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The first report of a vauxiid sponge from the Cambrian Chengjiang Biota

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Abstract.—Non-spicular sponges constitute >8% of the extant sponge biodiversity at the species level, yet their evolutionary history is poorly known due to a sparse fossil record. The genus *Vauxia*, previously only known from middle Cambrian (Miaolingian, Wuliuan) Lagerstätten, was regarded as the earliest fossil record of non-spicular demosponges. Here we describe the first vauxiid sponge, *Vauxia leioia* new species, from the early Cambrian Chengjiang Biota (Series 2, Stage 3). This sponge exhibits a double-layered fibrous skeleton: the mesh and fiber thickness of the endosomal layer are irregular while the dermal layer, which directly connects with the endosomal skeleton without intermediate supporting fibers, is regular in both aspects. Measurements using scanning electron microscope and Raman spectroscopy revealed that the endosomal fibers are composed of carbonaceous material, but are tomographically indiscernible from the host rock, while the dermal fibers are preserved as impressions without obvious accumulation of carbonaceous material. Although the original composition of the dermal skeleton is now hard to establish, we cannot rule out that it was siliceous. The morphological characters of *V. leioia* n. sp. represent an intermediate state between other *Vauxia* species and the recently established vauxiid genus *Angulosuspongia*. However, more data are required to reconstruct the phylogenetic relationship among these taxa.

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Introduction

Non-spicular taxa constitute a significant portion of the biodiversity of living sponges. The non-spicular demosponges (subclasses Verongimorpha and Keratosa, sensu Morrow and Cárdenas, 2015) are ~8.2% of known sponge species, equaling the contribution of the class Calcarea (8.4%), and surpassing that of the classes Hexactinellida (7.2%) and Homoscleromorpha (1.25%) (van Soest et al., 2018). In addition, some homoscleromorphs are also non-spicular (e.g., Gazave et al., 2013; Domingos et al., 2016). Although the absence of mineral skeletons in living demosponges and homoscleromorphs is probably apomorphic (Maldonado, 2009; Philippe et al., 2009; Botting et al., 2014), it is still in debate whether the common ancestor of sponges was spicular (e.g., Botting and Muir, 2018) or non-spicular (e.g., Wood, 2011; Luo, 2015). However, due to the low fossilization potential of non-biomineralized tissues, the evolutionary history of non-spicular sponges is still largely unexplored. Thus, any new discovery may influence our understanding of the evolutionary history of these clades.

The several species of *Vauxia* (family Vauxiidae, order Verongiida) from the middle Cambrian of Laurentia have been regarded as the earliest record of non-spicular demosponges (Rigby, 1986; Rigby and Collins, 2004; Botting and Muir, 2018), along with later Phanerozoic fossils preserved in carbonates (e.g., Luo and Reitner, 2014, 2016; Lee et al., 2015; Park et al., 2015; Friesenbichler et al., 2018). Ehrlich et al. (2013) confirmed that the skeleton of *Vauxia gracilenta* Walcott, 1920 is composed of chitin, consistent with the skeletal composition of modern verongiids. Recently, a new vauxiid genus, *Angulosuspongia* Yang et al., 2017a, was described from the Kaili Biota (Miaolingian, Wuliuan), which is slightly older than the Burgess Shale. These fossils possess an anastomosing, fibrous skeleton, which is claimed to have been exclusively composed of silica (Yang et al., 2017a, b). However, without a phylogenetic framework of vauxiid sponges and other closely related spicular taxa, it is difficult to interpret the evolutionary significance of these fossils.

Here we describe a new vauxiid sponge from the Chengjiang Biota (Cambrian Series 2, Stage 3), with a preserved carbonaceous endosomal skeleton. This material exhibits intermediate morphological characters between other *Vauxia* species and *Angulosuspongia*, although the data is still insufficient to establish a phylogenetic framework for these taxa.

Materials and methods

Fossils were collected from the upper part of the Maotianshan Shale Member, Yu'anshan Formation at the Malong Section during a one-month excavation. The location and sedimentary sequence of this site have been described in detail in Zhao et al. (2012). The age of the fossil layer was correlated to the uppermost part of the *Eoredlichia-Wutingaspis* Zone (Wang et al., 2012), meaning that the investigated materials belong to the Chengjiang Biota, but are slightly younger than the massively occurring, exceptionally preserved fossils in the Haikou and Chengjiang areas. The latest radiometric dates of detrital zircons from the base of the Chengjiang Biota in the Chengjiang area yielded a maximum deposition age of 518.03 ± 0.69/0.71 Ma (Yang et al., 2018).

