephanian B is dated between 302 and 301 Ma (Aretz *et al.* 2020).

The Stephanian C is the most deposited sub-stage in the Armorican Massif basins, with the Kergogne, Littry and St-Pierre-la-Cour Formations. They are correlated with the Igornay (Autun Basin), Bourran (Decazeville Basin), Lucenay (Decize-La Machine Basin), Lentin (Carmaux Basin), Esccoudarié (Réalmont Basin), Péroudel (Laguépie Basin), La Salvetat-Biau (Najac Basin), Grès Houillers (Brive Basin), Avaize (Saint-Étienne Basin), Ponsard (Blanzy-Montceau Basin) and Noyant (Bourbon-l'Archambault) formations (e.g., Jongmans & Pruvost 1950; Vetter 1968; Delsahut 1981; Doubinger & Vetter 1985; Debriette 1992; Pellenard *et al.* 2017; Izart *et al.* 2025). In the Bohemian Massif, the Lower Líně, Chvaleč and Semily formations are of the same age, as are the Puertollano and Douro basins in Iberia, the Siebigerode Formation in the Saale Basin and the Gehren Subgroup in the Thuringian Forest Basin (e.g., Pinto de Jesus 2003; Opluštil *et al.* 2016; Álvarez-Vázquez *et al.* 2018; Lützner *et al.* 2021; Mercuzot *et al.* 2023; Nádaskay *et al.* 2025). Radiometric datations for the Stephanian C are more numerous, giving an age between 300 and 299 Ma. Zircons of the Igornay, Avaize, Lucenay and lower Líně formations give ages close to 299.91 ± 0.38 Ma, 299.3 ± 1.3 Ma, 299.111 ± 0.076 Ma and 298.97 ± 0.09 Ma respectively (Opluštil *et al.* 2016; Pellenard *et al.* 2017; Gardien *et al.* 2022; Mercuzot *et al.* 2023). In the Thuringian Forest, rhyolites from the Gehren Subgroup yielded an age of 299.3 ± 0.3 Ma for the Ilmenau Formation, and 300.0 ± 0.5 Ma and 299.7 ± 0.4 Ma for the Möhrenbach Formation (Lützner *et al.* 2021). These ages between 300 and 299 Ma are contradictory with the international correlation of Aretz *et al.* (2020), which gives an age between 301 and 300.5 Ma for the Stephanian C. This difference can be explained by the ambiguous position of the boundary between the Stephanian C and the Autunian (e.g., Becq-Giraudon 1993; Pellenard *et al.* 2017), with sometimes even the existence of a Stephanian D between the two (e.g., Doubinger 1956), or the use of the names "Stephano-Autunian" and "Autuno-Stephanian" to designate the Stephanian C (e.g., Vandenberghe 1961; Delsahut 1981; Châteauneuf & Farjanel 1989; Becq-Giraudon 1993). The dating of the Igornay Formation of the Autun Basin illustrates this problem according to Pellenard *et al.* (2017), as a Lower Autunian (e.g., Heyler 1969; Broutin *et al.* 1999), or a Stephanian D (e.g., Doubinger, 1956), or a Stephanian C (e.g., Doubinger & Elsass 1979) age has been proposed. Furthermore, recalibrating the age of these macroflora-based regional stages by taking into account Iberian subdivisions may even assign the lower Igornay Formation to the Stephanian B while merging the Stephanian C with the early Autunian (Izart *et al.* 2025). However, this last interpretation, based on Bohemian Massif ages, is probably biased because it does not take into account the diachronism of the Autunian and Stephanian subdivisions at regional scale (Opluštil *et al.* 2022). This lack of clear delimitation also makes the correlation of the Stephanian C and early Autunian formations based on paleoflora alone fragile. However, despite these correlation issues, the dating of the Stephanian C in the Armorican Massif appears to be between 300.0 and 298.9 Ma, but may be also extended to 301 Ma.

