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The vertebrate fauna from the "stipite" layers of the Grands Causses (Middle Jurassic, France)

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The "stipites" are Bathonian (Middle Jurassic) coals that formed in an everglades-like environment and are now exposed in the Grands Causses (southern France). The vertebrate assemblage of the "stipites" and of the transitional layers to the carbonates in which they are interspersed are reviewed. To date, only small-sized and isolated vertebrate bones, teeth, and scales have been recovered. These record the presence of sharks (*Hybodus*, *Asteracanthus*), bony fishes (*Lepidotes*, Pycnodontiformes, *Caturus*, *Aspidorhynchus*), amphibians (Anura, Albanerpetontidae), and reptiles (Crocodylomorpha, Ornithischia, Theropoda). Despite its relatively limited taxonomic diversity, the vertebrate assemblage from the "stipites" and from their associated layers is notable for being one of the few of this age with both terrestrial and marine influences. Compared to other approximately coeval formations in Western Europe, the "stipites" vertebrate assemblage is surpassed in diversity only by those from the British Isles.

Keywords: Chondrichthyes, *Lepidotes*, Pycnodontiformes, *Caturus*, *Aspidorhynchus*, Amphibia, Crocodylomorpha, Dinosauria

INTRODUCTION

As a fuel source, the coal layers from the Middle Jurassic of the Grands Causses (southern France) have drawn human interest since prehistoric times (Théry et al., 1995) despite their thinness. Mining was already active in the 14th century (Vivier, 1959). Genssane (1776, p. 229) judged the mine of Les Gardies (Revens, Gard) to be profitable (this site was mentioned by latter authors as well, such as Dumas, 1876, pp. 226–227, 722, 1877, pp. 214, 505–506, and Parran, 1856, p. 106). The exploitation reached its apogee during the 19th century, but diminished at the beginning of the 20th century and ceased around the mid-20th century (see e.g., Rouire, 1946).

These deposits were called "stipites" by Brongniart (1829, p. 231) to distinguish them from lignites and other types of coal on the basis of the fact that they are due to "une végétation tout-à-fait différente, composée principalement de cycadées" ("a completely different vegetation, mainly made up of cycads"). This term has long been abandoned and these coals are usually called "lignites," but the analyses presented by Rouire (1928, p. 11, 1946, pp. 327, 353, 356, 357) and Bergounioux and Doubinger (1948, pp. 157, 159) suggest they would actually be much better termed bituminous coals. "Stipites" have formed in coastal swamps of the Massif Central land (see e.g., Fürsich et al., 1995). They are found scattered all over the Grands Causses in thin (always less than a meter) or even diminutive layers (**Figure 1**). The most significant outcrops are located in the center, in the axis of the "Grands Causses graben," near the Dourbie and Trevezel valleys (municipalities of Revens, Nant, and Causse Bégon) and in the surroundings of La Cavalerie (municipalities of La Cavalerie, Millau, Nant, and La Panouse de Cernon). The "Calcaires à stipites" are Middle to Late Bathonian in age (Charcosset et al., 1996, 2000; Ciszak et al., 1999).

The presence of fossil invertebrates in these layers was first mentioned by Rouville (1849), whereas Bleicher (1871) was the first to report the occurrence of vertebrate remains. Intensive sampling of a number of sites has been conducted from paleontologists from the Freie Universität Berlin in the 1960s in search of microvertebrates. Nevertheless, only a limited part of the material collected has been published to date (Seiffert, 1969a,b; Kriwet et al., 1997). We have also explored and sampled a variety of sites, which triggered additional publications (Knoll et al., 2013, 2014).

In the present article, we aim at providing a review of the vertebrate remains from the coal and associated marly and clayey layers of the "Calcaires à stipites" with a focus on the best determined components.

VERTEBRATE FAUNA

CHONDRICHTHYES

Hybodus *sp. (Figure 1A)*

Teeth (and, occasionally, dermal denticles) of hybodontiform sharks have been found at a number of sites such as "Les Gardies" (Nant, Aveyron), La Baume (La Panouse de Cernon, Aveyron), and Saint-Martin (Revens, Gard). Although a detailed systematic assessment of this material is definitely needed, the material is believed to be on the whole sufficiently close to the type species of *Hybodus*, *H. reticulatus* (Agassiz, 1837), as revised by Maisey (1987), to warrant a generic attribution. It is likely that several species are represented in the Grands Causses. Rees and Underwood (2006, Figure 4.1–3) described as *Hybodus* sp. a species from approximately coeval beds in Scotland that recall