Fossils were observed and photographed using a Nikon SMZ18 microscope coupled with a Nikon DS-Ri2 camera. Chemical composition of the fossils was investigated using a HITACHI SU3500 scanning electron microscope (SEM) equipped with an energy dispersive X-ray spectrometer (EDS) in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), and a Horiba Jobin-Yvon LabRam-HR 800 UV confocal Raman spectroscopy at the University of Göttingen (excitation wavelength 488 nm).

Repository and institutional abbreviations.—Types and figured specimens examined in this study are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China.

Systematic paleontology

Class Demospongiae Sollas, 1885
Order Verongiida Bergquist, 1978

Remarks.—The spelling of the order name follows the suggestion of Morrow and Cárdenas (2015), which changes “Verongida” to “Verongiida.” This spelling has been widely accepted (van Soest et al., 2018).

Family Vauxiidae Walcott, 1920

Diagnosis.—Thin-walled tubular to conical sponges, with or without branches. Single- or double-layered skeleton composed of fibrous elements, which fuse to produce a net. Discrete spicules absent. The meshes in the single-layered form or the endosomal meshes in the double-layered form are typically hexagonal or polygonal. Dermal layer, if present, is thin, irregularly or regularly reticular, often supported by radial fibers.

Remarks.—This family contains two genera: *Vauxia* Walcott, 1920 and *Angulosuspongia* Yang et al., 2017a. The presented diagnosis is emended from that of Yang et al. (2017a) for the reasons discussed below. The terms “dermal” and “ectosomal” in this diagnosis and the text below are following paleontologists’ usage since Rigby (1986), and not necessarily identical to biological terminology.

The family Vauxiidae was initially described as dictyonine hexactinellids with a single genus, *Vauxia* (Walcott, 1920; de Laubenfels, 1955), and later re-interpreted as a specialized offshoot of protospongiids (Finks, 1960) or as lithisitid demosponges (Rigby, 1980). Rigby (1986) re-investigated and illustrated the skeletal structures of the species in this family and established that: (1) the skeletal network of these sponges is composed of cored fibers like those in extant verongiids, instead of jointed triactinal or tetraxial spicules as previously described; and (2) the skeletons exhibit two differentiated layers connected by radial fibers—a relatively regular endosomal layer with polygonal meshes and an irregular dermal layer. Since then, “non-spicular” became a diagnostic character of the family Vauxiidae, which distinguishes it from similar taxa with fibrous skeletons (e.g., members of family Hazeliidae de Laubenfels, 1955).

Botting et al. (2013) observed that part of the skeleton of *V. bellula* Walcott, 1920 is composed of discrete elements and interpreted those as small monaxons. However, the diagnosis of family Vauxiidae was not emended in this study. Due to the suggested similarity between *V. bellula* and *Hazelia conferta* Walcott, 1920, even if this observation is confirmed by further paleontological and taphonomical studies, it would still require a phylogenetic analysis to determine whether to keep *V. bellula* in the family Vauxiidae and change the family definition, or to remove *V. bellula* from this family.

Yang et al. (2017a) established the genus *Angulosuspongia* for newly discovered sponge fossils which exhibit an anastomosing skeleton composed of siliceous “spicules.” This work modified the family diagnosis of Rigby (1986) by removing the word “keratose” and adding “spicules” to the description of skeletal components. In spite of the question whether it is appropriate in theory to resolve a “spicular” taxon under the family Vauxiidae, the figures in Yang et al. (2017a, b) actually did not show any proper structure indicating the existence of discrete skeletal elements (i.e., spicules). Thus, *Angulosuspongia* does comply with the old diagnosis of family Vauxiidae in exhibiting a fibrous skeleton, although the origin of silica in those fibers remains unknown.

In addition, although *Angulosuspongia* was described as an organism possessing a double-layered skeleton, the two layers were neither detailed in the text in how they differentiate from each other, nor identifiable from the illustrations. On the contrary, the illustrated specimens seem to show a compacted, single-layered skeleton (Fig. 3.3). The radial fibers of *Angulosuspongia* seem to have a free end and do not support any skeletal layer, unlike the radial fibers in other *Vauxia* species.

