New records of the archaic dolphin *Agorophius* (Mammalia: Cetacea) from the upper Oligocene Chandler Bridge Formation of South Carolina, USA (#26227)

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New records of the archaic dolphin *Agorophius* (Mammalia: Cetacea) from the upper Oligocene Chandler Bridge Formation of South Carolina, USA

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The stem odontocete *Agorophius pygmaeus* (Ashley Formation, lower Oligocene, South Carolina; 29.0-26.57 Ma) has been a critical point of comparison for studies of early neocete evolution owing to its early discovery as well as its transitional anatomy relative to archaeocete whales and modern odontocetes. Some time during the late nineteenth century the holotype skull went missing and has never been relocated; supplementary reference specimens have since been recently referred to the species from the Ashley Formation and the overlying Chandler Bridge Formation (upper Oligocene; 24.7-23.5). New crania referable to *Agorophius* sp. are identifiable to the genus based on several features of the intertemporal region. Furthermore, all published specimens from the Chandler Bridge Formation consistently share larger absolute size and a proportionally shorter exposure of the parietal in the skull roof than specimens from the Ashley Formation (including the holotype). Furthermore, these specimens include well-preserved ethmoid labyrinths and cribriform plates, indicating that *Agorophius* primitively retained a strong olfactory sense. These new crania suggest that at least two species of *Agorophius* are present in the Oligocene of South Carolina, revealing a somewhat more complicated taxonomic perspective.

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Abstract

The stem odontocete *Agorophius pygmaeus* (Ashley Formation, lower Oligocene, South Carolina; 29.0-26.57 Ma) has been a critical point of comparison for studies of early neocete evolution owing to its early discovery as well as its transitional anatomy relative to archaeocete whales and modern odontocetes. Some time during the late nineteenth century the holotype skull went missing and has never been relocated; supplementary reference specimens have since been recently referred to the species from the Ashley Formation and the overlying Chandler Bridge Formation (upper Oligocene; 24.7-23.5). New crania referable to *Agorophius* sp. are identifiable to the genus based on several features of the intertemporal region. Furthermore, all published specimens from the Chandler Bridge Formation consistently share larger absolute size and a proportionally shorter exposure of the parietal in the skull roof than specimens from the Ashley

Formation (including the holotype). Furthermore, these specimens include well-preserved ethmoid labyrinths and cribriform plates, indicating that *Agorophius* primitively retained a strong olfactory sense. These new crania suggest that at least two species of *Agorophius* are present in the Oligocene of South Carolina, revealing a somewhat more complicated taxonomic perspective.

Introduction

The holotype skull of *Agorophius pygmaeus* consists of a partial cranium and tooth (MCZ 8761) collected in January 1847 by F.S. Holmes (Curator, College of Charleston Museum) and L.R. Gibbes (Professor, College of Charleston) from exposures of the Ashley Formation at Greer's Landing near Middleton Place Plantation west of Charleston, South Carolina. Owing to its transitional morphology between Eocene archaeocetes and modern odontocetes, early studies often referred to *Agorophius* as a key comparative taxon (Whitmore and Sanders, 1977:308-310). Poor taxonomic practices led to the treatment of the Agorophiidae as a wastebasket taxon for many disparate early odontocete species now placed in other ~~such~~ families as the Xenorophidae, although that practice has now largely been abandoned (Whitmore and Sanders, 1977; Fordyce, 1981; Godfrey et al., 2016). The holotype originally belonged to F.S. Holmes, and after some initial study by Louis Agassiz in 1848-1850 the specimen was loaned to Joseph Leidy in 1869; by 1907, the specimen was realized to be lost (see Fordyce, 1981; Godfrey et al., 2016). In 1980 the holotype tooth was rediscovered and described by R.E. Fordyce (1981), though the skull is still missing. Fordyce (1981) published a supplementary description of the skull based on high quality illustrations.

Recently reported specimens of *Agorophius* have provided new reference specimens for the taxon as well as preserve aspects of the anatomy not represented in the now lost holotype cranium. These include ChM PV 4256, a partial skull and mandible with isolated teeth and associated postcrania from the Chandler Bridge Formation, and SC 2015.51.1, a partial skull from the Ashley Formation. The former specimen was identified and coded as *Agorophius pygmaeus* by Geisler and Sanders (2003) and figured by Godfrey et al. (2016); it remains undescribed. SC 2015.51.1 was described and referred to *Agorophius pygmaeus* by Godfrey et al. (2016). Godfrey et al. (2016) conducted a specimen-level cladistic analysis of *Agorophius*, and recovered a monophyletic *Agorophius* including these specimens and the holotype.

This study reports newly recovered specimens of *Agorophius* from the Chandler Bridge Formation include two incomplete skulls. These skulls raise questions about the identification of previously referred specimens of *Agorophius* and provide new information on ontogenetic variation and sensory anatomy in *Agorophius*.

