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SKULL ANATOMY AND NEUROMORPHOLOGY OF *HYPSOSTEIROMYS*, A COLHUEHUAPIAN ERETHIZONTID RODENT FROM ARGENTINA

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ABSTRACT—A relatively complete skull of *Hypsosteiromys* with a well-preserved natural cranial endocast was recovered from the Colhuehuapi Member, Sarmiento Formation (lower Miocene) at Gran Barranca, Chubut Province, Argentina. The only known skull of this genus, it differs from those of other erethizontids because it is continuously very low, the ascending ramus of the premaxillae extends behind the posterior margins of the nasals, and the external auditory meatus has a ventral furrow. Comparison of the endocast with the brains of extant Erethizontidae demonstrates remarkable neuromorphological homogeneity, despite differences in size. Erethizontid brains have rounded, telencephalic hemispheres with prominent frontal lobes and small olfactory bulbs, and lack temporal lobes and neocortical sulci. Thus, the Gran Barranca skull shows that the external neuromorphology of erethizontids has not changed substantially since at least the early Miocene.

INTRODUCTION

South American porcupines of the family Erethizontidae are one of the most primitive groups of hystricognath rodents (Wood and Patterson, 1959; Bryant and McKenna, 1995; Candela, 1999). This makes them important in understanding the origin and evolutionary history of the South American Hystricognathi (‘‘caviomorphs’’). However, their relationships to other families of this suborder are poorly understood, although their separation from other South American and Old World Hystricognathi is well established (Patterson and Wood, 1982; Bryant and McKenna, 1995; Candela, 1999, 2000). In addition, available data on the natural history of extant species and the diversity, distribution, and biology of extinct taxa are limited. Erethizontidae are currently represented in South America by *Coendou*, *Echinoprocta*, and *Chaetomys* (Mares and Ojeda, 1982), though some authors only regard *Coendou* and *Chaetomys* (McKenna and Bell, 1997) or *Coendou* and *Echinoprocta* (Woods, 1993) as valid.

Erethizontidae are recorded in South America since the Deseadan Age (late Oligocene) (Wood and Patterson, 1959; Candela, 1999, 2000), and reached their highest diversity during the Colhuehuapian Age (early Miocene), with *Eosteiromys*, *Hypsosteiromys*, *Parasteiromys* (Vucetich, 1986; Candela, 1999), and an undescribed fourth genus (Candela, 2000). Currently, Neotropical erethizontids are strictly arboreal, but some of the fossil species from Argentina probably were not (Candela, 2000; Candela and Vucetich, 2002).

A well-preserved skull of *Hypsosteiromys* was found during fieldwork along the southern cliff of Lake Colhué Huapi, Chubut Province, in the Colhuehuapi Member of the Sarmiento Formation. It is the first known skull of this genus, and exceptional for its well-preserved natural cranial endocast; the first recovered for this family. The new skull is especially interesting because *Hypsosteiromys* is unique among the Erethizontidae in showing a slight tendency towards hypsodonty (Patterson, 1958; Candela and Vucetich, 2002), and because brain endocasts of rodents have rarely been studied. Patterson and Wood (1982:491) stated, ‘‘Endocasts, so far as we are aware, have never been described for fossil caviomorphs, so fossil and Recent Old World hystricognath brains can only be compared with those of Recent New World genera.’’ Dozo (1997a, b, c) recently described brain endocasts and neuromorphology for members of the ‘‘caviomorph’’ families Caviidae, Cephalomyidae, and Dasyproctidae.

The purposes of this study are to describe the cranial anatomy and neuromorphology of *Hypsosteiromys*, to compare them with those of other erethizontids, to compare the brains and cranial endocasts of living and fossil hystricognath rodents from the Old and New World; and to explore the potential use of neuromorphology in the analysis of the phylogenetic relationships of the Erethizontidae with other hystricognath rodents.

Abbreviations—**FMNH**, The Field Museum, Chicago, USA; **MPEF**, Museo Paleontológico ‘‘Egidio Feruglio,’’ Trelew, Argentina; **MTD**, private collection of M. T. Dozo.