Therefore, the family diagnosis is modified in this paper from that of Yang et al. (2017a) with the following changes: (1) the expression “cored fibers or spicules” (Yang et al., 2017a, p. 1336) is changed to “fibrous elements;” (2) “single-layered form” is added; and (3) “often” is added in front of “(dermal layer) supported by radial fibers,” because the new species described below does not have the supporting radial fibers.

Genus *Vauxia* Walcott, 1920

Type species.—*Vauxia gracilenta* Walcott, 1920.

Vauxia leioia new species
Figures 1, 2, 3.2

Holotype.—Sample number: NIGPAS 169083 (including two counterparts NIGPAS 169083a and 169083b), collected from

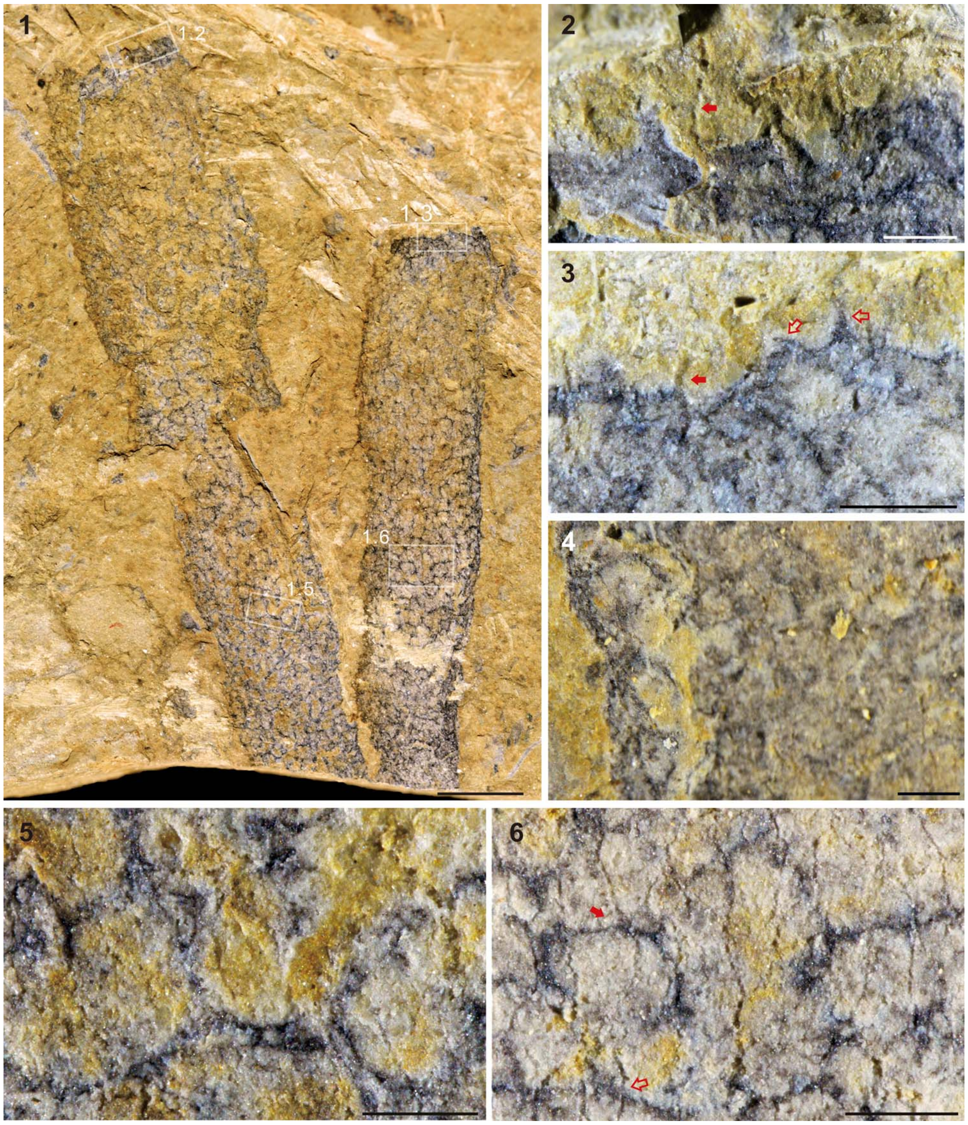

Figure 1. *Vauxia leioia* n. sp., NIGPAS 169083a and b, holotype: (**1**) overview of NIGPAS 169083a; areas in rectangles enlarged in (**2, 3**) and (**5, 6**); (**2, 3**) pinnacle-like and fibrous protrusions at the spongocoel margins, indicated by hollow and solid arrows, respectively; (**4**) a broken edge on NIGPAS 169083b showing that endosomal fibers penetrating into sediments; the well-focused part on the left is on a higher focal plane than the right part; (**5, 6**) endosomal and dermal skeletons; solid arrow in (**6**) indicates dermal fibers diverging from an endosomal fiber, hollow arrow indicates where dermal fibers imprints an endosomal fiber. Scale bars = 3 mm (**1**); 0.5 mm (**2–6**).

the Maotianshan Shale Member of the Yu'anshan Formation (Cambrian Series 2, Stage 3) at the Malong Section, Yunnan Province, China, now deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Diagnosis.—Thin-walled subcylindrical sponges, branching or not. Surface smooth, with pinnacle-like and fibrous forms of protrusions at spongocoel margin. Double-layered skeleton composed of reticulated fibrous elements. Endosomal skeleton irregular in both fiber diameter and the shape of polygonal meshes. Dermal fibers uniform in diameter, directly diverging from the endosomal skeleton and forming moderately regular, basically hexagonal meshes.

