



Endocranial morphology of the extinct Antillean shrew *Nesophontes* (Lipotyphla: Nesophontidae) from natural and digital endocasts of Cuban taxa

Johanset Orihuela

ABSTRACT

This paper describes the endocranial morphology of the extinct genus of Antillean shrews *Nesophontes*, based on natural and digital endocranial casts extracted from Cuban species. The endocranial casts show developed olfactory lobes without accessory bulbs, an exposed tectum with visible superior colliculi, a large cerebellum and vermis, and a smooth neocortex. Body mass was estimated from skull size to be between 97 and 114 g, yielding encephalization quotients between 0.33 and 0.57. Endocranial casts of *Nesophontes* are morphologically similar to those of *Solenodon* more so than to other lipotyphlans such as *Sorex*, *Blarina*, *Erinaceus*, or the afroinsectivoran *Tenrec*. The morphological similarity to *Solenodon*, not only in endocranial structures but also in the rest of the skeleton suggests a behavioral analogy between the two genera. The marked superior colliculi, prominent olfactory lobes, and facial musculoskeletal anatomy suggest that *Nesophontes* was most likely nocturnal and fossorial, relying on hearing, smell, and tactility to forage. Future analysis of the appendicular skeleton can help determine if this genus was solely terrestrial or if it also exploited arboreal habitats. All these morphologies can help elucidate *Nesophontes*'s behavior, ecology, and the osteological variation that is observed in the genus.

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INTRODUCTION

Nesophontidae (Anthony, 1916) and Solenodontidae (Gill, 1872) are so far the only two families of insectivorans known from the Antilles, of which only solenodons remain extant. *Nesophon-*

tes has been extinct since the late Holocene, but has left a rich fossil record in the Greater Antilles (Morgan and Wood, 1986; MacPhee et al., 1999; Whidden and Asher, 2001; Hutterer, 2005; Silva-Taboada et al., 2007). Most recent phylogenetic

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data suggests that Nesophontidae and Solenodontidae are sister taxa to a clade of Holarctic insectivorans that predate the K/T event which include moles, hedgehogs, and shrews (Roca et al., 2004; Asher et al., 2005; Douady and Douzery, 2009). MacPhee and Grimaldi (1996) reported Nesophontes-size lipotyphlan remains from late Oligocene/early Miocene amber from the Dominican Republic, in the Greater Antilles, but its classification remains uncertain. These ancient mammals are important to the understanding of Antillean land mammal biogeography and to discussions about insectivoran evolution (MacFadden, 1980; Asher et al., 2003, 2005; MacPhee, 2005).

Endocranial casts are relevant in the study of mammalian brains, and the evolution of endocranial morphology (Radinsky, 1968; Kielan-Jaworowska, 1984; Macrini et al., 2007a and b; Rowe et al., 2011; Silcox et al., 2011; Orliac et al., 2012). Endocranial casts do not represent actual brains. Instead, endocasts are impressions of external brain structures such as vessels and meninges (Bauchot and Stephan, 1967; Kielan-Jaworowska and Lancaster, 2004). Nevertheless, endocranial casts provide a unique opportunity for paleobiologists and paleoneurologists to study casts of soft tissue structures that are rarely preserved during fossilization. Particularly, endocasts allow investigators to infer the function, evolution, and behavior of extinct animals (Edinger, 1949; Clark, 1959; Eisenberg, 1981; Stephan et al., 1991; Jerison, 2009). Natural and digital endocasts have provided fundamental evidence of the neuroanatomy and behavior of primitive lineages such as multituberculates and insectivore-grade mammals, among other taxa, as a key to understanding mammalian evolution (Kielan-Jaworowska, 1984, 2004; Thewissen and Gingerich, 1989; Macrini et al., 2007a; Rowe, 1996; Rowe et al., 2011).

This paper reports the endocranial morphology of *Nesophontes* through the analysis of natural and digital endocranial casts. Although *Nesophontes* is known from well-preserved cranial specimens, their endocranial casts remained unreported and their morphology unstudied. The cranial osteology of *Nesophontes* has often been described in combination with that of *Solenodon*, with the most extensive treatments being those of Anthony (1916, 1918), McDowell (1958), MacPhee (1981, 2005), and Wible (2008). Other researchers have analyzed different features of nesophontid cranial morphology through the study of fossil crania, but not from endocranial casts (e.g., Gould and Garwood, 1969; Silva-Taboada et al., 2007). Through

the analysis of *Nesophontes* endocranial casts this research describes and illustrates their endocranial morphology for the first time. Additionally, this manuscript explains the sensorial and behavioral characteristics from *Nesophontes*'s neuromorphology, and compares it to that of *Solenodon* and other extant and extinct mammals. Such data provides basic information to evolutionary neurologists interested in mammalian or insectivoran neuroanatomy. Evolutionary signals and developmental drives (i.e., stages of brain evolution) lie outside the scope of this research. Nevertheless, the data presented here further enhance our knowledge and understanding of nesophontid systematics, paleoecology, and behavior.

MATERIALS AND METHODS

Locality

The specimens used in this study were extracted from a late Quaternary owl pellet deposit in Nesophontes Cave, Palenque Hill in northwestern Cuba. Specimens were excavated from a 50 cm x 50 cm x 50 cm test pit under the main doline (sinkhole). The association of the *Nesophontes* specimens with introduced rats (*Rattus* sp.) suggests a late Holocene age for the deposit (MacPhee et al., 1999). The cave's faunally-rich assemblage will be described elsewhere. All specimens are deposited in the National Museum of Natural History (MNHN Cu), Havana, Cuba (uncataloged). The numbers referred to here are field numbers.

Methodology

This study is based on eight incomplete natural endocranial casts and four digital reconstructions from four nearly complete skulls (Figures 1, 2, 3, 4, 5, 6, and 7). The analyses included the Cuban species *Nesophontes major* and *Nesophontes micrus*. All measurements are given in Table 1.

Natural endocasts (Steinkerns) were extracted from two nearly complete adult skulls; one *Nesophontes major* (C181) and one *Nesophontes micrus* (C145) (Figure 1.1). The maturity of the specimens was assessed from tooth wear and cranial sutures (McDowell, 1958). The natural endocasts were extracted through partial destructive sampling of the braincase after the specimens were x-rayed (Figure 1.2-3). Skulls with cemented sediment inside the endocranial cavity were specially selected. The posterior portion of the braincase was then carefully removed and the natural endocasts carefully extracted. These endocasts

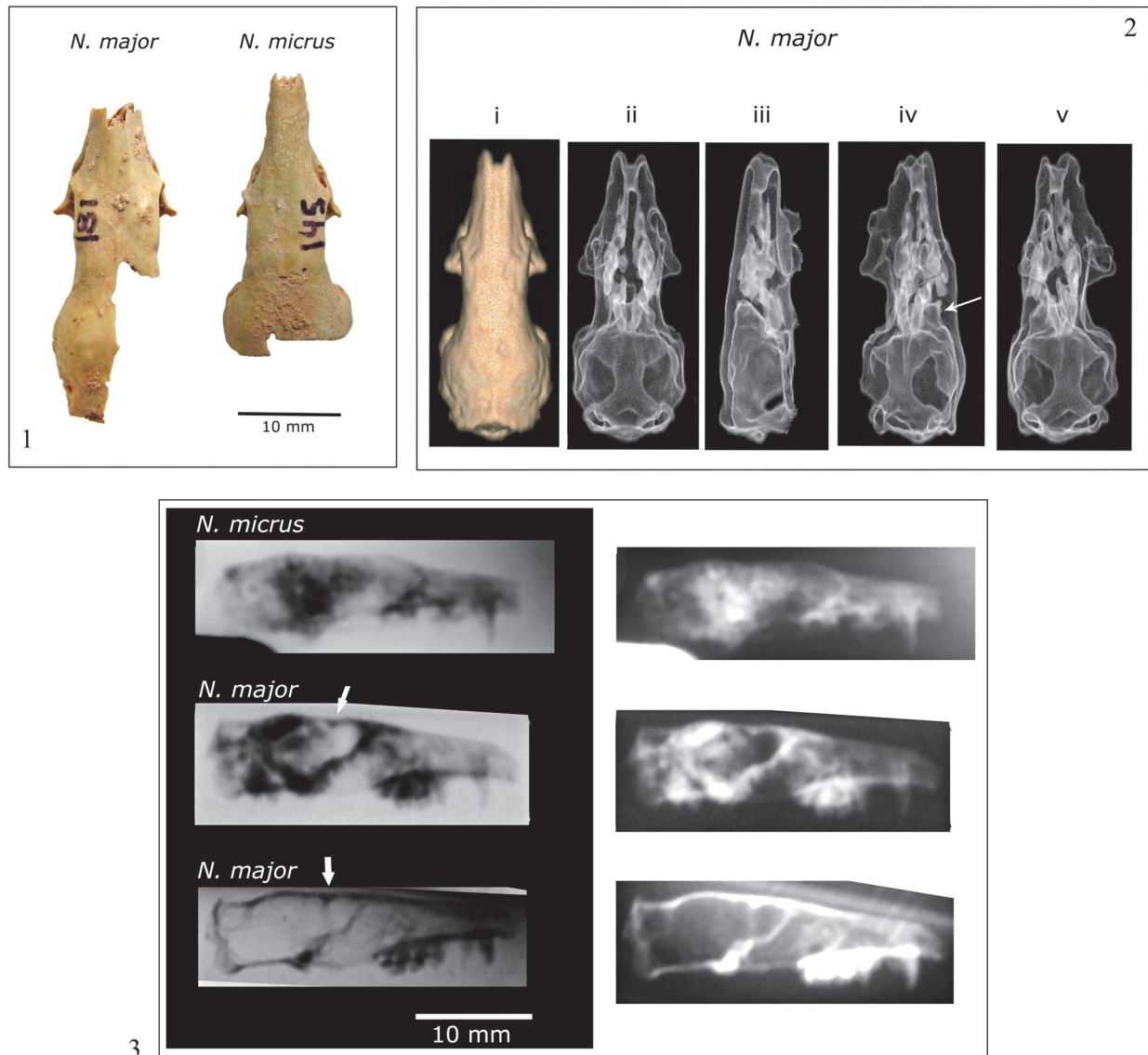


FIGURE 1. Natural (1), digital (2), and radiographic images (3) of *Nesophontes* spp. crania used in this study. 1, these skulls were the source of natural endocasts for *Nesophontes micrus* (C145) and *Nesophontes major* (C181) shown in Figures 1 and 2. 2, Digital rendering of *N. major* skull (C133) from which the digital endocast in Figure 5 was reconstructed. 3, are negative and positive lateral radiographs of *Nesophontes* spp. endocranial morphology and space.

