TWO CHIMAEROID EGG CASE REMAINS FROM THE LATE CRETACEOUS, MESA VERDE NATIONAL PARK, COLORADO, USA

G. WILLIAM M. HARRISON IV[1], JAMES I KIRKLAND[2], JAN FISCHER[3], GEORGE SAN MIGUEL[4], JOHN R. WOOD[5] and VINCENT L. SANTUCCI[6]

[1]Mesa Verde National Park, 3788 Ault Park Ave., Cincinnati, OH 45208; -email: g.william.m.harrison@gmail.com;
[2]Utah Geological Survey, 1594 W. North Temple, Salt Lake City, UT 84114; -email: jameskirkland@utah.gov;
[3]Urweltmuseum GEOSKOP, Burg Lichtenberg (Pfalz), Burgstraße 19, 66871 Thallichtenberg, Germany; -email: j.fischerl@yahoo.de;
[4]Mesa Verde National Park, PO Box 8, Mesa Verde, CO 81330; -email: George_san_miguel@nps.gov;
[5]National Park Service, Geologic Resources Division, 12795 W. Alameda Parkway, Lakewood, CO 80228; -email: john_wood@partner.nps.gov
[6]National Park Service, Geologic Resources Division, 1849 "C" Street, Washington, D.C. 20240; -email: vincent_santucci@nps.gov;

Abstract—In 2015, two fossil chimaeroid egg cases preserved as external molds were identified from the coastal facies of the middle Campanian (Late Cretaceous) Cliff House Sandstone at the top of the Mesaverde Group in Mesa Verde National Park, Colorado. The more complete specimen was unearthed earlier that year, while a fragmentary specimen containing only the tail was discovered in the repository and re-identified. Both specimens are most similar to a specimen collected in 1905 from the Lower Campanian Eagle Sandstone of the Mesaverde Group in Wyoming and described as *Elasmodus*? *gilli* Hay, 1929. Due to their characteristics, shapes and sizes, the new finds are assigned to the fossil egg case ichogenus and taxon *Chimaerotheca gilli* (Hay, 1929), expanding our knowledge of the chondrichthyan fauna of the Late Cretaceous Western Interior Seaway. The distinct corresponding producer is still unknown.

INTRODUCTION

While holocephalan chondrichthyans were extremely diverse and abundant during the Paleozoic (e.g., Stahl, 1999; Grogan et al., 2012; Coates et al., 2017), their extant representatives of the order Chimaeriformes comprise only ~ 4 % (54 species) within the living chondrichthyan fishes (Pollerspöck & Straube, 2019). The extant species are exclusively oviparous (egg-laying), producing characteristic protective egg cases (Fischer, 2018). The fossil record of holocephalans dates back to the Middle Devonian (Darras et al., 2008). Nevertheless, it is mostly based on isolated tooth plates and hyper-mineralized components (Stahl, 1999). Articulated remains are rare, and fossil chimaeroid egg cases are even rarer. So far, 11 distinguishable species have been described from Late Triassic to Oligocene marine strata of Eurasia, North America and New Zealand (e.g., Brown, 1946; Obruchev, 1967; Fischer et al., 2014; Gottfried and Fordyce, 2014; Fischer, 2018).

Here, we report on two chimaeroid egg case specimens from the Late Cretaceous (middle Campanian) Cliff House Sandstone in Mesa Verde National Park, Colorado. They are assigned to the ichnogenus *Chimaerotheca* Brown, 1946, belonging to an ichnospecies already collected over 100 years ago from the lower Campanian Eagle Sandstone of the Mesaverde Group in Wyoming (Gill, 1905). This work expands on a preliminary account of the Mesa Verde specimens by Harrison et al. (2016).

CHIMAEROID EGG CASE TERMINOLOGY, MORPHOLOGY AND NOMENCLATURE ISSUES

The descriptive terminology of the chimaeroid egg case morphology used here (Fig. 1) is made in accordance with the terminology used for other fossil chondrichthyan egg cases (Fischer et al., 2010, 2011, 2014) to assure consistent description. Chimaeroid egg cases are leathery, bilaterally symmetrical protective structures for the fertilized, yolky eggs composed of multilamellar collagen (Fischer, 2018). The up to 270 mm long cases are spindle-shaped, with a clear three-fold division consisting of a bulbous, ovoid central body (*trunk*) tapering gradually at the anterior end into a truncate beak (*snout*) and, at the posterior end, into a long and slender pedicle (*tail*) (Fig. 1). The anterior site is the hatching site (Fischer et al., 2014). The overall shape of the case perfectly corresponds with the spindle shape of the accommodated embryo (Dean, 1906). The lateral edges of the case are accompanied by a wing-like, lateral membrane (*web*) that tapers toward each end of the case. Its surface is conspicuously ornamented by multiply-branched or unbranched ribs (*costae*). Differences in shape and ratios of the egg case parts, the width of the web, as well as the number and shape of the ribs are diagnostic of each of the three living families: Callorhinchidae (plownose chimaeras or elephantfish), Rhinochimaeridae (longnose chimaeras or spookfish), and Chimaeridae (shortnose chimaeras or ratfish) (Fischer, 2018).