Occurrence.—The only known occurrence is from the Maotianshan Shale Member of the Yu'anshan Formation (Cambrian Series 2, Stage 3) at the Malong Section, Yunnan Province, China.

Description.—Only one specimen is known. Two subcylindrical fossils without the basal parts are preserved side by side, representing either two unbranched individuals or two branches of a single individual (Fig. 1.1). The larger cylindrical body is ~30 mm long, 6 mm wide at the top, 7 mm across at the widest place, and 4.5 mm at the base. The corresponding data for the smaller one is 22 mm, 4 mm, 5 mm, and 3 mm, respectively. These fossils retain a certain thickness after compaction, and the space among the skeletal fibers is filled with sediments. The shape of the spongocoel is not identifiable.

The endosomal skeleton is preserved as carbonaceous fibers of ~30–50 μm in diameter, which form irregularly

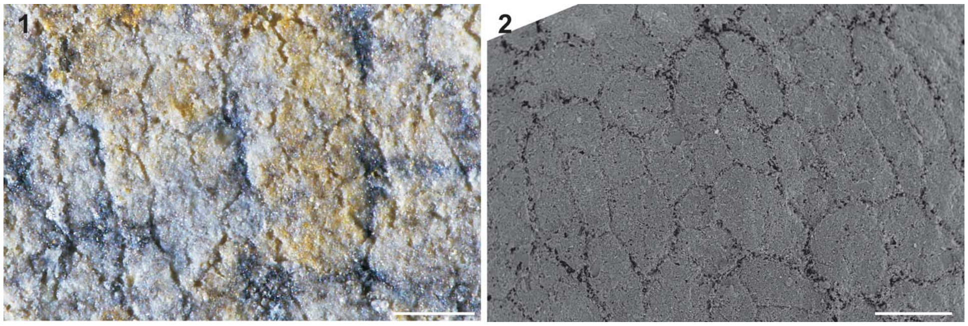

Figure 2. The same area in *Vauxia leioia* n. sp., NIGPAS 169083a, holotype, observed using (**1**) stereo microscope and (**2**) SEM (20.0kV, mode B.3 + UVD); showing the different preservation states of the endosomal and dermal skeletons. Scale bars = 0.3 mm.

polygonal meshes up to 850 µm, but mainly 350–600 µm across. These dark fibers are often thickened at the joints of the network. Viewed on the broken edge of the smaller body on NIGPAS 169083b, part of the endosomal skeletal layer is buried in sediments (Fig. 1.4). At the spongocoel margin, these carbonaceous skeletons extend to form pinnacle-like protrusions, which seem to be soft at some places (Fig. 1.3, hollow arrows).

