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SHORT COMMUNICATION

FIRST OCCURRENCE OF FOSSIL VERTEBRATES FROM THE CARBONIFEROUS OF COLOMBIA

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Data concerning Paleozoic vertebrates from the South American continent are still scarce. In Colombia, occurrences were until now restricted to the Late Devonian fish assemblage from Floresta and, principally, the Cucho Formation on the high plateau of the central part of the Eastern Cordillera at Floresta Massif, Boyacá. The assemblage comprises a diverse fauna, which includes placoderms, acanthodians, chondrichthyans, actinopterygians, and sarcopterygians (Janvier and Villarroel, 1998, 2000; Burrow et al., 2003; Janvier and Maisey, 2010; Mondéjar-Fernández and Janvier, 2014; Olive et al., 2019). These findings have proven to be important not only from paleobiological and taxonomic points of view but also in providing significant data to assert a global paleogeographic hypothesis (Dalziel et al., 1994; Dupret et al., 2005; Janvier and Clément, 2005; Janvier, 2007; Olive et al., 2015, and references therein).

Here, we describe a new Paleozoic vertebrate fauna from Colombia. Associated conodonts suggest a mid-Mississippian to earliest Pennsylvanian age for the carbonate levels where the vertebrates occur (see below). This represents, as far as we know, the first record of vertebrates from the Late Paleozoic of Colombia. The new assemblage consists of isolated microremains (teeth, scales, and denticles) of acanthodian and chondrichthyan fishes, which came from the acid dissolution of carbonate rocks. Paleogeographic and paleoecological context of the new findings is considered.

GEOGRAPHIC AND GEOLOGICAL SETTINGS

The material here described has been recovered from the Río Batá section (bottom coordinates: 1033459N, 1086961E, height: 1165 m; top coordinates: 1030650N, 1089700E, height: 1030 m), located 3.6 km north-northwest of the town of Santa María (Boyacá, Colombia; Fig. 1A), in the lower part of the eastern flank of the Cordillera Oriental.

The Río Batá exposes a very complete and continuous section belonging to the Farallones Group (Segovia and Renzoni, 1965), assigned to the Devonian–Carboniferous interval. It is constituted of a very thick sedimentary succession cropping out

approximately 2400 m along the canyon of the river. The predominantly siliciclastic accumulation consists of thick-bedded red sandstones interlayered with red, gray, and green siltstones and mudstones. A thick carbonate interval of about 200 m, mainly composed of black and dark gray wackestones and packstones with crinoids and brachiopods, crops out outstandingly in the upper part of the section (Fig. 1B, C).

Two members have traditionally been differentiated in the Farallones Group: the lowermost part, Middle–Late Devonian in age, and one upper part, dated as Carboniferous (see Royo and Gómez, 1945; Bürgli, 1958; Moreno et al., 2009, and references therein). The Devonian–Carboniferous boundary has been traced for around 400 m from the base of the group and identified on the basis of lithological changes (Moreno et al., 2009). In any case, the fossil content, lithostratigraphic succession and especially the chronostratigraphy of the Farallones Group have not yet been comprehensively studied.

The specimens reported here were obtained after etching in 5–10% acetic acid of limestone samples (12 kg approximately) collected from the median–upper part of the carbonate interval (Fig. 1C). A total of 110 kg of sediment was dissolved to gather all the material described below. All fossils studied are deposited at the Museo Geológico José Royo y Gómez, Servicio Geológico Colombiano (SGC-MGJRG).

SYSTEMATIC PALEONTOLOGY

Class ACANTHODII Owen, 1846
Order ACANTHODIFORMES Berg, 1940
Family ACANTHODIDAE Huxley, 1861
Genus ACANTHODES Agassiz, 1833

Type Species—*Acanthodes bronni* Agassiz, 1833.