Although all currently known fossil chimaeroid egg case specimens show clear accordance with extant callorhinchid or rhinochimaerid egg case types (Fig. 1; Obruchev, 1967, Stahl, 1999), distinct corresponding producers are unknown because they are isolated finds. Therefore, the classification of these fossils is parataxonomic, consisting of form groups because of their ambiguous orthotaxonomic position (Pruvost, 1930; Fischer & Kogan, 2008), as with fossil elasmobranch egg case types (e.g., *Palaeoxyris, Fayolia, Rajitheca, Scyliorhinotheca*). For that reason, Brown (1946) erected the ichnogenus *Chimaerotheca* to contain the whole variety of chimaeroid-type egg cases independent of their overall shape and relative proportions of body, beak, pedicle and membrane. In contrast, Obruchev (1966, 1967) attempted to assign the available fossils to extant genera to sustain the connection between taxonomy and phylogeny. According to this classification method, *Chimaerotheca* would be a subjective synonym of Brown's type species *Rhinochimaera gilli.* Obruchev's approach was subsequently applied by Stahl (1999). Although tempting in its execution, we follow Brown (1946), referring to the specimens as *Chimaerotheca* for practical reasons and future reference until the attribution of these fossils to distinct producers is unambiguously clarified.

GEOLOGIC SETTING AND LOCALITY

Mesa Verde National Park is located in Montezuma County, which is in the southwest corner of Colorado (Fig. 2A). The rocks exposed at the park span the Turonian to the Campanian (Griffiths, 1990) and were mostly deposited in the Western

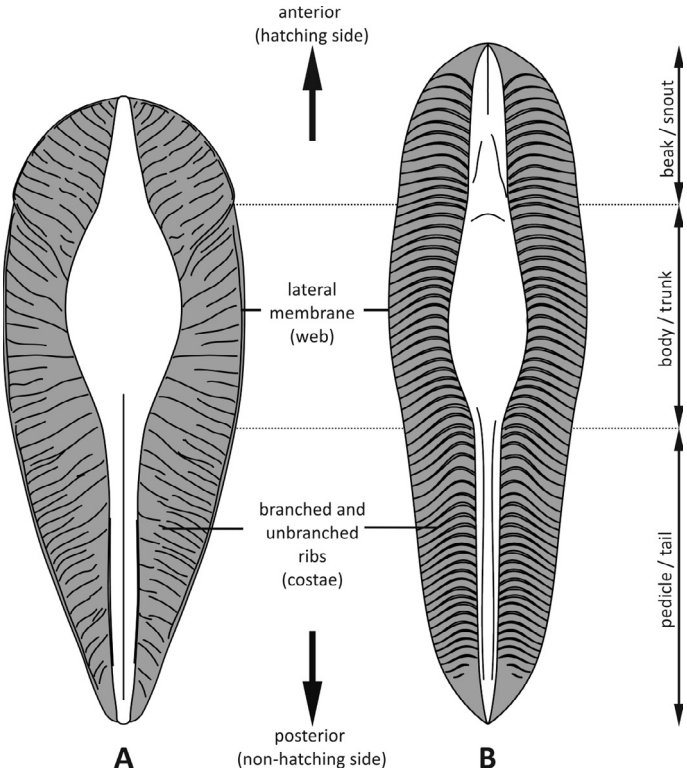

FIGURE 1. Descriptive terminology of callorinchid (**A**) and rhinochimaerid (**B**) egg case morphology used in the text according to Dean (1906), Brown (1946), and Fischer et al. (2014); egg cases are not scaled (diagrammatic drawing by Frederik Spindler).

Interior Seaway (Fig. 3). The base layer is the Mancos Shale (Fig. 2B), which was deposited in an offshore setting. Above it is the regressive Point Lookout Sandstone, which formed as the Cretaceous Inland Sea retreated. At the peak of the regression, the Mesa Verde area became a terrestrial environment (Griffiths, 1990), depositing the swampy Menefee Formation. Finally, the sea re-advanced, creating the transgressive Cliff House Sandstone (Fig. 2B). All rocks above the Mancos Shale formed in the Campanian (Carrara, 2014). Both chimaeroid egg cases were found in the fossiliferous Cliff House Sandstone (Fig. 2), known to contain ammonites, fish, shark, and mosasaur teeth, and fish and mosasaur bones. This points to a shallow marine, most likely marginal marine setting for the Mesa Verde area during the time when these egg cases were laid (Fig 3). Extant chimaeroid species commonly use shallow environments and/or bays for spawning, supporting this interpretation (e.g., Stahl, 1999; Boisvert et al., 2015). Leckie (1998) suggested on the basis of foraminiferal analyses that the Mesa Verde are was shallower than the surrounding sea.