MATERIALS AND METHODS

For the comparative study, we examined skulls and cranial endocasts of modern Erethizontidae (*Coendou bicolor*, *Echinoprocta rufescens*, *Erethizon dorsatum*) of the mammal collection of the Zoological Department of FMNH. Measurement of the skulls and endocranial casts are in Tables 1 and 2; specimen catalog numbers in Table 2. Brain endocasts of modern specimens from the families Dasyproctidae (*Dasyprocta*), Agoutidae (*Agouti*), Chinchillidae (*Lagostomus*, *Chinchilla*), Caviidae (*Dolichotis*, *Cavia*), Myocastoridae (*Myocastor*), Hydrochoeridae (*Hydrochoerus*), and Hystricidae (*Hystrix*, *Atherurus*) were also analyzed (Table 2). These data were supplemented with information from the Mammal Brain Collection Internet site of the University of Wisconsin (http://brainmuseum.org) and the literature (Brauer and Schober, 1970; Lavocat, 1973; Pilleri et al., 1984). Neuroanatomical terminology follows Butler and Hodos (1996); dental terminology follows Candela (1999).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tulberg, 1899
Family ERETHIZONTIDAE Thomas, 1897
Genus *HYPSOSTEIROMYS* Patterson, 1958
HYPSOSTEIROMYS sp.

Referred Specimen—MPEF-PV 6029, a nearly complete skull of a young adult individual with a complete dentition and

TABLE 1. Skull measurements of MPEF-PV 6029, *Hypsosteiromys* sp. (in mm) compared with other Erethizontidae.

	Hypsosteiromys sp.	*Coendou prehensilis*	*Coendou bicolor*	*Echinoprocta rufescens*	*Erethizon dorsatum*
Skull length*	~96	89.40	—	78.60	100.77
Diastema length	23.15	22.70	24.08	21.45	31.80
Rostrum height	17.22	25.65	—	20.30	31.70
Skull width at nasals level	20.67	24.09	—	16.25	20.80
Skull width**	47.24	42.75	46.75	37.00	48.40
Palate width at P4 level	6.34	6.07	5.10	4.30	3.30
Palate width at M2 level	9.84	8.20	7.65	7.95	12.50

*From the anterior end of the incisors to the preserved portion of the condyle.
**At the zygomatic arches, level with the paraorbital apophyses.

a well-preserved natural endocranial cast. The latter is exposed in dorsal and lateral view through a cross section of the skull.

Stratigraphic, Chronologic, and Geographical Occurrence—Colhuehuapi Member of the Sarmiento Formation. Puesto Almendra, southern cliff of the Lake Colhué Huapi, Chubut, Argentina. Colhuehuapian Age, early Miocene (Flynn and Swisher, 1995; Kay et al., 1999).

COMPARATIVE DESCRIPTION

Skull and Dentition

The skull is approximately the same size as that of the extant *Coendou prehensilis* (Table 1; Voss and Angermann, 1997), but much lower; the paranasal sinus is not inflated, and consequently, the dorsal profile is essentially flat (Fig. 1A). Paranasal sinus of the Colhuehuapian *Eosteiromys* (Ameghino, 1902), and the Santacrucian (early Miocene) *Steiromys* (Ameghino, 1887) is somewhat more inflated than that of *Hypsosteiromys*, but less than that of *C. prehensilis*, which is as inflated as that of the Huayquerian (late Miocene) *Neosteiromys* (Rovereto, 1914). Other fossil genera such as *Parasteiromys* (Ameghino, 1903), *Protosteiromys* (Wood and Patterson, 1959), *Microsteiromys* (Walton, 1997), and *Paradoxomys* (Vucetich and Candela, 2001) are known just by dentitions and mandibular fragments. The skull of *Hypsosteiromys* is narrower and longer than that of *C. prehensilis*, with the rostrum proportionally longer, and the orbit-temporal fossa smaller. The frontals of *Hypsosteiromys* are somewhat wider than the nasals, while they are substantially wider in *C. prehensilis*, and *Neosteiromys*. In this character, *Hypsosteiromys* is more similar to *Steiromys* and *Eosteiromys* (Candela, 2000). Nasals are long and almost flat, with the posterior ends rounded. The nasals in *Eosteiromys*, *Steiromys* and *Neosteiromys* are both transversely and anteroposteriorly convex. Unlike the other erethizontids, the ascending ramus of the premaxilla extends clearly behind the nasals. The lacrimal is small, but larger than in *C. prehensilis*. Postorbital process is as large as that of *Steiromys*, *Eosteiromys* and *Neosteiromys*, and larger than that of *C. prehensilis*. Frontals show a slight deepening in the middle dorsal area; their posterolateral margins show a marked post-orbital constriction. Frontoparietal sutures diverge anterolaterally from their origin. Zygomatic arches in dorsal view are straight and diverge posteriorly (Fig. 1C).