'ACANTHODES' sp.
(Fig. 2A–D)

Material—Ten isolated scales. Levels SM 1 (SGC-MGJRG.2020.V.1, SGC-MGJRG.2020.V.2, and SGC-

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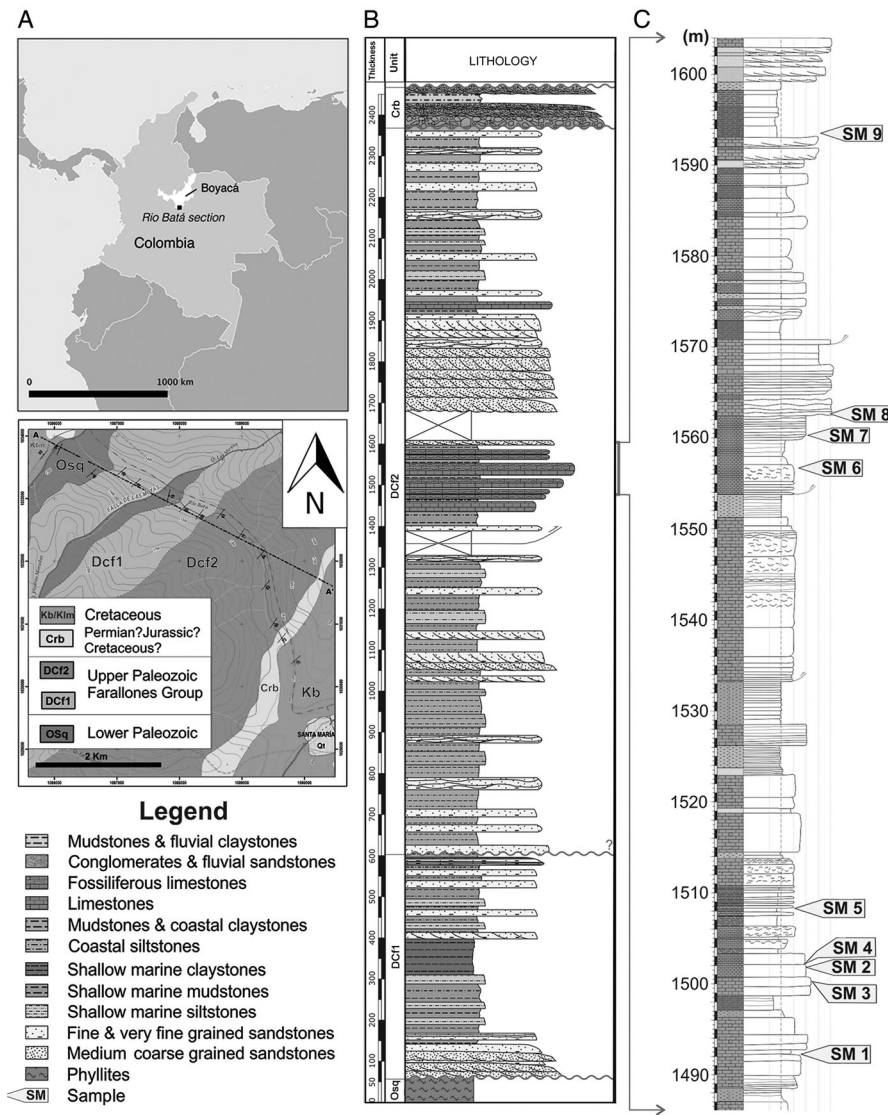


FIGURE 1. **A**, geographic and geological setting of the studied area. **B**, synthetic column of the Río Batá section with indication of carbonate levels (blue) that yield the vertebrate faunal associations. **C**, details of Carboniferous limestones with stratigraphic position of the sampled levels.

MGJRG.2020.V.18), SM 2 (SGC-MGJRG.2020.V.5), and SM 8 (SGC-MGJRG.2020.V.19), Río Batá section.

Description—Acanthodian scales of medium size (generally 500 μm anteroposterior dimension; 600 μm wide). The crown is symmetrical and diamond-shaped, with a rounded anterior margin. It is flat and parallel to the neck-base junction. The crown surface is totally smooth. Short and robust neck only a little narrower than crown. Neck-base interface clearly marked with similar anteroposterior and lateral dimensions to the crown. The base is deep (around 350 μm) and bulbous, slightly rostrally displaced.