Materials and Methods

Anatomical terminology follows Mead and Fordyce (2009) and Godfrey et al. (2013). All photographs were taken with a Canon EOS Rebel XS and 80 mm zoom lens.

Institutional Abbreviations: CCNHM, Mace Brown Museum of Natural History, College of Charleston, Charleston, South Carolina, USA; **ChM**, Charleston Museum, Charleston, South Carolina, USA; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **SC**, South Carolina State Museum, Columbia, South Carolina, USA.

Geologic Background

The new crania reported in this study (CCNHM 1921, 1922) were collected by Stephen Hildenbrandt in May 2017 from a construction site (now developed) in the Coosaw Preserve subdivision of North Charleston, Charleston County, South Carolina (Fig. 1A-B). Specimens were collected *in situ* from the Chandler Bridge Formation exposed in an excavated pond. Other specimens collected from the same pond include a possible squalodelphinid dolphin skull and skeleton (CCNHM 2115) and a partial shell of the sea turtle *Carolinachelys wilsoni* (CCNHM 1903). Sediment associated with these skeletons consists of lightly consolidated, tan, silty, fine-very fine friable sandstone, consistent with bed 2 of the Chandler Bridge Formation (Fig. 1C). Based on the lithology of this bed, its relationships to other facies, and micro- and macrofossils, Katuna et al. (1997) interpreted this bed forming in a bay or estuarine environment. At the Coosaw Preserve this bed was below the water level of the pond, thus observations of thickness, geometry, sedimentary structures, and ichnology were not possible.

The Chandler Bridge Formation is 24.7-23.5 Ma in age based on $^{87}Sr/^{86}Sr$ ratios from the same unit and from the overlying Edisto Formation reported by Weems et al. (2016; see also Boessenecker and Fordyce, 2016:456-458). The shark assemblage reported from the Chandler Bridge Formation, most likely from the basal marine facies, is suggestive of inner to middle shelf depths and temperatures ranging from 20-25 (Cicimurri and Knight, 2009). The billfish *Aglyptorhynhcus* similarly indicates middle shelf depths and temperatures of 20-24°C (Purdy et al., 2001; Fierstine and Weems, 2009). Overall deposition of the Chandler Bridge Formation reflects a regressive parasequence deposited over the Ashley Formation without a transgressive unit (Katuna et al., 1997), similar to other sequences further north on the Atlantic Coastal Plain with thin, entirely regressive parasequences are deposited under conditions of low subsidence rate (Kidwell, 1993). The unconformity between the Chandler Bridge Formation and the Ashley Formation represents approximately 2-3 million years (Weems et al., 2016). A rich assemblage of marine vertebrates is now known from the Chandler Bridge Formation including sharks, bony fish, an estuarine crocodile, freshwater and sea turtles, marine birds, cetaceans, and sirenians (Whitmore and Sanders, 1977; Sanders et al., 1982; Erickson and Sawyer, 1996; Sanders and Barnes, 2002; Cicimurri and Knight, 2009; Fierstine and Weems, 2009; Geisler et al., 2014; Weems and Knight, 2013; Weems and Sanders, 2014; Ksepka, 2014; Churchill et al., 2016; Godfrey et al., 2016; Weems and Brown, 2017).

Systematic Paleontology

Mammalia Linneaus, 1758

Cetacea Brisson, 1762

Odontoceti Flower, 1867

Agorophiidae Abel, 1914

Agorophius Cope, 1895

Agorophius sp.

Figures 2-4

Material: CCNHM 1921, partial skull including dorsal parts of parietal, supraoccipital, posterior part of frontal and incomplete right supraorbital process, partial ascending process of right maxilla, posterior tip of right premaxilla, and ethmoid; CCNHM 1922, partial skull including dorsal parts of parietal, supraoccipital, frontal, ethmoid, and a fragment of the ascending process of the right maxilla. Both specimens collected on June 19, 2017 by Steven Hildenbrandt.

Locality: Coosaw Preserve, exposure of Chandler Bridge Formation in excavated pond (now developed) on construction site, North Charleston, South Carolina, USA (Fig. 1). Detailed locality information on file at CCNHM, available on request to qualified researchers.

Age: early Late Oligocene (Chattian), dated to 24.7-23.5 based on $^{87}Sr/^{86}Sr$ ratios reported from mollusks by Weems et al. (2016).

Identification: CCNHM 1921 and 1922 preserve two features unique to *Agorophius* amongst all odontocetes with an intertemporal constriction (see diagnosis in Godfrey et al., 2016:157): 1) parietals exposed dorsally at the intertemporal constriction without a sagittal crest, and 2) region around the vertex including the frontal, parietal, ascending maxilla, and anterior occipital shield with a flat, planar margin in lateral view. A third feature is preserved only in CCNHM 1922: a deeply incised premaxillary cleft in the posterior nasal process of the premaxilla. Owing to their occurrence in a geochronologically younger stratum and an anteroposteriorly shorter exposure of parietal at the intertemporal constriction than the holotype and referred specimen SC 2015.51.1 from the Ashley Formation, these specimens are identified only to the genus level (see Discussion).