MATERIALS AND METHODS

Both fossil egg cases were discovered separately, and not in close association, during an internship in 2015 by the senior author (Harrison et al., 2016). The most complete specimen (MEVE 10335) was found as a piece of debris on a talus slope at the base of the Cliff House Sandstone cliff in Soda Canyon, while the fragmentary specimen, which never received a catalog number, was found on the top of a mesa formed from Cliff House Sandstone on Moccasin Mesa, approximately 15 km away from the Soda Canyon site (Fig. 2A). They are preserved as positive impressions on fine to very fine-grained sandstone. Both specimens are housed at the Mesa Verde National Park's repository.

Three-dimentional digital models were created for each of the specimens using photogrammetric techniques (cf. Falkingham et al., 2018). Images for the models were obtained using a Nikon D800 digital single-lens reflex camera fitted with a Nikkor 24mm f1/4 lens. Photography was completed using a set of matched LED (the MEVE specimens) or incandescent studio lights (USNM 5994), with the camera mounted on a tripod. Each specimen was positioned on a rotating pedestal, and was thusly photographed in a circular pattern. The functionality of the camera was set to aperture priority with the focal distance and ISO manually selected and locked down. Scaling in the imagery was provided by a set of calibrated control sticks (error ±0.05 mm) placed adjacent and level with each specimen; the controls use a non-coded but machine-readable marker that allowed for automated identification within the images by the photogrammetry processing software. The image sets for each of the fossils were processed to 3D models using AGISoft PhotoScan Professional; the images for the two specimens at Mesa Verde National Park were processed using 1.5.1 and the specimen USNM 5994 version 1.3.4. Photoscan was used for photograph alignment, sparse point-cloud creation and refinement, and creation of the 3D dense cloud and colored surface model data.

Institutional Abbreviations– MEVE = Mesa Verde National Park, Colorado, USA; NMKBR = National Museum of the Kabardino-Balkarian Republic, Nalchik, Russia; USNM = United States National Museum, Washington, D.C., USA

SYSTEMATIC PALEONTOLOGY

Ichnogenus: *Chimaerotheca* – Brown, 1946
Ichnospecies: *Chimaerotheca gilli* – Hay, 1929
Figs. 4-5

1905 chimaeroid ovicapsule – Gill, p. 601.
1910 chimaeroid egg case – Darton et al., p. 10.
1909 *Elasmodus*? – Dean, p. 267, plate XXXVII.
1912 chimaeroid egg case – Hussakof, p. 224.
1929 *Elasmodus*? *gilli* – Hay, p. 615.
1932 *Chimaeridae* (*Elasmodus*?) *gilli* – Kubacska, p. 55, plate VI no. 1.
1946 *Chimaerotheca wyomingana* – Brown, p. 263, plate 38 no 8.
1961 *Chimaerotheca gilli* – Estes, p. 1087.
1966 *Rhinochimaera gilli* – Obruchev, p. 121.
1967 *Rhinochimaera gilli* – Obruchev, p. 571.
1968 *Rhinochimaera wyomingana* – Vozin, p. 70.
1999 *Rhinochimaera gilli* – Stahl, p. 150, fig. 159b.
2016 *Chimaerotheca gilli* – Harrison et al., p. 149, Fig. 4.

Revised Diagnosis

Elliptical and spindle-shaped chimaeroid egg case of *Rhinochimaera* type of about 200 mm length and 70 mm width (with membrane) in complete state, with c. 60 unbranched ribs per side. Membrane outline is altogether oblong. The shape of the body is champagne glass-like with a slight constriction behind the end of the body section to a broad beak that equals the body in length. The body width is the same as the width of a lateral membrane. The long and narrow tail is slightly less in length than that of the body and beak combined. The numerous narrow tapering ribs on the lateral membrane are generally perpendicular anteriorly but distinctly bend backwards posteriorly on the web.

