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Cite this article: Degrange FJ, De Mendoza RS, Torres Etchegorry M, Demmel Ferreira MM, Witmer L, Tambussi CP. 2026 Unlocking the early evolution of brain and feeding strategies in Anseriformes: the case of *Conflicto antarcticus*. *R. Soc. Open Sci.* **13**: 252544.
https://doi.org/10.1098/rsos.252544

Received: 27 December 2025
Accepted: 22 May 2026

Subject Category:
Earth and environmental science

Subject Areas:
evolution, palaeontology, neuroscience

Keywords:
waterfowl, feeding, neuroanatomy, Palaeocene, Anseres

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Supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8517055.

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Unlocking the early evolution of brain and feeding strategies in Anseriformes: the case of *Conflicto antarcticus*

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The early Palaeocene *Conflicto antarcticus* reveals a mosaic pattern of brain and skull evolution relative to other Anseriformes. Despite its hyperinflated brain and ventrally displaced optic lobes, *Conflicto* lacks the Wulst, an absence shared with the Eocene *Presbyornis* and interpreted as a primitive trait for Neornithes. Enlarged olfactory bulbs suggest enhanced olfactory capabilities uncommon in modern birds, possibly compensating for the reduced visual and tactile specializations typically associated with filter feeding. The morphology of its straight, non-spatulate beak and the relatively undeveloped trigeminal system suggest a foraging strategy based more on ground-pecking than filtering. These findings provide critical insight into the early stages of anseriform evolution, indicating that key neural adaptations for filter feeding seen in modern taxa were absent or incipient in *Conflicto*. Moreover, *Conflicto*'s brain morphology suggests that several features evolved convergently across Neornithes.

1. Introduction

Recovered from freshwater sediments, *Conflicto antarcticus* is an Early Palaeocene medium-sized volant bird with a presumed wading lifestyle known from Western Antarctica. The original phylogenetic results [1] positioned it as the most basal anseriform, alongside presbyornithids (with a more basal branch leading to a clade uniting *Vegavis* and Dromornithidae—and thus, they should be considered stem-Anseriformes as well). Further phylogenetic analyses recovered *Conflicto* and presbyornithids in the same position [2]; or recovered the presbyornithids further apart from the basal *Conflicto* and nested within crown Anseriformes as the sister group of the magpie goose *Anseranas* [2]; or closer to the Late Cretaceous *Vegavis iaai* from Antarctica [3,4]. Other authors [5] positioned *C. antarcticus* nested with presbyornithids and *Nettapterornis*, recovering these as the sister groups of Anatidae—and thus, within Anseres—and within crown Anseriformes. All these analyses consistently place *Conflicto* as a sister taxon to the anseriform *Nettapterornis oxford*—recovered from the Eocene of England. By contrast [6], recovered *Conflicto* as sister taxon of presbyornithids, suggesting a more derived position than the basal *Nettapterornis*. The most recent analysis [4] presents *Conflicto* as a sister taxon either to *Vegavis* and Anatidae or to *Vegavis* and nested within a clade that includes *Nettapterornis* and the Presbyornithidae, all as sister taxa of the Anseres (Anatidae + Anseranatidae).

Conflicto antarcticus exhibits a ducklike general appearance, particularly its beak (although less spatulated), along with elongate hind limbs and a pectoral girdle and forelimbs typical of flying birds (e.g. [7]). It represents a substantial record (possibly the most complete skeleton) of a non-marine Palaeocene bird from the Southern Hemisphere. Therefore, its study is essential for inferring ancestral traits in anseriform lineages.

The 180 living species of Anseriformes are included in four families: the South American Anhimidae (screamers), the Australian Anseranatidae (magpie ducks), the recently proposed family Dendrocygnidae found mostly below the Equator, with some species in the Indian subcontinent, Indonesia and Southeast Asia, Cuba and the southern part of North America (whistling ducks) [8], and the most speciose worldwide Anatidae (swans, geese and ducks) [9]. The first known stem-anatid appeared about 34 million years ago, while crown Anatidae dates from the late Oligocene [10–12]. Along their evolutionary path, anseriforms developed a feeding strategy based on filtering, accompanied by a unique 'duck-type' beak shape [13]. The first stages in the evolution of this specialized beak type [1] are already evident in *C. antarcticus*, which underscores the significance of conducting further in-depth studies on this species.

The anatomy of the brain and sensory systems is extremely complex and impacts how animals perceive and interact with the world. This is especially significant for extinct species, for which inferring aspects of their lifestyle is challenging. Endocasts (reflecting the internal surface of the bony cavity housing the brain in life) constitute a critical proxy for qualitative and quantitative comparisons of brain shape and structure in extinct taxa, as well as modern birds facing conservation risks [14–16]. Here, we conducted a detailed study of the brain endocast of *C. antarcticus*, its bony inner-ear labyrinth morphology, and cranial and sensory anatomy, using computed tomographic (CT) scanning in a comprehensive comparative context that includes other species of extant (*Chauna*, *Dendrocygna*, *Cygnus*, *Lophonetta*) and extinct (*Presbyornis*) anseriforms. We compared total volume, regional surfaces (i.e. Wulst, olfactory bulb, rest of telencephalon, optic lobes, cerebellum, hypophysis), and the relative position of the main structures, to infer the lifestyle of *C. antarcticus*. *Presbyornis pervetus* represents an evolutionary branch of waterfowl that would have diverged earlier than the Anatidae or Anseranatidae [17]. In this context, we intend to provide new information that enhances our understanding of the early evolutionary history of waterfowl.