Description

Premaxilla

In CCNHM 1922, the nasal process of the premaxilla (Fig. 2A-B) is present is divided into a posterolateral plate and a posteromedial splint. Although the posterolateral plate is not preserved, its existence can be inferred from the sutural surface on the maxilla. The posteromedial splint is a narrow, vertical, and posteriorly tapering wedge between the frontal (medially) and the ascending process of the maxilla (laterally). A deeply incised premaxillary cleft is vertical, parasagittally oriented, and presumably separated the posteromedial splint (preserved) from the posterolateral plate (inferred). Part of the right nasal may be present but owing to damage it is unclear if ~~it~~ what is observed is actually the medial edge of the premaxilla. Though broken, the premaxilla transversely widens anteriorly based on the shape of the articular "buttress" for the premaxilla on the maxilla.

Maxilla

The ascending process of the maxilla is transversely expanded, dorsoventrally thin and sheet-like, and extends posteriorly to the level of the occipital shield apex (Fig. 2A-B). Medially, the ascending process of the maxilla forms a vertical plate that abuts the posteromedial splint of the premaxilla. This plate transitions anteriorly into a slightly raised platform that underlies the premaxilla adjacent to the nares. A single, large and posteriorly directed dorsal infraorbital foramina is present lateral to the posterior termination of the nasal, about 1 cm lateral to the premaxilla. A vertical fissure separates the maxilla from the premaxilla.

Frontal & Ethmoid

The median frontal suture is unfused in CCNHM 1922 and obliterated in CCNHM 1921 (Fig. 2A-B). The frontoparietal suture is transverse and W-shaped with a median point, bilateral anterior embayments, and an anterolaterally extending portion that contributes a small part to the supraorbital process. The latter part of the parietal resembles the morphology in *Ashleycetus* *planicapitis*, although in that taxon this part of the parietal expands further anterolaterally (Sanders and Geisler, 2016). Dorsally the frontal has a median, rectangular plateau outlined laterally by the premaxilla, the parietal posteriorly, and the nasals anteriorly. The frontal is anteriorly pointed with an anterolaterally facing articular surface for the nasal. In CCNHM 1921, the frontal is more acutely pointed and the rectangular median plateau is proportionally narrower. Given the higher degree of suture closure and inferred older ontogenetic stage of CCNHM 1921, this suggests that the premaxilla and maxilla grow dorsomedially, at the expense of the frontal, with age. Obviously this suggestion will be speculative until larger sample sizes are available. Dorsally, the frontal is very porous in comparison to the occipital shield and the ascending process of the maxilla.

A thin band of frontal was probably exposed posterior to the ascending process of the maxilla in CCNHM 1921, but damage to the maxilla obscures the extent. The dorsal surface of the supraorbital process of the frontal bears numerous radial, anteroposteriorly directed ridges and grooves for the ascending process of the maxilla.

The frontal forms most of the ventral surface of the compound supraorbital process (Fig. 2E-F). The posterior edge is formed by the anterolateral wing of the parietal. Posterior to the frontal groove the frontal is smooth and shallowly concave. This part bears a series of faint, radially oriented (i.e. lateral to posterolaterally directed) vascular sulci that emanate from the medial end of the orbit. The frontal groove is partially preserved in CCNHM 1921, widens from 3 mm to about 9-10 mm laterally, is deeply concave in cross-section, and oriented 35-40° from the sagittal plane.

Internally, the frontal articulates with the ethmoid and forms part of the ethmoid labyrinth (Fig. 2E-F); the ethmofrontal suture is evident dorsally, and fused internally within the olfactory nerve canal. The canal is subconical and transversely widens anteriorly; it is approximately circular in its anterior half. Posteriorly it narrows to a lensoidal, transversely constricted canal with a deeply incised dorsal fissure.

Although the cribriform plate (Fig. 2E-F) is not preserved in CCNHM 1921, a small part of the medial portion remains in CCNHM 1922 (Fig. 4). What is preserved is very porous and transversely oriented, and although damaged, it does not appear to completely bridge the canal, unlike the morphology seen in archaeocetes, extant mysticetes (Godfrey et al., 2013) and *Squalodon* (Godfrey, 2013). The ethmoturbinal recess and olfactory nerve canal are confluent via a pair of crescentic foramina – the cribriform plate is lenticular, perforate, anteroventrally facing and separated from the frontal by a deep transverse fissure. The plate bears a posteriorly directed conical projection.

The olfactory nerve canal is anteroposteriorly longer and transversely narrower in CCNHM 1921, where it is developed as a narrow fissure (Fig. 2F, 4). Longitudinal sulci are present in the anterior half of the canal. The ethmoturbinal recess has some poorly preserved turbinates, but the labyrinth and recess are small and separated by a low ridge immediately adjacent to the dorsal meatus. The preserved part of the meatus is a dorsally situated, lozenge-shaped, smooth cavity.