The incisor foramina are small, limited posteriorly by the maxillaries (Fig. 1B). Unlike *C. prehensilis*, the fossa behind these foramina is deep and wide as in *Steiromys* and *Eosteiromys*. The diastemal crest extends anteriorly from the anterior alveolar margin of the P4, terminating near the premaxillary-maxillary suture. The posterior margin of the ventral zygomatic root is located at the level of the P4, curving posteriorly very close to the dental series. Masseteric tuberosities are weakly developed, less than in *Steiromys* and *Eosteiromys*. The tooth rows are subparallel, slightly diverging posteriorly, and separated by a wide palate. Palatines extend anteriorly to the middle of the M1. The edges of the mesopterygoid fossa are missing. The posterior zygomatic roots are slender, less robust than in *Steiromys*, *Eosteiromys* and *Neosteiromys*. Pterygoid fossae are smaller and narrower than in *C. prehensilis*. The oval foramen is small, though clearly distinguishable. Bullae are slightly pos-

TABLE 2. Measurements (in cm) of cranial endocasts of Hystricognathi (**APL**, anteroposterior length; **THL**, telencephalic hemisphere length; **OBW**, olfactory bulbs width; **MTW**, maximum telencephalic width; **CW**, cerebellum width).

Specimens	APL	THL	OBW	MTW	CW
Hypsosteiromys sp. MPEF-PV 6029	4.58	2.78	1.24	3.37	—
Coendou bicolor FMNH 41204	5.00	3.22	1.40	3.30	2.69
Echinoprocta rufescens FMNH 88524	4.11	2.50	1.28	2.74	2.35
Erethizon dorsatum FMNH 146262	5.00	3.32	1.68	3.95	3.11
Erethizon dorsatum myops FMNH 20344	5.14	3.58	1.32	3.92	2.97
Agouti paca MTD 1	6.92	4.25	1.76	4.67	3.13
Agouti paca FMNH 35691	7.02	4.02	2.01	4.75	3.28
Dasyprocta azarae azarae FMNH 52334	5.57	3.39	1.18	3.22	2.07
Dasyprocta punctata MTD 2	5.50	3.51	1.19	3.38	2.14
Lagostomus maximus FMNH 24371	5.25	3.40	0.88	3.77	2.10
Lagostomus maximus MTD 3	5.21	3.45	0.68	4.15	2.28
Chinchilla lanigera MTD 4	3.64	2.15	0.74	2.39	1.55
Dolichotis patagonum FMNH 49086	5.69	3.91	1.50	4.18	2.29
Dolichotis patagonum MTD 5	6.14	4.52	1.60	4.67	2.41
Cavia porcellus FMNH 146265	3.13	2.10	0.75	2.10	1.42
Myocastor coypus FMNH 146264	5.20	3.46	—	3.45	2.58
Myocastor coypus MTD 6	5.28	3.33	1.26	3.24	2.29
Hydrochaeris hydrochaeris FMNH 146267	9.26	6.50	2.57	6.08	2.93
Hystrix indica indica FMNH 99379	6.89	4.26	2.69	4.41	3.11
Hystrix brachyura papae FMNH 39454	5.98	3.69	1.88	4.00	2.93
Hystrix crassispinis FMNH 32692	6.03	3.69	2.08	4.05	2.93
Atherurus africanus turneri FMNH 79420	5.22	3.15	1.75	3.45	2.47

