

An Oligocene chimaeroid egg capsule from western Washington State, USA, and priority of *Vaillantoonia* Meunier, 1891

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Introduction

Fossil egg capsules of chimaeroids (holocephalian fishes), although rare, have been known for more than 150 years (Bes-sels, 1869; Meunier, 1891a) and have been found in rocks as old as Upper Triassic (Gottfried and Fordyce, 2014). Egg capsules of extant chimaeroids are spindle shaped, with a smooth central body where the embryo develops, an elongate anterior beak through which the hatchling emerges, and an elongate posterior pedicle. The capsules are flanked by a lateral membrane or web on both sides, and the web is reinforced with branching or unbranching rib-like costae that extend laterally from the central body, beak, and pedicle. Specimens are typically about 10–30 cm long. Egg capsules of extant chimaeroids are made of collagen (Hamlett et al., 2005) and as fossils, chimaeroid egg capsules are typically preserved as external casts (Fischer et al., 2014).

There are two schools of thought on how to handle these fossils taxonomically. One assigns them to extant chimaeroid genera that produce morphologically similar egg capsules (Obruchev, 1967; Vozin, 1968; Stahl, 1999). However, it was pointed out that Mesozoic chimaeroid teeth are different from those of modern genera, hence, egg capsules with a morphology nearly identical to that of extant chimaeroids have apparently been produced by completely different genera (Jaekel, 1901; Fischer et al., 2014; Duffin et al., 2022). Therefore, the second school favors a parataxonomic scheme of ichnogenera and ichnospecies, already in use by the late 1800s (Meunier, 1891a) and adopted by most modern scholars (Brown, 1946; Fischer et al., 2014; Gottfried and Fordyce, 2014; Harrison et al., 2021; Duffin et al., 2022). Such a system is widely used and accepted for fossil shark egg capsules ranging as far back as the Carboniferous (Böttcher, 2010; Fischer et al., 2014; Krüger et al., 2021; Mottequin et al., 2021, 2022).

The currently used ichnogenus for chimaeroid egg capsules is *Chimaerotheca* Brown, 1946 (Brown, 1946; Gottfried and Fordyce, 2014; Harrison et al., 2021; Duffin et al., 2022). Here, we argue that *Vaillantoonia* Meunier, 1891a, being the first generic name introduced for a fossil chimaeroid egg capsule, has priority over *Chimaerotheca* and should be used instead.

The specimen reported here is from Oligocene deep-water deposits of the Lincoln Creek Formation in western Washington State, USA. Western Washington hosts a wide range of deep-water deposits of Eocene to Miocene age, which have produced a number of elasmobranch fossils (e.g., Jordan and Hannibal, 1923; Welton, 1974, 2015; Welton and Goedert, 2016; Goedert et al., 2024). This record includes egg capsules of catsharks, found at a late Eocene methane-seep deposit (Treude et al., 2011). The parataxon *Scyliorhinotheca goederti* Kiel, Peckmann, and Simon, 2013, was introduced for these fossils, which feature a mineralized capsule wall rather than being casts.

Material and methods

Specimens were measured with an analog caliper and were coated with ammonium chloride prior to photography.

Repositories and institutional abbreviations.—LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology, Los Angeles, USA. MNHN, Museum National d'Histoire Naturelle, Paris, France. NRM, Swedish Museum of Natural History, Stockholm, Sweden.

Systematic paleontology

Ichnogenus *Vaillantoonia* Meunier, 1891

1946 *Chimaerotheca* Brown, p. 262.

Type species.—*Cycadospadix virei* Meunier, 1891b, by monotypy; Upper Jurassic, Meuse, France. The holotype should be housed in the Geology collections of the MNHN in Paris (Leriche, 1914, caption of pl. 9). However, according to the records at MNHN, the specimen was loaned to Maurice Leriche ‘before the war’ and has apparently not been returned (C. Noyer, personal communication, 2024). At the time of Leriche’s (1914) publication, he was working at the Musée royal d’Histoire naturelle de Belgique (Royal Belgian Natural History Museum) in Brussels, Belgium, as well as the Université libre de Bruxelles and the University of Lille, France. But the specimen is not present in the Royal Belgian Natural History Museum (A. Folie, personal communication,

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2024), and it was neither found in the collection of the University of Lille, nor is it recorded in the database of the Lille Natural History Museum (J. Cuvelier, personal communication, 2024). Hence, the holotype must be considered lost, and Leriche's (1914, pl. 9) figure is here re-illustrated as [Figure 1.1](#).

