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TAXONOMY OF THE PLEISTOCENE GIANT BEAVER *CASTOROIDES* (RODENTIA: CASTORIDAE) FROM THE SOUTHEASTERN UNITED STATES

Richard C. Hulbert Jr. [1], Andreas Kerner[2], and Gary S. Morgan[3]

ABSTRACT

Two late Pleistocene skulls of *Castoroides* from Florida share a suite of morphologic features with two partial skulls from the early Pleistocene of Florida (including the holotype of *Castoroides leiseyorum* Morgan and White, 1995) and a late Pleistocene skull from South Carolina. These specimens are regarded as conspecific and can be readily distinguished from skulls of *Castoroides ohioensis* Foster, 1838 from the northeastern and midwestern United States by a number of characters including absence of a mesopterygoid fossa, shorter sagittal crest, lambdoidal crest strongly inflected anteriorly at midline of skull, larger postorbital process and incisive foramen, cheektooth rows less divergent posteriorly and located more anteriorly (relative to maxillary process of zygomatic arch), and a more massive premaxilla without an anterior protuberance. All Florida samples of *Castoroides* are now regarded as belonging to a single species that is not *Castoroides ohioensis*. The rule of nomenclatural priority requires raising *Castoroides ohioensis dilophidus* Martin, 1969 to the rank of species, *Castoroides dilophidus*, and regarding it as the senior synonym of *Castoroides leiseyorum* Morgan and White, 1995. The dental character which formed the basis for the subspecies name *dilophidus* is only known to occur in some late Pleistocene teeth from peninsular Florida and coastal Georgia, and is not present in all populations of the species *C. dilophidus*.

Key words: *Castoroides dilophidus*; Rodentia; Pleistocene; synonymy; taxonomy; Florida.

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INTRODUCTION

Along with the capybara *Neochoerus*, the giant beaver *Castoroides* is one of two large-sized rodents that is a member of the extinct Pleistocene megafauna of North America, with a mass currently estimated to have been about 60 to 100 kg (Reynolds, 2002; Hopkins, 2008). Historically, the genus was best represented by fossils from the northeastern and north-central United States (e.g., Wyman, 1846; Moore, 1890; Martin, 1912; Hay, 1914; Barbour, 1931; Engels, 1931; Erickson, 1962; Stirton, 1965), while its overall distribution ranged from southern Canada to Alabama and Florida in the east, to Oregon, the Yukon Territory, and Alaska in the west (Cahn, 1932; Kurtén and Anderson, 1980; Parmalee and Graham, 2002; Harington, 2011). Although several species were named in the nineteenth and very early twentieth centuries, through most of the twentieth century the general consensus was that the genus was monotypic, with *Castoroides ohioensis* Foster, 1838 as the valid species name (Hay, 1914, 1923; Stirton, 1965; Kurtén and Anderson, 1980; Martin, 1992).

In contrast to the skulls, mandibles, and two skeletons known from the northern part of its range, records of *Castoroides* from the southeastern United States long consisted of only isolated teeth and postcranial bones (Hay, 1923; Martin, 1969, 1975). Nevertheless, these specimens were routinely assigned to *Castoroides ohioensis*. Martin (1969) observed that some of the upper third molars (M3s) and most of the lower fourth premolars (p4s) of *Castoroides* from the Santa Fe River Basin in northern peninsular Florida had a split or divided loph/lophid, and used this character to diagnose the subspecies *Castoroides ohioensis dilophidus*. This subspecies name has been little used subsequently in the scientific literature. Morgan and White (1995) described the first crania of *Castoroides* from the Southeast, two early Pleistocene specimens from Leisey Shell Pit 1 in central Florida (Site 3 in Fig. 1). On the basis of several characters, most notably the lack of the distinctive mesopterygoid fossa that is present in *C. ohioensis* (Wyman, 1846; Stirton, 1965), Morgan and White (1995) proposed that the Leisey specimens belonged to a distinct species that they named *Castoroides leiseyorum*. Because of the older age of *C. leiseyorum* (early Pleistocene) relative to all then known skulls of *C. ohioensis* (middle or late Pleistocene), and because the features of *C. leiseyorum* appeared to be plesiomorphic relative to those of *C. ohioensis*, the assumption was that the differences between the two was primarily due to their different ages, not their geographic distributions. Thus, after the description of *C. leiseyorum*, late Pleistocene specimens of *Castoroides* from Florida continued to be referred to *C. ohioensis* and not *C. leiseyorum* (e.g., Hulbert, 2001; Schubert et al., 2010).

Parmalee and Graham (2002) were the first to describe a skull of *Castoroides* of late Pleistocene age from the southeastern United States; a specimen from the Cooper River, South Carolina. This specimen unexpectedly had the cranial features of *Castoroides leiseyorum* instead of *C. ohioensis*, which created a number of possible taxonomic options. As discussed by Parmalee and Graham (2002), these included: 1) a single, variable species, with northern and southeastern populations possibly distinguished as subspecies; and 2) two species, one in the southeast and one for the remainder of its range. Not discussed by Parmalee and Graham (2002) is a three-species option, with a widespread early Pleistocene species (i.e., *C. leiseyorum*) and two late Pleistocene species, one for southeastern North America and one for northern, midwestern, and western North America. Parmalee and Graham (2002) chose not select among these options, due to the absence of late Pleistocene skulls from Florida and lack of a link between crania with the features of *C. leiseyorum* and teeth with the features of C. *ohioensis dilophidus*. They recognized that the two species-level names based on Florida specimens of *Castoroides* might prove to be synonyms, with Martin's name having priority.

We report here two late Pleistocene crania of *Castoroides* from Florida, the first such specimens to be described, and discuss their taxonomic ramifications. We also analyze a much larger sample of teeth from Florida than were available to Martin (1969), to better determine the range