Description

Chimaerotheca from MEVE comprises two compressed specimens, one nearly complete (MEVE 1035) (Fig. 4A, B) and the other fragmentary (MEVE Fragment) (Fig. 4C). The most complete specimen is 204 mm long and 72 mm at its widest point. The fusiform body section is 64 mm long and shows a maximum width of 26 mm. With a length of 54 mm and a width of 9 mm most anteriorly, the beak is almost as long as

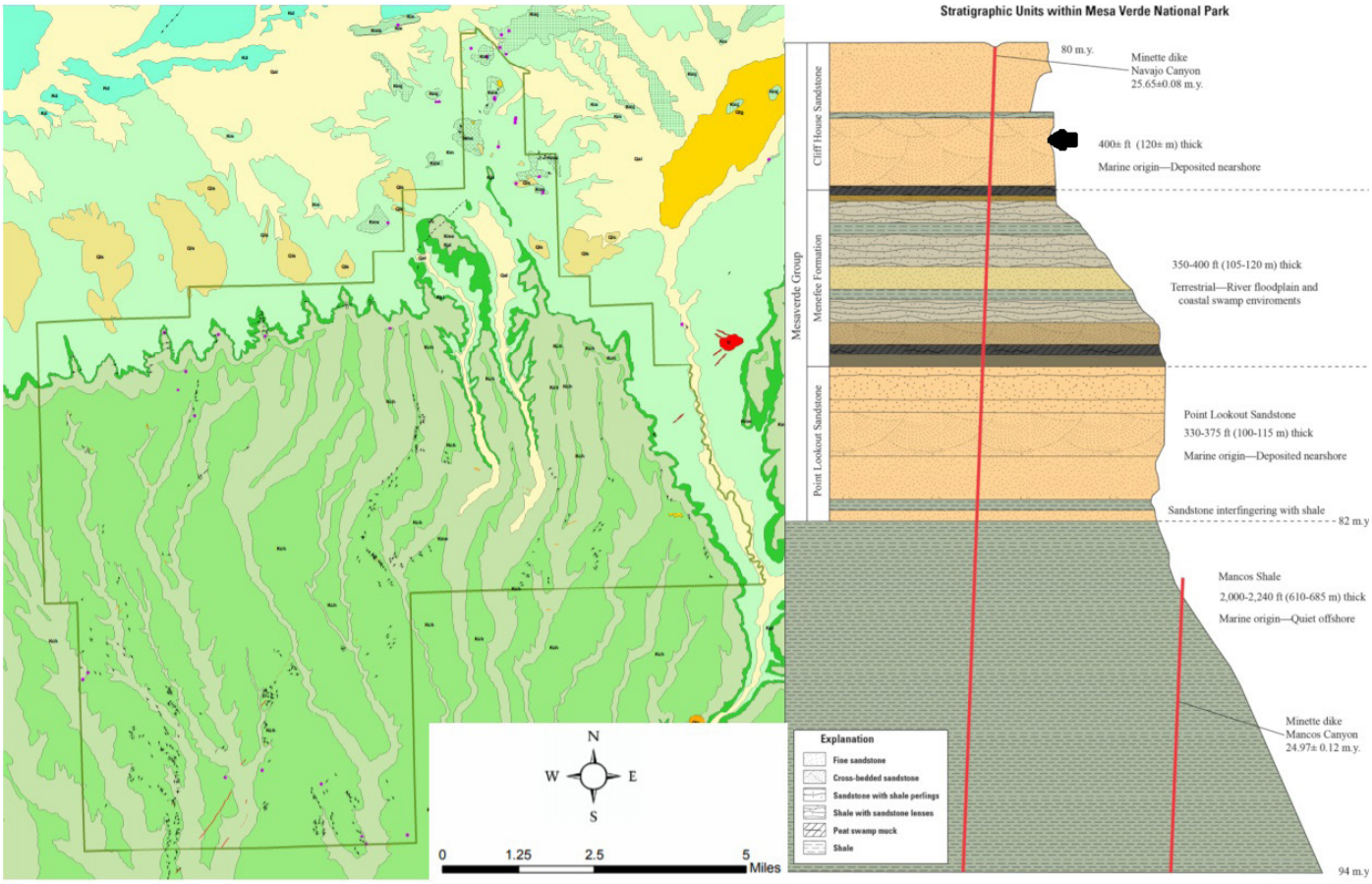

FIGURE 2. **A**, Map of Mesa Verde National Park. **B**, Stratigraphic section of Cretaceous formations with an arrow showing the level from which the fossil chimaeroid egg cases were discovered (modified from Griffiths, 1990).

the body. The long and slender pedicle measures 86 mm in length and 6 mm in width. Originally, it probably had about the same dimension as body and beak combined. The lateral membrane is preserved on both sides of the body. The width of the membrane is 26 mm at maximum, which is the same as the width of the body. It is covered with 58 narrow, unbranched ribs. While thicker at the anterior margin close to the central body (3 mm), they taper posteriorly (1.3 mm) where they become bended backwards. Superficially, it appears that the posterior margin forms a distinctly curved outline. This is the result of preservation since the most posterior part of the membrane is mostly not or weakly preserved. However, remnants of the left anterior end, as well as right from the body, show that the outer margin was originally more or less straight, not tracing the shape of the fusiform egg case.