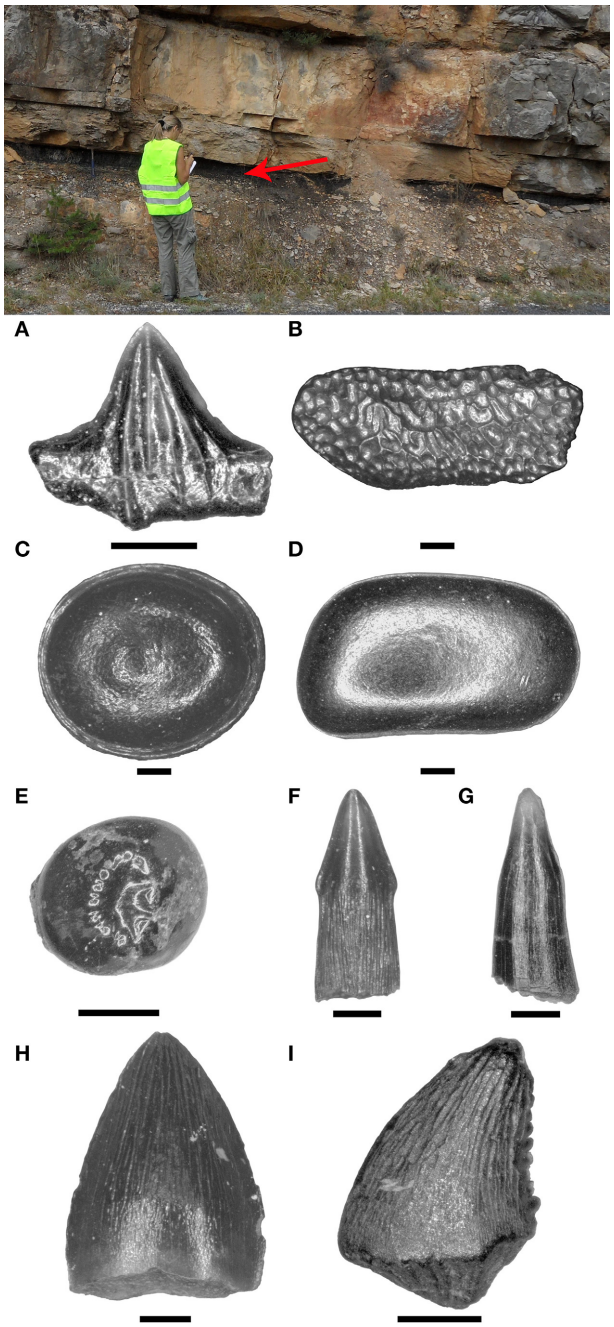

FIGURE 1 | Coal exposure (arrow) at "Les Gardies" (Nant, Aveyron) and representative sample of the teeth found at this site (all housed in the Museum für Naturkunde, Berlin, Germany). (A) *Hybodus* sp., labial view, **(B)** *Asteracanthus* sp., apical view; **(C)** *Lepidotes* sp., apical view; **(D)** *Macromesodon* sp., apical view; **(E)** Pycnodontidae indet. (cf. *Coelodus* sp.), apical view; **(F)** *Caturus* sp., lingual view **(G)** *Aspidorhynchus* sp., labial view; **(H)** Atoposauridae indet., labial view; **(I)** Theropoda indet., lingual view. Scale bars equal 500 μm.

specimens from the Grands Causses. The genus is well known in the Bathonian of France elsewhere (see e.g., Agassiz, 1837; Bigot, 1896; Coulon, 1903; Priem, 1908a). The genus *Hybodus* is not a reliable indicator of water salinity.

Asteracanthus *sp. (Figure 1B)*

Asteracanthus is a rare taxon, only known by a few teeth in Monplaisir (Le Rozier, Lozère) and "Les Gardies" (Nant, Aveyron). Even so, it is unclear whether only one species, not to mention which, is present. *Asteracanthus* is one of the most representative sharks from the Bathonian of France (see e.g., Agassiz, 1837; Sauvage, 1867, 1900; Owen, 1869; Bigot, 1896; Coulon, 1903; Priem, 1908a; Ligeron, 2007). The rarity of *Asteracanthus* in the "stipites" may be either due to taphonomic bias against the preservation of remains over a certain size or the reluctance of the species represented to venture from marine areas into brackish waters, or both.