1.1. Results

1.1.1. Endocranial anatomy

The brain of *C. antarcticus* shows a wide telencephalon, relatively small optic lobes, markedly large bulbus olfactorius, a short and wide cerebellum, stout flocculi and a wide medulla oblongata (figure 1). Viewed laterally, the main brain axis shows a slight flexure, deviating from the spinal cord's main axis. This flexure is more pronounced than in *Cygnus*, Anhimidae and Dromornithidae (in which the flexure is absent, [18]) and *Presbyornis*, but similar to *Crax*. This disposition is related to the extent to which the skull elongates in the rostrocaudal direction. In this regard, the elongation of the skull in *Conflicto* is similar to that of most anatids, greater than in species of *Chauna* and Cracidae. In dorsal view,

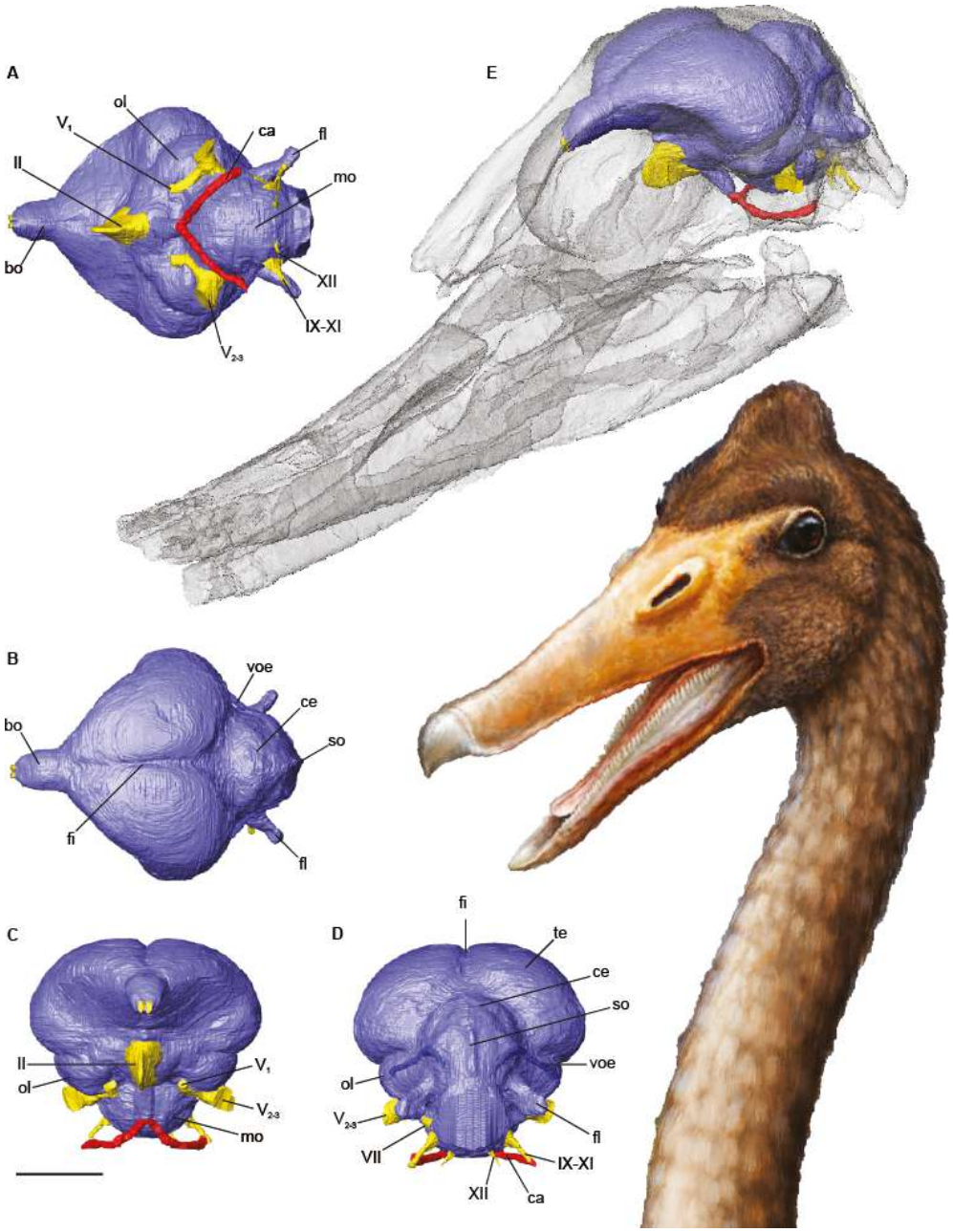

Figure 1. Three-dimensional reconstruction of the brain of *Conflicto antarcticus*, generated from CT scans in (A) left lateral, (B) ventral, (C) dorsal, (D) caudal and (E) frontal views. Abbreviations: bo, bulbus olfactorius (olfactory bulb); ca, cerebral carotid artery; ce, cerebellum; fi, fissura interhemispherica; fl, cerebellar flocculus; hy, pituitary gland (hypophysis); mo, medulla oblongata; ol, tectum opticum (optic lobe); so, sinus occipitalis; te, telencephalon; voe, vena occipitalis externa; I–XII, cranial nerves I–XII.