The fragmentary specimen (Fig. 4C) represents a part from the pedicle with accompanying ribbed membrane. Twenty-two unbranched ribs are preserved. The preserved pedicle has a length of 68 mm and a width of 6 mm. While the left part of the membrane is just fragmentary (17.5 mm wide at maximum), the right side shows the ribbing pattern up to the outer margin (32 mm at its widest). An apparent tapering of the outer margin towards the original end of the pedicle; however, is the result of exposure from the covering sandstone. The specimen was originally misidentified as a leaf, much like the early fossil elasmobranch egg case specimens (e.g. Crookall, 1932; Fischer & Kogan, 2008).

DISCUSSION

Due to shape and membrane characteristics, the Mesa Verde specimens unequivocally belong to the fossil holocephalian egg case morphotype *Chimaerotheca* Brown, 1946. Moreover, the numerous tapering and transversely backward bended ribs on the membrane, its straight outer margin, and the altogether spindle-shaped egg case with oblong body and broad beak section underline its resemblance with extant rhinochimaerid egg cases (Fig. 1B). Known fossil *Chimaerotheca* species of *Rhinochimaera* type are *C. newmexicana* Brown, 1946, *C. gilli* Hay, 1929, *C. caucasica* Obruchev, 1966, *C. arenicola* Vozin, 1968, and a so far unnamed species *C.* sp. Reichenbach-Klinke & Frickhinger, 1986. The MEVE finds are distinguished from the unnamed *C.* sp. by its smaller size < 300 mm, and from *C. arenicola* by the shape of the pedicle and the branching pattern of the ribs. *Chimaerotheca newmexicana* is different from the MEVE specimens by a much broader beak and a much larger width. *Chimaerotheca caucasia* differs by its slightly broader beak and pedicle as well as the more ribbed membrane. Most similarities exists with *C. gilli*, especially regarding pedicle and beak measurements, membrane size, and ribbing pattern. Differences in size are based on a more fragmentary preservation status of *C. gilli* that is based on a single specimen. Differences in the overall shape of the body seem to be the result of preservation. Other differences in the MEVE specimens are not sufficient to erect a new species but seem to reflect intraspecies variations. Therefore, the MEVE specimens are proposed to be homotaxial to *C. gilli* based on the available material. Moreover, MEVE 1035 is proposed as a epitype for *C. gilli* with better preservation in critical areas.

CONCLUSIONS

Altogether, *Chimaerotheca gilli* resembles in shape, size, and ribbing pattern egg cases of the modern-day Pacific spookfish (*Rhinochimaera pacifica*) (Dean, 1906, p. 38) and the straightnose rabbitfish (*Rhinochimaera atlantica*) (Chembian,