Remarks—The scales from Santa María are morphologically comparable to acanthodian isolate scales assigned, nonspecifically, to the genus *Acanthodes*, represented in the Carboniferous and Permian of North America (Zidek, 1976; Schultze, 1985, and references therein), Europe (e.g., Schultze, 1985; Soler-Gijón, 1993; Ginter et al., 2015), China (Wang and Turner, 1985), and Australia (Turner, 1993). Morphologically similar scales (i.e., with smooth rhombic crowns and bulbous bases) are sometimes present in species of other distant groups of acanthodians such

as the Ischnacanthiformes (e.g., in *Gomphonchus saneleensis*, *Ischnacanthus gracilis*, *Gomphonchoporus*), and histological studies are certainly critical for definite assignation (see, e.g., Valiukevičius, 1995; Botella et al., 2012, 2014). The level of preservation of our material does not allow for histological study. However, because other major groups of acanthodians apart from acanthodiforms are not known from the Carboniferous, we assign our scales to ‘*Acanthodes*’ sp. (Fig. 2A–D).

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Superorder XENACANTHIMORPHA Nelson, 1976
 Order BRANSONELLIFORMES Hampe and Ivanov, 2007
 Family INCERTAE SEDIS
 Genus *BRANSONELLA* Harlton, 1933

Type Species—*Bransonella tridentata* Harlton, 1933.

BRANSONELLA NEBRASKENSIS (Johnson, 1984)
 (Fig. 2E–J)