Ventrally, the frontal descends to terminate at large, articular surfaces for the basisphenoid; these facets are rectangular, face anteroventrally, and exhibit anteroposteriorly directed ridges and furrows forming a mortised frontal-sphenoid suture. Posterior to this in CCNHM 1921, the frontals form the anterodorsal margin of the endocranial surface with a median fissure-like opening for the olfactory nerve canal.

Parietal

Dorsally each parietal forms a triangular exposure, and medially they are connected by an anteriorly bowed, narrow band wrapping around the apex of the occipital shield (Fig. 2A-B). A distinct crease occurs between the supraoccipital and the parietal. The frontoparietal suture in CCNHM 1921 is open and anastomosing; the suture is more highly mortised and mostly closed in CCNHM 1922 (Fig. 2A-B). The parietal at the midline is pinched between the supraoccipital and frontal, and this exposure is reduced in CCNHM 1922, which we attribute to ontogenetic development of cranial telescoping.

The lateral edge of the parietal is concave in dorsal view, forming the medial margin of the temporal fossa; the anterolateral wing of the parietal extends along the posteromedial part of the compound supraorbital process of the frontal and buttresses it ventrally. The intertemporal region of the skull is dorsally flat with a nearly contiguous surface with the frontal (Fig. 3A-B). The intertemporal portions of the frontal and parietal are very cancellous in CCNHM 1922 (Fig. 2A). In CCNHM 1921, three small foramina are present on either side of the parietal (Fig. 2B), though less clearly developed in CCNHM 1922. The lateral side of the braincase is broadly concave and formed by the parietal, which posterodorsally forms the lateral part of the nuchal crest and overhangs the temporal fossa. The frontoparietal suture is sigmoidal and anterodorsally oriented in lateral view.

Supraoccipital

The occipital shield bears a triangular apex; the apex is somewhat more truncated in CCNHM 1922 than in CCNHM1921. A nuchal tuberosity is present and developed as a flat, diamondshaped plateau at the apex. The occipital shield is transversely concave, and at the midline is inclined anterodorsally at approximately 45° in CCNHM 1921 and 65° in CCNHM 1922.

Discussion

Olfactory anatomy

Several recent studies have investigated the anatomy of the ethmoid labyrinth and cribriform plate in extinct and extant cetaceans, and surprisingly found that modern mysticetes maintain a well-developed olfactory system complete with cribriform plate that differs little from archaeocete ancestors (Thewissen et al., 2011; Godfrey et al., 2013). Modern odontocetes lack such structures and as a result have probably lost their olfactory sense (Edinger, 1955; Berta et al., 2014). These anatomical changes are mirrored by molecular changes; cetaceans have a much higher proportion of olfactory receptors that are pseudogenes than many other mammals (Kishida et al., 2007; McGowen et al., 2008), and inactivation of individual genes is much more prevalent among odontocetes than in mysticetes (Springer and Gatesy, 2017). Unlike extant odontocetes, archaic Miocene odontocetes like *Squalodon* retain a cribriform plate and labyrinth (Godfrey, 2013). Obfuscating these matters somewhat is the apparent lack of a cribriform plate in xenorophids such as *Albertocetus meffordorum* and *Inermorostrum xenops* (Boessenecker et al., 2017a, 2017b). It remains unclear whether the condition in xenorophids detected thus far reflects true anatomy or postmortem taphonomic damage.

Skulls of *Agorophius* sp. reported herein shed new light on these matters, as *Agorophius* is typically recovered on the odontocete stem in an intermediate position between the basal position of xenorophids and later diverging *Squalodon* (Godfrey et al., 2016; Boessenecker et al., 2017b). Both specimens (CCNHM 1921, 1922) preserve a clear ethmoid labyrinth and an incomplete or incipient cribriform plate (Fig. 2, 4). It is unclear whether or not the cribriform plate completely or incompletely bridged the junction between the ethmoid labyrinth and olfactory canal, owing to damage. Regardless, some degree of a cribriform plate is present in *Agorophius* as well as later diverging stem odontocetes like *Squalodon* (Godfrey, 2013). Clarification regarding the condition in xenorophids is needed, as the apparent absence would imply two distinct losses of the cribriform plate, one due to lack of ossification (i.e. xenorophids) and the other due to closure of the olfactory foramina (crown Odontoceti).