were compared to brain images in scientific literature, plus the Comparative Brain Collection at www.brainmuseum.org and Digital Morphology Library (Digimorph: www.digimorph.org/) of the University of Texas at Austin. Detailed comparisons were made with several multituberculates, basal eutherians, and extinct insectivorans as a source or morphological comparison, and not for phylogenetic purposes. These included the species *Eoryctes melanus*, *Vincelestes neuquenianus*, *Hyopsodus lepidus*, the extant marsupials *Mondelphis domestica* and *Marmosa murina*, plus the

extant lipotyphlans *Solenodon paradoxus*, *Tenrec ecuadatus*, *Erinaceus europeus*, and *Sorex* sp. Cranial and natural endocranial casts linear measurements were taken with digital calipers. Brain percentage compositions and angle measurements procedures were adopted from Stephan and Andy (1982) and Macrini et al. (2006). Marsupials were included not as an ancient or “primitive” outgroup, but because of their endocranial similarities, and their value in the study of placental neuroanatomy (Ashwell, 2010). Because of known problems with insectivoran nomenclature and phylogeny



FIGURE 2. Natural endocranial casts of Cuban *Nesophontes* spp. **1**, superior, and right lateral view of *Nesophontes major* (specimen number C181) endocasts. **2-3**, superior and right lateral views of *Nesophontes micrus* endocasts. **2**, *Nesophontes micrus* (C145); **3-4**, are not cataloged.

(Asher and Helgen, 2010) some of the older classification systems (e.g., classification of “progressive insectivorans” using EQ values) have been included in the text to serve as comparisons with older literature and will be referred to as actual genera or species when appropriate.

Digital endocasts were reconstructed from x-ray computed tomography data (CT slices) acquired through the scanning of two nearly complete cranial specimens of *Nesophontes micrus* (C436, C437) and two of *Nesophontes major* (C133, C270). The specimens were scanned coronally with a General Electric Lightspeed scanner (VCT, 64 detectors), resulting in 120 images with a matrix size of 512². The techniques used were a 20 milliamperere current (mA), 80 peak kilovolts (KvP), a slice thickness of 0.625 mm, plus a 0.312 mm image overlap in a 32 mm field of view. The scan data were then reconstructed with a General Electric ADW (4.3) Workstation using an “air-structure” algorithm.

Encephalization quotients (EQ) were calculated using Jerison (1973) equation: $EQ = EV / 0.12 (Wt)^{0.67}$ and Eisenberg’s (1981) equation: $EQ = EV / 0.055 (Wt)^{0.74}$, where EV = endocranial volume in ml (cm³) and Wt the body mass in grams (g). Cal-

culated EQ values were based on a body mass range between 97 and 114 g (average 105.5), estimated from the formula: $y = 3.68x - 3.83$, where $y = \log_{10}$ (body mass in grams), and $x = \log_{10}$ (skull length in mm). This formula is based on the relationship between body mass and skull length documented in extant insectivore-grade mammals (Luo et al., 2001; Rowe et al., 2011). Skull lengths for *Nesophontes micrus* and *N. major*, plus other linear and volumetric features were measured (Table 1). Endocranial volumes and dimensions were measured directly from CT data with built-in measuring tools of the ADW software (Table 1). McFarlane (1999) provided a mass estimate for *Nesophontes* between 180 and 200 g. However, this estimate is based on correlations between the significantly larger *Nesophontes edithae* from Puerto Rico and chipmunk-sized rodents (e.g., Allen, 1942, Walker et al., 1975) and could be an overestimation.

The terminology for brain anatomy follows Butler and Hodos (2005), Rowe et al. (2011) and Orliac et al., (2012), and that for cranial osteological follows McDowell (1958), Wible (2008), and Macrini (2012). The use of Lipotyphla over Eulipotyphla follows the suggestions of Asher and Helgen

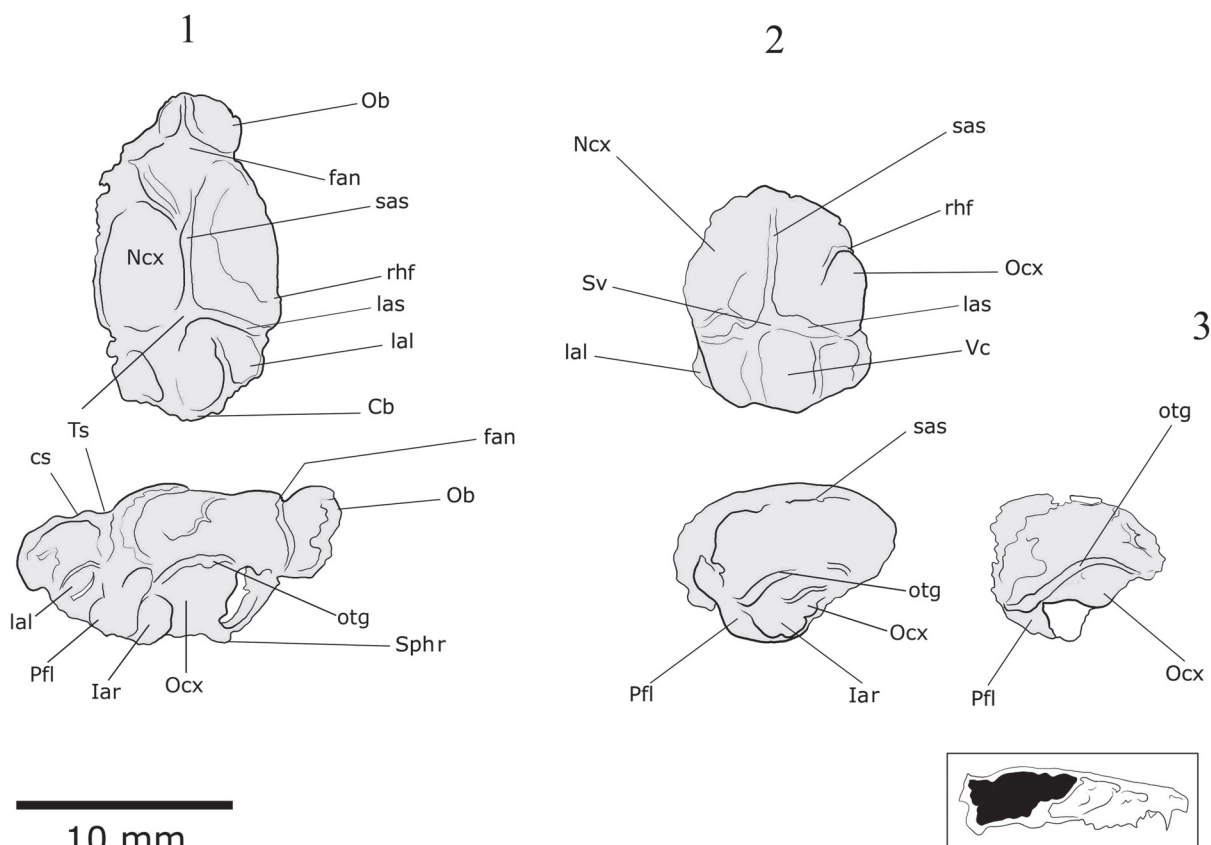


FIGURE 3. Anatomical terminology of *Nesophontes* endocranial casts. **1**, superior and lateral views of *Nesophontes major* endocranial cast (C181). **2**, superior and lateral views of *Nesophontes micrus* (C145) specimen. **3**, single view of partial endocranial cast extracted from an uncatalogued *N. micrus* skull. Abbreviations of anatomical terminology: **Cb** cerebellum; **cs** superior colliculi; **fan** annular or circular fissure; **iar** internal auditory region; **lal** lateral lobe of cerebellum; **las** lateral transverse sinus; **Ncx** neocortex; **Ob** olfactory lobes; **otg** orbitotemporal groove; **Ocx** olfactory (=piriform) cortex; **Pfl** paraflocculus; **rhf** rhinal fissure; **sas** sagittal sinus or longitudinal sinus; **Sphr** sphenorbital region; **Sv** confluence of the transverse and sagittal sinuses; **Vc** cerebellar vermis. **A** and **P** stand for anterior and posterior.

(2010). A list of character states for *Nesophontes* is provided in the Appendix.

RESULTS

Forebrain: The Olfactory Lobes and Ethmoid-cribriform Region

The casts of the olfactory lobes (Ob) are large, well-developed, elongated anteroposteriorly, non-continuous, and oval in shape (Figures 2.1 and 4.2). The olfactory lobe casts are less than one half the anteroposterior length of the neocortex, but constitute 20-25 % of the total endocranial volume. The sagittal or longitudinal sinus (sas) divides both lobe casts medially.

