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ENDOCRANIAL ANATOMY OF THE FOSSIL FURNARIID *Pseudoseisura cursor* (AVES, PASSERIFORMES): PALEOECOLOGICAL PERSPECTIVES AND EVOLUTIONARY IMPLICATIONS

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ABSTRACT: Furnariidae is a family endemic to the Neotropics and is one of the most diverse families of Passeriformes, and although it is one of the Neotropical families with the best fossil record, in Passeriformes in general the fossil record is scarce, which can make it difficult to interpret the evolution of the order in general. *Pseudoseisura cursor*, from the Ensenadan (Early–Middle Pleistocene) of Buenos Aires Province, Argentina, is considered the sister taxon of the extant species of the genus. This study describes the endocranial anatomy of this species and compares it with that of other extant Furnariidae to infer ecological aspects. A 3D model of the endocranium (i.e., a proxy for the brain) was created from micro-CT scans obtained from the holotype, which was described and measured (linear and surface-based measurements). Its body mass and endocranial volume were calculated, as well as its auditory capacities. Compared to the Brown Cacholote (*Pseudoseisura lophotes*), the endocranium of *P. cursor* shows general similarities but presents specific differences, such as greater dorsoventral development of the Wulsts and longer olfactory bulbs and flocculi, possibly related to its ancestral condition or functional adaptations. Although *P. cursor* had a greater body mass relative to the Brown Cacholote, its brain was proportionally smaller, with a volume of 9.73 times its body mass (23.59 times in the Brown Cacholote), which could be linked to the trend of body size reduction in extant species and the functional modularity of the brain. Additionally, *P. cursor* exhibited auditory capacities similar to those of Rufous Hornero (*Furnarius rufus*) and Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), possibly due to a similar habitat.

KEYWORDS: *evolution, Furnariidae, micro-CT, neuroanatomy, paleobiology, paleoecology*

Furnariidae corresponds to one of the most diverse families of Passeriformes within the order in the Neotropics (Winkler et al. 2020), including, to date, 318 described species, among which horneros and thornbirds stand out. It inhabits all types of environments, from deserts to tropical forests throughout the continent (Fjeldså et al. 2005). Their nests are usually complex and elaborate, a distinctive trait of the group (Olson 2001, Irestedt et al. 2006, Winkler et al. 2020). Most members of the family feed on insects and other small arthropods that they capture mainly from leaves or from the surface of trunks or by scratching the leaf litter (Ohlson et al. 2008, Winkler et al. 2020). Some species may feed on small vertebrates, such as frogs and lizards (Winkler et al. 2020), or include seeds and fruits in their diet (Lopes et al. 2003, Winkler et al. 2020).

Within this family, the genus *Pseudoseisura* groups species adapted to open or semi-open environments with xerophilous arboreal or shrubby vegetation. These furnariids are fundamentally terrestrial, as the prolonged daily activity of searching for food is carried

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out on the ground. The White-throated Cacholote (*Pseudoseisura gutturalis*) is the species that spends the most time on the ground and runs more easily than its congeners (Ridgely & Tudor 1994), whereas the more northerly species, the Brown Cacholote (*Pseudoseisura lophotes*) and the Caatinga Cacholote (*Pseudoseisura cristata*), are somewhat more arboreal, swaying abruptly while walking. Due to their nesting habits, the three species are closely associated with environments containing thorny trees or shrubs, being recognized in the ornithological literature as 'exaggerated thornbirds' (Ridgely & Tudor 1994), owing to these habits and their large body size (Tonni & Noriega 2001).

Paradoxically, despite their high diversity and abundance, the fossil record of Furnariidae is scarce compared to other groups of birds. Nevertheless, within Passeriformes, this family has a considerable record (Tonni 1977, Noriega 1991, Claramunt & Rinderknecht 2005, Tambussi 2011, Stefanini et al. 2016, Nascimento & Silveira 2024), although still insufficient to accurately reconstruct its evolutionary history (Noriega 1998). *Pseudoseisura cursor* (Fig. 1) (Furnariidae) is a fossil species that comes from the Ensenadan (Early–Middle Pleistocene) of Buenos Aires province, Argentina. Tonni & Noriega (2001) consider this fossil taxon to constitute the sister group of the extant species of the genus (Fig. 2); however, it is important to emphasize that the phylogenetic position of *P. cursor* is far from being considered established, since its position has not been rigorously tested. The events that gave rise to the genus *Pseudoseisura* would have begun during the glacial maximum following the late Ensenadan (after 1.0–0.9 Ma), coinciding with arid climatic conditions (Tonni & Noriega 2001). The material described by Tonni & Noriega (2001) consists of incomplete cranium and mandible; incomplete left humerus, distal extremity of right humerus; right and left carpometacarpus; left ulna, incomplete right ulna; right radius; phalanx 1 of wing digit II; incomplete left and right coracoids; incomplete sternum; incomplete left femur; left tibiotarsus; left tarsometatarsus; incomplete pelvis; and pygostyle. All belong to a single individual. In recent years, there has been renewed interest in understanding the early evolution of birds. However, the evolutionary history of their brain and sensory organs still presents numerous unanswered questions (Kurochkin et al. 2007). Endocasts of the neurocranium constitute fundamental tools to unravel this history, since they allow, through various quantitative and qualitative analyses, comparison of the size and shape of the brain of extinct species with extant ones, evaluating the degree of encephalization and its correlation with ecological habits (Jerison 2006). The application of endocranial models as proxies of brain structures allows, even in the absence of preserved brain tissue, the establishment of functional comparisons between fossil and extant species. This methodology has proven effective in previous studies on sensory and ecological evolution in birds (Witmer et al. 2008, Early et al. 2020).