The dermal skeleton is composed of thin, regular fibers that are ∼15 µm in diameter and forming moderately regular hexagonal, pentagonal, and tetragonal meshes that are mainly 100–250 µm and up to 300 µm across. These fibers seem to be distributed only on the sponge surface and do not penetrate into sediments as does the endosomal skeleton. Accordingly, some dermal fibers imprint the underlying endosomal skeleton, while in other places, the former clearly diverge from the latter (Fig. 1.6). Dermal fibers are mainly preserved as impressions. Fibrous protrusions of the same preservation are also observed at the spongocoel margin (Fig. 1.2, 1.3, solid arrows).

Etymology.—“*leio*-,” Greek, means smooth, referring to the smooth surface of the new species.

Remarks.—Although only one specimen has been collected so far, the morphological characters are elegantly preserved, and thus provide sufficient information for the taxonomic resolution.

The double-layered, anastomosing fibrous skeleton of the described fossils is in accordance with the definition of genus *Vauxia*. Six valid species have been described in this genus, including *V. bellula* Walcott, 1920, *V. densa* Walcott, 1920, *V. gracilenta* Walcott, 1920, *V. magna* Rigby, 1980, *V. venata* Walcott, 1920, and *V. irregulara* Rigby and Collins, 2004.

Most of these previously described species exhibit an endosomal skeleton with more or less regular meshes, different from that of *V. leioia* n. sp. Specifically, the endosomal meshes of *V. densa* and *V. venata* show a ladder-like pattern, those of *V. bellula* and *V. magna* are in a regularly hexagonal form, and those of *V. gracilenta* are subrectangular to hexagonal in shape (Rigby, 1980, 1986). Compared with these five species, the endosomal skeleton of *V. irregulara* is more irregular, showing circular to hexagonal or rectangular openings. However, the endosomal skeletal fibers of *V. irregulara* is much thicker (120–150 µm, up to 250 µm in diameter) than that of *V. leioia* n. sp., and the dermal skeletal fibers of the former species form an irregular network, different from the regular dermal meshes in the latter species (Rigby and Collins, 2004).

In previously described *Vauxia* species, the endosomal and dermal skeletal layers are typically connected by radial fibers. This was clearly illustrated in *V. bellula* and *V. gracilenta*, in which the radial fibers diverge from the endosomal layer and support the dermal skeleton (Rigby, 1986; Rigby and Collins, 2004). In the remaining four species, the connection between the dermal and endosomal layers was not described, partly due to unfavorable preservation. In contrast to these fossils, the dermal skeletal fibers of *V. leioia* n. sp. directly diverge from the endosomal layer.

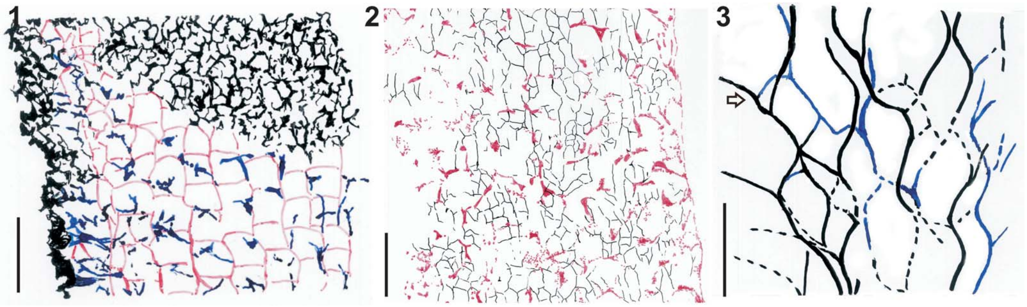

Figure 3. Skeleton architecture of three sponge species in the family Vauxiidae: (**1**) *Vauxia gracilenta*, USNM 66515, lectotype, drawn after the photo at https://burgess-shale.rom.on.ca, and courtesy of the Smithsonian Institution; indication of colors: red, endosomal skeleton; blue, radial fibers; black, dermal skeleton; (**2**) *Vauxia leioia* n. sp., NIGPAS 169083a, holotype; indication of colors: red, endosomal skeleton; black, dermal skeleton; (**3**) *Angulosuspongia sinensis*, GTBM17-765a, holotype, drawn after fig. 2b in Yang et al., (2017a); not all fibers can be clearly traced in the photo, the blue color indicates fibers that are beneath the others; arrow indicates a node at the edge, from which both blue and black fibers diverge. Scale bars = 1 mm.