Remarks.—*Vaillantoonia* was introduced by Meunier (1891a) after he was made aware that the Jurassic fossil he reported earlier as *Cycadospadix virei* Meunier, 1891b, was not a cycad fruit but a chimaeroid egg capsule. Thus, *Vaillantoonia* is the first generic name introduced for a fossil chimaeroid egg capsule. In his study on Jurassic chimaeroid fossils from Germany published ten years later, Jaekel (1901) overlooked Meunier's work and assigned two fossil egg capsules to the fossil chimaeroid *Aletodus ferrugineus* (Riess, 1887). The genus *Aletodus* was introduced in the same work (Jaekel, 1901, p. 548–551), but explicitly based on teeth rather than on the egg capsules. *Vaillantoonia* was subsequently mentioned by Leriche (1914), who illustrated the specimen for the first time. *Vaillantoonia* had also been listed by Jordan (1920) as a valid genus, but Brown (1946) was obviously unaware of this when he introduced *Chimaerotheca* Brown, 1946, an ichnogenus intended to encompass all fossil chimaeroid egg capsules.

Obruchev (1967, p. 571) dismissed *Vaillantoonia* using the following arguments: “The generic name *Vaillantoonia* Meunier, 1891 has priority over *Harriotta* Good et Bean, 1894 [sic], but, as a nomen dubium and nomen oblitum, based on a fossil capsule in incomplete state of preservation, should not be used instead of *Harriotta* Good et Bean, which is known from complete specimens of the fishes.” Considering that Obruchev belonged to the school that preferred assigning fossil egg capsules to extant genera, giving the name of an extant fish

priority over a fossil is understandable. However, the presently favored approach of using parataxonomic ichnogenera for such egg capsules makes a comparison to *Harriotta* Goode and Bean, 1895, irrelevant.

Obruchev's second argument (incomplete preservation) is also questionable because the holotype of *Vaillantoonia virei* (Meunier, 1891b) was actually quite complete. The specimen, as illustrated by Leriche (1914, pl. 9) and herein ([Figure 1.1](#)), is only missing the tip of the beak and part of the lateral web at the pedicle. It is thus as complete as the holotype of *Chimaerotheca wyomingana* Brown, 1946, which is the type species of *Chimaerotheca*. Subsequently, workers have followed Obruchev (1967) in regarding *Vaillantoonia* as invalid and used *Chimaerotheca* for fossil chimaeroid egg capsules (Warren, 1948; Fischer et al., 2014; Gottfried and Fordyce, 2014; Harrison et al., 2021; Duffin et al., 2022).

However, *Vaillantoonia* is the oldest generic name based on a fossil chimaeroid egg capsule, and it was used by Leriche in 1914 and Jordan in 1920. This point is critical because a necessary condition for suppressing an older name: “the senior synonym or homonym has not been used as a valid name after 1899” is not met (ICZN, 1999; Article 23.9.1.1). Hence, *Vaillantoonia* remains valid and should be used as the ichnogenus for fossil chimaeroid egg capsules instead of *Chimaerotheca*.

Vaillantoonia sp.
[Figure 1.2, 1.3](#)

Description.—The specimen is a fragment preserving a part of the central filament, and a lateral web on one side. It is approximately 52 mm long and 22 mm wide, and the central axis is 5.5 mm wide. It preserves nine bifurcating costae, with an average distance of 3 mm between them. The costae start pointing anteriorly(?) at the central axis; about 4 mm away