The olfactory lobe casts are divided anteriorly and anterodorsally by the crista galli and postero-

dorsally by an annular or circular fissure (fan) on the posterior frontal bone (Figures 1.2-3, 2.1 and 4.2). Small sections of the olfactory peduncle casts were observed in well-preserved natural casts (Figure 4.2) and implied in digital endocasts (Figures 5.1, 6.1). Casts of olfactory nerve fibers were not observed in either natural or digital endocast. The olfactory lobes rest on a thick and inclined cribriform plate, rich in nasoturbin and ethmoturbin foramina (Figures 1.2-3, 6 and 8). Possible casts of olfactory extensions [onf] are visible superiorly and anteriorly on the olfactory lobes of digital renderings (Figure 5 and Figure 6). The dorsalmost might be a negative cast of the cribroethmoidal foramen (cef), which seems to be largest of the cribriform foramina in *Nesophontes* (Figure 8). The annular or circular fissure (fan), which separates the olfac-

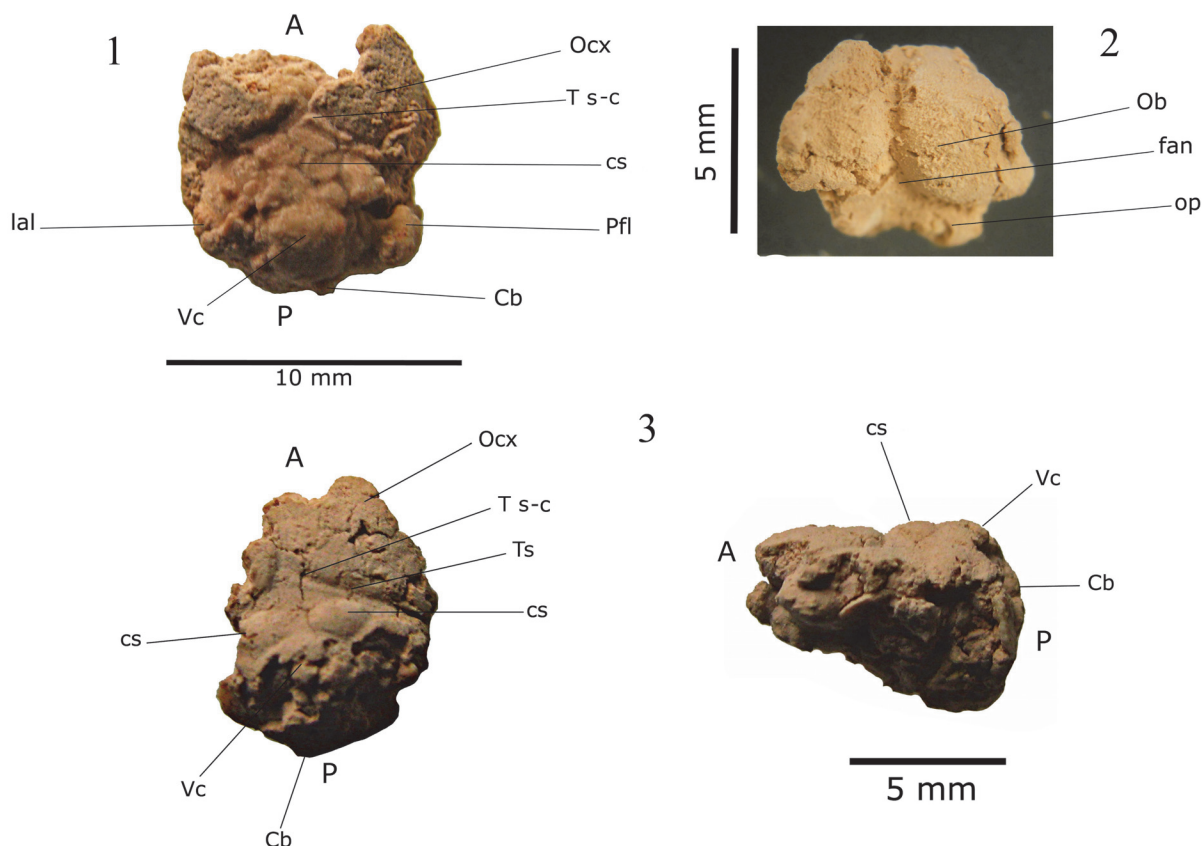


FIGURE 4. Natural endocranial casts extracted from *Nesophontes* spp. skulls. (4.1) *Nesophontes major* hindbrain fragment; (4.2) *N. major* olfactory lobes; (4.3-4.4) *Nesophontes micrus* superior (4.3) and left lateral (4.4) views of a partial hindbrain. **Cb** cerebellum; **cs** superior colliculi; **lal** lateral lobe of cerebellum; **Ob** olfactory lobes; **op** olfactory peduncle; **Pfl** paraflocculus; **Ts** transverse sinus canal; **Ts-c** confluence of the transverse and sagittal sinuses. **A** and **P** stand for anterior and posterior.

tory lobes from the neocortex, is apparently deep as it can be seen in radiographs, and digital and natural endocranial casts. The olfactory lobes are aligned to the rest of the brain, but with an endocranial flexure between 25 and 29 degrees. No evidence of accessory olfactory lobes were observed in *Nesophontes* casts.

Forebrain: Cerebrum

The cast of the neocortex (Ncx) is lissencephalic or smooth (poor gyrification). Only slight indications of sulci are visible on natural and digital cast specimens. These are superficial, and probable indications of the rhinal fissure (rhn) above the olfactory (= piriform) cortex (Ocx), and superiorly, behind the circular fissure (fan). The latter seems to be the sylvian fissure (Sf) (Figures 1.2, 5, and 6).

The cast of the neocortex is ovoid and divided by a shallow superior sagittal sinus. The casts of the hemispheres are elongated anteroposteriorly, narrower anteriorly, and wider posteriorly, at the

level of the olfactory cortex (Ocx). The cerebral hemispheres are well defined.

A marked orbitotemporal groove (otg) cast is visible on most natural endocasts (Figure 2), but not on digital renderings (Figures 5 and 6). Such a structure is often defined as a sinus canal or meningeal vessel, and is visible on the endocranial face of the squamosal bone (Thewissen and Gingerich, 1989; Silcox et al., 2011). This feature is a probable marker of the rhinal fissure, delimiting between the paleo and neocortex (Rowe, 1996; Silcox et al., 2011). The transverse sinus seems deeper and wider than the sagittal sinus. Traces of the sagittal and transverse sinuses meet just before the tectum (Figures 2 and 4).

Diencephalon

The digital renderings show a hypophyseal fossa (hyf) and sphenoid tracts with optic nerves in the anterior-inferior region that can represent the optic chiasm (Och). The sphenoid tracts seem to

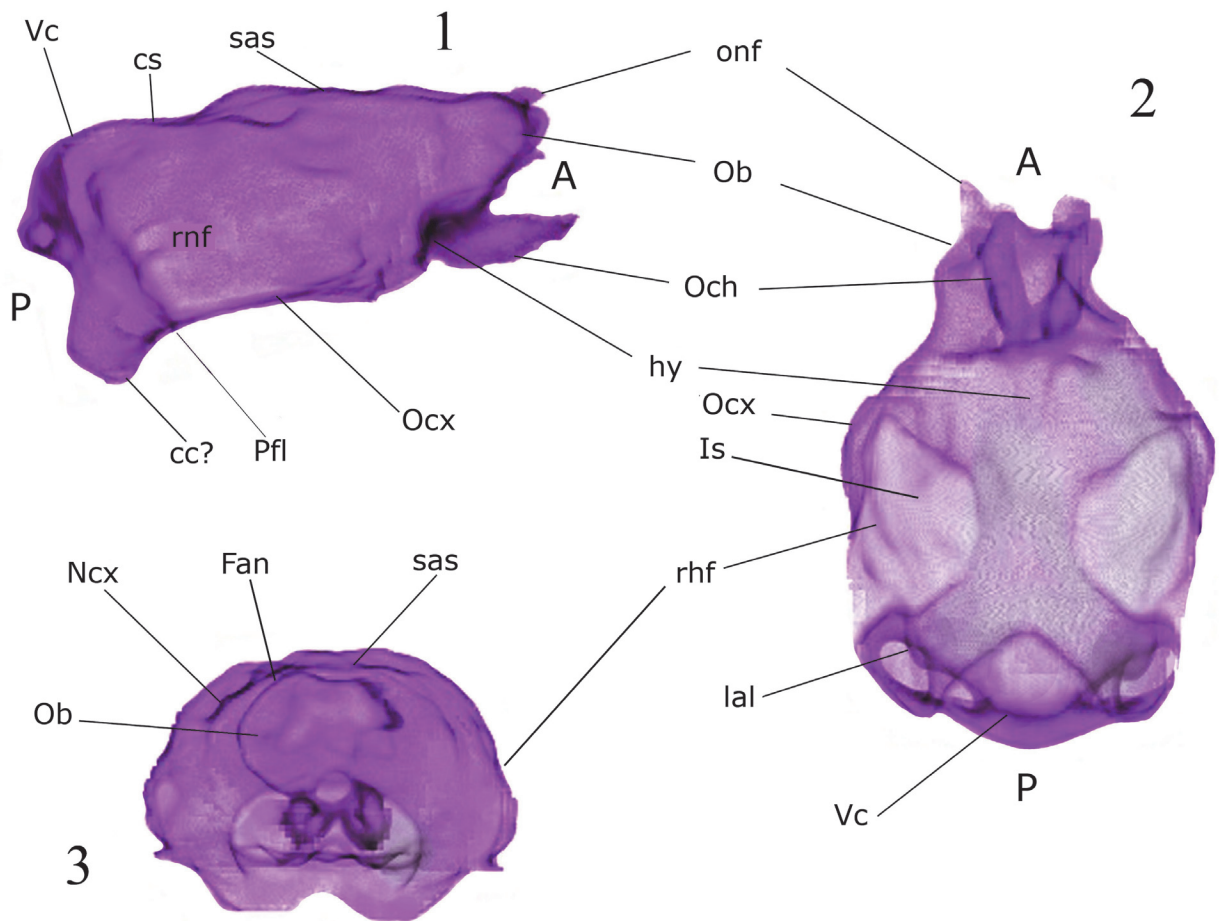


FIGURE 5. Digital endocranial cast of *Nesophontes major* (C133) in right lateral (1), anterior (2), and inferior (3) views. Abbreviations: **Cb** cerebellum; **cc** possible cast of spinal cord space; **cs** superior colliculi; **fan** annular or circular fissure; **hy** hypophyseal fossa; **lar** internal auditory region; **lal** lateral lobe of cerebellum; **las** lateral transverse sinus; **Ncx** neocortex; **Ob** olfactory lobes; **Och**, optic chiasm; **Ocx** olfactory (=piriform) cortex, **onf** olfactory nerve fiber, **otg** orbitotemporal groove; **Pfl** paraflocculus; **rhf** rhinal fissure; **sas** sagittal sinus or longitudinal sinus; **Sphr** sphenorbital region; **Sv** confluence of the transverse and sagittal sinuses; **Vc** cerebellar vermis. **A** and **P** stand for anterior and posterior.

be divided anteriorly by the alisphenoid, and are separate from the optic foramina (Figure 5). The olfactory cortex cast and the sphenorbital region are visible, but were not well delimited on natural or digital endocasts (Figure 9 and 10).

Midbrain: Tectum

The midbrain shows marked superior colliculi casts posterior to the confluence of the transverse sinus (Figures 2.1-2, 4.1, and 4.3). The midbrain seems to have been exposed with very little or no space between cerebrum and cerebellum. The tectum seems to be continuous superiorly and through between the cerebrum and cerebellum, unlike *Solenodon* or *Tenrec*, in which the tectum is exposed, but separated from both cerebrum and cerebellum (Figure 9, 10, 11, 12; see Discussion).