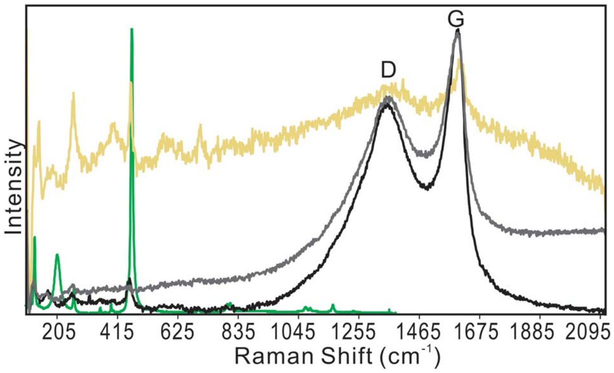

Figure 4. Raman spectra measured from *Vauxia leioia* n. sp., NIGPAS 169083a, holotype. Colors: black and gray, measured from endosomal skeletal fibers; yellow, from host rock; green, referential spectrum of quartz, from Handbook of Minerals Raman Spectra (http://www/wns-lyon.fr/LST/Raman).

For these reasons, the specimen described here is assigned to a new species under the genus *Vauxia*.

Discussion

The endosomal and dermal skeletons in *V. leioia* n. sp. are preserved in different ways: the former is preserved in dark-colored carbonaceous material, without discernible topographic differences from the host rock under SEM (Figs. 2, 4); while the latter is impressions, generally devoid of the dark carbonaceous material (Fig. 2). The protrusions at the spongocoel margin also exhibit these two different preservation states (Fig. 1.2, 1.3). These facts indicate that these skeletal elements probably had different compositions. Although it is impossible to confirm the original compositions based on the current material, the impressions were probably produced by mineralized tissues. Silica and carbonates, both commonly utilized in sponge skeletal construction, are often diagenetically dissolved in Chengjiang fossils (e.g., Forchielli et al., 2012).

Authigenic crystalline aragonite and amorphous silica have recently been reported from the chitinous skeleton of some extant verongiids (Ehrlich et al., 2010). In light of this fact, it is conceivable that there might have been some fossil keratose sponges that incorporated a higher proportion of minerals in their fibrous skeletons. On the other hand, chitin and spongin, the basic components of the organic skeleton of keratose sponges (e.g., Gross et al., 1956; Ehrlich et al., 2007), have been used in material science as templates for in vitro mineralization, including calcification and silicification (e.g., Wysokowski et al., 2015; Szatkowski and Jesionowski, 2017). This indicates that some favorable diagenetic physio-chemical conditions also have a potential to trigger mineralization of the originally non-mineralized organic skeletons. However, if further investigations confirmed the mineralization in *V. leioia* n. sp., it would be more likely a biological feature than a diagenetic product, because the distinct compositional difference between the dermal and endosomal skeletons should invoke some biological regulation.

With the description of *V. leioia* n. sp. and the discussion above, it is now possible to establish a continuous spectrum of morphological characters in the family Vauxiidae: (1) from double-layered skeleton separated by radial fibers (e.g., *V. gracilenta*) to a double-layered skeleton without intermediate radial fibers (*V. leioia* n. sp.), and to single-layered skeleton (*Angulosuspongia sinensis* Yang et al., 2017a); and (2) if the mineralization in *V. leioia* n. sp. and *A. sinensis* were confirmed by future studies, from organic skeleton (e.g., *V. gracilenta*) to a partly mineralized (possibly silicified) skeleton (*V. leioia* n.sp.), and to completely mineralized siliceous skeleton (*A. sinensis*). In both aspects, *V. leioia* n. sp. represents an intermediate state between other *Vauxia* species and *Angulosuspongia*. Considering the older age of *V. leioia* n. sp., this species may represent an ancestral form, from which other *Vauxia* species and *Angulosuspongia* derived from. However, other possible phylogenetic relationships still cannot be excluded at this stage, such as that *V. leioia* n. sp., *Angulosuspongia*, and other *Vauxia* species were parallel, contemporaneous derivatives of a common ancestor.

Rather than resolving any existing questions, this study reveals unexpected complexity in the early evolutionary history of sponge skeletons. Further data are required to forge a more comprehensive picture.

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