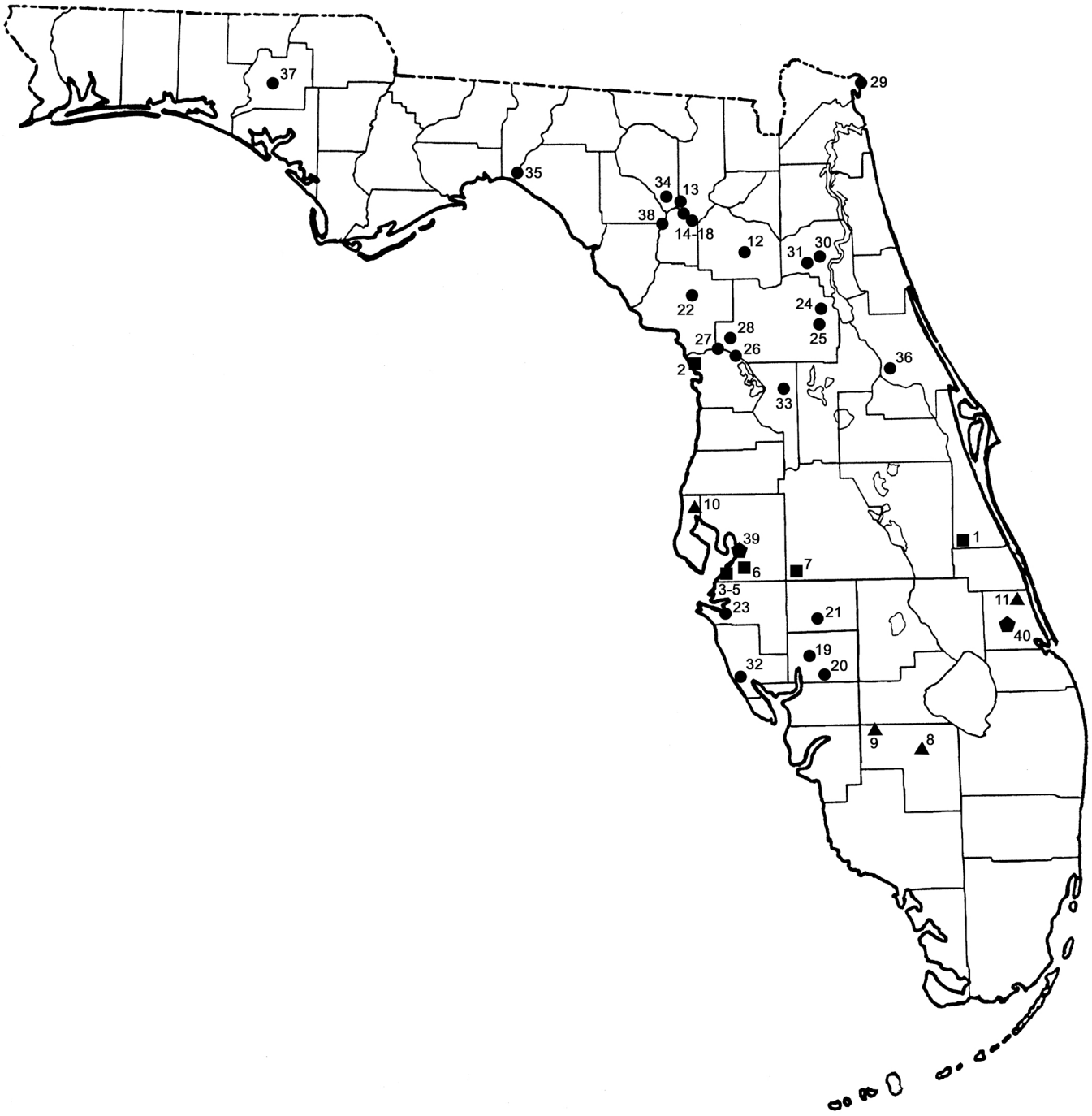

Figure 1. Locations of fossil sites in Florida containing specimens of *Castoroides dilophidus*. Numbers correspond to those in the Appendix, which lists each site's name and referred specimens. Squares are early Pleistocene localities; triangles, middle Pleistocene; circles, late Pleistocene; and pentagons, undifferentiated Pleistocene.

of variation in the dental characters he used to diagnose *Castoroides ohioensis dilophidus* and their geographic and chronologic distributions. All currently known fossil localities in Florida with *Castoroides* are indicated in Figure 1 and listed in the Appendix..

MATERIALS AND METHODS

Dental terminology and measurements follow Woodburne (1961); terminology for cranial features follows Stirton (1965). Standard dental abbreviations are used (i, lower incisor; I, upper incisor; m, lower molar; M, upper molar; p, lower premolar; P, upper premolar; following numeral indicates tooth position). All measurements in mm. Chronologic boundaries for the Pleistocene Epoch follow Gibbard et al. (2010).

Of the two skulls of *Castoroides* that form the primary basis for this report, one was collected by scuba divers from submerged deposits in Lake Rousseau, a dammed reservoir of the Withlacoochee River in north-central Florida (Site 27 in Fig. 1). Fossils recovered from Lake Rousseau were previously discussed by Schubert et al. (2010), and include many of the common late Pleistocene mammals found in Florida, such as *Holmesina septentrionalis*, *Tapirus veroensis*, and *Palaeolama mirifica*. No taxa characteristic of the early or middle Pleistocene (late Blancan or Irvingtonian) have been found in Lake Rousseau. The second new cranium of *Castoroides* was collected in the lower Aucilla River in northern Florida (Site 35 in Fig. 1), a region with numerous latest Pleistocene deposits with abundant vertebrate fossils (Mihlbachler et al., 2002; Webb and Simons, 2006). As was the case with Lake Rousseau, no early or middle Pleistocene fossils are known from this region. The Aucilla River skull is housed in a private collection, but a high fidelity cast is in the UF collection. Furthermore, the owner of the original specimen has agreed to make it available for study to other workers (contact RCH to make arrangements).

The cranial morphology of *Castoroides ohioensis* has been thoroughly described by Wyman (1846), Martin (1912), Hay (1914), and especially Stirton (1965). Their observations were confirmed through direct examination of a very well preserved specimen from Indiana, USNM 1634.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York; **SC**, South Carolina State Museum, Columbia; **MMNS**, Mississippi Museum of Natural Science, Jackson; **UF**, Vertebrate Paleontology Division, Florida Museum of Natural History, University of Florida, Gainesville; **UF/FGS**, Florida Geological Survey collection, now housed at UF; **UF/TRO**, Timberlane Research Organization collection, now housed at UF; **USNM**, United States National Museum, Smithsonian Institution, Washington, DC.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA BOWDICH, 1821
Family CASTORIDAE HEMPRICH, 1820
Subfamily CASTOROIDINAE ALLEN, 1877
Genus *CASTOROIDES* FOSTER, 1838
CASTOROIDES DILOPHIDUS MARTIN, 1969 new rank

Castoroides ohioensis dilophidus Martin (1969); Martin (1975).

Castoroides leiseyorum Morgan and White (1995); Hulbert Jr. (2001); Parmalee and Graham (2002); Hopkins (2008); Rinaldi et al. (2008); Samuels (2009); Rinaldi et al. (2012).

Castoroides ohioensis Foster, Hulbert Jr. (2001), in part; Schubert et al. (2010), in part.

Holotype.—UF 12404, a left p4 (Fig. 2A).

Type Locality.—Santa Fe River 2, on the Columbia-Alachua county boundary, north-central Florida, approximately 29.8° N; 82.7° W (Site 15 in Fig. 1). Fossils from Santa Fe River 2 are predominantly late Pleistocene (Rancholabrean) taxa, with a small percentage of early Pleistocene (late Blancan) taxa. In this it differs from other stretches on the Santa Fe River, such as Santa Fe River 1, where Blancan mammals are abundant. A late Pleistocene age is inferred for UF 12404 (and all other Santa Fe River specimens of *Castoroides*) not only because of the rarity of Blancan specimens along Santa Fe River 2, but also because none of the many purely late Blancan sites in Florida

have produced a single specimen of *Castoroides* (Morgan and Hulbert, 1995; Hulbert, 2010). Also, two specimens of *Castoroides* from the Santa Fe River were analyzed for rare earth isotopes (REE) as part of the study by MacFadden and Hulbert (2009) and they both had relative abundances of REEs matching late Pleistocene species (e.g., *Megalonyx jeffersoni*, *Bison* sp., *Mammuthus columbi*), and significantly different from Blancan taxa.

Chronologic and Geographic Range.—The species is known from the early Pleistocene (early Irvingtonian) to late Pleistocene (late Rancholabrean) of Florida and the late Pleistocene of coastal South Carolina. Records from geographically intermediate coastal Georgia are assumed to represent *Castoroides dilophidus*, but crania to confirm this are lacking (one p4 with a divided second lophid is known from this region, supporting referral to this species). *Castoroides dilophidus* may have been more widespread in the southeastern United States, but crania or lower p4s are needed to distinguish it from *Castoroides ohioensis*, so records from intervening regions such as Tennessee, Mississippi, and Arkansas cannot be confidently referred to a species at this time. Supposed very early Pleistocene (late Blancan) records listed by Martin (1969) are actually late Pleistocene (Morgan and White, 1995).