Casts of colliculi appear posterior to the confluence of the transverse and sagittal sinuses at the same level. Colliculi are not visible on all natural specimens, and are also not visible on the digital endocasts. The variation in presence or absence of colliculi casts seems to be an artifact of preservation, and indicates the low resolution of both the natural and digital endocasts in which they are not evident. However, they are suggested by the presence of impressions inside the osseous roof of the braincase (Figure 9). However, on the digital renderings, there is indication of only one set of colliculi, which most probably represents superior colliculi. Presumably, inferior colliculi were present in the living animal, as in all extant mammals, but not visible on the endocasts (Macrini

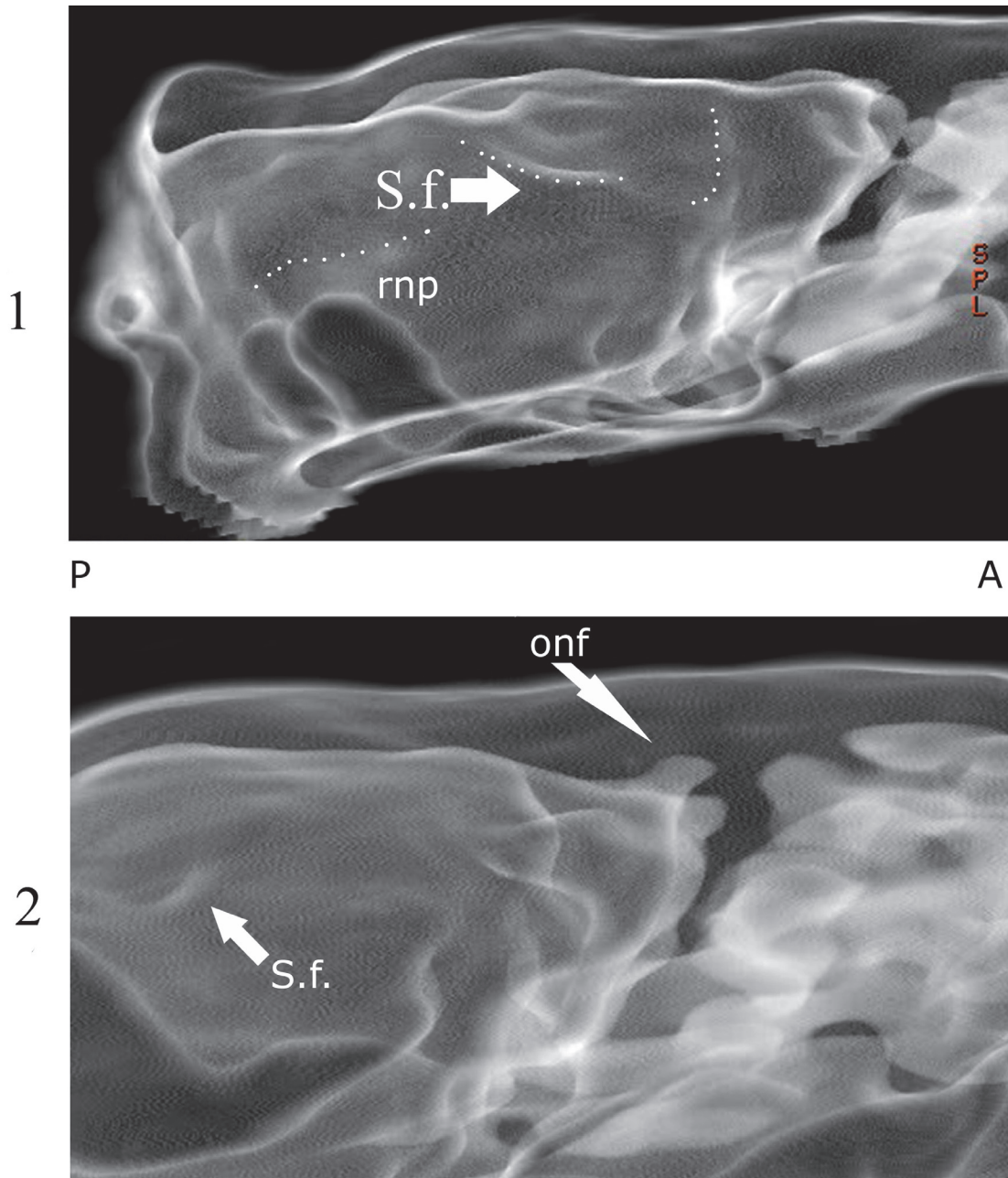


FIGURE 6. Volume rendering of *Nesophontes major* (C133) endocranial space in lateral (1) and oblique (2) views showing possible olfactory nerve fibers (**onf**), sylvian fissure (**S. f.**), and rhinal fissure (**rhf**). **A** and **P** stand for anterior and posterior.

pers. comm., 2012). There was no osseous tentorium in any of the specimens studied.

Hindbrain: Cerebellum

The cast of the cerebellum is large and as wide as the neocortex. The vermis's cast is thick, wide, and lies slightly higher than the rest of the cerebellum (Figures 2 and 4). Folia or fissures are not visible on either natural or digital casts of the cerebellum. There are two prominent casts of lat-

eral lobes (=cerebellar hemispheres), and paraflorculi. The casts of the paraflorculi are ovoid, much smaller than the cerebellar lobe and project laterally (Figures 2 and 4).

Endocasts extracted from *Nesophontes micrus* and *Nesophontes major* crania seem to be slightly different morphologically. The endocranial casts of *N. major* (C181) show a narrower cerebrum and cerebellum than those of *N. micrus* (C145). The tectum is wider and more conspicuous

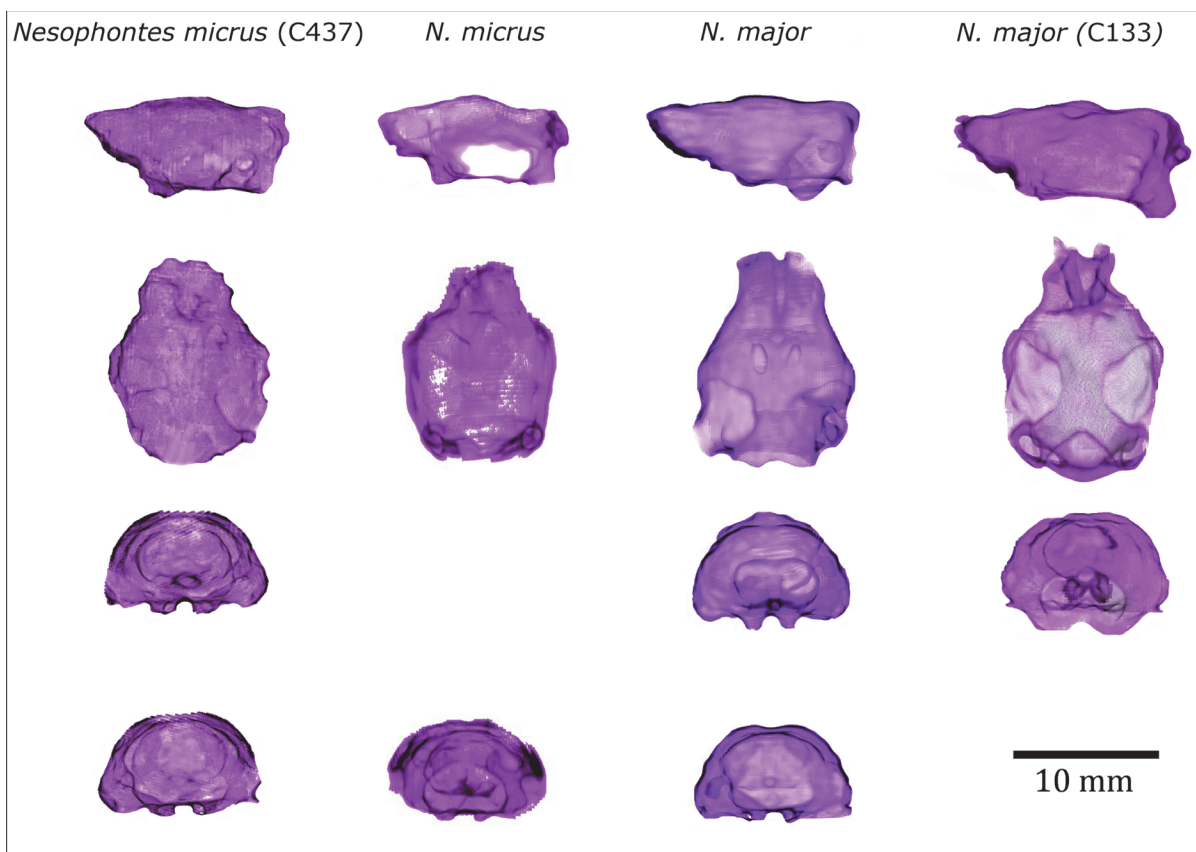


FIGURE 7. Endocranial casts of Cuban *Nesophontes* spp. *Nesophontes micrus* (C437) first column. Endocast volume: 0.580 mL, encephalization quotients (EQ 2 and 3): 0.21 and 0.33. *Nesophontes micrus* (C436), second column. Endocast volume: 1.231 mL, EQ 2 and 3: 0.33 and 0.52. *Nesophontes major* (270), third column. Endocast volume: 0.729 mL, EQs: 0.27 and 0.43. *Nesophontes major* (C133), fourth and last column. Endocast volume: 0.888 mL, EQs: 0.36 and 0.57.

in *N. micrus* than in *N. major* (Figure 9). The cerebrum and the vermis are wider and rounder in *N. micrus* (C145). The colliculi impressions on the braincase are deeper and slightly more separated in *N. major* than in *N. micrus*. The confluence of the transverse sinus appears to be deeper and wider in *N. major*. Differences are visible in the x-ray images and inner molds of their braincase (Figures 1.3 and 9).

Measurements and EQ Values

The volume of all endocasts was estimated between 0.76 and 1.23 ml, which suggest a brain mass of nearly, or slightly heavier than 1 g ($\approx 1 \text{ g/cm}^3$). Encephalization quotients calculated from Eisenberg's (1981) equation (EQ^3) ranged between 0.33 and 0.57 ($n=4$; $\text{mean}=0.46$) for both species. The EQ estimates calculated with Jerison's (1973) formula (EQ^2) are slightly smaller with values between 0.21 and 0.36 ($n=4$; $\text{mean}=0.29$) (Table 1) and Figure 12 (Appendix). Of these, and

despite the overlap, *Nesophontes major* seem to have larger EQ scores, probably due to their larger brain mass and volume.