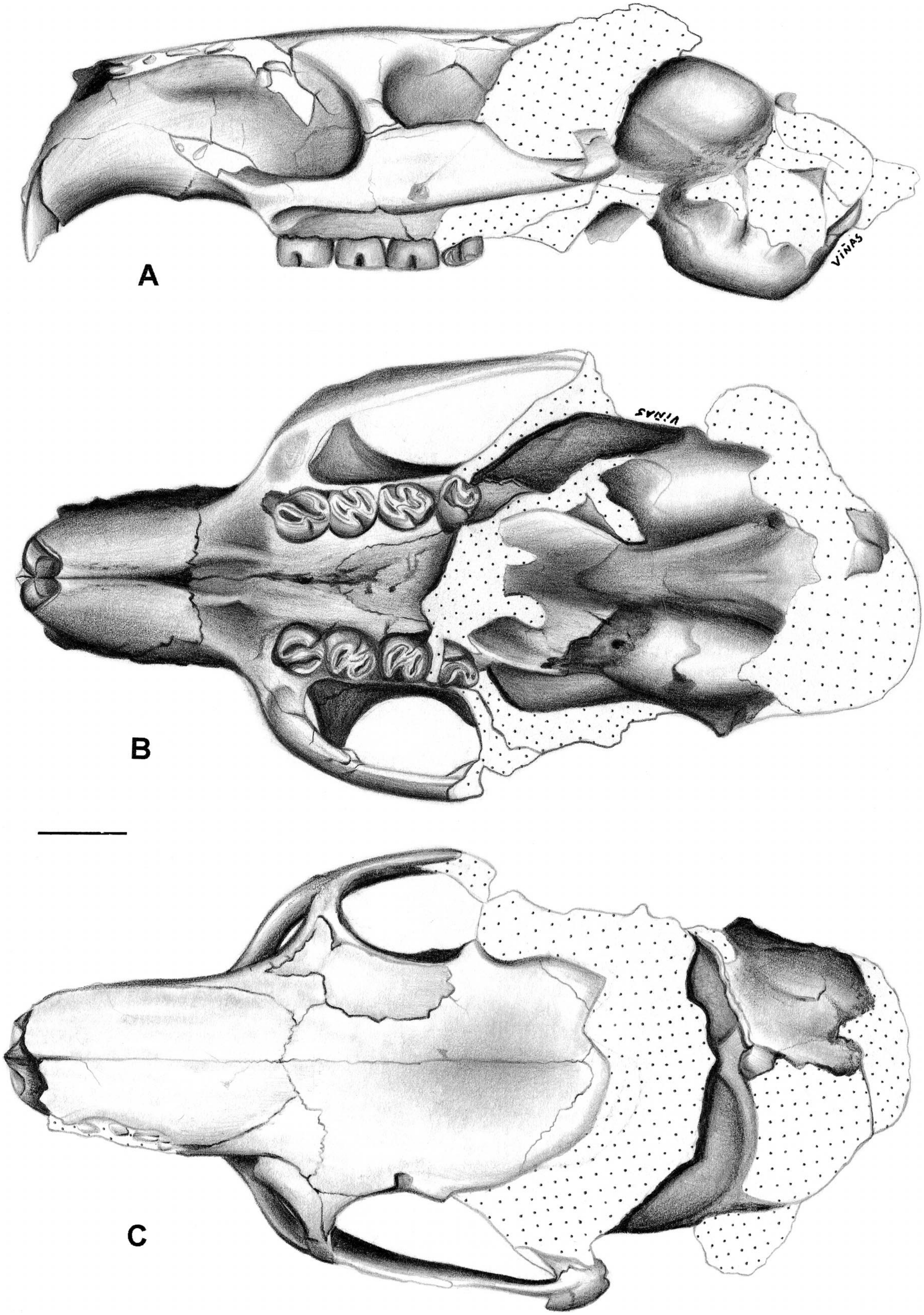

FIGURE 1. Lateral (**A**), ventral (**B**), and dorsal (**C**) views of the skull of *Hypsosteiromys* sp. (MPEF-PV 6029) from the Colhuehuapi Member, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina. Scale equals 1 cm.