the telencephalon completely covers the mesencephalon, and the mediolateral extension is greater than the distance between both small cerebellar flocculi. However, the cerebellum is mainly located caudal to the telencephalon, making the disposition of the brain clearly orthoencephalic [19,20], as in dromornithids [18].

The telencephalon tapers rostrally to the enlarged bulbus olfactorius of *C. antarcticus*, which is a one-lobe type (i.e. both lobules are fused into one as is typical of anatids, and similar to that of anhimids). It shows a slight ventral inclination, is wide at the base and tapers rostrally, with the olfactory nerves (I) entering at that end. This anatomy is dissimilar to the condition observed in extant anatids where the smaller lobe has a medial furrow that separates it, and to the bifurcated bulbus of dromornithids and *Anseranas* [18]. Galliforms exhibit both types [21]. Regrettably, the endocast of *Presbyornis* has been difficult to reconstruct and does not allow a clear identification of the type of olfactory bulb, although it looks similar to the others in largely being a single cavity housing the two

neural structures. The paired dorsal telencephalic swelling known as the Wulst (i.e. eminentia sagittalis or hyperpallium) is not discernible in *C. antarticus*. Most modern birds have Wulsts with different shapes and sizes (e.g. dromornithids have extremely well-developed rostrally placed Wulsts, [18]), separated by a median groove (the fissura interhemispherica), and bounded laterally by the vallecula telencephali. Although the first is well defined, the second is indistinguishable in *C. antarcticus*.

The optic nerve (II) canal in *C. antarcticus* is well expanded. The hypophysis (i.e. pituitary) is quite elongate, being uniformly wide throughout its entire length and slenderer than in *Anseranas* and modern anatids. The paired cerebral carotid arteries are well visible, entering the pituitary fossa at its distal end (type X of [22] as in anatids, dendrocygnids and anhimids; type I in *Crax*). This divergence is quite variable among crown anseriforms as they are quite divergent in *Cygnus* (similar to *Conflicto*) and less divergent in *Dendrocygna*.

The optic lobes are fairly projected laterally, unlike in *Presbyornis*, where they are poorly developed in this direction. These lobes are extended rostrocaudally, although more caudally positioned than in *Presbyornis*. The optic lobes in *Conflicto* are quite different to those of anatids and dendrocygnids in which the optic lobes are shorter and more rostrally positioned (especially in *Dendrocygna*). *Anseranas'* optic lobes are markedly bulkier, rostrally placed and more ventrolaterally projected.

The cerebellum is dorsally rhomboid, more expanded mediolaterally than rostrocaudally. No cerebellar folia can be discerned—suggesting that the sinusoidal/meningial tissue was thick and wide enough to prevent the cerebellar surface from contacting the endocranium—and the occipital dural venous sinus is quite marked, being sharp and protruded caudally. The paired cerebellar flocculi project laterally at an angle of approximately 45° relative to the sagittal plane. Their bases are broad and not twisted, more similar to species of *Chauna* than to those of Cracidae or Anatidae. They narrow distally, not exceeding the caudal limit of the cerebellum. They appear to belong to type 5 of [23], the most frequent of all types of flocculi present in birds from both aquatic and terrestrial environments, gliders or with active flight, nocturnal or crepuscular.

The brainstem region has a rounded shape, being slightly longer than wider, and strongly projected ventrally. The trigeminal nerve (V) arises from the lateral surface of the pontine region. The maxillomandibular ramus (cranial nerve $V_{2\text{-}3}$) of the trigeminal nerve diverges widely from the ophthalmic ramus (cranial nerve V_1). Caudolaterally on the medulla oblongata, the nerves IX–XI exit the brain. On the caudoventral surface of the medulla, only a single pair of nerves corresponding to the cranial nerve XII can be observed.

Conflicto exhibits the surface area of the olfactory bulbs as large as those of the galliform species in *Crax* but not as extensive as that of *Presbyornis* (figure 2; tables 1 and 2, electronic supplementary material, table S2). The surface area of the flocculus is similar in all the species compared except in *Chauna*, in which it is notably larger. The surface area of optic lobes is larger in *Crax* but is similar in size in *Conflicto*, *Chauna* and *Presbyornis*.