Discussion

This study supports that the endocranial morphology of *Nesophontes* resembles that of placental, insectivore-grade mammals, especially the lipotyphlans. Within this clade, it is most morphologically similar to *Solenodon* despite their different molar morphology (Figure 12). Unfortunately, because endocranial casts of juvenile specimens were not available, developmental variation was not studied.

The olfactory lobes seem continuous in the digital endocasts, but are markedly separated by the circular fissure in natural endocasts and lateral radiographs (Figures 1.1, 1.3, and 4.2). Casts of olfactory nerve fibers are visible only on digital casts and could be negative renderings of the cribroethmoidal foramen (cef) (Figure 6). Such an

TABLE 1. Linear and volumetric mean values of *Nesophontes* natural and digital endocasts.

¹ Total cranium length range (minimum and maximum) taken from *N. major* (n = 24) and *N. micrus* (n = 12) from the same assemblage. * Estimated body mass calculated from the relationship $y = 3.68x - 3.83$, where $y = \log_{10}$ (body mass in grams), and $x = \log_{10}$ (skull length in mm) following Luo et al. (2001) and Rowe et al. (2011); EQ² formula from Jerison (1973), and EQ³ formula from Eisenberg (1981). Greater than (>) and less than (<) signs used are to indicate measurements on incomplete specimens. The number given after the sign is the minimum measurement that was taken on the specimen. The labels L (=left) and R (=right) are applied to the measurements of bilateral structures such as the olfactory lobes.

Measurement	<i>N. micrus</i>	<i>N. major</i>	<i>N. major</i>	<i>N. micrus</i>
	(C145)	(C181)	(C133)	(C436)
	Natural Endocasts		Digital Endocasts	
Cranium length (mm) from specimen	> 27.5	> 31.0	32.1	28
Cranium length min. (mm) ¹	26.9	30.3	30.3	26.9
Cranium length max. (mm) ¹	29.1	32.5	32.5	29.1
Estimated body mass (g)*	97.37	110.2	114.3	99.21
Estimated body length (mm)	≈ 110-135	≈ 120-140	≈ 120-140	≈ 110-135
y=Log10 value* (Body mass units)	1.99	2.04	2.05	2
x=Log10 value* (Cranial length)	1.44	1.49	1.51	1.45
Estimated endocast volume (ml)	> 0.76	1.09	0.888	1.231
Calculated endocast volume (ml) (from formula)	0.844	0.997	1.043	0.856
Endocast total length (mm)	> 14.48	> 15.18	15.2	14
Endocast total width (mm)	9.86	9.65	9.4	9.7
Olfactory bulb length (mm)	3.65 - 3.69	R 3.60	L 3.0 - R 3.1	incomplete
Olfactory bulb width (mm)	7 (both)	R 3.86	6.4 (both)	incomplete
Cerebellum length (mm)	5.97	4.58 - 5.22	6.2	5.9
Cerebellum width (mm)	7.45 - 8.4	7.32	7.7	7.4
Brain-Cranium length ratio	52.6	49	47.3	50
Encephalization Quotient (EQ) ²	0.33	0.35	0.36	0.33
Encephalization Quotient (EQ) ³	0.52	0.56	0.57	0.52

intricate system of cribriform foramina is reminiscent of *Solenodon* as illustrated in Wible (2008, figure 23).

The neocortex of *Nesophontes* is ovoid and nearly lissencephalic in both the natural and digital endocasts. There are faint indications of sylvian and rhinal fissures (Figures 2.2, 5, and 6). Gyrencephalic brains of mammals, such as apes, are known to produce lissencephalic endocasts due to the covering of thick meninges (Clark, 1959; Macrini et al., 2007a). Presently, gyrification is correlated with brain mass and size (Pillay and Manger, 2007). The low gyrification seen in endocranial casts of *Nesophontes* is plausibly an artifact of its small brain size and mass (Martin, 1981; Pillay and Manger, 2007).

The traces of the rhinal fissure in *Nesophontes* separates the neocortex from the olfactory cortex very low and laterally as in *Solenodon*, but not

as superiorly as in *Erinaceus* or *Tenrec* (Figure 12) (Leche, 1907; Allen, 1910; Stephan and Andy, 1982). The orbitotemporal groove seen on natural and digital endocasts (Figures 2, 3, and 5) marks the location of the rhinal fissure and suggests that the olfactory cortex was lower in the neocortex than the extant lipotyphlan *Sorex*, *Blarina*, and *Scalopus*. Overall, it resembles the extent observed in *Solenodon* and *Condylura* (Stephan and Andy, 1982).

Exposed colliculi are reported for most tenrecids and ericnaceids (Clark, 1932; Stephan et al., 1991; Orliac et al., 2012). In the afroinsectivoran *Tenrec*, and the lipotyphlans *Ericaceus*, *Sorex*, and *Condylura*, the tectum is not superiorly continuous with the cerebellum. Instead, it arises, exposed, from under the neocortex (telencephalon) to join the cerebellum. There is a small gap between the telencephalon and the cerebellum in three men-

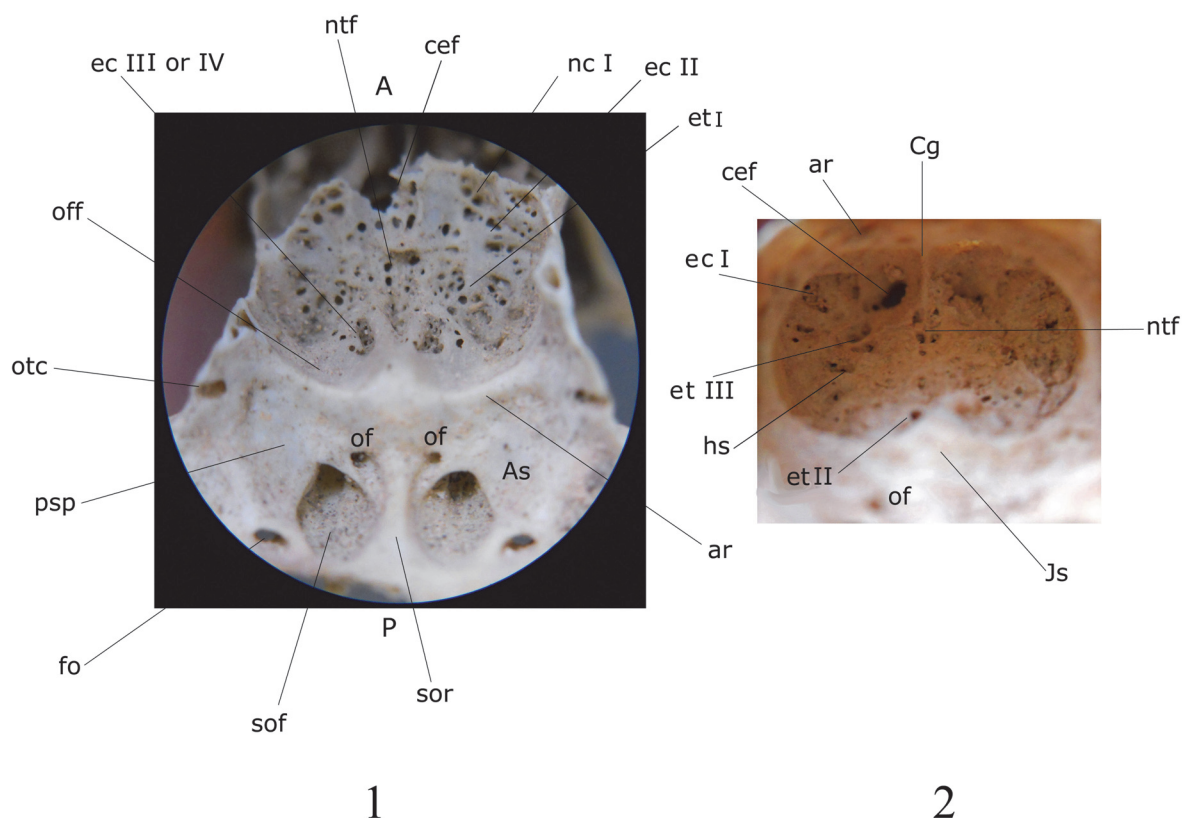


FIGURE 8. Cribriform and olfactory regions in *Nesophontes major* (1) and *Nesophontes micrus* (2). Abbreviations: **ar** annular ridge; **As** alisphenoid; **cef** cribroethmoidal foramen; **cg** crista galli; **ec** ectoturbinal foramina; **etI** ethmoturbinal foramina; **fo** foramen ovalae; **hs** horizontal sulcus; **Js** jugum sphenoidalis; **nc** nasocribriform foramina; **ntf** nasoturbinar foramina; **of** optic foramen for optic nerve; **off** olfactory fossa; **otc** orbitotemporal canal; **psp** parasphenoid plate; **sof** sphenorbital fossa; **sor** sphenorbital ridge. **A** and **P** stand for anterior and posterior.

tioned species, where the tectum is nearly totally exposed, and thus visible (Stephan and Andy, 1982; Macrini et al., 2007 b; Figures 9 and 10). Conversely, the tectum in *Nesophontes* is not as exposed as in *Solenodon*, *Erinaceus*, or *Tenrec* (Figures 10, 11, and 12). Natural endocasts suggest a slight and shallow gap between *Nesophontes*'s telencephalon and cerebellum (Figures 2 and 4.3), in which the tectum is not completely exposed. In the endocranial casts of *Nesophontes* only one set of colliculi casts are visible (Figures 10 and 11). These were presumably present, but hidden under the telencephalon or cerebellum, or poorly preserved in the endocranial casts studied. The state of *Nesophontes* resembles that of *Solenodon paradoxus* as shown in Allen (1910) and Stephen and Andy (1982) in which the tectum is exposed superiorly, but one set of colliculi are covered by the neocortex.

The endocranial casts of *Nesophontes* resembles that of the extinct condylarth *Hyopsodus* and

the palaeoryctid *Eoryctes* in being nearly superiorly continuous, and having partially or totally exposed colliculi (Figures 10 and 11). The gap between the tectum and cerebellum was not wide enough to expose all sets of colliculi in *Nesophontes*. This state, as observed in *Nesophontes* endocasts, is intermediate with that present in *Tenrec* (totally exposed) and *Microgale* or *Sorex* (totally hidden) (Figures 11 and 12). In *Tenrec*, there is a wide gap between the posterior part of the cerebral hemispheres and the cerebellum from which the midbrain appears, exposing the tectum (Figure 12). In *Microgale*, however, there is no gap between the neocortex and the cerebellum. This feature seems hidden in *Sorex*, *Blarina*, and *Scalopus* (Figure 12).