Cranial variation and stratigraphic origin of *Agorophius* specimens

These newly described partial crania are incomplete but represent the first formally described specimens of *Agorophius* from the Chandler Bridge Formation. CCNHM 1921 and 1922 are identifiable as *Agorophius* but notably differ from the holotype of *Agorophius pygmaeus* and SC 2015.51.1 in exhibiting an anteroposteriorly shorter exposure of the parietal in dorsal view. In fact, in all specimens of *Agorophius* from the Chandler Bridge Formation (ChM PV4256, CCNHM 1921, CCNHM 1922), the length of the parietal at the midline is only 11.9-14.7 % of the minimum parietal breadth at the intertemporal constriction. In crania from the Ashley Formation (holotype, SC 2015.51.1), the parietal is somewhat anteroposteriorly longer and constitutes 22-46.4% of the intertemporal width (Table 1). Another feature differentiating ChM PV4256 from *Agorophius pygmaeus* is the presence of a triangular rather than parabolic or convex apex of the occipital shield (Godfrey et al., 2016: 165). A triangular apex is also present in CCNHM 1921 and 1922. Given that the holotype is from the late early Oligocene Ashley Formation (Whitmore and Sanders, 1977; Godfrey et al., 2016), these consistent differences raise the possibility that specimens from the late Oligocene Chandler Bridge Formation (including ChM PV 4256) represent a geochronologically younger and as-yet undescribed species of *Agorophius*. For the time being, CCNHM 1921, CCNHM 1922, and ChM PV4256 are considered conspecific and identified as *Agorophius* sp., pending further study.

Ontogenetic trends are apparent within Chandler Bridge *Agorophius* sp. CCNHM 1922 and ChM PV4256 both possess open median frontal sutures and clear frontoparietal sutures; both are mostly or totally closed in CCNHM 1921. CCNHM 1922 and ChM PV 4256 likely represent similar ontogenetic stages, though neither are juveniles owing to their large size (~84-87% intertemporal width of CCNHM 1921; Fig. 3D, 4). Thus, we tentatively identify these specimens as subadults and CCNHM 1921 as an adult. If correct, then ontogenetic trends within this species include a steeper occipital shield, an anteroposteriorly longer median dorsal exposure of the frontal, an anteroposteriorly longer olfactory nerve canal, and blunted apex of an otherwise triangular occipital shield apex in CCNHM 1921. Curiously, the ratio of the anteroposterior length to transverse width of the parietal appears stable (anteroposterior length equals 6.25-8.34% of transverse width) throughout this crude growth series (CCNHM 1921, 1922, ChM PV 4256), suggesting minimal change in parietal exposure during postnatal ontogeny.

Further questions arise regarding the size of reported *Agorophius* crania. A smaller cranium from the Ashley Formation, ChM PV 5852, was tentatively considered to belong to *Agorophius* by Geisler and Sanders (2003) and identified as *Agorophius* sp. by Deméré et al. (2005). In fact, Geisler and Sanders (2016) recovered a sister-group relationship between ChM PV4256, which all studies agree can be referred to *Agorophius* (Geisler and Sanders, 2003; Godfrey et al., 2016), and ChM PV5852 in some of their phylogenetic analyses. Godfrey et al. (2016) considered this specimen as Odontoceti indet. because they recovered it as the sister taxon of *Simocetus rayi*. Although those authors did not report support values, the same relationship was also recovered by Lambert et al. (2017), and the branch support for this relationship was low. Thus we consider the generic attribution of ChM PV5852 a question that requires further investigation.

This cranium of ChM PV5852 measures 186.8 mm in bizygomatic width, slightly smaller than SC 2015.51.1 (206 mm) and the holotype of *Agorophius pygmaeus* (approximately 190 mm). ChM PV 5852, SC 2015.51.1, and the holotype cranium are all much smaller than ChM PV 4256 (248 mm). Newly referred crania CCNHM 1921 and 1922 lack squamosals but are similar to ChM PV4256 in intertemporal width. Whereas the holotype specimen exhibits a number of open and incipiently fused cranial sutures indicating immaturity, ChM PV 5852 does not and has a greater degree of suture closure than one of the skulls reported here (CCNHM 1921), suggesting the presence of a large and small morphotype of *Agorophius* (if ChM PV5852 is a species of *Agorophius*) If correct, then SC 2015.51.1 and ChM PV 5852 represent a small morph and ChM PV 4256, CCNHM 1921, and CCNHM 1922 all represent a much larger morph. However, owing to fact that the holotype is immature and smaller than adults of each morphotype, it is unclear which, if any, of these morphotypes represents *Agorophius pygmaeus*. Formal description of ChM PV 5852 and recently discovered *Agorophius*-like crania from the Ashley Formation is required to resolve these questions.

Conclusions

New specimens of *Agorophius* include two fragmentary crania preserving the intertemporal region and 'vertex' and constitute the first formally described remains of this odontocete from the Chandler Bridge Formation. These specimens share with *Agorophius* *pygmaeus* an intertemporal constriction, pointed occipital shield, and a flattened frontal-occipital 'table' in lateral view. The broken nature of these specimens reveals that *Agorophius* had a cribriform plate and large ethmoturbinal recess, suggesting a well-developed olfactory sense. The larger size and proportionally shorter exposure of parietal at the midline suggests that there are in fact two species of *Agorophius*, which differ in size. A better understanding of cranial ontogeny is needed to determine how these two species relate to the holotype of the genus, which is almost certainly an immature individual.