There is broad consensus regarding the significant correlation between brain size and the development of cognitive abilities in vertebrates (Møller 2010). This relationship suggests that brain size directly influences behavior, which has important implications for ecological and evolutionary processes (Dukas 2004). It has been demonstrated that more developed brain areas are associated with increased information-processing capacities of those areas (Brenowitz & Arnold 1986, Iwaniuk & Wylie 2006). In the case of birds, the study of brain anatomy through computed tomography has revealed a direct relationship between the size and shape of brain regions and the structures of the endocranium (Early et al. 2020), understood as the internal surface of the skull that contains and protects the brain. This allows inference of the sensory and

Figure 1. Illustration of the external appearance of *Pseudoseisura cursor*, based on skull morphology. Digital reconstruction by doctoral candidate Jesús María Dorado.

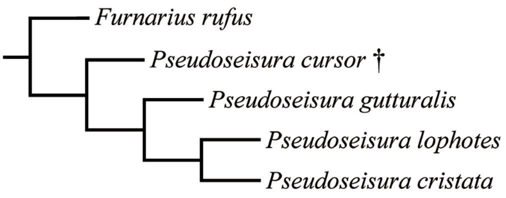

Figure 2. Phylogenetic tree of *Pseudoseisura* species. The Rufous Hornero (*Furnarius rufus*) represents the outgroup. Figure taken and modified from Tonni & Noriega (2001). It should be noted that this is only a proposal, and that in the absence of other studies evaluating the phylogenetic position of the fossil taxon, alternative hypotheses cannot be ruled out.

motor capacities of different groups of birds from the analysis of endocranial models, regardless of the presence of the brain (Witmer & Ridgely 2008, Tambussi et al. 2014, 2015). During embryonic development, the interaction between the brain and the bony material produces an interface surface that exactly replicates the surface of the brain and that, in many fossil specimens, is preserved and can be studied through casts or digital models (Balanoff & Bever 2017). Therefore, the endocranial cast is an excellent proxy for studying the brain surface of birds (Early et al. 2020).

Within this framework, the main objective of this study was to estimate possible life habits of *P. cursor* based on the description of its endocranial cast and its comparison with the endocranial casts of other furnariids. Under the premise proposed by Tonni & Noriega (2001) regarding the close relationship of this fossil taxon with extant species of the genus, and considering that extant species of *Pseudoseisura* show significant ecological and behavioral similarities—such as preference for semiarid environments, terrestrial behavior, and similar vocal patterns—it could be assumed that these traits are also reflected in endocranial morphological homologies. Therefore, it is hypothesized that the morphology and relative size of the endocranium of *P. cursor* are similar to those of other species of the genus *Pseudoseisura*, such as the Brown Cacholote, as well as the relative surfaces of the endocranial structures and their auditory capacities.

METHODS

Specimens. The holotype of *Pseudoseisura cursor* MLP-XI-14-1 is housed in the collection of the División Paleontología de Vertebrados of the Museo de Ciencias Naturales de La Plata. For comparisons, data from specimens of the family Furnariidae published in Demmel Ferreira et al. (2024) were used. No live animals were used in this study.

Processing. X-ray microtomography of the skull of *P. cursor* was performed using a commercial Bruker Skyscan 1272 system belonging to the Facultad de Odontología de la Universidad de Buenos Aires (FOUBA). The resolution used was 25 µm, with an energy of 100 µA and 100 kV. The resulting DICOM files were processed in the software Avizo (Version 7.1), where anatomical structures were manually segmented and a three-dimensional model of the endocranium was generated.

Description and measurements

Based on the generated three-dimensional model, a detailed description of the endocranium was carried out, including the inner ear, nerves, and blood vessels. The description follows the anatomical terminology for the central nervous system proposed mainly by Breazile & Kuenzel (1993). The number of cerebellar folds refers only to those exposed. Both linear (Fig. 3A) and surface (Fig. 3B) measurements of the different anatomical structures were taken following Demmel Ferreira et al. (2024). Linear measurements were taken in millimeters using tools in the Avizo software. In order to achieve a better representation of shapes, indices were calculated from the linear measurements. Surface measurements were taken using the software Geomagic Studio (version 2012). These measurements are expressed as percentages relative to the total endocranial surface, in order to provide quantitative information mainly on the size of the different brain structures. Body mass (BM) of *P. cursor* was calculated following the method proposed by Field et al. (2013). According to the authors, the most accurate indicator for estimating body mass in flying birds is the maximum diameter of the humeral articular facet of the coracoid (the glenoid cavity). Field et al. (2013) suggest that, in most cases, this indicator can provide the most accurate estimates of body mass for fossil flying birds. Based on this, the maximum diameter of the articular facet of the right and left humerus of *P. cursor* was measured and both measurements were averaged. The formula indicated in the study was then applied: $\ln(BM) = 2.44*(\ln HAF) + 2.00$, where BM is body mass and HAF is the measurement of the humeral articular facet. Brain volume (BV) was calculated using the software Avizo. Hearing range (Hz) and mean hearing (Hz) were calculated following Walsh et al. (2009).