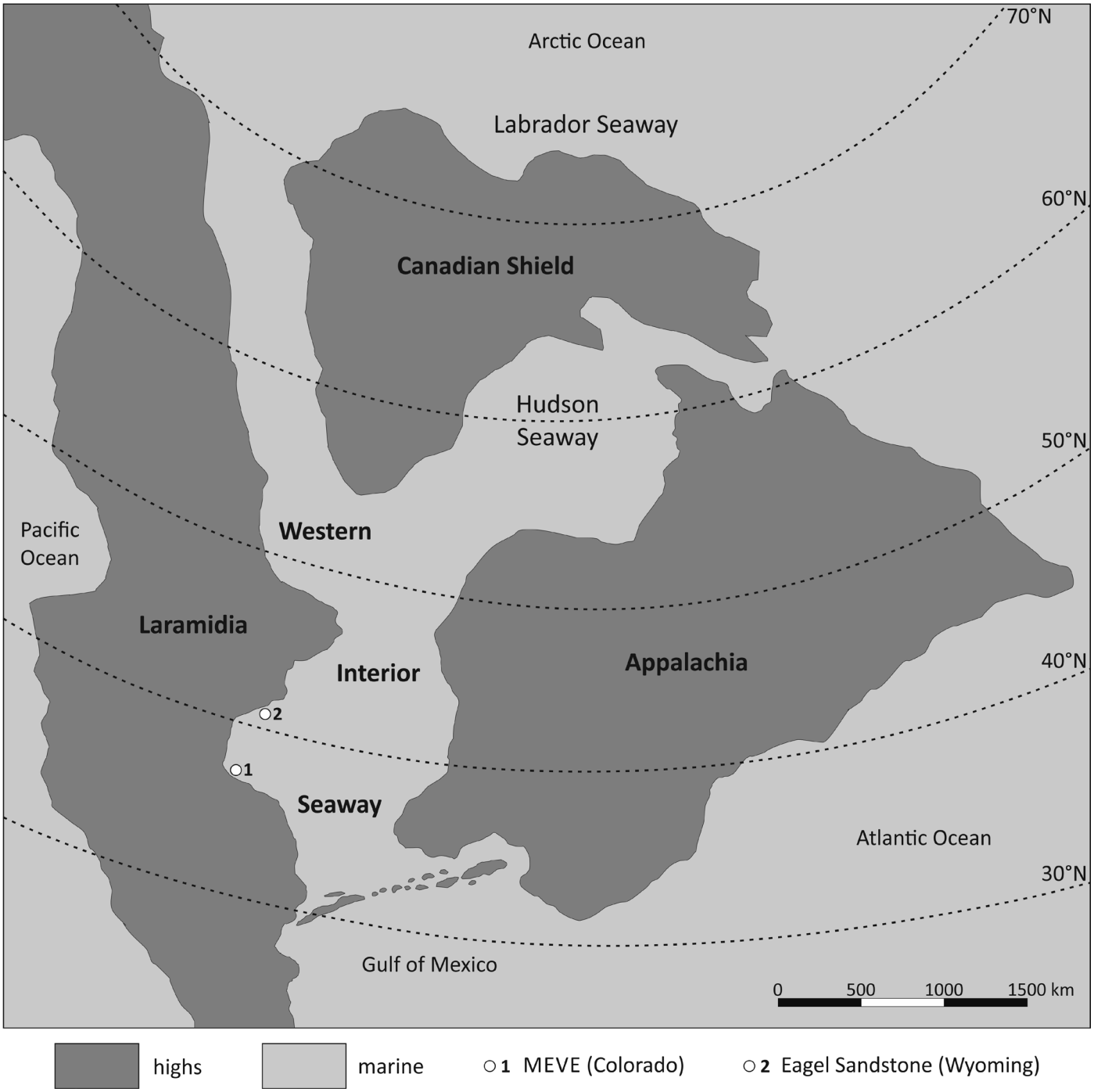

FIGURE 3. General paleogeographic map of North America during the Late Cretaceous (modified from Everhart, 2017). The general position of the find sites of the MEVE specimens (1) and the Gill (1905) specimen (2) at the western margin of the Western Interior Seaway are marked with a circle.