Referred Specimens.—UF 81736, braincase, Leisey Shell Pit 1A, Hillsborough Co., FL (holotype, *Castoroides leiseyorum*); UF 60868, braincase, Leisey Shell Pit 1, Hillsborough Co., FL; UF 256059, braincase, Lake Rousseau, Marion Co., FL; UF 258638, nearly complete skull with broken portions of right and left incisors, Aucilla River 1, Taylor Co., FL. (cast); SC75.33.1, nearly complete skull with incisors (missing cheekteeth), Cooper River, Charleston Co., SC. Additional specimens listed in Appendix.

Revised diagnosis.—Member of *Castoroides* that differs from *Castoroides ohioensis* in having shorter sagittal crest; lambdoidal crest strongly inflected anteriorly at midline of skull; better developed postorbital process; cheektooth rows less divergent posteriorly and located more anteriorly (relative to maxillary process of zygomatic arch); larger incisive foramen; and more massive premaxilla with greater distance between the alveoli for incisors and the external nares. Also differs from *C. ohioensis* in lacking mesopterygoid fossa in basisphenoid and pronounced medial protuberance on the premaxilla ventral to external nares.

Description and comparison of new Florida skulls.—Morgan and White (1995) and Parmalee and Graham (2002) previously described crania of *Castoroides leiseyorum* (= *Castoroides dilophidus* herein). Many aspects of the cranial and dental morphology of *Castoroides dilophidus* and *Castoroides ohioensis* are the same, so these features will not be emphasized here. Differences in the development of the internal choane between the two species were noted by Rinaldi et al. (2012), and will presumably be described in detail by those authors in a future work. The two new Florida crania of *Castoroides*, along with the two Leisey braincases, are smaller than average specimens of *C. ohioensis* and the Cooper River skull from South Carolina (Table 1). Some of this can be attributed to the relatively young age of UF 81736 and 256059, based on open sutures between the major bones of the two skulls, but the other specimens have closed sutures and had apparently reached their final adult size. The two sagittal crests have completely fused to form a single ridge only in UF 60868, while the others have paired sagittal crests, suggesting they were not fully mature. But the much larger South Carolina skull also has paired sagittal crests, so the difference in size between specimens from peninsular Florida and more northern regions appears to be real.

Viewed anteriorly, the external bone surface of the premaxillae of *Castoroides dilophidus* is extremely rugose (Fig. 3). Despite this, in lateral view the anterior surface of the premaxilla overall is relatively flat (Fig. 4), without the prominent, anteriorly protruding medial process found just ventral to the external nares on the premaxillae of *Castoroides ohioensis* (Engels, 1931:fig. 3; Stirton, 1965:fig. 1). The height of the premaxilla between the external nares and the anterior border of the

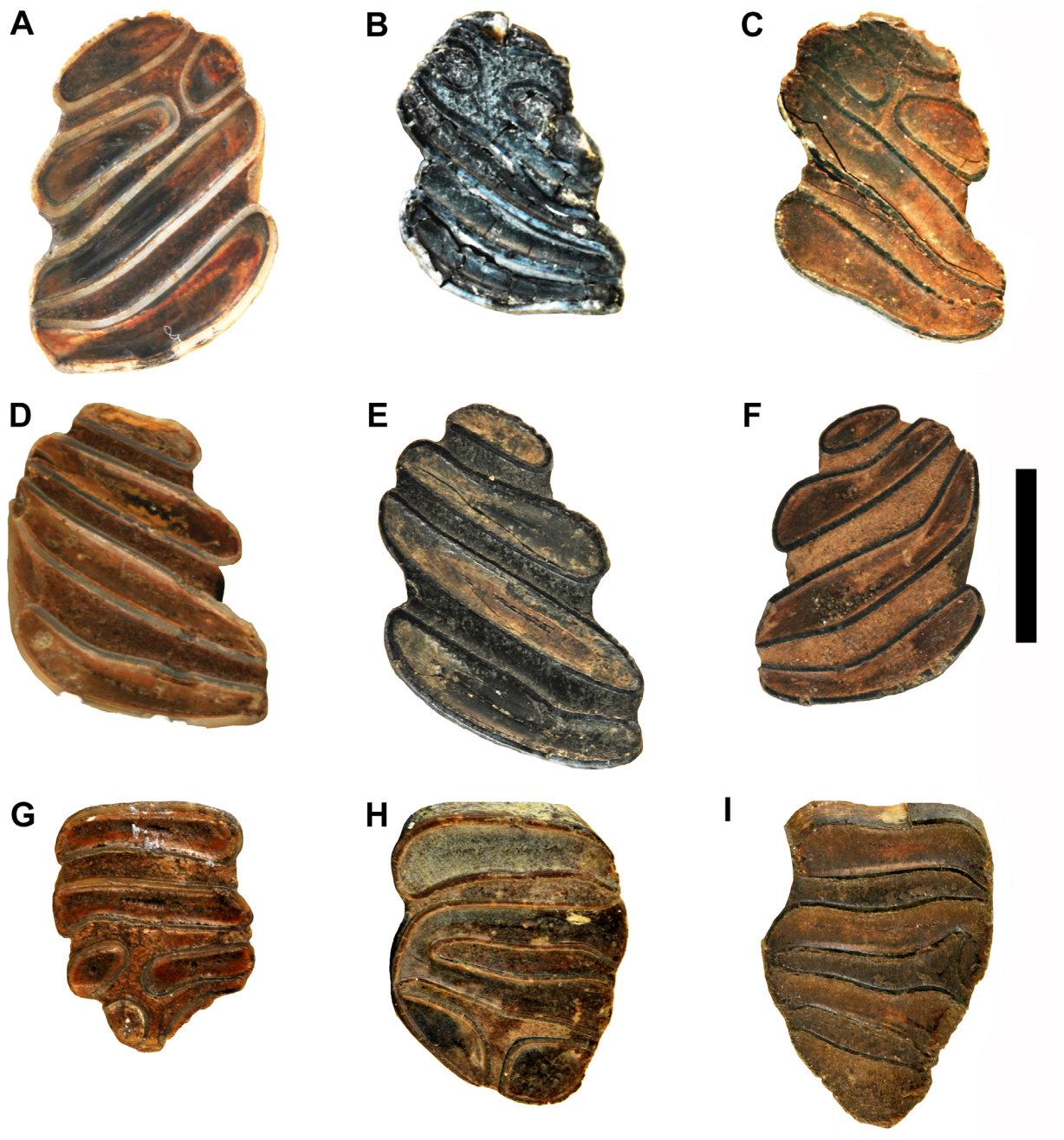

Figure 2. Cheekteeth of *Castoroides dilophidus* from the Pleistocene of Florida in occlusal view, anterior to top of page in all images. **A**, UF 12404, right p4, Santa Fe River 2, holotype. **B**, UF 261933, left p4, Withlacoochee River, **C**, UF/TRO 5, left p4, Waccasassa River. **D**, UF 166637, left p4, Santa Fe River 1. **E**, UF 261934, left p4, Lake Rousseau. **F**, UF 217396, right p4, Sun City Shell Pit. **G**, UF 12405, left M3, Santa Fe River 2. **H**, UF/TRO 4, right M3, Peace River. **I**, UF/TRO 9, right M3, Waccasassa River. Teeth in A–C and G–H have the anomalous 'dilophid' enamel pattern; others show the normal *Castoroides* pattern. Scale bar is 1 cm.