The Saint-Martin-de-Blagny Formation of the Carentan Basin is early Autunian, an age similar to that of Muse (Autun), Buxières (Bourbon-l'Archambault), Cantemerle (Réalmont), Bosc du Soulié (Cérou Valley), Mazet-La Boulp (Najac) and Usclas-St-Privas (Graissessac-Lodève) formations (e.g., Delsahut 1981; Châteauneuf & Farjanel, 1989; Pellenard *et al.* 2017; Mercuzot *et al.* 2023). The lower Autunian is also found in the Lower Glan Group (Saar-Nahe), the Halle Subgroup (Saale), the Guardia Pisano, Punta lu Caparoni and Rio su Lunda (Sardinia), Padochov, Upper Líně, Vrchlabí and Broumov (Bohemian Massif) formations (e.g., Opluštil *et al.* 2016; Mercuzot *et al.* 2023; Izart *et al.* 2025; Nádaskay *et al.* 2025; Rossignol *et al.* 2025). The Autunian is also a stage for which radiometric datings have been measured within the Variscan basins. Gore I, Gore VII and Gore La3 of the Muse Formation (Autun Basin) are dated respectively at 298.05 ± 0.39 Ma, 298.57 ± 0.38 Ma and 298.91 ± 0.08 Ma (Pellenard *et al.* 2017), the "Lien Vert" of the Buxières Formation (Bourbon-l'Archambault Basin) is dated to 298.592 ± 0.075 Ma (Mercuzot *et al.* 2023), a tonstein near the top of the Líně Formation (Central and Western Bohemian basins) is dated to 297.16 ± 0.17 Ma (Opluštil *et al.* 2016), in the Glan Group, a tonstein from the Altenglan Formation (Saar-Nahe Basin) is dated to 298.7 ± 0.4 Ma (Voigt *et al.* 2022), the age of the Rio su Lunda Formation (Perdasdefogu Basin) fill is dated to be between 297.9 ± 0.9/3.1 and 295.7 ± 0.7/3.0 Ma (Rossignol *et al.* 2025), and an ash level from Guardia Pisano Basin is dated to

297 ± 5 Ma (Pittau *et al.* 2002). These ages between 298.9 and 295.7 Ma allow for an approximation of the possible dating for the Saint-Martin-de-Blagny Formation.

The deposits above the Saint-Martin-de-Blagny Formation are dated on the basis of their sedimentological facies, which makes these datings discussable (L'Homér & Pareyn 1989). These Autuno-Saxonian deposits are similar to those found in the Autun, Brive, Réalmont, Najac, Cérou Valley and Graissessac-Lodève basins (e.g., Feys 1976; Delsahut 1981; Châteauneuf & Farjanel, 1989).

CONCLUSION

The Stephano-Permian basins of the Armorican Massif show similar profiles, with sparse outcrops, sometimes disappeared since the end of the mining activity, and coarse deposits over a short period. These factors may be responsible for the low palaeontological interest in this region and the few available fossil occurrences. Nevertheless, these few occurrences allow to date and correlate these basins on a Variscan scale, remaining cautious due to the diachronism of continental regional stages. The Carentan and Saint-Pierre-la-Cour basins are exceptions, as they are better known and more explored. The Carentan Basin underwent a long phase of almost continuous sedimentation from the Stephanian C to the Saxonian. Although the faunal remains are lost, they suggest a faunal composition very similar to that of the better-known Variscan basins from the French Massif Central, Bohemian and Rhenish massifs. The presence of *Anthraconaia carbonaria* in the Carentan and Saar-Nahe basins alone indicates a close proximity to the fluvial networks of the Armorican and Rhenish massifs. As for the Saint-Pierre-la-Cour basin, although the deposits only correspond to the regional sub-stage of the Stephanian C, the rich fauna discovered highlights a strong relationship with the Autun and Decazeville basins, and to a lesser extent with other basins of the western Variscan Belt. The presence of *Aeduella blainvillei* in the Saint-Pierre-la-Cour basin indicates that this taxon was more widely distributed than previously known, and that its range exceeds that of all other aeduellids, with the possible exception of *Westollia crassa*. This study highlights the need to review old discoveries and visit little-known collections in order to better understand the history of the Variscan Belt. It thus provides a solid basis for comparison of the Armorican Massif in the context of broader studies of the paleobiogeography of the Variscan mountain range in the Permo-Carboniferous.