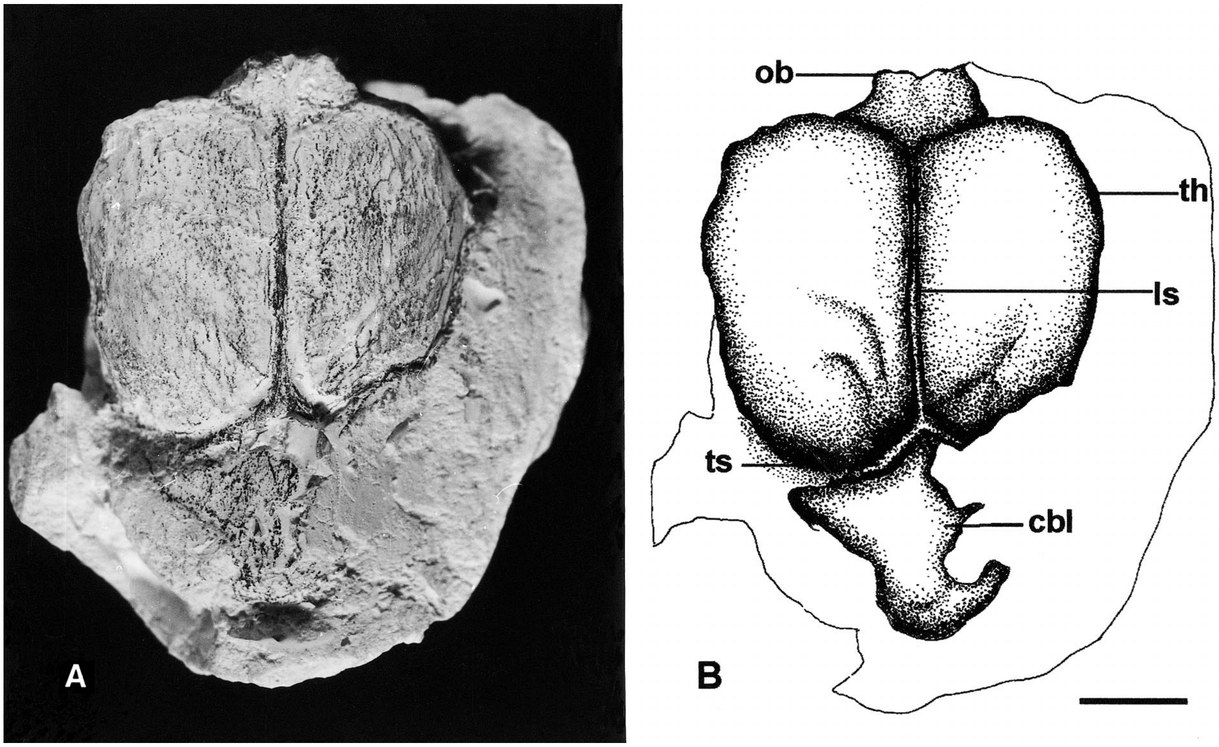

FIGURE 2. Natural cranial endocast of *Hypsosteiromys* sp. (MPEF-PV 6029) from the Colhuehuapi Member, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina. **A**, dorsal view. **B**, schematic representation in dorsal view. **Abbreviations**: **cbl**, cerebellum; **ls**, longitudinal sinus; **ob**, olfactory bulbs; **th**, telencephalic hemispheres; **ts**, transverse sinuses. Scale equals 1 cm.

teriorly divergent and more elongated than those of *C. prehensilis*. The external auditory meatus has a well-developed anterodorsal border, while the ventral edge is even and interrupted by a deep notch. The stylomastoid foramen is small and the mastoid area is moderately bulky.