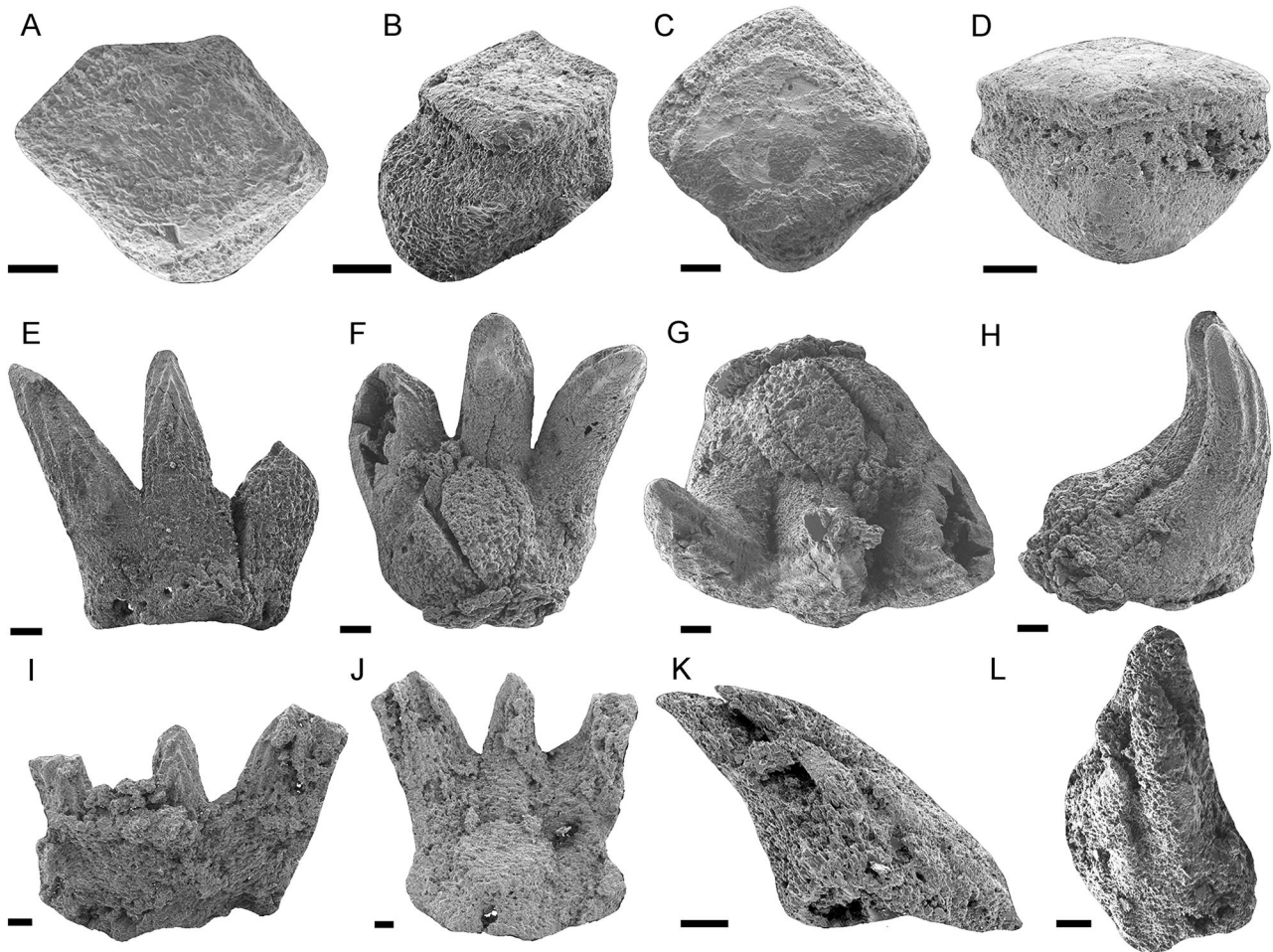


FIGURE 2. Carboniferous vertebrate microremains from the Río Batá section. **A–D**, ‘*Acanthodes*’ sp.: **A**, **B**, scale (SGC-MGJRG.2020.V.1) in crown and lateral views, respectively; **C**, **D**, scale (SGC-MGJRG.2020.V.5) in crown and anterior views, respectively. **E–J**, *Bransonella nebraskensis* (Johnson, 1984): **E–H**, tooth (SGC-MGJRG.2020.V.3) in labial, lingual, occlusal, and lateral views, respectively; **I–J**, tooth (SGC-MGJRG.2020.V.12) in labial and lingual views, respectively; **K–L**, Chondrichthyan indet. mucous membrane denticle (SGC-MGJRG.2020.V.8) in lateral and crown views, respectively. Scale bars equal 100 μm .

Material—Two teeth, SGC-MGJRG.2020.V.3 and SGC-MGJRG.2020.V.12, and several broken cusps. Levels SM 1 and SM 8, Río Batá section.

Description—The specimens are highly eroded. Even so, the overall morphology of the teeth has been preserved. SGC-MGJRG.2020.V.3 is a small tricuspidate tooth with a broken lateral cusp. The crown is higher than the base. All three cusps have similar diameter, and the two completely preserved also display equal height. The cusps present a chevron-like ornamentation with five straight cristae on the labial side that reach the base. Additional, shorter cristae in the proximal parts of the cusps where the inverted-‘V’ pattern becomes less distinct and the cristae more sigmoid (Fig. 2E). Soft fine cristae can also be identified on the distal-most lingual margins of both preserved cusps (Fig. 2F). The cusps are subcylindrical in cross-section, slightly compressed proximally (Fig. 2G) and lingually arched (Fig. 2H). The base is subcircular (800 μm linguolabial dimension; 730 μm anteromedial-posterolateral dimension). At least four small labial foramina open above the basolabial projection, and two larger ones are present symmetrically on either side of it (Fig. 2E). The lingual part of the base is dominated by a rounded oral-lingual button that is in contact with both the intermediate and the lateral cusps. This oral-lingual button does not

reach the lingual rim of the base (Fig. 2F–H). The lingual margin of the base is covered by sedimentary particles, not allowing a clear identification of a central nutrient channel.

SGC-MGJRG.2020.V.12 (Fig. 2I–J) is more poorly preserved than SGC-MGJRG.2020.V.3, with the proximal part of the cusps as well as the lateral part of the left cusp (in labial view) hidden by sediment. The teeth are tricuspidate, with the intermediate cusp slightly smaller than the lateral cusps. The intermediate cusp is complete, whereas in both lateral cusps the distal part is broken. All three cusps show an inverted-‘V’ pattern of ornamentation on their labial side, with at least four identifiable straight cristae in the complete intermediate cusp (Fig. 2I). Ornamentation seems to be absent on the lingual side, but this area is extremely eroded (Fig. 2J). Cusps are narrower and more gracile than in SGC-MGJRG.2020.V.3. The base is rounded (900 μm labiolingual dimension; 1000 μm anteromedial-posterolateral dimension), and the labial margin is severely damaged. This alteration affects the basolabial projection, which seems reduced in comparison with SGC-MGJRG.2020.V.3. A pair of large foramina are present labially placed symmetrically on each side of the basolabial projection (Fig. 2I). The lingual part of the base shows a prominent oval apical button, which is in contact with the intermediate cusp

and does not reach the lingual margin of the base. A large central foramen (main nutrient channel) is present on the lingual margin close to basal rim, forming an incipient notch (Fig. 2J).