Estimation of possible habits

The inference of potential behaviors and ecological habits of *P. cursor* was carried out qualitatively, assisted by comparison with extant species of the same genus and of other genera within the same family.

Unless otherwise specified, the terms 'endocranium', 'endocranial cast', 'endocranial model', and derived terms will be used interchangeably to refer to the brain proxy.

RESULTS

Anatomical description

The endocranium corresponds to a pneumocephalic brain type (Hofer 1952), which implies that the brain is positioned dorsally to the rostrum and has a marked dorsoventral overlap of the telencepha-

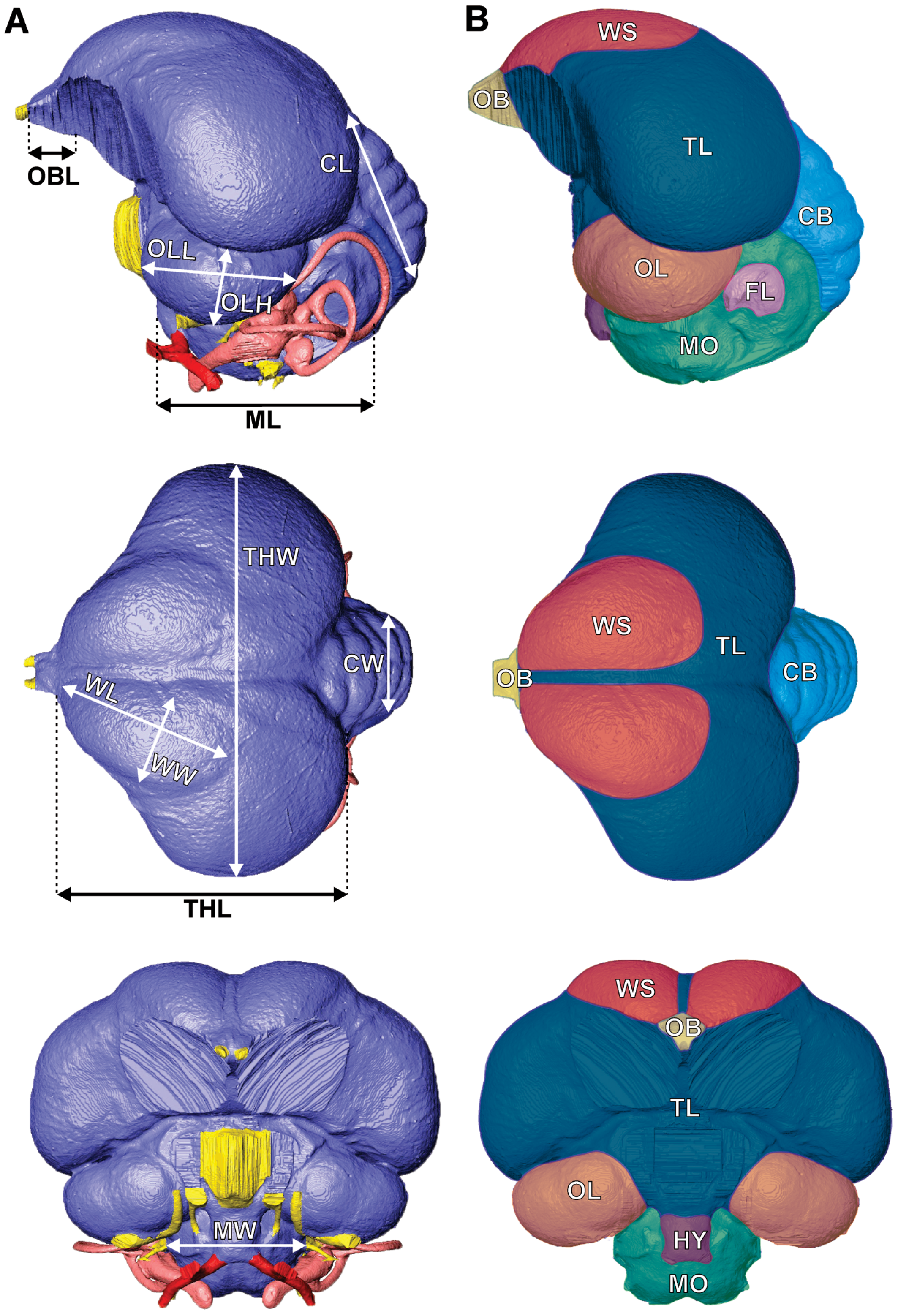

Figure 3. Linear and surface measurements taken from the 3D endocranial model of *Pseudoseisura cursor*. Figure taken and modified from Demmel Ferreira et al. (2024). The endocranial model shown in the image belongs to the Great Kiskadee (*Pitangus sulphuratus*). Views: A, linear measurements; B, surface measurements. Abbreviations: CB, cerebellum; CL, cerebellar length; CW, cerebellar width; FL, flocculi; HY, hypophysis; ML, medulla length; MO, medulla oblongata; MW, medulla width; OB, olfactory bulb; OBL, olfactory bulb length; OL, optic lobes; OLH, optic lobe height; OLL, optic lobe length; THL, telencephalic hemisphere length; THW, telencephalic hemisphere width; TL, remaining telencephalon; WL, Wulst length; WS, Wulsts; WW, Wulst width.

lic hemispheres over the optic lobes and the medulla oblongata (Fig. 4). In dorsal view and in general terms, the endocranium has a subrounded shape (Fig. 4).