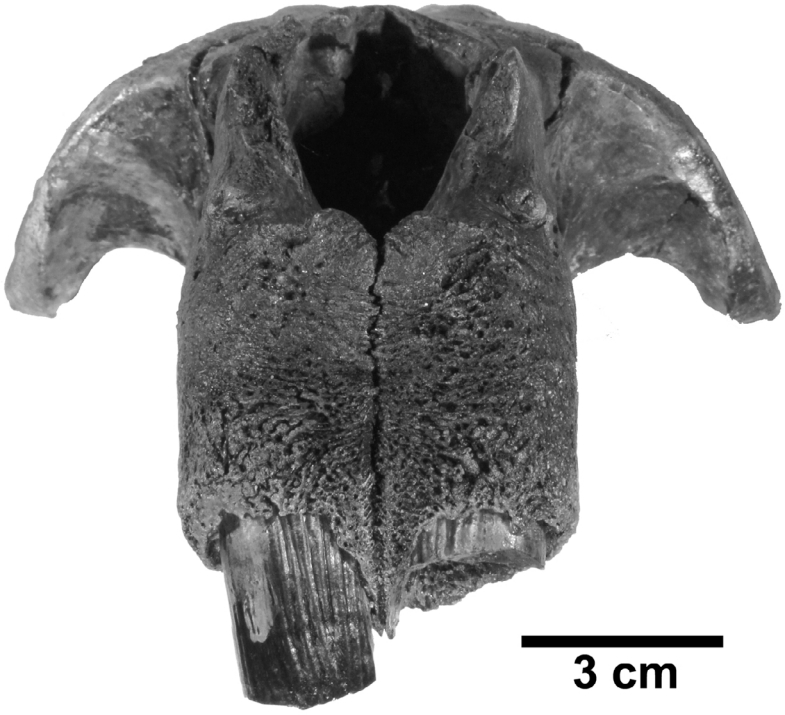

Figure 3. Anterior view of UF 258638, skull of *Castoroides dilophidus* from the late Pleistocene of Florida, showing very rugose, tall premaxillae.

Figure 4. Right lateral view of UF 258638, skull of *Castoroides dilophidus* from the late Pleistocene of Florida.

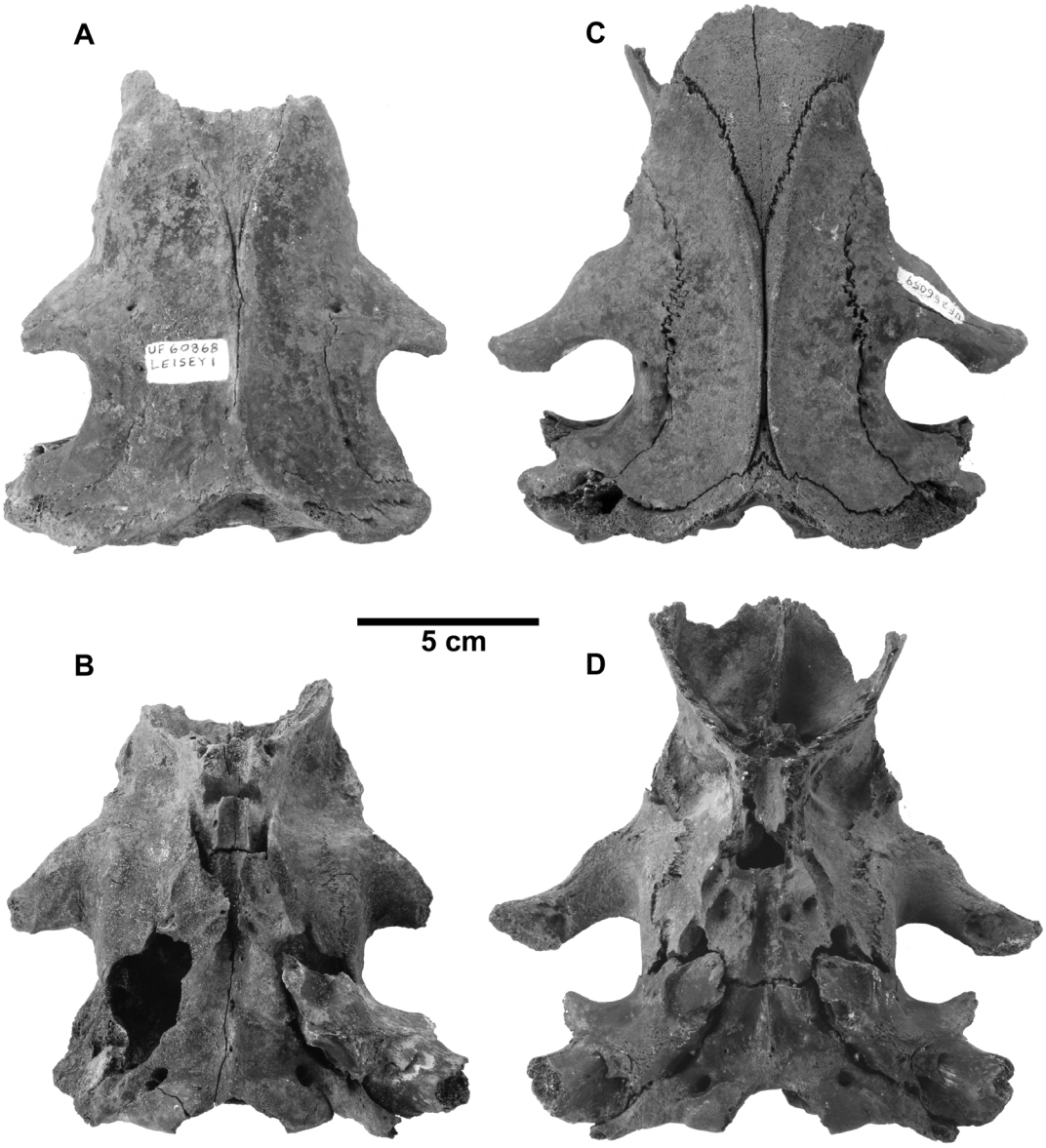

Figure 5. Partial skulls (braincases) of *Castoroides dilophidus* from the Pleistocene of Florida. **A**, dorsal, and **B**, ventral views of UF 60868, Leisey Shell Pit 1, Hillsborough County, early Pleistocene. **C**, dorsal, and **D**, ventral views of UF 256059, Lake Rousseau, Marion County, late Pleistocene.

incisor is 45–58 mm, compared to about 27 mm in *C. ohioensis*.

In dorsal view (Figs. 5A,C; 6A), *Castoroides dilophidus* has a relatively small but distinct postorbital process formed on the squamosal, just posterior to its suture with the frontal (postorbital process absent or much weaker in *Castoroides ohioensis*; Hay, 1914; Stirton, 1965). The development of the sagittal crest in *C. dilophidus* shows some variation. As in *C. ohioensis*, the sagittal crest in *C. dilophidus* begins with the union of the right and left frontoparietal crests at the midline of the skull. In *C. dilophidus* this junction occurs at a point even with or posterior to the zygomatic process of the squamosal, posterior to the parietal-frontal suture at the midline (Figs. 5C; 6A; also Parmalee and Graham, 2002:fig. 4A). In contrast, the sagittal crest in *C. ohioensis* begins at the location of the parietal-frontal suture, well anterior to the zygomatic process of the squamosal.