Remarks—Despite the high erosion of the tooth surfaces, their overall preservation allows for a good identification of all the characteristic features of bransonelliforms: i.e., inverted-‘V’ nested cusp ornamentation on the labial side of all three cusps; dominant orolingual button; labially positioned foramina; and lingual large central opening often forming a distinct notch at the margin of the base (see Hampe and Ivanov, 2007; Elliott and Hodnett, 2013). The teeth from Colombia fit well into the size and the morphological variability described by Johnson (1984) in *Xenacanthus* (*Bransonella*) *nebraskensis* from the Pennsylvanian of Nebraska, with teeth of similar-sized cusps and others where the central cusp is slightly smaller than the lateral cusps. In fact, our teeth are particularly similar to those from the Viséan of England and Poland (Ginter et al., 2015:figs. 8a1–a3, 9a1–a2, 14c1–c2), which show the pair of large nutrient canal openings (symmetrically placed on either side of the basolabial; Ginter et al., 2015:fig. 14c2).

CHONDRICHTHYES indet. (Fig. 2K–L)

Material—One denticle from level SM 3 (SGC-MGJRG.2020.V.8), Río Batá section.

Description—A small denticle (580 µm high; 510 µm length; 350 µm wide) with a multicuspidate crown consisting of conical pointed slightly recurved cusps. At least four cusps can be identified that successively overlap each other, increasing in height. They seem distributed in a pair of rows. The eroded preservation of the specimen does not allow for the identification of any kind of ornamentation (if it existed). The base of the denticle is flat or slightly concave and wider than the crown.

Remarks—Multicuspidate mucous membrane denticles are common in several Paleozoic chondrichthyan groups, such as Symmoriiforms or Xenacanthiformes. In both groups, significant variation in morphology occurs, including, for example, the number of cusps, their pattern of arrangement, or their ornamentation.

The disposition and overall morphology of the cusp of the Colombian specimen is somewhat similar to that present in some mucous membrane denticles of *Orthacanthus* and other xenacanth (Johnson, 2018:fig. 6a) with overlapping conical smooth cusps, although xenacanth usually (but not always) present a large compact base. Symmoriiform branchial/mucous membrane denticles (*Stemmatias* St. John and Worthen, 1875) often present cusps bearing cristae and lateral carinae, but forms with weakly ornamented or smooth cusps are not rare (e.g., Williams, 1985). For instance, Ginter et al. (2015:fig. 15e, 1, n; ‘*S. bicristatus*’) reported symmoriiform branchial denticles with a double row of cusps and flat bases from the Viséan of northern Europe, similar to our SGC-MGJRG.2020.V.8. Moreover, multicuspidate dermal denticles (scales) with a conical shape cusp and a thin, concave, basally open basal plate are also present in the dermal skeleton of *Sphenacanthus* (e.g., Dick, 2008). In any case, the poor preservation and erosion of our specimen SGC-MGJRG.2020.V.8 does not allow for a confident assignment to any major group of chondrichthyans.

DISCUSSION

Age of the Fauna

The Farallones Group consists of a thick succession of rocks still not finely subdivided stratigraphically, which includes rocks of wide-ranging ages. Existing dating studies, however, are scarce, with no detail, and are poorly regionally integrated. Royo and Gómez (1945) assigned a Carboniferous age to

samples collected from the upper part of the Farallones Group on the basis of their fossil content. Later, Bürgl (1958) determined an age from Middle Devonian to Carboniferous to the complete Paleozoic sequence in the Río Batá section. Our finding of the conodonts *Cavusgnathus* sp., *Rhachistognathus* sp., and *Neognathodus* sp. in the same samples where the vertebrates occur permits reasonably close age constraints on these levels within the Osagean to Chesterian (Mississippian; uppermost Tournaisian to Serpukhovian in the International Chronostratigraphic System). This age range agrees with the currently known stratigraphic ranges for the vertebrate taxa. Thus, *B. nebraskensis* (Johnson, 1984) displays a ‘noticeably’ large range, from the Middle Mississippian to the lower Permian (see Hampe and Ivanov, 2007; Johnson and Thayer, 2009; Elliott and Hodnett, 2013, and references therein). On the other hand, *Acanthodes* is a widespread genus (see above) known from the Carboniferous and Permian.