1.1.2. Inner ear

Differences between the left and right inner-ear labyrinths of *C. antarcticus* were barely appreciable, and indeed the labyrinths of extant birds tend to be highly symmetrical [25]. The average total volume of the endosseous labyrinth is 40.46 mm^3; and the percentage of endosseous labyrinth volume relative to brain endocast volume (which is 4381.19 mm^3) is considerably higher in *Conflicto* (0.95%) than in the extant anatid *Cygnus* (e.g. 0.33%, whose inner ear has a similar absolute volume to that of *Conflicto*, considering that swans are larger birds and have larger brains). As in *Presbyornis*, the three semicircular canals (SCCs) are thicker than in anatids and dendrocygnids (figure 3). Posterior and anterior SCCs show subcircular cross-section, meanwhile the horizontal SC has a sub-elliptical one. The anterior SCC is conspicuously shorter (about half as wide as it is tall) and less expanded caudally than in crown representatives. In most living taxa, the anterior SCC is often larger than the other two. In *Cygnus*, the anterior SCC does not lean caudally, all SCCs are extremely thin, and their corresponding ampullae are very noticeable. The anterior and posterior SCCs communicate towards the midpoint of the major axis of the anterior SCC. From that place and towards the posterior SCC, the crus communis is located. It is long, thick and vertically disposed in *Conflicto* (slanted posteriorly in *Presbyornis*, vertical and thick in *Cygnus*, thinner in *Lophonetta* and *Dendrocygna*). All ampullae are stout and prominent (the posterior especially). The cochlea is relatively short and bends slightly medially (considerably more extended in our comparative sample). The ends of both cochleae approach each other at the base of the cranium.

Conflicto antarcticus has the thickest canals of all the compared species, especially regarding the anterior semicircular canal (electronic supplementary material, table S2). A similar situation occurs in *Dendrocygna* but in other stem-Anseriformes such as *Presbyornis*, canals are thinner.