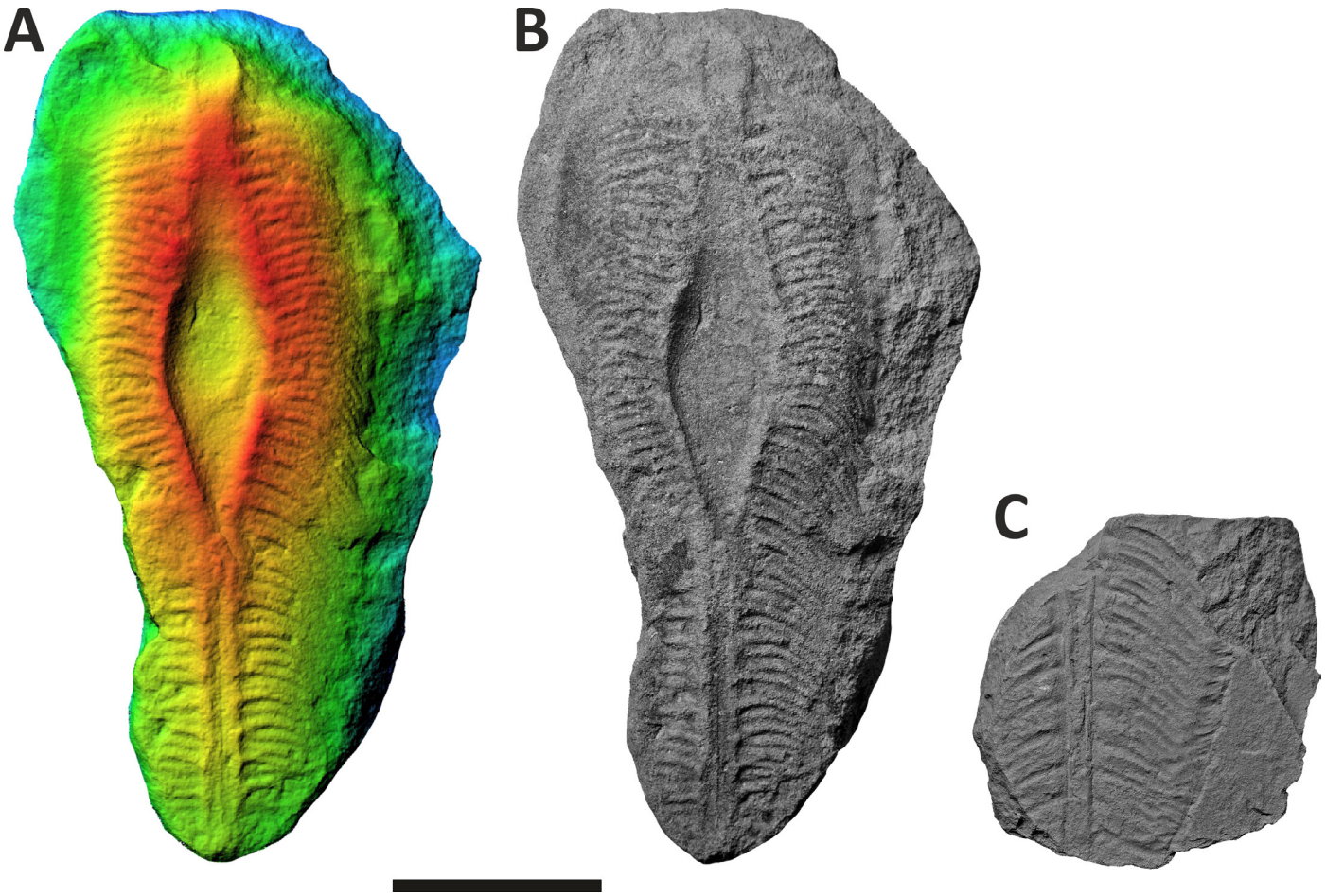

FIGURE 4. Photographs of the chimaeroid egg case *Chimaerotheca gilli* from the middle Campanian Cliff House Sandstone at the top of the Mesaverde Group in Mesa Verde National Park, Colorado. **A,** Nearly complete specimen (MEVE 1035) as photogrammetric picture; **B**, As normal photo; **C**, Fragmentary specimen (MEVE Fragment). Scale bar equals 50 mm.

TABLE 1. Table of measurements comparing the holotype of *Chimaerotheca gilli* (USNM 5994) with the Mesa Verde specimens (MEVE 1035 and MEVE Fragment). Components that are incomplete are noted with an "*".

Egg Case Dimensions	*Chimaerotheca gilli* (USNM 5994)	*Chimaerotheca gilli* (MEVE 1035)	*Chimaerotheca gilli* (MEVE Fragment)
Overall Length	145mm*	199mm	81mm*
Overall Width	73mm	72mm	62mm*
Membrane Width	26mm	26mm	32mm
Body Length	60mm	54mm	N/A
Body Width	27mm	26mm	N/A
Pedicle Length	59mm*	86mm	68mm*
Pedicle Width	6.8mm	6mm	6mm
Beak Length	38mm*	54mm	N/A
Beak Width	9.5mm	9mm	N/A
Number of Ridges	49*	57*	22*
Distance Between Ridges	2.9mm	2.7mm	3mm