Telencephalon (Fig. 4): The telencephalon is slightly longer than it is wide (Tables 1 & 2). The hemispheres are domed and pyriform in dorsal view and are mediolaterally expanded. The interhemispheric fissure is wide and deep and is uniform along its entire length. The eminentiae sagittales (Wulsts) correspond to type A (Stingelin 1957), that is, they are positioned rostrally in relation to the length of the telencephalic hemispheres. The Wulsts are elongated and subrounded in shape, and their contact with the interhemispheric fissure is straight, with well-defined margins. The vallecula could not be identified. The olfactory bulb is wide at its origin and narrows rostrally, being conical in shape.

Diencephalon (Figs. 4C & D): The hypophysis is wide, robust, and hourglass-shaped in rostral view. The pineal gland could not be identified because it does not leave an impression on the endocranium, as in most birds.

Mesencephalon (Figs. 4A, B, C & D): The optic lobes are subspherical and globose in lateral view and are positioned rostrally in relation to the caudal limit of the Wulsts. The contact between the optic lobes and the telencephalon forms a line that curves markedly ventrolaterally; therefore, in rostral view they show a dorsoventral orientation. The telencephalic hemispheres 'wrap' the dorsal surface of the optic lobes, as

Table 1. Linear measurements in millimeters (mm) of the different anatomical structures of the endocranium.
* Data obtained from Demmel Ferreira et al. (2024).
Abbreviations: CL, cerebellar length; CW, cerebellar width; FL, flocculus length; ML, medulla length; MW, medulla width; OBL, olfactory bulb length; OLH, optic lobe height; OLL, optic lobe length; THL telencephalic hemisphere length; THW, telencephalic hemisphere width; WL, Wulst length; WW, Wulst width.

Species	TLH	THW	WL	WW	OBL	OLL	OLH	CL	CW	FL	ML	MW
Pseudoseisura cursor	16.79	21.63	13.61	8.39	2.66	6.46	4.61	7.31	5.31	3.59	8.43	6.29
Cinclodes fuscus *	12.28	13.99	9.97	4.37	1.22	5.85	3.24	5.84	4.68	1.26	7.33	4.61
Coryphistera alaudina *	14.51	11.44	8.53	4.46	1.12	5.42	3.28	5.97	4.32	0.91	5.28	4.09
Drymornis bridgesii *	17.15	20.57	13.67	7.84	1.33	6.38	3.27	8.3	4.83	1.28	7.03	5.36
Furnarius rufus *	13.55	16.57	11.23	4.68	0.64	7.42	3.96	7.1	4.77	1.92	6.08	4.62
Lepidocolaptes angustirostris *	12.06	15.72	11.06	5.81	0.74	5.91	2.77	6.72	4.81	1.54	6.09	4.58
Pseudoseisura lophotes *	15.38	19.3	11.2	6.12	1.15	6.16	3.71	7.41	4.99	1.5	6.67	5.66
Syndactyla rufosuperciliata *	14.09	16	9.91	5.53	1.2	5.92	3.21	7.28	4.86	1.31	6.4	4.77

Table 2. Indices calculated from linear measurements.
* Data obtained from Demmel Ferreira et al. (2024).
Abbreviations: CL, cerebellar length; CW, cerebellar width; FL, flocculus length; ML, medulla length; MW, medulla width; OBL, olfactory bulb length; OLH, optic lobe height; OLL, optic lobe length; THL telencephalic hemisphere length; THW, telencephalic hemisphere width; WL, Wulst length; WW, Wulst width.

Species	THL/ THW	WL/ WW	OBL/ THL	OLL/OLH	CL/ CW	FL/ CW	ML/ MW
Pseudoseisura cursor	0.776	1.622	0.158	1.401	1.377	0.676	1.34
Cinclodes fuscus *	0.878	2.281	0.099	1.806	1.248	0.269	1.59
Coryphistera alaudina *	1.268	1.913	0.077	1.652	1.382	0.211	1.291
Drymornis bridgesii *	0.834	1.744	0.078	1.951	1.718	0.265	1.312
Furnarius rufus *	0.818	2.4	0.047	1.874	1.488	0.403	1.316
Lepidocolaptes angustirostris *	0.767	1.904	0.061	2.134	1.397	0.32	1.33
Pseudoseisura lophotes *	0.797	1.83	0.075	1.66	1.485	0.301	1.178
Syndactyla rufosuperciliata *	0.861	1.792	0.085	1.844	1.498	0.27	1.342