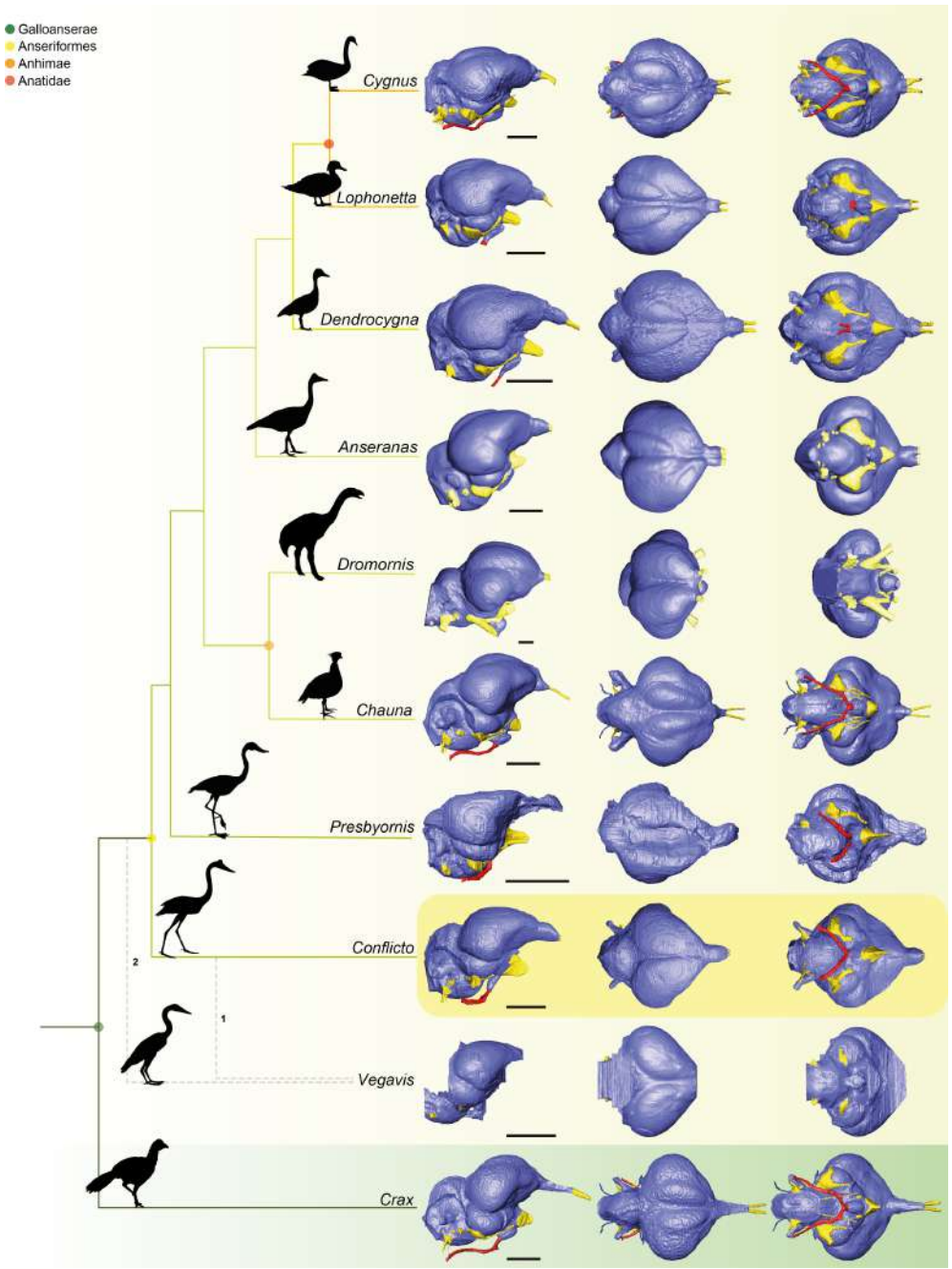

Figure 2. Anseriformes brain evolution in left lateral, dorsal, ventral, rostral and caudal views. Main phylogenetic proposal follows [1]. Alternative phylogenetic positions of *Vegavis* are indicated by 1, Torres *et al.* [4] and 2, Worthy *et al.* [17]. Anhimae relationship follows [24].

We calculate that *Conflicto* would have had a mean range of approximately 4454.1 Hz, which is considerably larger than extant species, and a mean hearing of 2633 Hz. The estimations of hearing capacity showed that *Presbyornis* is the species with the widest hearing range, with *Conflicto* in second place (table 3).

Spatial occupation imposes a strong constraint on the geometry of the semicircular canal system in birds. Following this idea, Benson *et al.* [26] proposed a method to quantify how much the labyrinth curves in response to cranial flexion. In large birds like *Struthio*, for example, this angle is 90°, while in small birds, it is typically smaller. Our measurements showed that in Anseriformes, this angle is highly variable, and its biological significance remains unclear.

Table 1. Linear measurements (mm) taken in the endocast of *C. antarcticus* as in comparative taxa. Abbreviations: BL, olfactory bulb length; CL, cerebellum length; CW, cerebellum width; FL, flocular lobe length; HL, telencephalic hemispheric length; ML, medulla oblongata length; MW, medulla oblongata width; OH, optic lobe máximum height; OL, optic lobe maximum length; TW, telencephalic width; WL, Wulst length; WW, Wulst width.

taxa	HL	TW	WL	WW	BL	OL	OH	CL	CW	FL	ML	MW
Chauna	20.81	30.49	16.94	7.23	3.96	11.04	7.15	16.13	10.28	9.36	12.7	10.37
Conflicto	18.32	25.04	—	—	5.46	10.58	6.26	11.97	9.8	6.63	11.33	10.23
Crax	21.27	30.38	15.67	6.73	9.95	11.72	7.86	15.02	8.59	5.93	13.55	10.86
Cygnus	28.35	33.05	20.21	8.32	4.66	11.06	6.7	9.84	12.24	5.31	14.9	12.73
Dendrocygna	21.46	23.63	13.54	5.35	5.03	8.45	5.09	11.49	9.03	4.74	11.16	9.86
Lophonetta	22.75	24.89	15.04	6.81	3.83	8.83	7.12	8.1	9.38	4.73	13.74	9.34
Presbyornis	12.61	15.89	—	—	5.1	7.17	3.75	7.76	6.77	3.75	9.2	6.94

Table 2. Surface measurements (mm^2) taken in the endocast of *C. antarcticus* as in comparative taxa. Abbreviations: C, cerebellum; F, flocculus; H, hypophysis; MO, medulla oblongata; OB, olfactory bulbus; OC, optic chiasm; OL, optic lobe; T, telencephalon (without the Wulst); W, Wulst. Compare with electronic supplementary material, table S2.

taxa	W	OB	H	OL	C	F	M	OC	T
Chauna	246.26	46.92	73.37	263.655	148.67	214.88	415.05	35.67	1215.31
Conflicto	—	68.51	27.28	153.13	144.17	85.21	352.36	24.96	1000.06
Crax	268.12	102.81	45.38	336.97	182.38	98.33	422.32	44.96	1269.55
Cygnus	318.87	49.95	94.1	215.24	164.95	136.45	521.88	37.62	1706.97
Dendrocygna	130.19	56.15	43.05	127.88	131.38	73.05	298.42	16.05	942.73
Lophonetta	199.73	47.37	51.63	165.09	95.01	92.38	294.22	21.85	1044.77
Presbyornis	—	64.69	—	75.28	42.26	46.98	113.93	7.41	498.91

1.1.3. Trigeminal nerve

The area of the foramen for the ramus ophthalmica (V_1) splits the analysed taxa into two groups. *Conflicto* belongs to the group with a small value, which also includes *Presbyornis*, *Dendrocygna*, *Crax* and *Chauna*. By contrast, the analysed anatids, *Cygnus* and *Lophonetta*, exhibit a much larger value of this foramen (see electronic supplementary material, table S4). The maxillary and mandibular rami ($V_{2\text{-}3}$), which share the same exit at the base of the neurocranium, follow a similar trend in their values, with the analysed anatids having a significantly larger area than the other taxa, including *Conflicto*. The ratio between the areas of the exiting foramina of $V_{2\text{-}3}$ and V_1 also divides the analysed taxa into two roughly distinct groups: those with a consistently larger ratio (i.e. a relatively larger $V_{2\text{-}3}$ compared with V_1), which include *Dendrocygna*, *Presbyornis* and *Chauna*, and those with smaller ratios, which include the anatids and *Crax*. In this case, *Conflicto* exhibits intermediate values (electronic supplementary material, table S3). Regarding the size of the foramen of the nervus opticus (II), *Conflicto* has the largest one of all the examined taxa. Nevertheless, considering the ratio of the foramina of the nerves II and V_1, a pattern emerges similar to that of the size of the trigeminal rami themselves, as the ratio is clearly smaller in the anatids (*Cygnus* and *Lophonetta*) and larger (meaning an optic nerve being much larger than the ophthalmic nerve) in the non-anatids.