ACTINOPTERYGII

Lepidotes *sp. (Figure 1C)*

Bleicher (1871, p. 795) first reported the finding of "une dent palatine très-belle de *Sargus* et des écailles de *Lepidotus*" ("a very beautiful palatine tooth of *Sargus* and scales of *Lepidotus*") (see also Bleicher, 1872a, p. 298, 1872b, p. 409). Ganoid scales and teeth like those described by Mudroch and Thies (1996) and other authors as from *Lepidotes* have been collected at "Les Gardies," La Baume, Les Moulinets (Nant), Saint-Martin, the lower level of Cornhes (Mostuéjouls, Aveyron) and other sites. The fish scales mentioned by Fürsich et al. (1995, p. 138) possibly belong to the same taxon. The number of species represented in the material from the Grands Causses and whether it incontrovertibly belongs in *Lepidotes*, i.e., if it is closely related to the Early Jurassic species *Lepidotes elvensis* (Blainville, 1818), *Lepidotes gigas* Agassiz, 1832, *Lepidotes semiserratus* Agassiz, 1836, and *Lepidotes bülowianus* Jaekel, 1929 (see López-Arbarello, 2012, pp. 26–27), cannot be currently settled. Outside the Causses, *Lepidotes* has been reported from several Bathonian sites in France (e.g., Agassiz, 1836; Sauvage, 1867, 1880b; Priem, 1908b), but all in all European Middle Jurassic species of *Lepidotes* remain poorly known.

Pycnodontiformes (Figures 1D,E)

Teeth of Pycnodontiformes have been collected at sites such as "Les Gardies" and Cornhes. Kriwet et al. (1997) suggested the presence of two genera, the primitive *Macromesodon* (for prehensile and "molariform" teeth without apical indent) and the more derived *Coelodus* (for "molariform" teeth with apical indent). However, isolated "molariform" teeth of Pycnodontiformes are difficult to determine with accuracy, being always low and robust (Poyato-Ariza, 2005). Moreover, whereas the type species of *Macromesodon* is from the Late Jurassic (about 15 myr younger), that of *Coelodus* is from the Late Cretaceous (about 73 myr younger) (Poyato-Ariza and Wenz, 2002). Gérard (1936, p. 190) listed teeth of *Microdon* sp. that may come from the Bathonian of Larzac. This genus is now referred to as *Proscinetes* (see Poyato-Ariza and Wenz, 2002). A diversity of Pycnodontiformes is present in the Bathonian of France outside the Causses, most or all of which probably representing the genus *Macromesodon* (see e.g., Agassiz, 1836; Sauvage, 1867, 1880a,b; Woodward, 1895; Priem, 1911). The Pycnodontiformes from the Grands Causses probably favored shallow seas.

Caturus *sp. (Figure 1F)*

Specimens that match the teeth attributed to *Caturus* by Mudroch and Thies (1996) have been collected from "Les Gardies" and the upper layer of Cornhes. Similar material is known from the Late Bajocian site of Larnagol (Lot, France; Kriwet et al., 1997). *Caturus* is usually considered a marine amiiform. However, the genus is also known from beds of freshwater origin (Bogan et al., 2013, p. 194).

Aspidorhynchus *sp. (Figure 1G)*

Kriwet et al. (1997) identified a few blunt conical teeth from "Les Gardies" as *Aspidorhynchus* sp. The oldest known species of the genus is certainly Bathonian in age: *Aspidorhynchus crassus* Woodward, 1890. As in the case of *Asteracanthus*, the presence of such a sea dweller at "Les Gardies" may reveal a strong marine influence.

AMPHIBIA

Anura

Seiffert (1969a) described from "Les Gardies" an omosternum that he identified as from an ancestral Ranidae. This record was critically reappraised by Estes and Reig (1973, p. 29). Sanchiz (1998, pp. 89, 155) considered this specimen as from a non-ranid indeterminate anuran.

No other anuran remains from the "stipites" has been described. However, Sciau et al. (2006, p. 31) alluded to "la découverte dans une grotte des Causses par une équipe de spéléologues, d'un amphibien anoure (Rouire and Rousset, 1973)" ("the discovery in a cave of the Causses by a team of speleologists, of an anuran amphibian (Rouire and Rousset, 1973)") in the 1970s. Rouire and Rousset (1973, p. 26) actually mentioned "les restes d'un amphibien anoure (J. Seiffert)" ("the remains of an anuran amphibian (J. Seiffert)"), but this "amphibien anoure" would have been a distinct find made in a cave of the Trèvezel valley according to Sciau (pers. comm., 2010). Although it is unquestionable that the "stipites" are exposed in some caves of the Grands Causses, it is suspicious to 'stumble upon' a fossil frog in this manner, especially because the vertebrate from the "stipites" are always very small and disarticulated.