Acknowledgements

First and foremost we thank S. Hildenbrandt for collecting the cetacean specimens reported within, and M. Brown for donating the specimens to CCNHM. This study benefited from discussions with B.L. Beatty, S.J. Boessenecker, M. Churchill, M. Gibson, and A.E. Sanders. Thanks to S. Boessenecker (CCNHM) and M. Gibson and J. Peragine (ChM) for access to specimens under their care. Thanks to X anonymous reviewers and the editor [name] for critical comments which improved the quality of this paper.

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Figures

Figure 1. Geographic and geologic context of *Agorophius* sp. specimens in South Carolina (A). Generalized geologic map of Oligocene strata in the Charleston area with star indicating the locality that produced CCNHM 1921 and 1922 (B), map modified from Weems and Lewis (2002) and Boessenecker et al. (2017a); (C) idealized stratigraphic section of the Chandler Bridge Formation, with silhouette indicating bed that produced the new specimens, modified from Katuna et al. (1997).

Figure 2. Skulls of *Agorophius* sp. (CCNHM 1921, 1922) from the Chandler Bridge Formation (A-E); CCNHM 1922 in dorsal view (A); CCNHM 1921 in dorsal view (B); line drawings of CCNHM 1922 and 1921 in dorsal view (C, D); CCNHM 1922 in ventral view (E); CCNHM 1921 in ventral view. Abbreviations: fr, frontal; m, maxilla; n, nasal; p, parietal; px, premaxilla; so, supraoccipital.

Figure 3. Skulls of *Agorophius* sp. in lateral view; CCNHM 1922 (A), and CCNHM 1921 (B); size comparison of *Agorophius* spp. Crania in dorsal view (C); scatterplot of parietal width and parietal length at the midline, in millimeters (D). Closed circles denote specimens from the Ashley Formation and open circles denote specimens from the Chandler Bridge Formation.

Figure 4. Skull of *Agorophius* sp. (CCNHM 1922) in anterior view.

Table 1(on next page)

Measurements of the intertemporal constriction of *Agorophius*.

Table 1. Measurements of the intertemporal constriction of *Agorophius*.

Specimen	Minimum Parietal width (mm)	Anteroposterior length of Parietal at midline (mm)	Parietal width/parietal length
MCZ 8761	49.5	23	46.46%
SC 2015.51.1	54	11.9	22.04%
ChM PV 4256	72	4.5	6.25%
ChM PV 5852	66.1	10.5	15.89%
CCNHM 1921	74.5	6.2	8.32%
CCNHM 1922	85.1	7.1	8.34%

Figure 1

Geographic and geologic context of *Agorophius* sp. specimens in South Carolina (A)

Generalized geologic map of Oligocene strata in the Charleston area with star indicating the locality that produced CCNHM 1921 and 1922 (B), map modified from Weems and Lewis (2002); (C) idealized stratigraphic section of the Chandler Bridge Formation, with silhouette indicating bed that produced the new specimens, modified from Katuna et al. (1997).

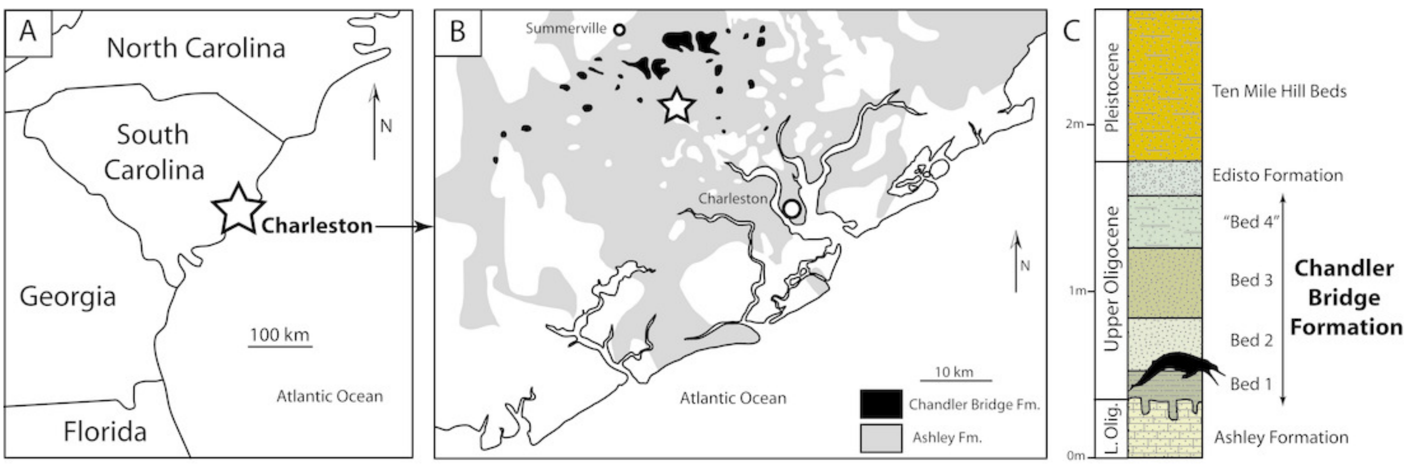

Figure 2

Skulls of *Agorophius* sp. (CCNHM 1921, 1922) from the Chandler Bridge Formation (A-E;