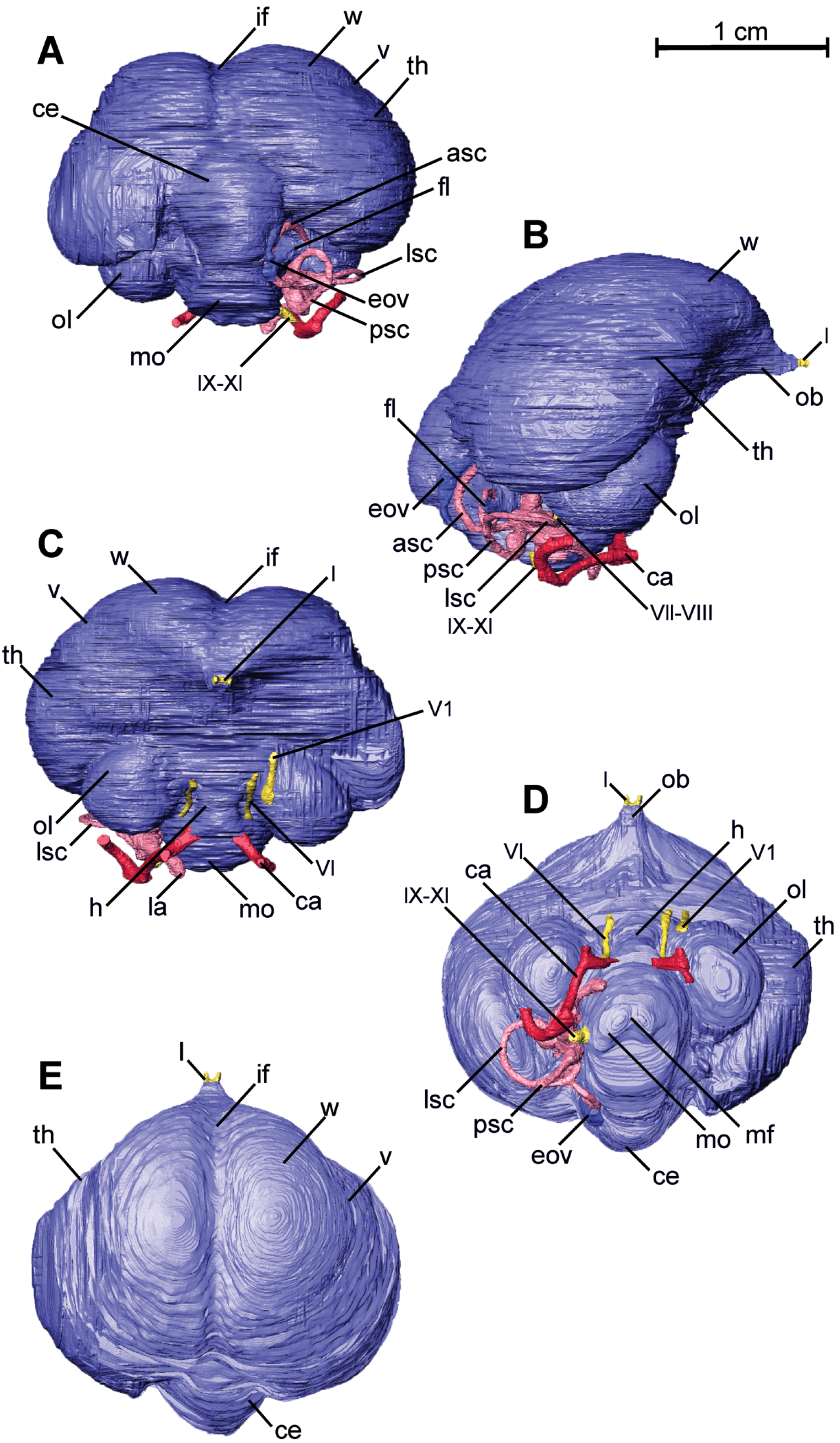

Figure 4. Virtual 3D reconstruction of the endocranial cast of *Pseudoseisura cursor* produced from computed microtomography, with anatomical structures indicated. Abbreviations: asc, anterior semicircular canal; ca, carotid; ce, cerebellum; eov, external occipital vein; fl, flocculus; h, hypophysis; I, nerve one; IX–XI, exits of nerves nine to eleven; if, interhemispheric fissure; la, lagena; lsc, lateral semicircular canal; mf, median fissure; mo, medulla oblongata; ob, olfactory bulb; ol, optic lobe; psc, posterior semicircular canal; th, telencephalic hemisphere; v, vallecula; V1, branch one of nerve five; VI, nerve six; VII–VIII, exits of nerves seven and eight; w, Wulst.

in most Neornithes (Chiappe et al. 2024).

Metencephalon (Figs. 4A, B, D & E): The cerebellum is short and wide, and the contact with the telencephalon has the shape of an inverted open 'U'. It was not possible to reconstruct the cerebellar folds due to the state of preservation of the skull. The flocculi are wide at their origin and extend laterocaudally, without curvatures or folds.

Myelencephalon (Figs. 4A, C & D): The medulla oblongata is elongated in the rostrocaudal direction. The median fissure is shallow and poorly marked. The medulla has a globose appearance in rostral view.

Cranial nerves (Figs. 4A, B, C & D): Due to the state of preservation of the skull, it was not possible to reconstruct all cranial nerves. The olfactory nerve (I) projects rostrally from the olfactory bulb. The origin of this nerve is common to both branches, with the common portion being short and subtle. Of the trigeminal nerve (V), only the ophthalmic branch (1) could be reconstructed; it runs over the medial portion of the optic lobes. This branch is slender, with a rounded cross section. The abducens nerve (VI) originates in the most rostral portion of the medulla and extends dorsorostrally, parallel to branch 1 of nerve V. It is slender and circular in cross section. The facial and vestibulocochlear nerves (VII and VIII) have a shared origin on the lateral sides of the medulla, partially covered by the inner ear. The glossopharyngeal, vagus, and accessory nerves (IX, X, and XI) have a common origin, as in most birds (Breazile & Kuenzel 1993), located in the ventrolateral region of the medulla. The common origin of these nerves is rounded and oval in cross section. The optic (II), oculomotor (III), and trochlear (IV) nerves could not be reconstructed.