Albanerpetontidae

Seiffert (1969b) described an atlas of urodele from "Les Gardies", which was first recognized as related to *Albanerpeton* by Estes and Hoffstetter (1976, pp. 297, 316, 321). This specimen is still regarded as the earliest definitive albanerpetontid known (see e.g., Gardner and Böhme, 2008, p. 193, tab. 12.2; Sweetman and Gardner, 2013, p. 320), together with an articular and an axis from a possibly slightly older, Early Bathonian, lens at Snowshill (Gloucestershire, United Kingdom). Gardner and Böhme (2008, p. 193) identified the atlas from "Les Gardies" as from an indeterminate albanerpetontid.

REPTILIA

Crocodylomorpha (Figure 1H)

Teeth of crocodylomorphs are common, in proportion to other vertebrate remains, at specific places such as Les Moulinets and, especially, "Les Gardies." The "petites dents de sauriens" and "dent de petit saurien" ("small teeth of saurians"/"tooth of small saurian") mentioned by Bleicher (1872a, p. 298, 1872b, p. 409) were probably from crocodylomorphs and so would be the "reptile teeth" observed by Fürsich et al. (1995, p. 138). Kriwet et al. (1997) suggested the presence of a single species at "Les Gardies", close in morphology to atoposaurids as described by Brinkmann (1992) and other authors. Early atoposaurid teeth are also found in abundance in approximately coeval sites, for instance in the Ambondromamy area (Boeny, Madagascar; Flynn et al., 2006).

Dinosauria

Ornithischia. Kriwet et al. (1997) reported the finding of one ornithischian tooth at "Les Gardies." It is unclear from the text and figure caption if this specimen is among those illustrated by these authors, which are mostly coarsely denticulated crowns devoid of sharp apicobasal ridges on the lateral surface. Kriwet et al. (1997) identified both the tooth from "Les Gardies" and the numerous, allegedly comparable, teeth from Larnagol as from a hypsilophodontid ornithischian. However, continuous improvement of our understanding of ornithischian phylogeny since the late 1990s strongly supports that *Hypsilophodon* is actually the only member of Hypsilophodontidae (see e.g., Boyd, 2012). For the time being, the affinities of the ornithischian teeth from the Causses described by Kriwet et al. (1997) remains indeterminate. Sciau et al. (2006) described possible ornithopod footprints close to the coal layers at La Verrière (Trèves, Gard) and La Garène (La Roque-Sainte-Marguerite, Aveyron). The single tooth from "Les Gardies" is the only direct remains of Ornithischia from the Bathonian of France.

Theropoda (Figure 1I). Kriwet et al. (1997) reported the finding of a few theropod teeth and tooth fragments at "Les Gardies." The most complete specimens were minuscule unserrated crowns, but portions with chisel-like serrations had also been recovered. Whereas the latter cannot be reasonably identified beyond Theropoda, the former might indicate a Maniraptoriformes (see e.g., Knoll and Ruiz-Omeñaca, 2009; Gianechini et al., 2011). However, the recent description of a pristine Late Jurassic juvenile megalosaurid specimen with some teeth devoid of serrations suggests that the apparition of this character is a more intricate issue than could have been conceived (Rauhut et al., 2012). Theropod footprints were described by Sciau et al. (2006) close to the coal layers at Capelan (Meyrueis, Lozère) and La Garène (La Roque-Sainte-Marguerite, Aveyron). Gand et al. (2007, p. 49) reported an additional theropod footprint near Salles-la-Source (Aveyron). Theropod remains from the Bathonian of France have been mentioned, depicted, and/or described since the beginning of the 19th century and habitually ascribed to *Megalosaurus*, *Poekilopleuron* or *Dubreuillosaurus* (e.g., Caumont, 1828; Eudes-Deslongchamps, 1837; Sauvage, 1900; Mercier, 1937; Rioult, 1978; Buffetaut, 1995; Allain, 2002, 2005). Most of the remains come from the Middle Bathonian Calcaire de Caen, which was deposited in a coastal swamp of the Armorican Massif, not dissimilar to the depositional environment inferred for the "stipites" of the Grands Causses (Rioult, 1963).