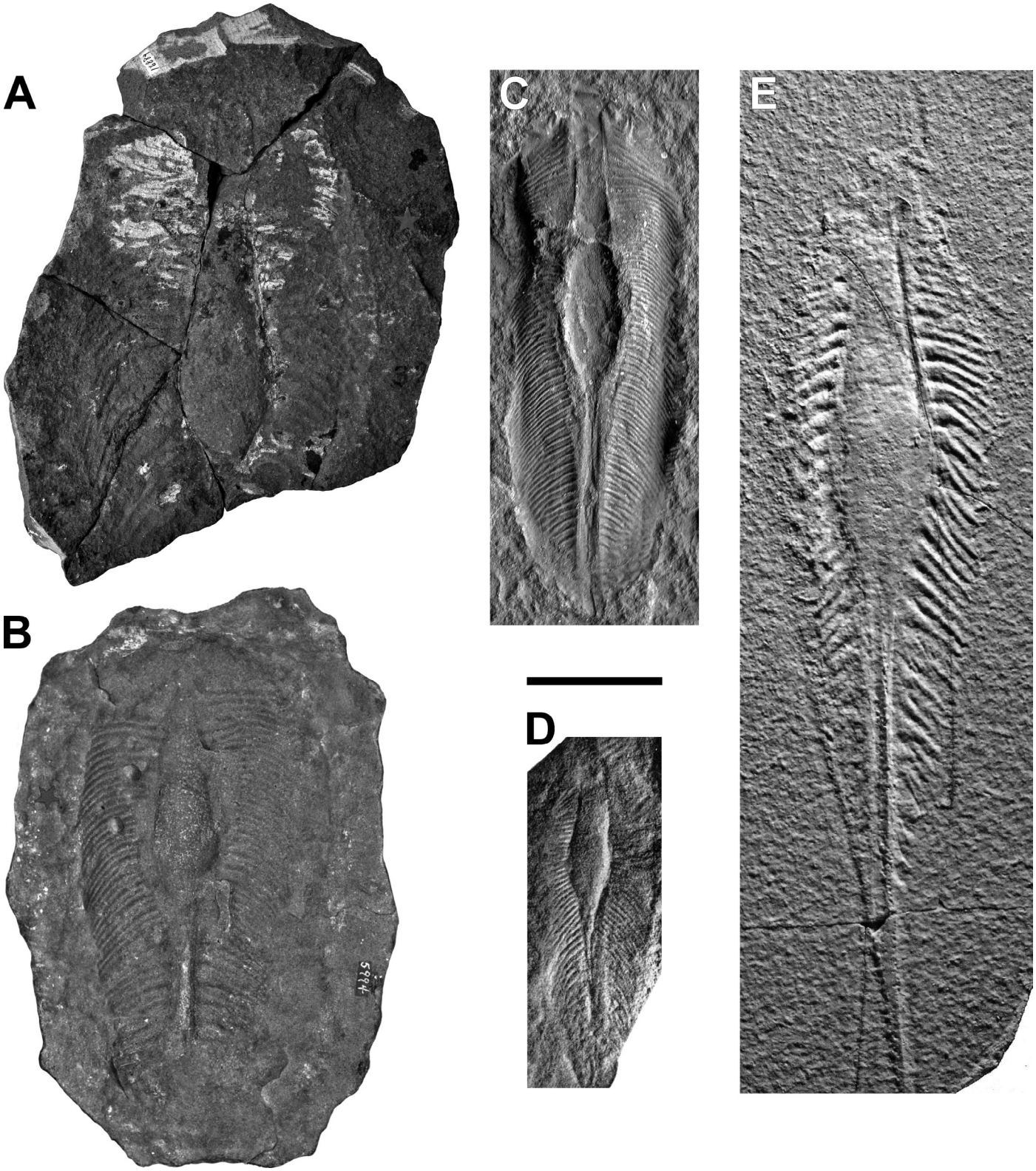

FIGURE 5. Photographs of the known fossil *Rhinochimaera* type *Chimaerotheca* egg cases. **A**, *C. newmexicana* Brown, 1946 (USNM 16889); **B**, *C. gilli* (Hay, 1929) (USNM 5994); **C**, *C. caucasica* Obruchev, 1966 (NMKBR IKP-25, counterprint of the holotype); **D**, *C. arenicola* Vozin, 1968 (92/1 from Vozin 1968, p. 74, Fig. 1); **E**, Lost specimen *C.* sp. (from Reichenbach-Klinke & Frickhinger 1986, p. 257). Scale bar equals 50 mm.

2007). These extant species congregate in large breeding aggregations in inshore spawning grounds for several weeks before they migrate back to their normal deep-water life habits. The eggs are laid in pairs directly on the flat, sandy seafloor (Didier, 2004) at a depth of 200–500m. Incubation may last between 6 to 12 months (Chembian, 2007), as in elasmobranchs (Compagno, 1990), without maternal care.

Dean (1909) remarked that modern chimaeras lay eggs roughly one fourth their size, which implies that *C. gilli* was probably laid by an approximately 80 cm long hypothetical adult holocephalian fish. This distinct corresponding producer; however, is still unknown. No chimaeroid tooth plates or other commonly found chimaeroid remains (fin spines, head claspers) are known from the Cliff House Sandstone of Mesa Verde National Park, although remains of the chimaeroid *Ischyodus bifurcatus* Case, 1978, which reached a suitable adult size, have been reported from the Late Cretaceous of Wyoming (Johnson-Ransom et al., 2018). Moreover, *Ischyodus* Egerton, 1843 belongs to the callorhinchid chimaeroids, while *C. gilli* represents characteristics of rhinochimaerid egg cases. Nevertheless, both specimens represent the only known chimaera remains from the MEVE area. Since the egg case shape is specialized in accordance with the shape of the young fish (Dean, 1906; Chembian, 2007), the fusiform body implies that the Mesa Verde hatchlings would have had a long tapered snout and streamlined build as in extant rhinochimaerids (Finucci et al., 2017).

Egg cases are a minor but significant portion of the fossil record (Fischer et al., 2014). Not only do they give valuable information about the reproductive habits of ancient animals, they can provide a record of a taxon's existence when no other specimens were found (Fischer et al., 2011; 2019). However, while it is proper to assign these charismatic egg cases to chimaeroid chondrichthyans, giving them a non ichnogenus name remains problematic due to its parataxonomic position without the unequivocal corresponding producer from the fossil record of the related strata. This is especially true of specimens such as those of *C. gilli*, which were found in an area in which no other known chimaera remains have been found to date. Therefore, egg cases are important contributions to the fossil record but must be considered with caution.

ACKNOWLEDGMENTS

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