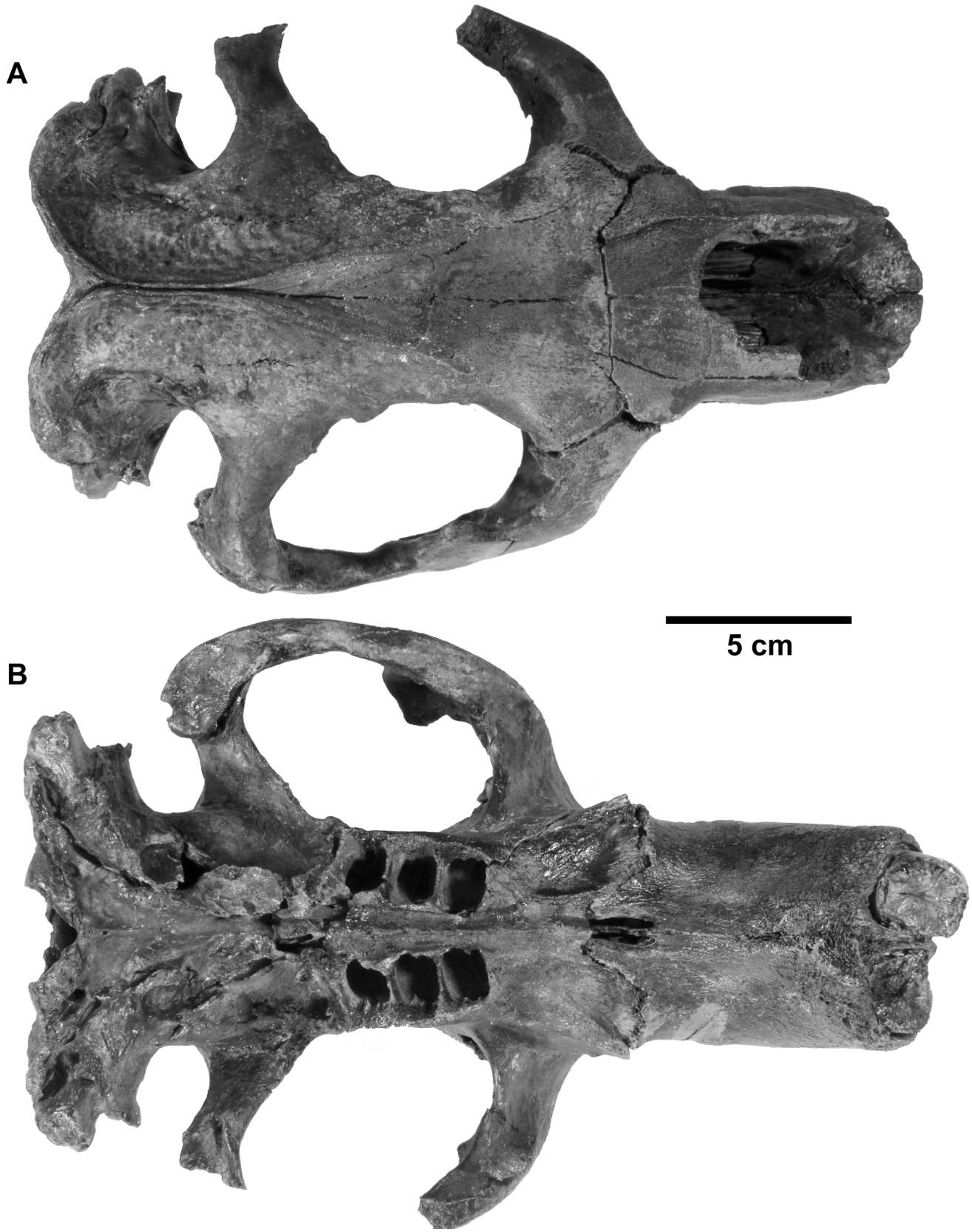

Figure 6. A, dorsal, and **B**, ventral views of UF 258638, skull of *Castoroides dilophidus* from the late Pleistocene of Florida.

Table 1. Measurements on crania of *Castoroides dilophidus* from Florida and South Carolina, with comparative values of *Castoroides ohioensis* from the northern United States.

	UF 258638	UF 256059	UF 81736	UF 60868	UF 258889	SC75.33.1[1]	*C. ohioensis*[2]
greatest length, tip of premaxilla to post. end of occipital condyle	262	—	—	—	—	289	242–298[3]
I1 to P4 diastema length	103.2	—	—	—	—	112.9	98.5–118.5
width of postzygomatic constriction	63.9	71.7	77.7	79.9	72.5	81.6	71.5–88.2
width between outer edges of mastoid processes	128.9	144.1	141.2	~135	145.4	150.6	136.5–167.0
height of occiput from base of basi-occipital to middle of lamboidal crest	59.2	55.3	59.8	62.5	63.6	68.5	62.2–68.0
height of rostrum above incisive foramen	83.2	—	—	—	—	98.0	78.5–100.0
angle of cheektooth row divergence	23°	—	—	—	—	22°	36–47°[4]

[1]after Parmalee and Graham (2002).

[2]range of 5 individuals from Stirton (1965) except where indicated.

[3]Stirton's (1965) longest skull, UMMP 3110, is listed as having a length of 397.5 mm, about 100 mm more than the next longest skull. As other dimensions of this specimen are only slightly larger or in some cases less than the other specimens in his sample, it is assumed that the provided length is a typographic error and that 297.5 is the correct value.

[4]range of 5 individuals, USNM 1634 and crania figured by Wyman (1846), Martin (1912), Engels (1931), and Stirton (1965).

As a result, the overall length of the sagittal crest is greater in *C. ohioensis*. The lambdoidal crest in *C. dilophidus* is deeply indented anteriorly at the midline where it intersects the terminus of the sagittal crest, whereas in *C. ohioensis* it is relatively straight or only slightly indented. The postzygomatic crest in *C. dilophidus* has a sharp margin anteriorly, but fades near the middle of the postzygomatic constriction; in *C. ohioensis*, a sharp postzygomatic crest encircles nearly the entire constriction.

In ventral view (Fig. 6B), *Castoroides dilophidus* and *Castoroides ohioensis* differ in the location of the toothrow in relation to the zygomatic processes of the maxilla and squamosal. The toothrow is located more anteriorly in *C. dilophidus*, with the anterior border of the P4 alveolus even with the zygomatic process of the maxilla, and the posterior border of the M3 is anterior to the level of the zygomatic process of the squamosal. The toothrow starts posterior to the zygomatic process of the maxilla in *C. ohioensis*, and the posterior border of the M3 is even with the zygomatic process of the squamosal. In both species the toothrows diverge posteriorly, such that the distance between the right and left M3s is much greater than the distances between the P4s (Fig. 6B). However, the degree of divergence in *C. dilophidus* is about half that observed in *C. ohioensis* (Table 1). In the two specimens in which it is preserved, UF 258638 and SC75.33.1, the incisive foramen is both wider and longer than in USNM 1634 and other skulls referred to *C. ohioensis* (Wyman, 1846; Martin, 1912; Stirton, 1965). All skulls from Florida lack the prominent mesopterygoid fossa on the basisphenoid (Figs. 5B, 5D, 6B), resembling the Cooper River skull, and differing from all known skulls of *C. ohioensis* (Stirton, 1965; Parmalee and Graham, 2002).

Another character used to distinguish *Castoroides dilophidus* from *Castoroides ohioensis* by Morgan and White (1995) and Parmalee and Graham (2002) was a weaker or less developed median ridge on the ventral surface of the basioccipital. However, the two Rancholabrean skulls for Florida, UF 256059 and 258638, have moderately well-developed medial ridges on the basiocciptial (Figs. 5D, 6B), within the observed range of variation of *C. ohioensis*. Therefore this character is not considered to be diagnostic for *C. dilophidus*.