DISCUSSION

Although relatively scarce, the vertebrate microremains from the coal and associated layers of the Grands Causses (**Table 1**) are of great interest given their age. Indeed, the best known record of Bathonian microvertebrates is by and large restricted to the United Kingdom (England, mostly, and Scotland; see e.g., Evans, 1991; Metcalf et al., 1992; Evans and Milner, 1994; Metcalf and Walker, 1994; Evans and Waldman, 1996; Evans et al., 2006; and references therein). The British sites were formed under shallow marine conditions (e.g., Stonesfield, Oxfordshire) or in swampy coastal regions (e.g., Kirtlington, Oxfordshire). In contrast to those localities, the Grands Causses are yet to yield definitive remains of salamanders, turtles, lepidosauromorphs, choristoderes, pterosaurs, and therapsids. Although no direct sauropod fossils have been found so far, it should be pointed out that possible footprints from these animals are known at some levels next to coal layers (Sciau et al., 2006; but see discussion in Gand et al., 2007, pp. 48–49) at Capelan (Meyrueis, Lozère), La Verrière (Trèves, Gard), La Garène (La Roque-Sainte-Marguerite, Aveyron), Saint-Véran (La Roque-Sainte-Marguerite, Aveyron), Bombes (Nant, Aveyron), Montméjean (Saint-André-de-Vézines, Aveyron), Mas Nau (Millau, Aveyron), Les Crottes (Saint-Georges-de-Luzençon, Aveyron), and Ravin de Raves (Peyreleau, Aveyron). The French Bathonian sauropod record is, in fact, relatively poor as a whole (Sauvage, 1900; Läng, 2008; Buffetaut et al., 2011).

The meager fossil record of the French sites compared to those in the United Kingdom may be, at least in part, because they have drawn much less attention. However, genuine observations about the microvertebrates for the Grands Causses can be made. Firstly, the fossil content can vary considerably between different localities as well as between layers within the same site. For instance, crocodiles are the most common remains at "Les Gardies," whereas hybodont sharks prevail in the nearby locality of Saint-Martin. Furthermore, of the two levels examined at Cornhes, one is dominated by ginglymodian fishes and the other by amiiforms. Ecological causes (degree of marine influence) can well account for these faunal dissimilarities. The second remark that can be made is that, crocodile teeth aside, the remains of tetrapods are, as a rule, largely outnumbered by those of fishes *sensu lato* (either ginglymodians, amiiforms, or hybodonts, depending on the very site and layer). As in British localities (see e.g., Metcalf and Walker, 1994, Figure 19.5), crocodiles are the most common or the only tetrapods present at most sites of the Grands Causses. However, in contrast with the former, there is no evidence of crocodiles other than atoposaurids (which is a minor group of crocodiles in the British Isles) in the latter. A taphonomic bias against 'large' specimens would not satisfactorily explain the lack of non-atoposaurid crocodiles as the teeth of juvenile individuals would still be found. The absence of other crocodiles may, therefore, be genuine, and might be due to the fact that these taxa are either of more marine (teleosaurids) or, conversely, less aquatic (goniopholidids) habits than atoposaurids. At the best known locality ("Les Gardies"), the bulk of the specimens are atoposaurids and ginglymodian fishes. However, the site has also yielded a very small number of a priori mutually exclusive taxa, such as an albanerpetontid amphibian, a bank of freshwater pond inhabitant, together with the teleost *Aspidorhynchus*, a definite marine taxa. This suggests that a minor part of the remains are allochthonous, that marine flooding took place episodically, or this could just be due to the mixing of taxa from the coal itself and from the transitional beds to the carbonates.

Table 1 | Vertebrate fauna from the "stipites" of the Grands Causses.

Chondrichthyes
Hybodontiformes
Hybodus sp.
Asteracanthus sp.
Actinopterygii
Ginglymodi
Lepidotes sp.
Pycnodontiformes
Macromesodon sp.
Pycnodontidae indet. (cf. *Coelodus* sp.)
Amiiformes
Caturus sp.
Teleostei
Aspidorhynchus sp.
Amphibia
Anura
Anura indet.
Albanerpetontidae
Albanerpetontidae indet.
Reptilia
Crocodylomorpha
Atoposauridae indet.
Dinosauria
Ornithischia indet.
Theropoda indet.

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