CCNHM 1922 in dorsal view (A); CCNHM 1921 in dorsal view (B); line drawings of CCNHM 1922 and 1921 in dorsal view (C, D); CCNHM 1922 in ventral view (E); CCNHM 1921 in ventral view. Abbreviations: fr, frontal; m, maxilla; n, nasal; p, parietal; px, premaxilla; so, supraoccipital.

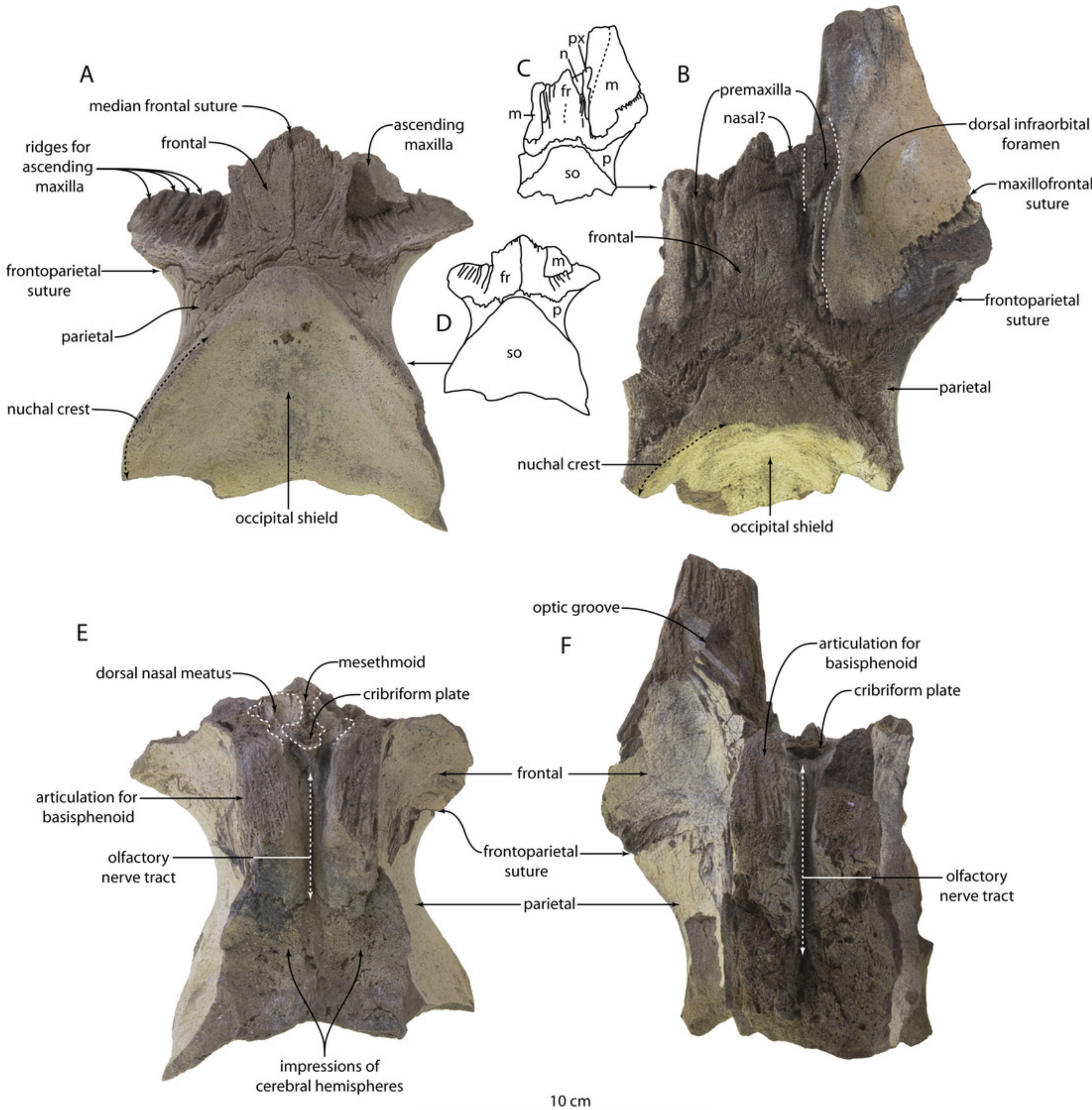
A
median frontal suture
frontal
ascending maxilla
ridges for ascending maxilla
frontoparietal suture
parietal
nuchal crest
occipital shield
C
px
n
fr
m
so
p
B
premaxilla
nasal?
dorsal infraorbital foramen
maxillofrontal suture
frontal
frontoparietal suture
parietal
nuchal crest
occipital shield
D
fr
m
p
so
E
dorsal nasal meatus
mesethmoid
cribriform plate
articulation for basisphenoid
olfactory nerve tract
impressions of cerebral hemispheres
F
optic groove
articulation for basisphenoid
cribriform plate
frontal
frontoparietal suture
parietal
olfactory nerve tract
10 cm