Unfortunately, no beak tip is preserved in the holotype of *Conflicto*, making it impossible to appreciate any distal pattern of ramification of the ramus ophthalmica, which is (at least the reconstructed part) quite similar in thickness and length to that of modern anatids (figure 4).

2. Discussion

Conflicto antarcticus exhibits avian brain synapomorphies [27] such as a hyper-inflated brain with optic lobes ventrolaterally displaced. Across Anseriformes, there seems to be a trend towards a more

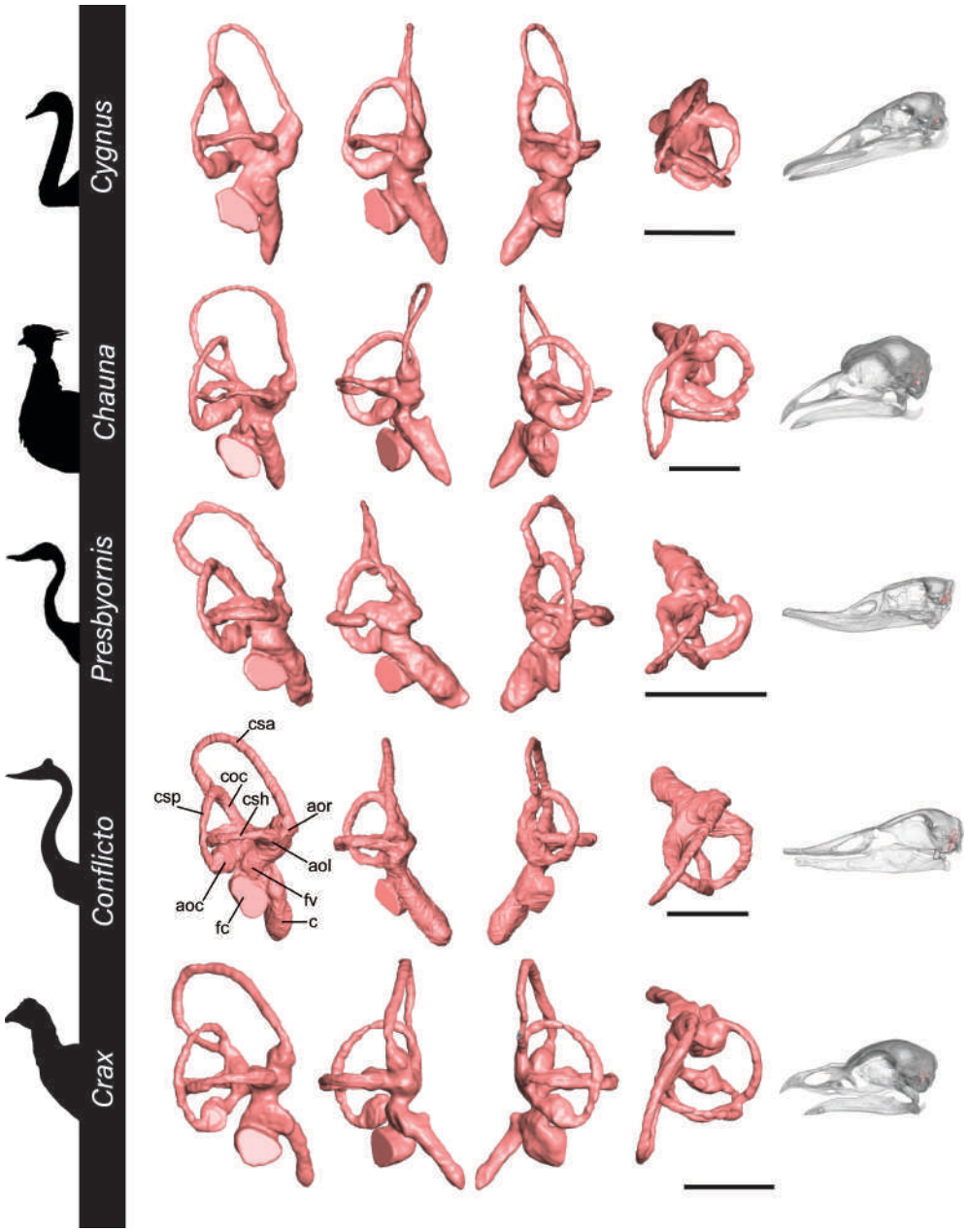

Figure 3. Inner ear morphology of Anseriformes in right lateral, cranial, caudal and dorsal views. Abbreviations: aoc, ampulla ossea caudalis/posterior; aol, ampulla ossea lateralis; aor, ampulla ossea rostralis/anterior; c, cochlea; coc, crus osseum commune; csa, canalis semicircularis anterior/rostralis; csh, canalis semicircularis horizontal/lateralis; csp, canalis semicircularis posterior/caudalis; fc, fenestra cochlearis; fv, fenestra vestibularis. Scale-bar = 5 mm.