Tectum exposure of the midbrain is correlated with a slight neocortical extension, and secondary sensory specialization as documented in bats (Edinger, 1964; Orliac et al., 2012). Yet, this exposure usually leaves faint, if any, marks on the braincase (Orliac et al., 2012). However, there are slight

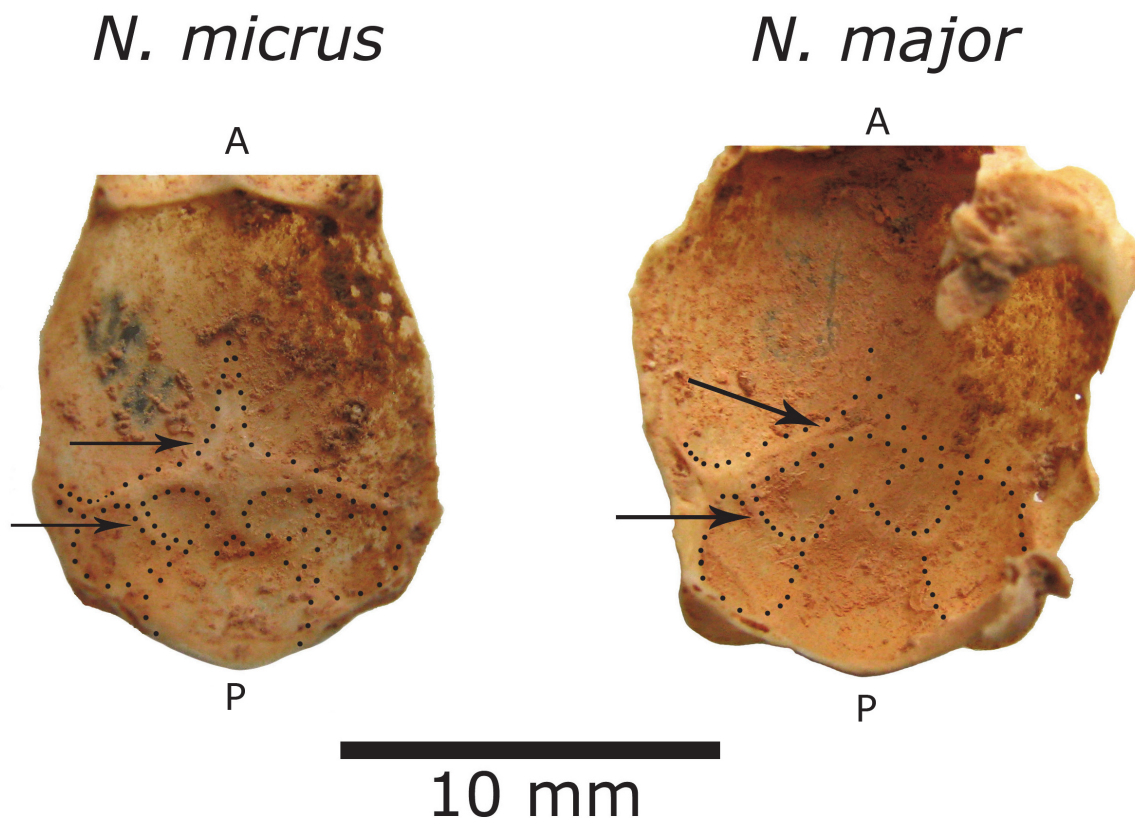


FIGURE 9. Endocranial morphology of *Nesophontes micrus* and *Nesophontes major* calotte showing slight differences in tectum and transverse sinus. Top arrows point to the confluence of the transverse sinus and the colliculi fossae. **A** and **P** stand for anterior and posterior.

collicular imprints inside of the *Nesophontes* braincase (Figure 9). The slight differences noted between *N. micrus* and *N. major* endocranial casts lie especially in the neocortex and tectum. The neocortex of *N. micrus* is slightly wider, with more visible sylvian and rhinal fissures, plus orbitotemporal groove (otg). The confluence of the transverse sinus is less angled, deeper, and wider in *N. micrus*. The superior colliculi seem more pronounced in *N. micrus* (Figure 9). Unfortunately, there is not enough evidence now to support that these differences are of interspecific value considering the high level of intraespecific variation in *Nesophontes* (Figure 7) (Silva-Taboada et al., 2007 and literature cited therein).

Cerebellar hemispheres or lateral lobes, vermis and paraflocculus are all visible in the endocranial casts of *Nesophontes* as in other placentals (Macrini et al., 2007 b; Rowe et al., 2011). Widening of the cerebellar hemispheres, and distinction between its parts in *Nesophontes*'s casts, resemble *Solenodon* and tenrecids in general. The casts of the vermis are not round and centrally located

such as that of the stem therian *Vincelestes*, but are elevated and medially located like those of *Solenodon*, *Erinaceus*, and *Sorex* (Figure 12) (Stephan and Andy, 1982; Macrini et al., 2007 b). Unfortunately, casts of the paraflocculi were not all complete, but indications on natural and digital casts suggest that these were round structures, projecting postero-laterally and low in the cerebellum (Figures 2.1, 4.1, and 5.1). Future study on the ear structure of *Nesophontes* can shed light on the relationship between the paraflocculi and the semi-circular canal within the inner ear.

Characters such as enlargement and widening of the cerebellum with marked cerebellar parts are considered derived conditions in ancestral therians (Kielan-Jaworowska et al., 2004; Rowe et al., 2011). The neocortex covering of the midbrain tectum is apparent in many different lineages of extant mammals; such dorsal exposure of the tectum is considered a likely condition of ancestral or early mammals (Kielan-Jaworowska et al., 2004; Macrini et al., 2007 b).

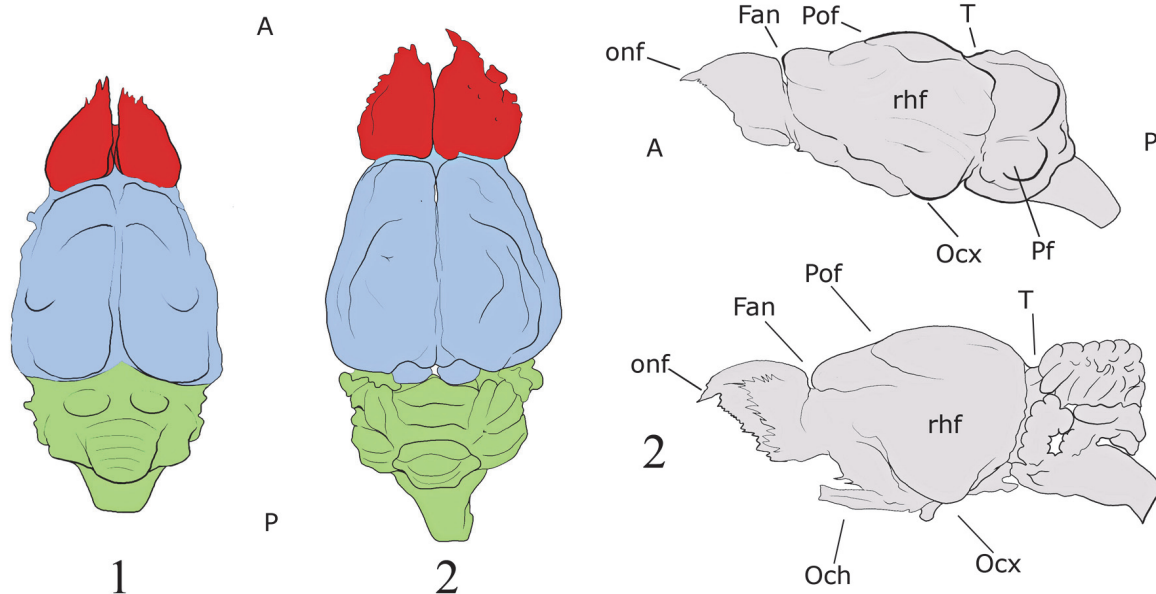


FIGURE 10. Idealized brain reconstruction of *Nesophontes* spp (1), and *Solenodon paradoxus* (2) in superior and lateral views. The brain of *Nesophontes* is a composite reconstruction based on natural and digital casts. *Solenodon paradoxus* was drawn from photographs of Stephan and Andy (1982:541, figures 20-22). Lines and labels on the lateral views indicate similar morphologic features. Olfactory lobes are in red, neocortex is in blue, and posterior brain (part of midbrain and cerebellum) is in green. Specimens are not to same scale. Abbreviations: **Cb** cerebellum; **cs** superior colliculi; **Fan** annular or circular fissure; **lar** internal auditory region; **lal** lateral lobe of cerebellum; **las** lateral transverse sinus; **Ncx** neocortex; **Ob** olfactory lobes; **Och** optic chiasm; **Ocx** olfactory (=piriform) cortex; **onf** olfactory nerve fiber; **otg** orbitotemporal groove; **Pfl** paraflocculus; **Pof** post-orbital fissure; **rhf** rhinal fissure; **sas** sagittal sinus or longitudinal sinus; **Sphr** sphenorbital region; **Sv** confluence of the transverse and sagittal sinuses; **T** tectum; **Vc** cerebellar vermis. **A** and **P** stand for anterior and posterior.

For comparative purposes with older methodology and literature, encephalization quotients (EQ) of insectivoran-grade mammals are compared to that of *Nesophontes*. These “progressive insectivorans” are said to be progressive because of larger brains, and higher EQ estimates related to specialized behavior seen in fossorial and semi-aquatic adaptations (Stephan and Andy, 1982). The EQ estimates for both *N. micrus* and *N. major* lie below those for the “evolved insectivorans” of Bauchot and Stephan (1967), and are intermediate to the “progressive insectivores” of Stephan and Andy (1982), and most of the crown mammals in Rowe et al. (2011). The “progressive insectivores” of Stephan and Andy (1982) included the following taxa: *Desmana*, *Talpa*, and the semiaquatic *Potomogale*, whereas *Solenodon*, *Oryzoryctes*, and *Microgale* were considered “slightly progressive” or intermediate between groups. *Nesophontes* EQ values lie within the range of the extant *Solenodon paradoxus*, *Erinaceus* spp., plus the marsupials *Monodelphis* and *Didelphis*. Their range is also

comparable to the extinct multituberculate *Kryptobaatar*, *Chulsanbaatar*, and the also extinct primitive eutherian *Asioryctes*, but is larger than the stem therian *Vincelestes* and the primitive eutherian *Kennalestes* (Kielan-Jaworowska et al., 2004; Rowe et al., 2011).