The dorsal branch of the zygomatic root rises at the level of P4–M1 (Fig. 1A) and joins the ventral branch at the level of M1. Therefore, the infraorbital foramen is located lateral to the axis of the skull. The zygomatic arch is moderately deep anteriorly, while behind the paraorbital apophyses its dorsal edge descends posteriorly. Its ventral edge, instead, is consistently subhorizontal. The maxillary-jugal suture is located anteriorly in the zygomatic arch.

In anterior view, the infraorbital foramen is subtriangular with a subhorizontal base. The nasal fossa is small and subtriangular.

The incisors are higher than wide and their anterior faces are slightly convex, and they are narrower in relation to the size of cheekteeth than in *Eosteiromys*, *Steiromys* and *Neosteriomys*. P4 is tetralophodont and longer and wider than M1. The P4 anteroloph is transverse, while the protoloph is anterolabially oriented. The metaloph is joined labially and lingually to the posteroloph, forming a small, ephemeral posterofossette that opens posteriorly. The hypoflexus is short and oriented toward the protoloph. The labial flexi are wide and oriented anterolabially. At this stage of wear, the posteroloph is not connected to the hypocone.

The M1 is tetralophodont, with a transverse anteroloph and anterolabially oblique protoloph and mesolophule. The hypoflexus is narrow and deeper than in P4. The labial end of the mesolophule (Candela, 1999) joins that of the posteroloph, which is slightly widened in the middle, perhaps reflecting a metaloph lost with wear. On the right M1, the mesolophule is separated from the mure, although very close to it. The mesoflexus widens labially.

The M2 is similar in size and occlusal pattern to the M1, although it has a small but distinct metaloph. The posterofossette is small and subcircular.

The M3 is shorter and narrower than the M1 or M2. The hypocone is located more labial than the protocone. The hypoflexus is weakly connected to the anterofossette. The mesolophule is short, separated from the mure, although very close to it, and its labial end joins the metacone, which is the single distinguishable cusp. The metaloph is oriented from the posteroloph towards the metacone. The labial portion of the posteroloph is much lower than the metaloph and metacone.

Brain Endocast

The cranial endocast reflects the brain surface morphology together with the meninges and the main blood vessels. The exposed portion of the endocast reveals most of the olfactory bulbs, telencephalic hemispheres, and cerebellum (Fig. 2). The latter is partially covered by bone. The telencephalic hemispheres form the major part of the exposed endocast. In dorsal view, they are rounded, widened in the frontal region, and somewhat divergent in the occipital region. Faint impressions of vascular structures are present on the telencephalic surface. The filling of the longitudinal sinus is visible at the midline between the hemispheres and bifurcates at the caudal end of the hemispheres in two transverse structures corresponding to transverse sinuses (Fig. 2B).

The impression of the rhinal fissure, which separates the pyriform lobe from the neocortex or isocortex, cannot be seen because of preservation. The telencephalon is interpreted as lissencephalic because of the lack of impressions of neocortical