airencephalic, flexed or 'packed' type of brain (figure 2). While *Conflicto* has an orthoencephalic disposition, as observed in several marine neoavians (e.g. [28]), species of *Presbyornis* and Anhimidae deviate from this with airencephalic brains. Nevertheless, modern anatids seem to have an intermediate type of brain, where, although the optic lobes are rostrally positioned and the cerebellum is tightly packed against the telencephalon, the brainstem region is developed caudally and not fully disposed under the telencephalon. Dendrocygnidae has more rostrally displaced optic lobes and brainstem, and a more packed cerebellum against the telencephalon, indicating a variable airencephalic condition across Anatidae.

The proposed sister-group relationship between *Conflicto* and *Vegavis* proposed by Torres *et al.* [4]—or a close relationship as suggested by Mayr [29]—is intriguing but challenging to support. *Vegavis* exhibits morphological traits indicative of a diving lifestyle, such as a short, curved femoral shaft and a reduced tibiotarsus, along with piscivorous trophic adaptations hypothesized [4] based on the presence of well-expanded temporal fossae—in skull material that has been referred to this species based on

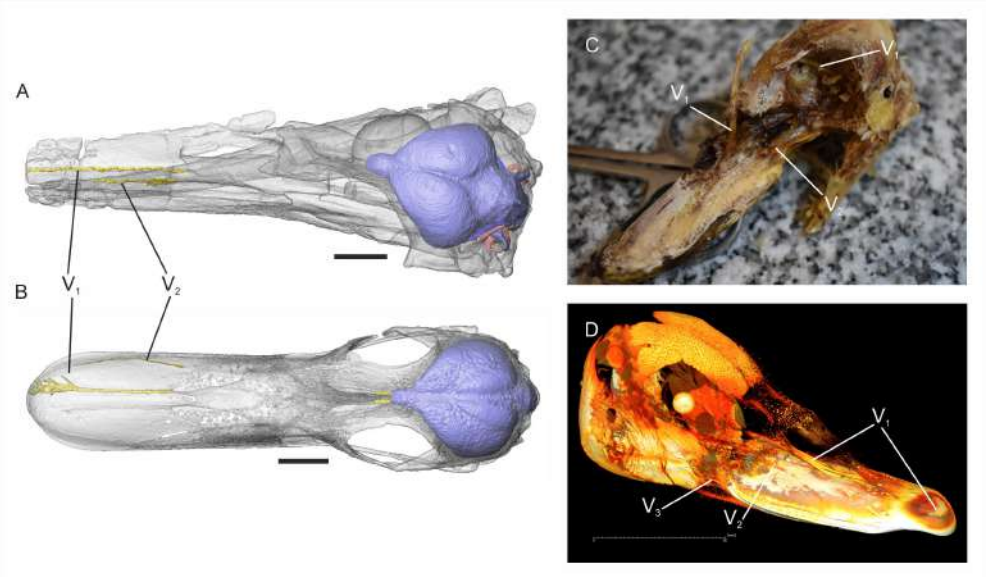

Figure 4. Skull in dorsal view indicating the ophthalmic nerve (V_1), maxillary nerve (V_2) and mandibular nerve (V_3) in *Conflicto* (A) compared with that of *Dendrocygna* (B), *Anas* (C), and *Melanitta* (D) —CT rendering.

Table 3. Hearing capabilities (in Hz) in Anseriformes. Abbreviations: BL, basicranium length; CL, cochlear length; HR, hearing range; MBH, mean hearing range. BL and CL are expressed in mm.

	CL	BL	HR	MBH	hearing range	
					upper	lower
Conflicto	5.61	14.52	4454.1	2633.22	4860.27	406.17
Presbyornis	4.64	10.92	4706.2	2769.98	5123.08	416.88
Dendrocygna	5.23	14.49	4273.64	2535.54	4672.36	398.77
Cygnus	6.19	18.55	4065.56	2422.63	4455.41	389.85
Lophonetta	5.06	15.58	3993.75	2383.56	4380.43	386.69
Chauna	6.20	12.26	5166.02	3020.32	5603.33	437.31
Crax	6.08	12.26	4274.29	2536.60	4673.74	399.45

minimal overlap of elements with the known skeletons of *Vegavis*—and the absence of a processus retroarticularis. *Conflicto* lacks these features, instead displaying long, straight femoral and tibiotarsal shafts, shallow temporal fossae, and a well-developed processus retroarticularis along with abundant evidence for a flying lifestyle [1].