Vasculature (Figs. 4A, B, C & D): The carotid canals have a subrounded cross section. Both carotids reach the hypophysis independently; therefore, there is no intercarotid anastomosis. The external occipital vein follows the lateral margins of the cerebellum. It is robust and conspicuous in appearance. Due to the state of preservation, it was not possible to identify the occipital sinus.

Inner ear (Fig. 5): All semicircular canals have a subrounded cross section. The posterior semicircular canal (PSC) is the least developed (i.e., the one with the smallest diameter), whereas the anterior (ASC) and lateral (LSC) canals show similar development. All three

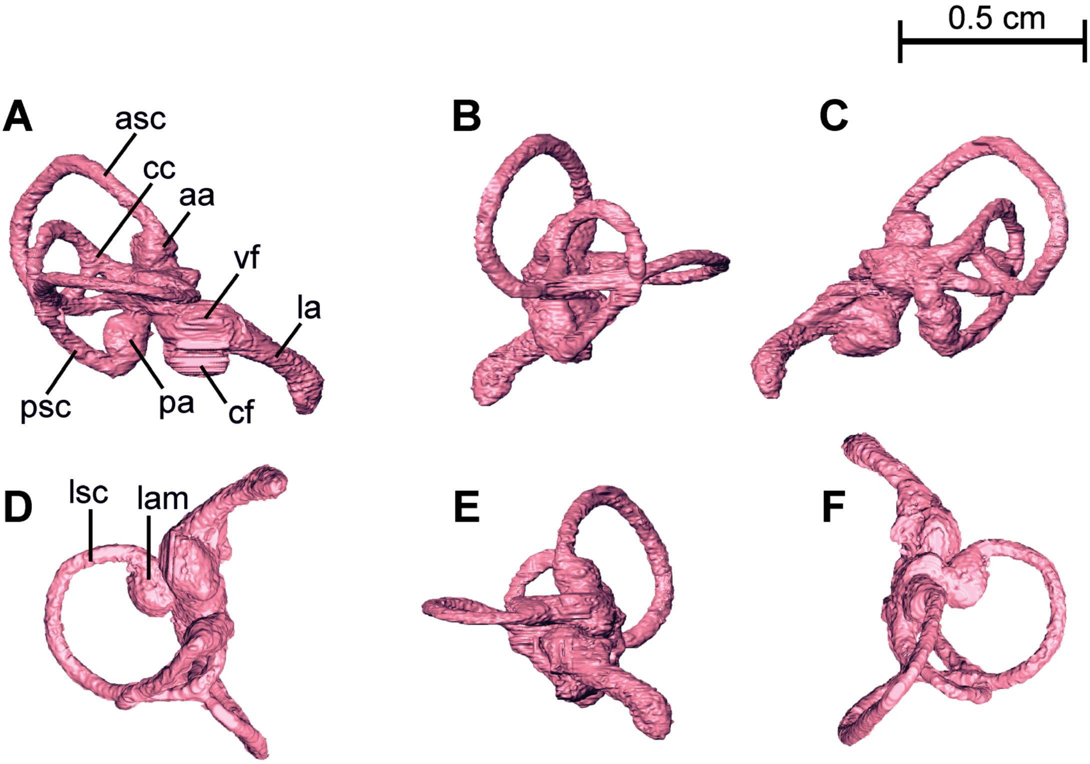

Figure 5. Virtual 3D reconstruction of the endocranial cast of the right inner ear of *Pseudoseisura cursor*, with anatomical structures indicated. Abbreviations: aa, anterior ampulla; asc, anterior semicircular canal; cc, common crus; cf, cochlear fovea; la, lagena; lam, lateral ampulla; lsc, lateral semicircular canal; pa, posterior ampulla; psc, posterior semicircular canal; vf, vestibular fovea.

ampullae are globose and oriented caudally. The common crus is short and robust and is oriented obliquely relative to the LSC. The lagena curves slightly medially, and its cranial end is oriented ventrally. The vestibular fenestra is oval and conspicuous; it is clearly marked. The cochlear fenestra is smaller than the vestibular one; it is also oval and slightly more elongated.

DISCUSSION

The proposal of Tonni & Noriega (2001) places this species as the first extinct species of the genus *Pseudoseisura*, and they postulate its condition as the sister taxon of the other species of the genus. When comparing the shape of the endocranium of *Pseudoseisura cursor* (Fig. 4) with that of the Brown Cacholote (Demmel Ferreira et al. 2024), it is possible to state that, in general terms, the endocrania are similar. However, due to the lack of specific and rigorous phylogenetic studies, there is some phylogenetic uncertainty, and therefore the results should be interpreted with the caution that such uncertainty requires. Regarding the linear measurements (Table 1) and the indices of those measurements (Table 2), there are no major differences indicating that the shape of the different anatomical structures varies markedly. By analyzing Table 2, it can be observed that the olfactory bulb of *P. cursor* is considerably longer relative to telencephalon length than in the Brown Cacholote, which could be due to a greater predominance of olfaction in *P. cursor* than in extant furnariids. The flocculi are also longer relative to cerebellar width in *P. cursor* than in the Brown Cacholote. This could be explained by an increase in neuronal density in specific regions, which facilitates the incorporation of additional brain pathways or the elaboration or increased acuity of existing pathways (Ksepka et al. 2020). Some authors suggest that there is differential growth of individual brain regions, which could be divided into distinct functional regions, indicating a certain degree of modular evolution (Iwaniuk et al. 2004, 2005, Healy & Rowe 2007, Balanoff et al. 2016, Smaers & Vanier 2019).