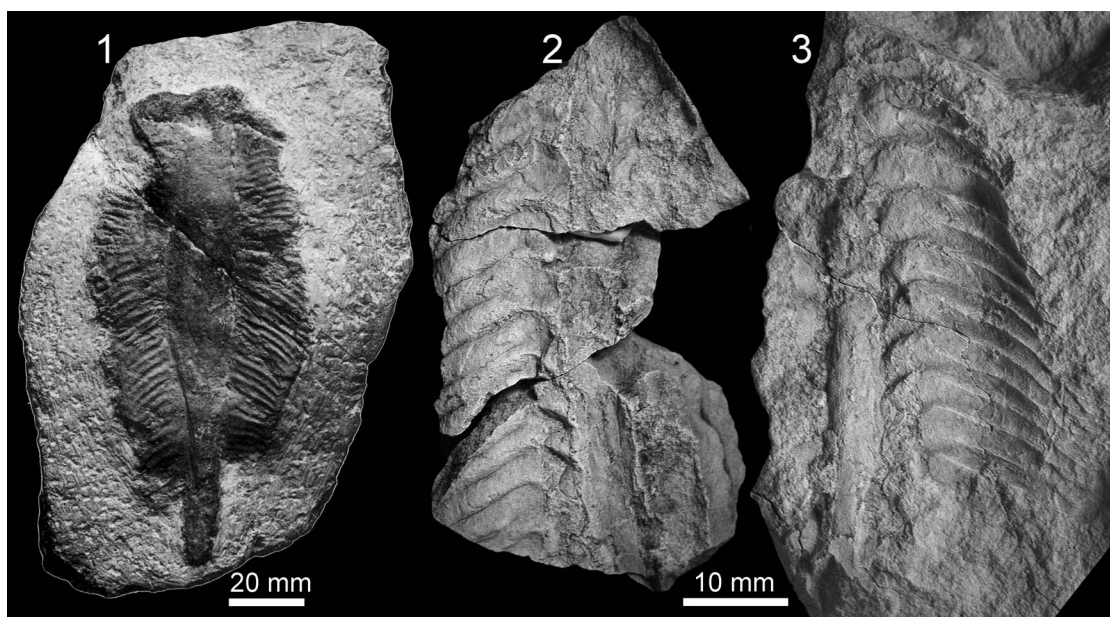


Figure 1. Fossil chimaeroid egg capsules. (1) Holotype of *Vaillantoonia virei* (Meunier, 1891b), Upper Jurassic, France (reproduced from Leriche, 1914, pl. 9). (2, 3) *Vaillantoonia* sp. from the Lincoln Creek Formation in western Washington State, USA (NRM PAL P19808), probably representing part of the pedicle and attached web.

from the axis, they bifurcate and bend posteriorward(?) at an angle of ~60–70°.

Material.—One specimen from the upper part of the Lincoln Creek Formation, found in weathered talus, north-facing roadcut in the southwest corner of Sec. 31, T.17N., R.6W., Grays Harbor County, Washington State; coordinates: 46.909866°N, 123.489352°W. The specimen is housed at the Swedish Museum of Natural History, Department of Paleobiology, under catalog number NRM PAL P19808. The only identifiable fossil associated with the egg capsule is a heterodont bivalve, possibly belonging to *Astarte*.

The locality is approximately 30 m or less stratigraphically below LACMIP loc. 17102, upper part of the Lincoln Creek Formation, possibly latest Oligocene. Squires et al. (1999) assigned LACMIP loc. 17102 to the early Miocene on the basis of overlapping age ranges of several invertebrates, including the gastropod *Turritella oregonensis* (Conrad, 1865), known from early to middle Miocene rocks of Oregon and Washington (e.g., Moore, 1963; Addicott, 1976a, b). However, *T. oregonensis* has been reported from rocks of the Clallam Formation and along with the associated molluscan fauna formed the basis of the regional Pillarian molluscan stage, previously thought to encompass most of the early Miocene (Addicott, 1976a, b; Moore and Addicott, 1987). Magnetostratigraphic work in Oregon and Washington has shown that the Pillarian might actually have been of very short duration, and entirely or mostly latest Oligocene (Prothero et al., 2001; Prothero and Burns, 2001). Deposition is thought to have occurred at depths of as much as 200 m (Squires et al., 1999); however, a concentrated zone of reworked and bivalve-bored fossiliferous concretions encrusted by bryozoans, barnacles, and serpulids at LACMIP loc. 17102 indicates an abrupt shallowing and depositional hiatus of unknown duration in this part of the Lincoln Creek Formation (Feldmann et al., 2018).

Remarks.—The missing embryo cavity makes interpretation of this fossil as being part of either the beak (anterior part of the capsule) or the pedicle (posterior part of the capsule) difficult. We interpret it as part of the pedicle because the preserved central filament shows no widening in any direction, which seems more commonly the case in the pedicle than in the beak of chimaeroid egg capsules. The apparent shortening of the costae toward the anterior (in the orientation in our figures) is likely an artifact because the lateral ends of the costae are not preserved in the more anterior costae.

Vaillantoonia sp. is most similar to the Late Cretaceous *V. newmexicana* (Brown, 1946), whose costae are also somewhat bent and point posteriorly after the bend. The only other Cenozoic chimaeroid ichnospecies, the Oligocene *V. alaskana* (Brown, 1946) from the Katalla Formation in Alaska, differs by having more densely spaced costae that hardly bend. Ichnospecies with similar bifurcating costae include *V. stelcki* (Warren, 1948) from the Upper Jurassic of Alberta, Canada, *V. schernfeldensis* (Duffin et al., 2022) from the Upper Jurassic of southwestern Germany, and *V. gilli* Hay, 1929 from the Upper Cretaceous of Wyoming and Colorado, USA (Hay, 1929; Harrison et al., 2021).

A more complete specimen with the same morphological features as *Vaillantoonia* sp. from Washington was found in

the early Oligocene part of the Keasey Formation in Oregon. It is curated in the Condon Fossil Collection (University of Oregon) as no. 42802, from locality no. 3951. Unfortunately, this specimen was not available to us for study.

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Declaration of competing interests

The authors declare no competing interests.

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