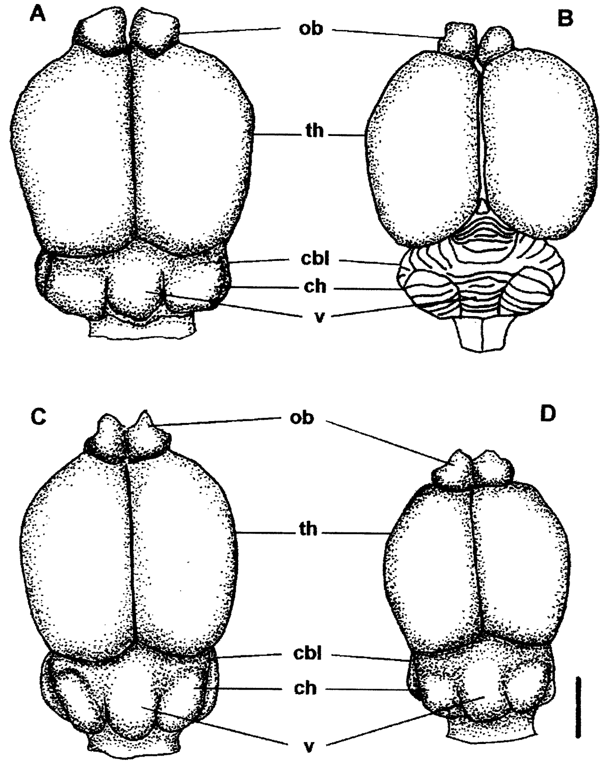

FIGURE 3. Dorsal views of the brain (B) and endocasts (A, C, D) of living Erethizontidae. **A** and **B**, *Erethizon dorsatum* (FMNH 146262) (modified from Brauer and Schober, 1970). **C**, *Coendou bicolor* (FMNH 41204). **D**, *Echinoprocta rufescens* (FMNH 88524). **Abbreviations**: **cbl**, cerebellum; **ch**, cerebellar hemispheres; **ob**, olfactory bulbs; **th**, telencephalic hemispheres; **v**, vermis. Scale equals 1 cm.

sulci, but it shows a clear expansion of the frontal lobe. Unlike most ''caviomorphs,'' the temporal lobe and sylvian region are not distinguished. A slight depression in the occipital region may correspond to the posterior end of the lateral sulcus.

The telencephalic hemispheres do not cover the olfactory bulbs, which are small and rounded, but connect to them through short olfactory peduncles. The transverse diameter of the olfactory bulbs is much less than the maximum telencephalic width.

The cerebellum is only partially exposed, and the relative size of the vermis and the cerebellar hemispheres cannot be determined. Its transverse diameter is somewhat less than the maximum width of the telencephalon.

DISCUSSION

This specimen is referred to *Hypsosteiromys* because of its more hypsodont cheek teeth (which easily distinguish this genus from other erethizontids), more oblique lophs, deeper fossettes, reduced or absent cusps in relation to the other erethizontids, and P4 not molariform and lacking mesolophule and rudimentary metaloph (Patterson, 1958:fig. 1A; Candela and Vucetich, 2002). In addition, the incisors of this specimen are narrower, in relation to the size of cheek teeth, than in *Parasteiromys*, *Eosteiromys*, *Steiromys*, and *Neosteiromys*. We do not refer this specimen to any described species of *Hypsosteiromys*, because they are all based on lower tooth characters (Candela and Vucetich, 2002). However, the larger size of P4 in relation to M1 suggests that it may be *Hypsosteiromys axiculus* (Candela and Vucetich, 2002).

The skull of *Hypsosteiromys* has several distinctive features among the Erethizontidae that increase the known morphological diversity of the family: it is continuously very low with a small olfactory sinus, the ascending rami of the premaxillaries are located behind the posterior margins of the nasals, and the external auditory meatus has a well-developed ventral furrow.

From a neuromorphological point of view, *Hypsosteiromys* has rounded telencephalic hemispheres in dorsal view, with prominent frontal lobes and small olfactory bulbs, and lacks temporal lobes and neocortical sulci. It shares these features with *Erethizon dorsatum* (Pilleri et al., 1984), *Coendou bicolor*, and *Echinoporcta rufescens*. These characters separate these genera from other New and Old World Hystricognathi (Pilleri et al., 1984).

Paleoneurological studies of rodents are rare. One of the first reports is the paper by Wood (1937) on the brain of *Ischyromys*. Later, Dechaseaux (1958) briefly described cranial endocasts of Eocene and Oligocene rodents from the Northern Hemisphere and Lavocat (1973) described several cranial endocasts of the extinct Thryonomyidae. Dozo (1997a, b, c) studied brain endocasts of several families of South American Hystricognathi.

Although rodents display a wide range of variation in brain structures, each traditional suborder shows some general neuromorphological patterns. Pilleri et al. (1984) recognized lissencephalic brains for Myomorpha and Sciuromorpha, except for a few cases in which a lateral sulcus is present (see also Dechaseaux, 1958). Hystricognathi have several neuromorphological patterns (Pilleri et al., 1984). They apparently underwent an early neopallial fissuration (Landry, 1957; Lavocat, 1974; Hoffstetter, 1975), and an increase in the degree of cortical folding, which correlates, at least partially, with body weight (Pilleri et al., 1984).