Figure 3

Figure 3. Skulls of *Agorophius* sp. in lateral view;

CCNHM 1922 (A), and CCNHM 1921 (B); size comparison of *Agorophius* spp. Crania in dorsal view (C); scatterplot of parietal width and parietal length at the midline, in millimeters (D). Closed circles denote specimens from the Ashley Formation and open circles denote specimens from the Chandler Bridge Formation.

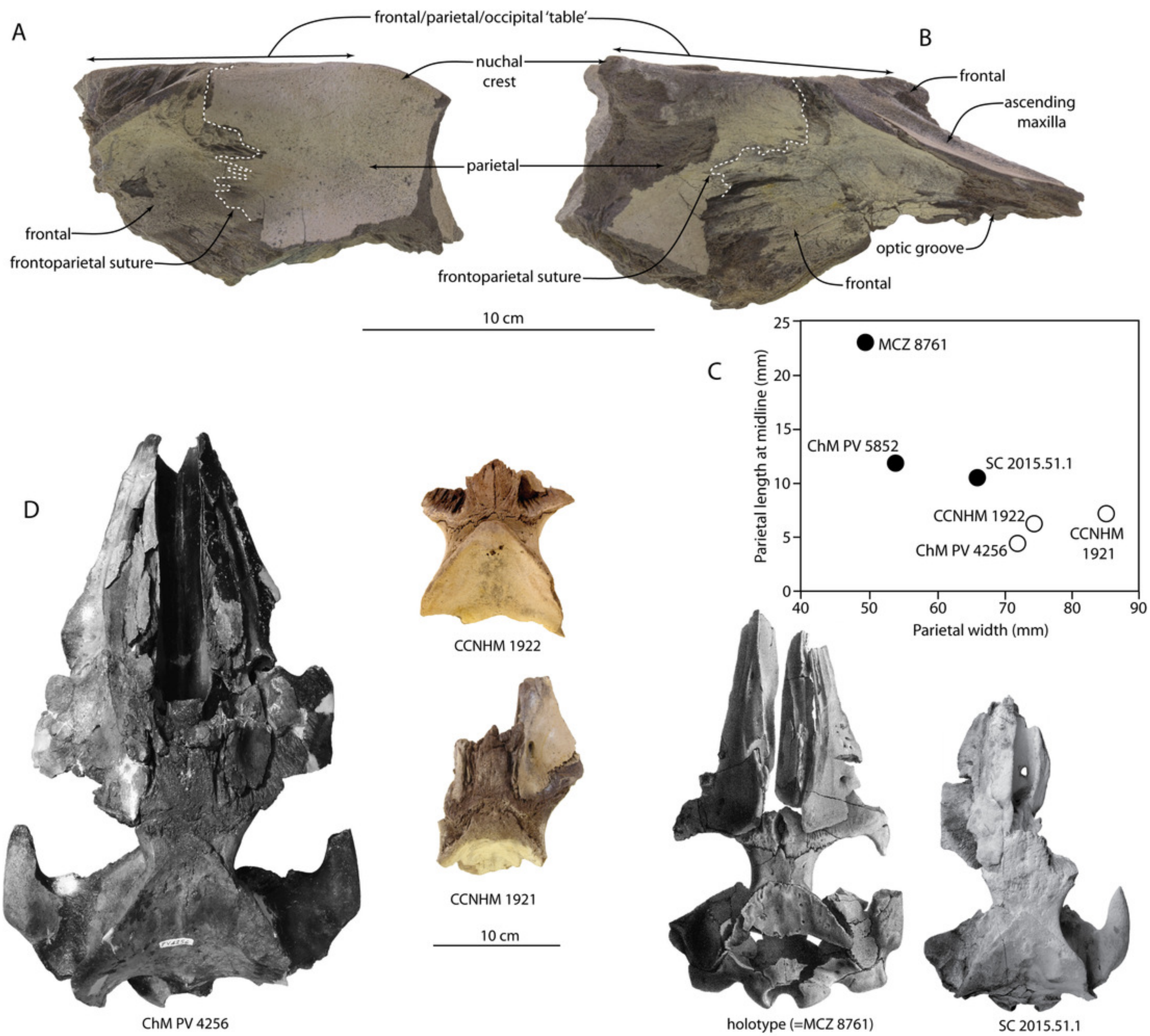

Figure 4

Skull of *Agorophius* sp. (CCNHM 1922) in anterior view.