When analyzing the relative percentages of surface measurements (Table 3), it can be observed that the Wulsts represent more than twice the surface occupied by the optic lobes. This comparison is made because the Wulsts (histologically corresponding to the hyperpallium) process visual information (caudal region) and somatosensory information (rostral region) (Atoji et al. 2016). This could indicate that both vision and somatosensory information were of great importance. The amount and type of information received by the Wulsts is closely linked to both locomotor and trophic habits (Wylie et al. 2015, Stacho et al. 2020). This, together with the idea of a highly cursorial locomotor habit (Tonni & Noriega 2001), could indicate it foraged on the ground, searching for food among grass or leaf litter. When comparing Wulst and optic lobe values with those of other furnariid species, the Scimitar-billed Woodcreeper (*Drymornis bridgesii*) shows the most similar values, and although this species also feeds on tree trunks and branches, it primarily forages on the ground (Belton 1984, Kratter et al.

Table 3. Surface measurements expressed as percentages (%) relative to the total endocranial surface.
* Data obtained from Demmel Ferreira et al. (2024).
** Structure that could not be reconstructed in the endocranial model.

Species	Wulsts	Olfactory bulb	Hypophisis	Optic lobes	Cerebellum	Flocculi	Medulla	Optic chiasm	Remaining telencephalon
Pseudoseisura cursor	19.88	1.03	1.16	9.97	5.59	2.26	7.38	**	52.73
Cinclodes fuscus *	14.71	1.23	1.01	16.73	6.07	2.69	11.81	0.87	44.89
Coryphistera alaudina *	15.3	1.01	1.12	13.05	6.2	2.2	11.91	1.08	48.14
Drymornis bridgesii *	20.01	1.11	0.82	9.15	5.73	1.12	10.78	0.8	50.48
Furnarius rufus *	14.51	0.86	1.17	13.93	6.57	2.62	12.1	1.26	46.98
Lepidocolaptes angustirostris *	19.59	1.01	0.89	11.56	7.14	2.32	11.42	0.69	45.37
Pseudoseisura lophotes *	17.65	0.59	0.85	11.83	6.06	2.08	12.04	0.91	47.99
Syndactyla rufosuperciliata *	19.02	1.05	0.94	9.6	7.38	2.03	10.22	0.85	48.89

1993, Juárez 2021). The Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*) also shows similar values, but this species has different foraging behaviors, as it searches for food mainly in the understory, occasionally extending into the canopy and only rarely on the ground. It collects items from branches, dead leaves, and other debris; occasionally it hammers branches (Remsen 2020). In this case, it is likely that the similarity in Wulst surface values is more related to the processing of sensory information. The cerebellar surface value of *P. cursor* is striking when compared with the other species: it is the smallest value, and the closest value is the one that corresponds to the Scimitar-billed Woodcreeper. Cerebellar size is strongly linked to the size of the different folds or folia, which in turn are related to different functions and different habits (Sultan & Glickstein 2007). Walsh et al. (2013) recognize that a large cerebellum may have contributed to flight capability, as well as to all modes of avian locomotion. Hall et al. (2013) found a positive correlation between the degree of folding of the cerebellar cortex and nest complexity. This suggests that a cerebellum with a higher degree of folding allows greater neuronal density (especially of Purkinje cells), better fine motor processing, and possibly greater learning capacity and motor sequencing. Given that the cerebellum is also involved in fine motor control (Hall et al. 2013), this can influence both flight performance (for example, in precise maneuvers or flight in complex environments such as dense forests) and swimming (Balanoff et al. 2016), or even the construction of complex nests. In the case of *P. cursor*, the relatively small cerebellar surface compared to other furnariids could be related to a lifestyle less demanding in terms of fine motor skills and behavioral complexity. It may have inhabited more open or less structurally complex areas, perhaps with a more terrestrial lifestyle or less dependence on flight, or it may not have built highly

Table 4. Body mass in grams (g) and endocranial volume in cubic millimeters (mm^3).
* Data obtained from Demmel Ferreira et al. (2024).
** According to the formula used (Field et al. 2013), the mean percent prediction error is 12.95, and the 95% confidence interval of the percent prediction error is 1.07.
Abbreviations: BM, body mass; EV, endocranial volume.

Species	Body mass	Endocranial volume	EV/BM
Pseudoseisura cursor	262.52**	2554.99	9.73
Cinclodes fuscus *	30	804.49	26.82
Coryphistera alaudina *	30	809.48	26.98
Drymornis bridgesii *	94	2181.33	23.21
Furnarius rufus *	43.7	1130.25	25.86
Lepidocolaptes angustirostris *	31.5	931.45	29.57
Pseudoseisura lophotes *	72.4	1707.83	23.59
Syndactyla rufosuperciliata *	25.6	1157.94	45.23

Table 5. Frequencies and hearing ranges expressed in Hertz (Hz).
* Data obtained from Demmel Ferreira et al. (2024).