DISCUSSION

The original description of the subspecies *Castoroides ohioensis dilophidus* was based on the discovery of a high incidence of a dental anomaly in p4s and M3s collected from the bed of the Santa Fe River in north-central Florida (Martin, 1969). The original sample consisted of only six p4s (of which five showed the anomaly) and seven M3s (of which two showed the anomaly). Anomalous p4s have a divided or split second anterior lophid (Fig. 2A–C; a single individual is known with a divided first anterior lophid, Table 2), while the M3s can have either a divided first (Fig. 2G) or second (Fig. 2H) posterior loph (or more rarely both). Such teeth are referred to here as having the 'dilophid' pattern. In most such teeth, the divided loph/lophid can be observed on both the occlusal surface and at the base of the crown. In a few individuals (e.g., UF 12405), the loph/lophid is pinched but not completely divided on the occlusal surface, but is fully divided at the base of the crown. In others (e.g., UF 166634), the 'pinched' condition remains consistent through the entire tooth. An M3 with a pinched first posterior loph on the occlusal surface and the dilophid pattern at the base of the crown was described by Woodburne (1961) for a Blancan specimen of *Procastoroides sweeti* from Sand Draw, Nebraska. Woodburne (1961) figured a second specimen in the same Blancan population with a pinched anterior loph on a P4, something we have not observed on any Florida *Castoroides* P4. While it is tempting to interpret this as an indication that the presence of the dilophid pattern is a retained primitive character in *Castoroides* samples from Florida, it is worth noting that all 13 p4s of *P. sweeti* observed by Woodburne (1961) had the normal dental pattern, as do all known early Pleistocene teeth of *Castoroides* from Florida.

We have greatly increased the size of the known sample of p4s and M3s of *Castoroides* from

Florida since the publication of Martin (1969), as well as their geographic coverage through much of peninsular region of the state (Fig. 1; Table 2; Appendix). As observed by Martin (1969), the dilophid pattern is more common in p4s (64%, n=36) than in M3s (23%, n=39) throughout late Pleistocene samples from Florida (Table 2). This difference in frequency of the dilophid pattern between p4s and M3s is highly significant ($p= 0.0012$, $X^2=10.45$, d.f.=1). This difference remains significant even if the four M3s with the incipient dilophid pattern are grouped with the fully dilophid individuals ($p<0.01$, $X^2=7.00$, d.f.=1). The dilophid pattern is now known to occur much more widely in peninsular Florida than just the Santa Fe River basin, including individuals from the Withlacoochee and Rainbow rivers in west-central Florida, the Peace River in southwestern Florida, and the Oklawaha River in northeastern Florida (Fig. 1). Teeth with the dilophid pattern have been found only in late Pleistocene samples from Florida (Appendix) and coastal Georgia. Irvingtonian sample sizes for p4s and m3s are much smaller than for the Rancholabrean, but all four known specimens (two p4s, two M3s) are of 'normal' morphology (e.g., Fig. 2F). In a small sample of p4s of *Castoroides dilophidus* from Andrews Island, Glynn County, Georgia, one has the dilophid pattern (UF 277389), while three do not (UF 265146–265148). To date, none of the many known specimens of *Castoroides ohioensis* from the northern and midwestern USA display the dilophid pattern. Clearly, if dilophid individuals do exist in *C. ohioensis*, they must be very rare. There is no obvious selective advantage of the dilophid pattern versus the normal one; indeed it would seem to structurally weaken the tooth and decrease the amount of functional enamel to process food, albeit to a minor degree. A reasonable explanation is that the unusual high frequency of the dilophid condition in Rancholabrean samples is the result of a population bottleneck caused when high sea levels covered much of peninsular Florida during Marine Isotope Stage 5 (and perhaps other earlier high stands) resulting in a population crash, followed by limited gene flow to and from more continental areas of the USA. This may explain

Table 2. Enamel patterns observed in teeth of late Pleistocene (Rancholabrean) *Castoroides dilophidus* from Florida.

	lower fourth premolars	upper third molars
normal pattern	UF 14486, 36625, 46486, 166637, 261931, 261934, 261928, 266253, 276997, 277385, 278364; UF/TRO 28; MMNS VP-3587 [n = 13]	AMNH 94547, 97801a, 97801b; UF 12407–12410, 12463, 14912, 21016, 36622, 36634, 46670, 68339, 261930, 262201, 263661, 265076; 270850, 277386; 278367 UF/TRO 6–9; MMNS VP-3659 [n = 26]
incipient dilophid pattern[1]		UF 12411, 12412, 166634, 261951 [n = 4]
dilophid pattern	UF 12404, 12406, 12417, 12427, 12440, 16177, 36628, 258889, 261932, 261933, 261938, 261939, 261949, 261967, 261983, 266321, 266322, 271213, 278363, 278365, 299668; UF/TRO 5, 10 [n = 23]	1st posterior loph divided: UF 14915, 261703, 265141; UF/TRO 4 2nd posterior loph divided: UF 261929, 261950, 262202, 278366 Both posterior lophs divided: UF 12405 [n = 9]

[1]Second posterior loph partially but not completely divided.

why the dilophid pattern is rarer in late Pleistocene samples from coastal Georgia than in those from peninsular Florida.

The late Pleistocene crania of *Castoroides* from Lake Rousseau and the Aucilla River demonstrate that characters formerly believed to be limited to the early Pleistocene species *Castoroides leiseyorum*, and which differed in many ways from those observed in *Castoroides ohioensis*, persisted into the late Pleistocene in Florida. This is in agreement with the morphology and presumed late Pleistocene age of the Cooper River skull from South Carolina described by Parmalee and Graham (2002). There is no morphological evidence separating the early Pleistocene Leisey specimens of *C. leiseyorum* and the late Pleistocene specimens of *Castoroides* from Florida and South Carolina into separate species, although recovery of more complete early Pleistocene material will test this hypothesis. We do not consider the presence or absence of the dilophid pattern by itself a valid, diagnostic feature for distinguishing species of *Castoroides*. Current fossil evidence only supports the presence of a single species of *Castoroides* in Florida with a chronologic range of 1 to 1.5 million years. Following the principal of priority, *Castoroides leiseyorum* is here regarded as the junior synonym of *Castoroides dilophidus*. If more complete early Pleistocene skulls are found in Florida that differ in the morphology of the premaxilla and toothrow from the Cooper River and Aucilla River skulls, then this synonymy could be reversed and both species regarded as valid. If a larger sample of early Pleistocene p4s and M3s from Florida or the Southeast becomes available, and they prove to completely lack the dilophid pattern, or have it in a significantly lower frequency than in late Pleistocene samples, then the older population could be recognized as a distinct subspecies.

The company Bone Clones© manufactures and sells a reproduction of a skull and mandible of *Castoroides* (their product number BC-071). It is marketed under the name *Castoroides ohioensis*, and as being "among the largest and most complete" specimens known, but without information regarding its place of origin (http://www.boneclones.com/BC-071A.htm). A brief discussion on this specimen is needed because copies likely reside in a number of museum collections and because it apparently displays a mixture of cranial features of *Castoroides ohioensis* (widely diverging tooth rows) and *Castoroides dilophidus* (absence of mesopterygoid fossa, short sagittal crest, tall premaxillae lacking anterior process, etc.). The original specimen is now in a private collection and not available for study. However, we have had discussions with the collector of the specimen, as well as the individual who did the preparation and restoration of the specimen. The collector revealed that it was found in Lake Rousseau, Florida, and provided us with drawings of the specimen made prior to its restoration. Photocopies of these drawings are stored in the UF collection along with a cast of the specimen under the number UF 258889. The drawings reveal that the cranium was originally recovered in two major parts, the braincase and the premaxillae with the incisors, but without the intervening section that includes the orbits, zygomatic arches, maxillae, and upper cheekteeth. The missing portions of the skull, most notably the palate and orbits were reconstructed based on those of *Castor canadensis* and *C. ohioensis*. The real parts of the cranium have the features described above for *C. dilophidus*. The reconstruction also likely exaggerates the length of the skull. Measurements taken on those portions of the cast which are based on original fossil material fall within the range of *C. dilophidus* and the lower half of the range of *C. ohioensis* (Table 1). For example, the width between the outer edges of the mastoid processes on UF 258889 is 145.4 mm, which is less than in the Cooper River specimen SC75.33.1 (Parmalee and Graham, 2002). According to the collector, the original fossils of the right and left mandibles sold with Bone Clones© skull BC-071 were found within a few meters of the skull portions and almost certainly represent the same individual. The cheekteeth were found in the mandibles, and both p4s have the dilophid pattern.