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Appendix 1. — Measurements (in cm) of the body and scales of *Aeduella blainvillei* from Saint-Pierre-la-Cour Basin. Dash (**–**) is used when data is missing and asterisk (*****) when the measure is made on an incomplete element. Institutionnal abbreviation: **ML**, Musée de Laval, Laval, France.

Specimen	**Growth stage (GS)**	**Body length (BL)**	**Body depth (BD)**	**BL/BD**	**Skull length (SL)**	**BL/SL**	**Skull-Anterior fin base distance (SFD) (Dorsal, Pelvic, Anal, Caudal)**	**Fin leading edge length (FL)**	**Fin base length (FB)**	**FL/FB (Dorsal, Pectoral, Pelvic, Anal)**	**Caudal fin length (CL)**	**BL/CL**	**Dorsal lobe length (DLL)**	**Ventral lobe length (CLL)**	**DLL/CLL**	**Scale count (Dorsal/Pelvic – Anal – Caudal) Scale inversion**	**Number of scales rows between Pelvic and Anal fin**	**Number of scales rows between Dorsal and Anal fin**	**Number of scales rows between Anal and Caudal fin**	**Number of scales rows between Caudal fin and Scale inversion**
ML-PAL-0451a	GS3	13.2	4.1	3.2	2.8	4.7	D4.2, –, A4.7, C6.4	D1.8, –, P0.8, A1.3	D1.2, –, P0.5, A1.3	D1.5, –, P1.6, A1.0	4.2	3.1	3.6	2.4	1.5	(23/8 – 23 – 34) 38	11	0	11	4
ML-PAL-0451b	GS3	5.7*	2.5*	–	1.6	–	D1.7, P1.4, A2.6, C3.9	D0.9, –, P0.7, A1.0	D0.9, –, P0.4, A0.8	D1.0, –, P1.8, A1.3	–	–	–	–	–	(21/8 – 21 – 34) ?	13	0	13	?

Appendix 2. — Measurements (in mm) of the skull elements of *Aeduella blainvillei* from Saint-Pierre-la-Cour Basin. Dash (–) is used when data is missing and asterisk (*) when the measure is made on an incomplete element. Institutionnal abbreviations: **ML**, Musée de Laval, Laval, France.

Specimen	Parietal length (PaL)	Parietal width (PaW)	PaL/PaW	Postparietal length (PpL)	Postparietal width (PpW)	PpL/PpW	PaL/PpL	PaW/PpW	Intertemporo–dermosphenotic length (DsphL)	Supratemporal length (StL)	Supratemporal width (StW)	DsphL/StL	StL/StW	Preoperculum bending angle	Preoperculum inclination	Maxilla length (ML)	Maxilla depth (MD)	ML/MD	Maxillary plate length (MpL)	MpL/MD	ML/MpL	Maxillary plate bending angle	Dentary length (DL)
ML–PAL–0451a	6.6*	2.9	–	5.8	2.8	2.1	–	1.0	6.5*	5.8	2.9	–	2.0	156°	52°	13.5	2.5*	–	–	–	–	–	–
ML–PAL–0451b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.2	2.7	3.0	4.6	1.5	1.8	17°	7.2

Specimen	Dentary depth (DD)	DL/DD	Dentary plate length (DpL)	DpL/DD	DL/DpL	Dentary plate bending angle	Operculum dorsal margin length (OpdL)	Operculum ventral margin length (OpvL)	OpdL/OpvL	Operculum depth (OpD)	OpD/OpvL	Operculum bending angle	Operculum posteroventral angle	Operculum inclination	Suboperculum ventral margin length (SopvL)	Suboperculum anterior margin depth (SopaD)	Suboperculum posterior margin depth (SoppD)	SoppD/SopaD	OpD/SoppD	OpvL/SopvL	Supracleithrum length (SclL)	Supracleithrum depth (SclD)	SclD/SclL
ML–PAL–0451a	–	–	–	–	–	–	5.1	7.7	0.7	12.0	1.6	126°	132°	45°	–	4.4	8.1	1.8	1.5	–	–	–	–
ML–PAL–0451b	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–