Especial Comparison with *Solenodon*

Except for their difference in size and dentition, the brain and facial anatomy of *Nesophontes* is similar to that of tenrecids, and even more so to *Solenodon* (Figure 11). This similarity extends to cranial rostral musculature and its osseous morphology (Anthony, 1918; McDowell, 1958; Asher, 2001). These similarities seem to suggest *Nesophontes* and *Solenodon* are ecomorphs. The faci-maxillary morphology of *Nesophontes* is similar to that of *Solenodon* in having similar muscular arrangements, cranial osteology, and grooved anterior dentition. In *Nesophontes*, the maxillary canines are grooved. In *Solenodon*, the second inferior incisor (i2) is grooved for venom delivery

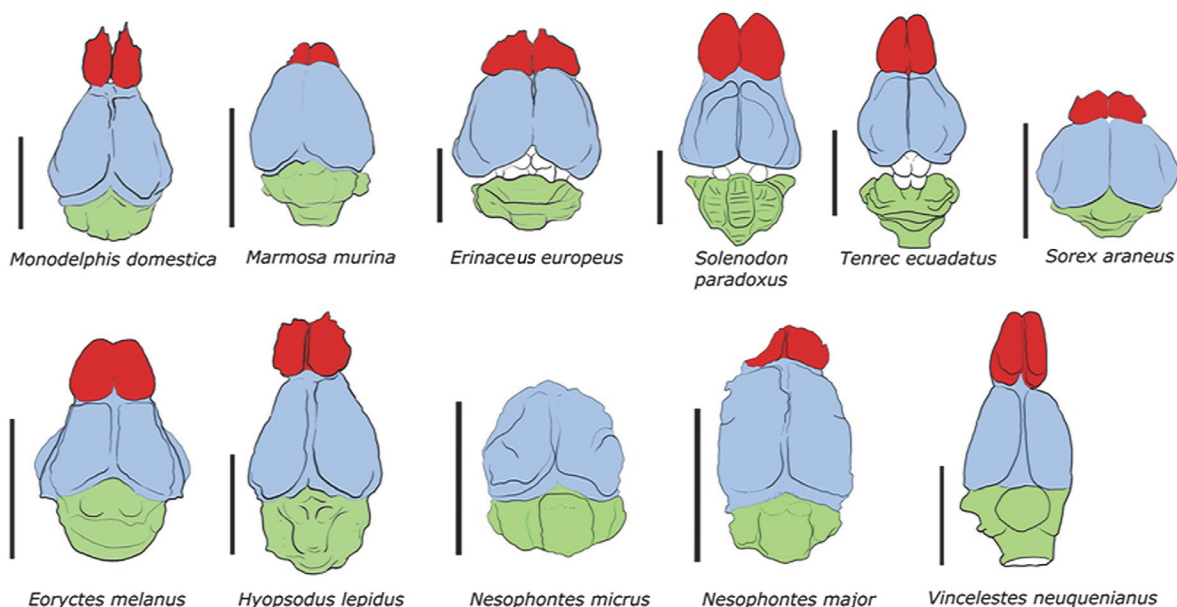


FIGURE 11. Brain morphology of selected extinct and extant mammals, including *Nesophontes* spp. Upper row contains extant placentals and marsupials. Lower row contains extinct taxa and *Nesophontes*. Olfactory lobes are in red, neocortex is in blue, and hindbrain is in green. Scale bar equals 10 mm. Sources: *Monodelphis domestica* drawn from Rowe et al. (2011); *Solenodon paradoxus* from Allen (1910); *Tenrec ecuadatus* from Stephan and Andy (1982); *Eoryctes melanus* from Thewissen and Gingerich (1989); *Hyopsodus lepidus* from Orliac et al. (2012); *Vincelestes neuquenianus* from Macrini et al. (2007a) *Nesophontes* taxa reported here, and the remaining from the Comparative Brain Collection at www.brainmuseum.org. **A** and **P** stand for anterior and posterior. Scale bar = 1 cm.

(Gundlach, 1877; McDowell, 1958; Silva-Taboada et al., 2007; Ligabue-Braun et al., 2012). The similar characteristics include pronounced faciomaxillary musculature scars for the levator labii, levator labii, and erector vibrissarum on the superior-lateral aspects of the maxilla (Allen, 1910; MacDowell, 1958; Wible, 2008). Other characters, such as the absence of accessory bulbs on olfactory lobes and the presence of prootic canal seem to be unique states in *Solenodon* and *Nesophontes* in comparison to other lipotyphlans (Stephan and Andy, 1982; Wible, 2008). Casts of the olfactory lobes in *Nesophontes* do not show presence of accessory olfactory lobes, as also not reported for *Solenodon* (Stephan and Andy, 1982: 540). In addition, *Nesophontes* has a double prootic canal (canalis prooticus), whereas *Solenodon* has a single canal (Wible, 2008). Prootic canals are not reported from other placental mammals, but have been widely reported in Cenozoic mammaliaforms (Wible, 2008).

Behavioral and Ecologic Inferences

By considering the marked similarities of the nesophontid endocranium with those of *Solenodon* and the *Tenrec* it is possible to deduce its sensitiv-

ity to auditory and olfactory stimuli. Barton and colleagues (1995) showed that nocturnal species tended to have larger olfactory structures than diurnal species; fossorial species had smaller optic nerves than those of non-fossorial adaptations. They did not find optic nerve size exclusive of either nocturnal or diurnal adaptation. The marked development of the olfactory lobes and superior colliculi in *Nesophontes* suggests that it lived in habitats where olfaction and acoustic capabilities were crucial (Scalia and Winons, 1975; Catania, 2005). *Nesophontes* was probably nocturnal, as indicated by its abundance in owl pellet remains (Silva-Taboada et al., 2007) and fossorial as suggested by its minute optic nerve foramen (0.27-0.58 mm, n= 8) (Barton et al., 1995), plus well-developed auditory and tactile systems as in other mammals adapted to nocturnal environments (Jerison, 1973; Scalia and Winons, 1975; Kielan-Jaworowska et al., 2004; Catania, 2005). The presence of superior colliculi suggests that the vision of *Nesophontes* was probably not as poor as in other lipotyphlans (e.g., *Sorex*) (May, 2005). Instead, it implies that *Nesophontes* depended on inputs from the retina and from head- eye movements such as seen in the gazing, foraging, and defensive behav-

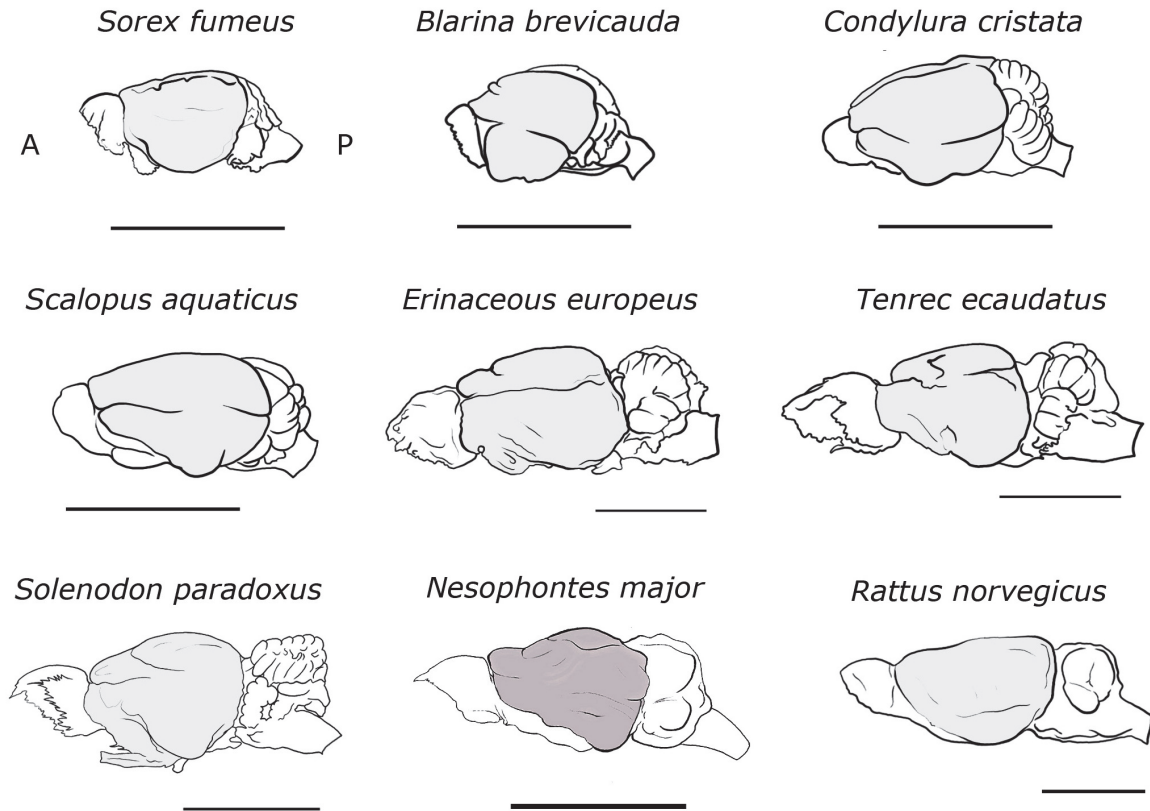


FIGURE 12. Idealized brain reconstruction of *Nesophontes major* compared to other insectivorous mammals, plus the Norway rat *Rattus norvegicus*. *Sorex*, *Blarina*, *Condylura*, *Scalopus*, and *Rattus* specimens were redrawn and modified from specimens in the Comparative Brain Collection at www.brainmuseum.org and Sarko et al. (2009). *Erinaceus*, *Tenrec*, and *Solenodon* were drawn from Stephen and Andy (1982). **A** and **P** stand for anterior and posterior. Scale bar = 1 cm.

ior of *Solenodon* and *Tenrec* described by Eisenberg and Gould (1966) and Stephen and Andy (1982). *Nesophontes* probably had a long, mobile nasal snout with movable vibrissae or whiskers for foraging and the detection of prey similar to that of *Solenodon*, *Hemicentetes* and *Tenrec*, (True, 1886; Beddard, 1901; Allen, 1910; McDowell, 1958; Eisenberg and Gould, 1966; Wible, 2008). Altogether, most of these characteristics suggest that *Nesophontes* was most likely nocturnal, terrestrial, and probably a very specialized fossorial insectivorous mammal. Moreover, the scars for the levator labii and erector vibrissarum in the maxilla of *Nesophontes*, as in *Solenodon* (Allen, 1910; Jolicœur et al., 1984; Sánchez-Villagra and Asher, 2002; Catania, 2005), suggest the use of vibrissae and mobile snouts in similar foraging and defensive behavior.