In published abstracts of an as yet unpublished study, Rinaldi et al. (2008; 2012) also

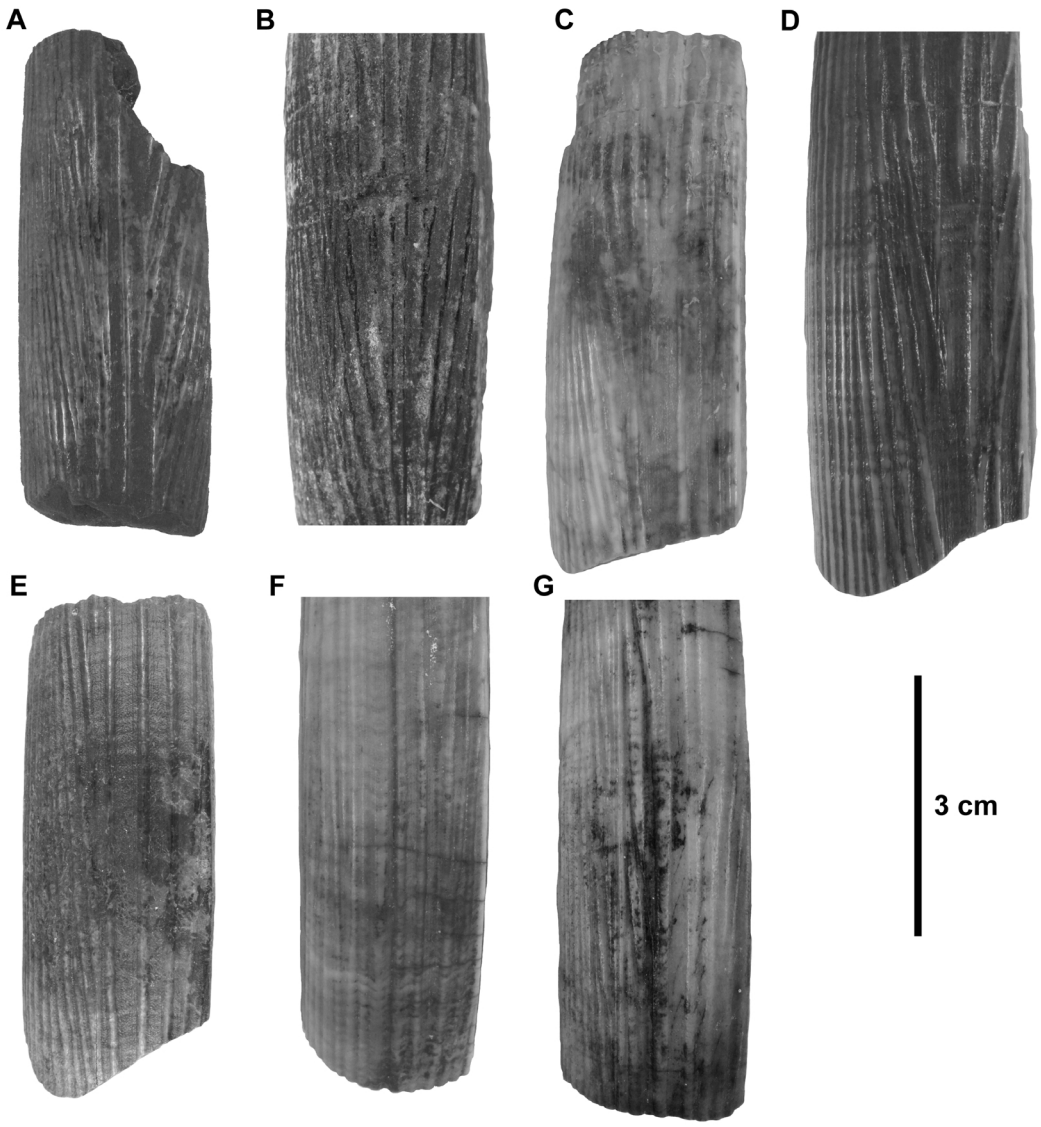

Figure 7. Upper incisors of *Castoroides dilophidus* from Florida in anterior view. **A**, UF 12872. **B**, UF 19412. **C**, UF 13030. D, 17318. **E**, UF 46529. **F**, UF/TRO 25. **G**, UF 166631. Distal cutting edge complete in C, D, and E. A–B and E–G are rights; C and D are lefts, but are reversed so as to appear to be from the right side. In all cases, lateral is to the left on the images, medial to the right, and distal to the bottom.

supported the separation of *Castoroides* into two species, *Castoroides ohioensis* and what they termed *Castoroides leiseyorum*. In addition to unlisted differences in cranial features, Rinaldi et al. (2008) concentrated on supposed differences in the upper incisors between the two species. They stated that the I1s of "*C. leiseyorum*" differed from those of *C. ohioensis* by having a more pinnate system of ridges on the anterior enamel and a more sharply angled distal cutting edge. In addition to SC75.33.1, we have five available specimens from Florida with the intact distal cutting edge of the I1 (UF 1708, 13030, 17318, 46529, and 258889) and 11 additional specimens preserving sections of the I1 >70 mm long (UF 12872, 19412, 46411, 46412, 166631, 268283, 268284, 268285; UF/FGS 7254; UF/FGS 4888; UF/TRO 25). The enamel ridge pattern on the anterior face of these 16 specimens is highly variable (Fig. 7). Only three individuals, UF 12872, 19412, and 46411

have a highly pinnate ridge pattern (one or two central ridges straight, medial and lateral ridges slanted). In the other 12, some had predominantly slanted medial ridges and straight lateral ridges (e.g., UF 17318, 268284), some predominantly straight medial ridges and slanted lateral ridges (e.g., UF 13030, 46529, 268285), and some with predominantly straight ridges on both sides of the tooth (UF 46412, 166631, UF/TRO 25). Likewise, the angle made by the distal cutting edge relative to the long axis of the tooth is highly variable, ranging from about 25 to 45°, and broadly overlapping the range observed in *C. ohioensis*. The large range of individual variation observed in these characters, some between individuals from the same locality, suggests that they are not suitable for distinguishing between species. Also, the claim by Rinaldi et al. (2008) that most of the enamel ridges meet the distal cutting edge of the I1 at right angles in "*C. leiseyorum*" is not observed in our specimens from Florida (Fig. 7C–E).

Until diagnostic cranial specimens are described from other regions of the southern US, the geographic range of *Castoroides dilophidus* is best considered to be limited to Florida and coastal regions of Georgia and South Carolina. Likewise, the range of *Castoroides ohioensis* should be restricted to the area and chronologic interval from which it is known from skulls, namely the late Pleistocene of New York, the Great Lakes region (Indiana, Ohio, Illinois, Minnesota, and southern Michigan), and the northern Great Plains (specifically Kansas and Nebraska; Martin, 1912). Fossils from other regions or different geologic intervals are best referred to *Castoroides* sp.