Paleobiogeography

Bransonelliforms reached a wide geographic distribution during the Carboniferous, including occurrences in North America, Europe, Siberia, China, Australia, and Greenland (for detailed occurrences and references, see recent reviews of paleogeographic distribution of bransonelids in Hampe and Ivanov, 2007; Johnson and Thayer, 2009; Elliott and Hodnett, 2013; Ginter et al., 2015; Ivanov et al., 2017; Hodnett and Elliott, 2018; Ivanov and Lucas, 2019). Findings in South America were limited, until now, to a putative occurrence in Brazil (?*Triodus* in Duffin et al. [1996], recognized latterly as *Bransonella* by some authors [Hampe and Ivanov, 2007; Johnson and Thayer, 2009; Elliott and Hodnett, 2013]). The new data from Colombia, therefore, confirm the presence of bransonelliforms in Western Gondwana.

Bransonella nebraskensis is known from North America, Siberia, and Europe. However, remarkably, until now, Mississippian occurrences were restricted to the Viséan–Serpukhovian of Europe, whereas most occurrences in North America are Pennsylvanian or Permian in age (references above). The reported findings herein in the Mississippian of Colombia represent the first occurrence of the species in Gondwana, being one of its earliest records, similar in age to occurrences in the Viséan sediments of Europe and Siberia.

Similarly, isolated scales of *Acanthodes* type, like those found in Colombia, are common microremains in Carboniferous sediments from North America, China, Australia, and Europe (see above). The scales from Río Batá represent the first record of the genus *Acanthodes* in western Gondwana—South America (but see Mutter and Richter, 2007), illustrating worldwide distribution of the genus during Carboniferous times. In sum, this first vertebrate fauna described from the Lower Carboniferous of Colombia shows clear similarities to faunas from Europe and North America (Laurasia). In fact, *B. nebraskensis* teeth, chondrichthyan branchial/mucous membrane denticles, and *Acanthodes* scales appear to be also associated with several ‘Laurasian’ localities: e.g., Holy Cross Mountains, Poland; Derbyshire, England, (Ginter et al., 2015); or the Flint Hills of central Kansas, U.S.A. (Schultze, 1985), as part of a more diverse assemblage.

The Mississippian age of the Colombian faunas supports the presence at that time of, at least, narrow marine corridors between the Paleotethys Ocean and the oriental margin of the Panthalassa Ocean (e.g., Scotese, 2004).

Paleoenvironment

According to its lithofacies, the Farallones Group has been considered to be deposited in shallow-water marine to coastal

environments. The sampled limestones and overlying arenaceous levels with wavy parallel and nonparallel lamination can fit with a regressive event in a depositional model of carbonate platform with limestones deposited in a shallow open platform environment and sandstones in a foreshore and coastal channel area (e.g., Boggs, 2011). The conodont genera *Cavusgnathus* and *Rhachistognathus* are characteristic of shallow marine waters, although occurrences in open marine and open platform environments are common, especially for the latter genus (e.g., Krumhardt et al., 1996).

Bransonella nebraskensis (as well as all other bransonelliforms) is undoubtedly a true marine xenacanthimorph (Johnson and Thayer, 2009; Hodnett and Elliott, 2018). However, occurrences in Europe come mainly from pelagic sediments, whereas in North America it occurs typically in shallow water, or even in estuarine environments. Thus, *B. nebraskensis* has been reported from deep-water facies of Europe: Holy Cross Mountains, Poland; Derbyshire, England (Ivanov and Ginter, 1996; Ginter et al., 2015); the Dinant synclinorium in Belgium (Derycke et al., 2005); the Urals (Ivanov and Ginter, 1996); and Siberia, the Kuznetsk Basin (Hampe and Ivanov, 2007). In North America, however, *B. nebraskensis* occurs mostly in more coastal facies (e.g., Schultze, 1985; Hodnett and Elliott, 2018), or even in estuarine environments (Johnson and Thayer, 2009).

Therefore, the paleoenvironmental context of *B. nebraskensis* in the Farallones Group seems to be more similar to those of North America rather than the deep-water facies where it appears in Europe. Nevertheless, further studies on both fossil content and sedimentology of the Farallones Group are needed to clarify this issue. In any case, the data presented here testify the potential of the Farallones Group to provide stratigraphically/phylogenetically relevant early vertebrate fossil remains.

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