With the available endocasts it is not possible to infer whether *Nesophontes* used echolocation as reported for many lipotyphlans (Eisenberg and Gould, 1966; Orliac et al., 2012). Pathway connec-

tions between superior colliculi and optic layers have been supported by Lee and Hall (1995). The relationship of visual-motor guidance involved in eye/head movement and the development of superior colliculi has been compared to those of fructivorous megabats, monkeys, and in echolocating mammals such as microbats and several shrews (Valentine et al., 2002; Silcox et al., 2011; Orliac et al., 2012). Alternatively, the trace of these structures on the endocasts of *Nesophontes* indicates poor development of its cerebral hemispheres (Kielan-Jaworowska et al., 2004; May, 2005), but not vision directly.

Study Limitations

The study presented here is limited by several factors, but most especially by preservation. The detail of the natural endocasts in this case depended on taphonomic processes, such as the fragmentation of the fossil crania, and the extent to which the braincase filled with sediment during

burial. Complete compaction and hardening of finer clay inside the braincase would have resulted in better casts. Most of the natural endocranial casts studied were incomplete.

The study of the digital endocasts reported here is also limited by their relatively low resolution, a result of equipment selection and the small size and density of *Nesophontes* crania. Specimens were scanned and reconstructed from data acquired with a multidetector CT (MDCT) designed for humans, and not from micro-computed tomography (micro-CT). Micro-CT would allow for the rendering of higher resolution casts due to their acquisition of thinner slices (Abel et al., 2012). Additional scanning with such better technology is already part of a future study to understand the morphological variation of the genus. The volume rendering of *Nesophontes* endocasts are based on an “air-structure” algorithm designed to visualize air-filled cavities, which allows only for the reconstruction of negative impressions inside the braincase, and can help approximate the original brain structures (Abel et al., 2012). The absence of a feature on these endocasts cannot be considered as indication of the nonexistence of such a feature. All scanned specimens are included in Figure 7 for further comparison.

Nevertheless, despite the limitations, studies have shown that the digital and natural endocranial casts give a fairly accurate approximation of brain morphology (Edinger, 1949; Macrini et al., 2007b; Abel et al., 2012). The measurements and morphology recorded from *Nesophontes*'s digital endocasts are congruent with those observed in the natural endocasts. Together, the two types of endocasts provide an unreported approximation of *Nesophontes* endocranial characteristics that are comparable to other extinct and extant taxa (Macrini et al., 2007a; Jerison, 2009; Abel et al., 2012)(Figures 7, 11, and 12).

Conclusions

The endocranial morphology of *Nesophontes* spp. reported here allows for a generalized inference of their ecology, behavior, diversity, and evolution. Additionally, it adds data to the developing corpus of evidence on mammalian brain evolution in extant and extinct forms (see cited literature in Bauchot and Stephan, 1967; Macrini et al., 2007a; Jerison, 2009; Rowe et al., 2011).

Brain characters observed in the natural and digital endocranial casts of *Nesophontes* suggested that this taxon was probably as specialized as the lipotyphlan *Solenodon*, with well-developed

olfactory, auditory, and tactile senses that are most likely associated to nocturnal habits. *Nesophontes* was most likely terrestrial and fossorial. Like *Solenodon* and *Tenrec*, it had a sensible mobile snout (proboscis) used as tactile and olfactory to sense its environment. However, with the present data, it is not possible to deduce whether *Nesophontes* used echolocation, like it has been documented for *Solenodon* and other insectivoran-grade mammals (Eisenberg and Gould, 1966; Orliac et al., 2012).

The endocranial morphology of *Nesophontes* is most similar to that of other lipotyphlans, especially *Solenodon*, rather than erinaceids, soricids, and talpids (Figure 12). Encephalization quotients and general brain characteristics superficially support its phylogenetic association to basal insectivoran-grade mammals and lipotyphlans. Foremost, the morphological similarities of *Nesophontes* to species that are considered “primitive” within the clade such as *Solenodon* and erinaceids incipiently support its position among other basal Holarctic insectivorans, where *Nesophontes* seems to be a sister taxon of a *Solenodon*-talpid-soricid clade (Robles et al., 2004; Asher et al., 2005; Douady and Douzery, 2009).

The future availability of better preserved natural endocasts and the scanning of the remaining Antillean taxa can help confirm these initial conclusions about nesophontid brain morphology and derived characteristics. Furthermore, such data can help detect interspecific differences between all other Antillean *Nesophontes* and help resolve the slight differences detected between the natural and digital endocasts. Such data can help reconstruct the relationship of Nesophontidae to other mammals, especially to other extinct insectivorans, and their evolution in the Antilles.

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APPENDIX

List of endocranial character states from *Nesophontes* (several characters were adopted and modified from Macrini et al., 2007a).

Character 1

Olfactory bulb cast percent composition: 6% or greater = 0; less than 6% = 1

Nesophontes olfactory lobe percent composition from total brain volume ranges from 20-25% (score of = 0). *Nesophontes* approaches the overall percent composition of *Tenrec* and *Hemicentetes* the most (Stephan and Andy, 1982). That of *Solenodon* is 17.95%, and from other insectivorans reported by Stephan and Andy (1982).

Character 2

Width to length ratio of olfactory lobes: longer than wide (aspect ratio < 0.9) = 0; wider than long (aspect ratio > 1.1) = 1; equivalent (aspect ratio between 0.9 and 1.1) = 2. *Nesophontes* sp. scores = 2.

Character 3

Accessory olfactory bulb casts: absent=0; present=1.

Accessory olfactory bulbs are not always present in the endocranial casts of extinct or extant mammals (Bauchot and Stephan, 1967; Macrini et al., 2007a). Stephan and Andy (1982) reported "no accessory bulbs" on the olfactory lobes of *Solenodon paradoxus*. This state is scored = 0 here, was considered unique in *Solenodon* in comparison to other insectivoran-grade mammals such as *Erinaceus*, *Sorex*, *Tenrec*, *Hemicentetes*, and *Microgale*. It also scores = 0 in *Nesophontes*.

Such accessory bulbs apparently receive nerve fibers (or projections) from the vomero-nasal organ and are involved in the detection of pheromones (Nieuwenhuys et al., 1998; Macrini et al., 2007a).

Character 4

Olfactory bulb tracts (or peduncles): not visible on endocasts = 0; visible on endocasts = 1. *Nesophontes* sp. scores = 1.

Character 5

Circular fissure: Absent or shallow on endocast = 0; marked or deep on endocast = 1. *Nesophontes* sp. scores = 1.

Character 6

Surface of cerebral hemisphere endocasts: lissencephalic or smooth = 0; gyrencephalic or convoluted = 1. *Nesophontes* sp. scores = 0.

Character 7

Rhinal fissure seen on endocast: not visible or absent = 0; visible or present on endocast = 1. *Nesophontes* sp. scores = 1.

Character 8

Lateral extent of the cerebral hemisphere cast: medial to or even with the parafloccular casts = 0; clearly extending laterally beyond the parafloccular casts = 1. *Nesophontes* sp. scores = 1.

Character 9

Cast of the superior sagittal sinus: not visible on dorsal surface of the endocast = 0; visible = 1.

Nesophontes sp. scores = 1. Note: this character is often not visible on endocasts if located deep or thickly covered by the meninges (Macrini et al., 2007a).

Character 10

Ossified falx cerebri: absent = 0; present = 1. *Nesophontes* sp. scores = 0.

Character 11

Ossified tentorium: absent = 0; present posteromedially = 1; present laterally = 2; completely present = 3. These stages are explained in Macrini et al. (2007a). *Nesophontes* sp. scores = 0.

Character 12

Wide gap between the neocortex and cerebellum casts: absent = 0; present = 1. *Nesophontes* sp. scores = ? But probably = 1.

This character is problematic in *Nesophontes* because there are slight discrepancies between the natural and digital endocasts. Natural endocasts show a slight indentation or gap between the neocortex and cerebellum that seems very shallow in the digital endocast. However, imprints within this region of the osseous braincase support a shallow gap between these structures.

Character 13

Extent of the tectum and colliculi casts: below = 0; at the same level of the vermis = 1; above = 2. *Nesophontes* sp. scores = 1.

Character 14

Extent of vermis cerebelli: cast of vermis extending to or even with the parafloccular casts = 0; vermis remains behind the parafloccular casts = 1; vermis extends beyond parafloccular casts = 2. *Nesophontes* sp. scores = 2.

Character 15

Extent of cerebellar hemisphere casts not visible on endocasts = 0; visible = 1. *Nesophontes* sp. scores = 1.

Character 16

Shape of parafloccular casts: cone-shaped = 0; broad and round = 1; ovoid, large, and oriented posterolaterally = 2; long and cylindrical = 3. *Nesophontes* sp. scores = 2.

Character 17

Prootic canal visible on squamosal bone of the skull (character taken from Wible, 2008): absent = 0; present = 1. Both Cuban *Nesophontes* score = 1. The orbitotemporal groove may be associated

with this structure in *Nesophontes*, as it is in *Solenodon* (**ecps**: Wible, 2008: figure 21, p. 349).

Prootic canals are not known from any other placental mammal. They are reported from Mesozoic mammaliaforms and several Cenozoic eutherians, monotremes, and some marsupials. See Wible (2008) for discussion of this character and literature.

Character 18

Canal for carotid arteries relative to the hypophysis: posterolaterally positioned = 0; anterolaterally positioned = 1. *Nesophontes* sp. scores = 0.

Character 19

Orbitotemporal groove not visible over periotic portion of squamosal cast = 0; visible on endocast = 1. *Nesophontes* sp. scores = 1. This groove can represent the cast of a meningeal vessel.

Character 20

Nasoturbinal foramina located inferior to ectoturbinal foramina II not on a depression = 0; on depression = 1. *Nesophontes* sp. scores = 1.