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APPENDIX

Florida fossil localities with referred specimens of *Castoroides dilophidus*. Site numbers match those in Figure 1.

Early Pleistocene (early Irvingtonian Land Mammal Age)

1. Tucker Borrow Pit, Brevard County. UF 137999, phalanx.

2. Crystal River Power Plant, Citrus County. UF 17318, I1; UF 17319, M3; UF 17320, molar; UF 133904, axis vertebra.

3. Leisey Shell Pit 1, Hillsborough County. UF 60868, braincase; UF 80464, partial pelvis; UF 81736, braincase; UF 83119, 86862 astragali.

4. Leisey Shell Pit 2, Hillsborough County. UF 125214, partial cheektooth.

5. Leisey Shell Pit 3, Hillsborough County. UF 115965, mandible with i1, p4-m3 (Morgan and White 1995:fig. 2); UF 124563, lower molar; UF 132047, 219950, 241862 partial cheekteeth; UF 225740, M3; UF 160757, pelvis.

6. Sun City Shell Pit, Hillsborough County. UF 217395, M3; UF 217396, p4.

7. Fort Green Mine, Polk County. UF 24016, molar; UF 95637, femur.

Middle Pleistocene (late Irvingtonian or early Rancholabrean Land Mammal Ages)

8. Tri-Britton Site, Hendry County. UF 209380, astragalus.

9. La Belle Highway Pit, Hendry County. UF 214399, astragalus.

10. Oldsmar 1, Pinellas County. UF 143695, distal i1; UF 266757, lower molar.

11. Dickerson Coquina Pit, St. Lucie County. UF 266750, P4.

Late Pleistocene (late Rancholabrean Land Mammal Age)

12. Paynes Prairie 1, Alachua County. UF 12457, lot of 11 cheektooth and incisor fragments; UF 13030, I1; UF 265141, M3.

13. Ichetucknee River, Columbia County. UF 1708, I1.

14. Santa Fe River 1, Columbia County. UF 10537, 166631–166633, 166648, 268284–268285, I1s; UF 166637, p4; UF 12410, 166634, M3s; UF 166638, lower molar; UF 11871, 166634–166636, upper molars; UF 10536, 10597, molars; UF 16782, humerus; UF 244579, metacarpal 5; UF 10433, 10538, 10541, 157021, partial femora.

15. Santa Fe River 2, Columbia County. UF 12404, 12406, 12417, 12421, 12427, 12440, UF/TRO 28, p4s; UF 12405, 12407–12409, 12411, 12412 M3s; UF 12413, 12416, 12420, upper molars; UF 12419, 12422, 12423, 12442, 12450, 14925, lower molars; UF 12414, 12415, 12418, 12424–12426, 12428, 12429, 12441, 12443–12449, 12451, 12452, 12453, 54351–54359, 54361, molars; UF 12430–12436, 268283, incisors; UF 12437–12439, mandible fragments; UF 16782, distal humerus; UF 12454–12455, partial femora; UF 54360, distal tibia. UF 244580–244581, calcanea.

Santa Fe River 3, Columbia County. UF 277385, p4; UF 277386, M3; UF 277389–277340, molars.

16. Santa Fe River 8, Columbia County. UF 12964, partial incisor.

17. Santa Fe River 9, Columbia County. UF 16176, incisor fragment; UF 16177, p4.

18. Santa Fe River (no specific locality), Columbia County. UF/FGS 4888, I1; UF 261928, 266321, 266322, 278363, MMNS VP-3587 p4s; UF/FGS 4867, lower molar; UF 261929, 261930, 262201, M3s; UF 11477, UF/FGS 4792, upper molars; UF 135779, i1.

19. Peace River, De Soto County. UF 266253, p4; UF 265076, 263661, UF/TRO 4, M3s; UF 224037, incisor fragment; UF 238549, astragalus.

20. Prairie Creek, De Soto County. UF 156797, incisor fragment.

21. Peace River, Hardee County. UF 261703, M3.

22. Waccasassa River, Levy County. UF 19196, 299668, UF/TRO 5, UF/TRO 10, p4s; UF 14912, 14915, 270850, UF/TRO 6–9, M3s; UF 13978, 14911, 14913, upper molars; UF 46667–46669, 299669-299670 molars; UF 14909, 14910, 46663–46666, 299667 I1s; UF 203815, i1.

23. Bradenton, Manatee County. AMNH 97801 lot of six cheekteeth including two M3s and eight incisor fragments.

24. Eureka Lock, Marion County. UF/FGS 7258–7261, upper molars; UF/FGS 7262, lower molar; UF/FGS 7254, I1; UF/FGS 7255–7256, i1s.

25. Oklawaha River, Marion County. UF 68338, mandible with m2-m3; UF 36625, 36628, 261949, 261967, 261983, p4s; UF 68340, 261958, 261968, lower molars; UF 68341, 261952–261957, 261969, 261970, 261981, 261996, upper molars; UF 36622, 36634, 68339, 261950, 261951, M3s; UF 36623, 36624, 36626–36633, 68165, 68166 molars; UF 261959, 261960, I1s; UF 261961, i1; UF 68344, 261962, partial humeri; UF 68345, partial radius; UF 36660, 261994, ulnae; UF 68346, partial femur; UF 261965, partial tibiofibula; UF 261995, astragalus; UF 68347, 261966, calcanea; UF 261963, metatarsal; UF 36612, 36620, 68167, 68348, phalanges.

26. Withlacoochee River, Marion County. UF 14486, mandible with p4-m1; UF 46486, 261932, 261933, p4s; UF 12463, MMNS VP-3659, M3s; UF 46528, lower molar; UF 46529, I1; UF 60847, distal humerus.

27. Lake Rousseau, Marion County. UF 256059, braincase; UF 261934, p4; UF 258889, cast of associated braincase, premaxillae with I1s, and mandibles with right and left i1, p4-m3.

28. Rainbow River, Marion County. UF 243542, 243543, partial incisors; UF 271213 p4.

29. North Fernandina Beach, Nassau County. UF 223127–223131, partial cheekteeth, UF 223123–223126, partial incisors.

30. St. Johns Lock, Putnam County. UF/FGS 8732, 8837, upper molars; UF/FGS 8731, I1; UF/FGS 8734, four partial incisors; UF/FGS 8838, distal tibiofibula; UF/FGS 8733, astragalus.

31. Cross Florida Barge Canal near Rodman, Putnam County. UF/FGS 10062, lower molar.

32. Venice Ditch, Sarasota County. AMNH 94547, M3.

33. Coleman 3, Sumter County. UF 16647, lower molar.

34. Branford 2A, Suwannee County. UF 261940, partial i1; UF 261937, petrosal; UF 261938, partial mandible with p4; UF 261939, p4; UF 261941, lower molar; UF 261942, astragalus.

35. Aucilla River 1, Taylor/Jefferson counties. UF 258638 (cast), skull; UF 204915, 245044, partial incisors.

36. Blue Springs, Volusia County. UF 276997, p4.

37. Cypress Spring Run, Washington County. UF/FGS 4718, incisor.

38. Suwannee River, exact county unknown. UF 261931, 278364, 278365 p4; UF 262202, 278366, 278367 M3.

Pleistocene (Irvingtonian or Rancholabrean Land Mammal Age)

39. Apollo Beach, Hillsborough County. UF 60860, frontals and parietals; UF 61912, molar.

40. Rim Ditch Canal, St. Lucie County. USNM 244229, partial I1.

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