Among New World Hystricognathi, with the exception of the Erethizontidae (see above), brains are characterized by a rhombic telencephalon in dorsal view, approximately triangular in lateral view, that tends to form a genuine temporal lobe and a conspicuous sylvian region (Pilleri et al., 1984). ''Caviomorph'' brains have lateral and suprasylvan sulci, with the former more extended and sinuous in larger species (Dozo, 1997a). Comparative analysis of brains and cranial endocasts of Caviidae and Chinchillidae suggests that larger taxa tend to display more neocortical sulci, giving them the appearance of higher encephalic complexity (Hofman, 1989). For example, *Hydrochoerus*, the largest modern rodent, has a gyrencephalic brain with a conspicuous neocortical fissuration, and both primary and secondary sulci (Pilleri et al., 1984). This pattern is clearly seen in Cavioidea and Chinchilloidea, and is also present, though somewhat more diffuse, in Octodontoidea. In this sense, the telencephalon of *Myocastor* (Pilleri et al., 1984) and *Capromys* (Brauer and Schober, 1970), the only middle-sized octodontoids in which the encephalic morphology has been studied, is somewhat more rounded anteriorly, with a less developed temporal lobe and a weak lateral sulcus.

Among Old World Hystricognathi, the Thryonomyidae display the most complex brain morphology, very similar to that of the Chinchilloidea and Cavioidea, with an extended neocortex, developed temporal lobe, and evidence of a lateral sulcus. The brain morphology of the Hystricidae is similar, but, despite the considerable development of the neocortex, there is no temporal lobe. Unlike other Hystricognathi, hystricids have a conspicuous diagonal sulcus on the frontal region (Brauer and Schober, 1970; Pilleri et al., 1984). The extremely primitive brain of the Bathyergidae (e.g., *Heterocephalus*) differs conspicuously from those of the other Hystricognathi: complete absence of the neocortical sulci, dorsal exposure of the mesencephalon, and a remarkable development of the olfactory bulbs (Pilleri et al., 1984). This neuromorphological diversity is consistent with the adaptive diversity and wide size range displayed by this clade. The Cavioidea, Chinchilloidea, Thryonomyidae, and, to a lesser extent, the Octodontoidea, show the most complex brain morphology among rodents, with regards to the development of the temporal lobe, sylvian region, and presence of the lateral and suprasylvian sulci. This does not necessarily mean a closer phylogenetic relationship of the Thryonomyidae with the Caviida (Octodontoidea, Cavioidea and Chinchilloidea; Bryant and McKenna, 1999) than with other Hystricognathi, as these shared characters may represent homoplasies (Lockwood and Fleagle, 1999), or allometric effects (Hofman, 1989).

Despite differences in size and ecological adaptations, the Erethizontidae has remarkable neuromorphological homogeneity (see above). This is especially noteworthy in *Hypsosteiromys*, because, compared with the remaining living and extinct porcupines, it has several autopomorphic features. Thus, it might be inferred that the brain in the Erethizontidae is more conservative than in other groups of ‘‘caviomorphs,’’ although brain morphology remains unknown in several fossil genera.

The phylogenetic distinction of the Erethizontidae from the other ‘‘caviomorphs’’ is well established. Woods (1972:191) considered that, from a myological point of view, *Erethizon* is the most primitive living hystricognath, and that it is isolated from the other New and Old World taxa. Bugge (1974), on the basis of the cephalic arterial system pattern, even suggested that the Erethizontidae should be placed in a different suborder. Bryant and McKenna (1995), using cranial characters, especially those of the middle ear, and Candela (1999, 2000), using molar structure, both placed the Erethizontidae at the base of the radiation of the Suborder Hystricognathi. The primitive condition of the erethizontid brain, with the absence of neocortical sulci (Johnson et al., 1982) and temporal lobe, is consistent with this hypothesis.

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