Species	Optimal frequency	Mean frequency	Minimum frequency	Maximum frequency
Pseudoseisura cursor	5385.8	3138.62	445.72	5831.52
Cinclodes fuscus *	5617.83	3264.49	455.57	6073.41
Coryphistera alaudina *	6176.63	3567.61	479.3	6655.93
Drymornis bridgesii *	4476.19	2645.2	407.11	4883.3
Furnarius rufus *	5448.09	3172.41	448.37	5896.46
Lepidocolaptes angustirostris *	5190.04	3032.43	437.41	5627.45
Pseudoseisura lophotes *	4944.42	2899.2	426.99	5371.41
Syndactyla rufosuperciliata *	4954.19	2904.5	427.4	5381.59

complex nests. It is also important to mention that the low relative surface values for the cerebellum could be due to limited space within the skull, in which some structures increase their surface area at the expense of others, or to a phylogenetic constraint.

A striking aspect of the relative surface values is that those of *P. cursor* are considerably different from those of the species of the same genus, the Brown Cacholote. Although the values of the species considered here do not show large variation, it is possible to state, as shown above, that there are species with values more similar to *P. cursor* than the Brown Cacholote. Again, this could be due to ancestral conditions of the fossil species. A comparison with the other members of the *Pseudoseisura* clade would be interesting in order to obtain a more complete picture.

Regarding the relationship between relative endocranial volume and body mass (in which *P. cursor* showed a smaller value than other Furnariidae; Table 4), Ksepka et al. (2020) propose that the trend toward relatively larger brain sizes along the phylogeny was driven by selection for smaller body sizes. Evolutionary rates appear to have stabilized over time, while directional selection acted on individual clades. Although body size is a possible explanation for variation in relative brain size, some authors suggest that high levels of encephalization could be due to differential growth of individual brain regions, which could be divided into distinct functional regions, indicating a certain degree of modular evolution (Iwaniuk et al. 2004, 2005, Healy & Rowe 2007, Balanoff et al. 2016, Smaers & Vanier 2019). This may be linked to ancestry and could indicate, as proposed by Ksepka et al. (2020), that extant furnariids experienced a more pronounced decrease in body mass than in endocranial volume, compared to fossil species. It is worth mentioning that the body mass estimate of *P. cursor* is unprecedented prior to the publication of this work and represents a novel result in itself. Although the calculated value is striking in relation to the body mass of other furnariids, it is currently the estimate that provides the greatest precision for this parameter (Field et al. 2013). Tonni & Noriega (2001) described *P. cursor* as a large species, at least 'larger than the three known species of *Pseudoseisura*', so the body mass value could be consistent with that idea.

With respect to hearing, the Acoustic Adaptation Hypothesis (AAH) proposes that habitat structure has shaped the evolution of the acoustic properties of bird songs (and therefore hearing; Morton 1975, Hansen 1979, Boncoraglio & Saino 2007). Warm, dry air improves sound transmission (Harris 1966, Michelsen & Larsen 1983), whereas dense foliage increases attenuation (Aylor 1972, Martens 1980). Tonni & Noriega (2001) infer that *P. cursor* inhabited open or semi-open Chaco-type environments, where sound would have been transmitted without major difficulties. The auditory capabilities of *P. cursor* (Table 5) showed intermediate values within the comparative framework, and its optimal hearing frequency is close to that of the Rufous Hornero (*Furnarius rufus*) and the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*). This may be explained by the fact that the Rufous Hornero inhabits a variety of open habitats: disturbed areas with bare ground, secondary scrub, grasslands, and agricultural lands, as well as urban parks and gardens (Remsen & Bonan 2020), showing some similarity to the habitat proposed for *P. cursor*. The latter occurs in slightly more vegetated habitats, such as open forests, scrublands, and savannas (Marantz et al. 2020). These similarities in habitat types could explain the similarity in hearing frequencies among *P. cursor*, the Rufous Hornero, and the Narrow-billed Woodcreeper. The reason why the Brown Cacholote has lower hearing frequencies than *P. cursor* could be due to the fact that this species inhabits different types of habitats (mainly tropical deciduous forests, forest edges, and secondary scrub, among other forested environments; Remsen 2024), which differ from those proposed for the fossil species. According to the AAH, different habitats imply different acoustic properties. The meta-analysis carried out by Boncoraglio & Saino (2007), while supporting the AAH, warns that habitat structure only weakly predicts the acoustic properties of bird songs. Therefore, other potentially relevant factors should be included in realistic models of the evolution of avian song acoustics.

In conclusion, there are strong similarities in the general morphology of the endocranium of *P. cursor* compared to other furnariids. However, it is important to emphasize that, to date, there are no specific and rigorous phylogenetic studies regarding its assignment to the genus *Pseudoseisura*; therefore, alternative hypotheses of its affiliation cannot be ruled out, and the results presented here should be interpreted with appropriate caution. Analysis of its endocranial anatomy allows inference of a strong predominance of olfaction in *P. cursor* compared to extant furnariids, accompanied by a notable relevance of vision and somatosensory information. These traits are related both to its cursorial locomotion (Tonni & Noriega 2001) and to its trophic habit, indicating that foraging occurred on the ground, among grass or leaf litter. From the relative surface of the cerebellum, it can be inferred that it may have had a lifestyle less demanding in terms of fine motor skills and behavioral complexity, more terrestrial or with less dependence on flight, and perhaps did not build highly complex nests. Analysis of the auditory range suggests that this species primarily inhabited open or semi-open Chaco-type environments, more open or less structurally complex areas, in agreement with Tonni & Noriega (2001). The remarkable preservation of the brain and skull of *P. cursor*, together with its age of approximately 2.5 million years and its taxonomic position, make it a key specimen within the fossil record of Neotropical birds, especially of Passeriformes, the avian group with the greatest biodiversity.

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