Additional skeletal features further challenge this proposed phylogenetic relationship, particularly the morphology of the palate. In *Conflicto*, the os palatinum differs notably from that of *Vegavis*, displaying a well-developed, vertically disposed fossa ventralis, a pronounced angulus caudalis and a markedly slender processus rostralis. Neuroanatomical differences also underscore these distinctions: *Vegavis* has a more depressed brain with a wider telencephalon, and proportionally larger and more laterally expanded optic lobes, which are also shorter than those of *Conflicto* (figure 2). However, the most striking difference is the absence of the Wulst in *Conflicto* (as well as in *Presbyornis*), a feature present in *Vegavis*.

The size, shape and position of the Wulst vary considerably across avian lineages, including Anseriformes. Throughout extant Anseriformes, the Wulst is well developed and sharply delimited, being more restricted to the posterior region of the telencephalon in the analysed Anatidae. Meanwhile, some extinct anseriforms such as dromornithids—a group recently proposed to be related to screamers [24]—exhibits highly developed rostrally placed Wulsts [18]. The phylogenetic framework proposed by Torres *et al.* [4] suggests that *Conflicto* and *Vegavis* represent a later branching event than Anseres, which shows a more derived avian brain. Based on this, the evolutionary trajectory of the

anseriform brain appears rather complex, as this would imply that *Conflicto* (along with presbyornithids) retained basal avian brain features such as the absence of Wulst [27,30,31] or that the evolution of the Wulst consisted in a multiple event, convergently acquired by Galliformes, *Vegavis*, crown Anseriformes and Neognathae.

The Wulst is a swelling of the dorsal pallium with two main regions: a larger caudally located part associated with processing visual information and a smaller rostrally located somatosensory part. Together, these parts integrate binocular vision [32,33], spatial orientation [34], motion perception [35] and somatosensory inputs [36,37]. On the other hand, the optic lobes reflect the underlying tectum opticum [15,38], which is part of the tectofugal visual pathway. This path is considered the 'main' visual path and is the primary source of visual input to the avian brain [39] as it receives 90% of the retinal projections [40,41]. It is involved in the processes of brightness, colour and shape discrimination in pattern processing as well as in simple and complex motion [41,42]. Thus, both structures (i.e. Wulst and optic lobe) process visual information, among others. It has been demonstrated that the sizes of both the Wulst and optic lobe are correlated with the development of the underlying tissues (the hyperpallium and the tectum opticum, respectively), and its expansion is a characteristic trait of avian brain evolution [15].

The absence of a Wulst and the presence of a small optic lobe seem to indicate that stem Anseriformes were not strongly visually oriented birds whereas their large olfactory bulbs would denote significant olfactory capabilities. In crown Anseriformes (as in most modern birds), the condition is the opposite. Consequently, the brain morphology of *C. antarcticus* is consistent with morphological trends seen in living birds: replacement of olfactory sensory input by enhanced vision, indicating a shift that occurred multiple times within birds [43].

Contrary to what the absence of the Wulst and the proportionally smaller size of the optic lobes (compared with most extant Anatidae) would indicate, the relatively large orbit size of *Conflicto* (and *Presbyornis*; see electronic supplementary material) could be suggesting some reliance on vision. This might suggest a crepuscular or nocturnal lifestyle; although such a lifestyle is uncommon in extant anseriforms, a larger eye can enhance light capture in low-light conditions. More plausibly, it could indicate a visually guided foraging strategy. Some shorebirds, like scolopacids and charadriids, have large to very large eyes [44], developed optic lobes, but reduced Wulsts [45]. In both cases, their feeding strategy follows a 'watch, run, peck' pattern, which implies both visual and tactile aptitudes. Most anatids, such as *Anas* and *Oxyura*, rely on tactile feeding and have relatively small eyes compared with non-anatid anseriforms. Most taxa with large eyes also have large Wulst and/or optic lobes [46], so the apparent incongruence of the large eyes and the brain shape in *Conflicto* remains a mystery, although it could be suggested that the tectofugal visual pathway could balance the absence of Wulsts, as optic lobes seem to be developed enough. The orientation of the orbits and the shape of the frontals in extant and extinct anseriforms is related to several biological factors, including feeding, vigilance and head posture. During feeding, some anatids tilt their bill downwards, enhancing peripheral vision. When foraging on the ground or in shallow water, their upward-facing eyes help them remain aware of their surroundings, watching for predators.

Additionally, changes in the relative size of the Wulst are indicative of enhanced somatosensory and motor processing capabilities [47] in species that rely on tactile information originating from the beak for foraging. Based on this, if *Conflicto* were a filter feeder, its neuroanatomy suggests that its capabilities were still incipient compared with those of modern anatids and dendrocygnids. Moreover, while *Dendrocygna* is a capable filter feeder, despite not having a particularly well-developed trigeminal nerve, anatids also rely on this nerve for food detection while filtering. A possible explanation that integrates these observations is that *Conflicto* was a wading bird that relied on vision as well as its enhanced olfactory capabilities—a common trait in ancient birds—to detect and capture prey. Its large eyes may have also helped it detect movement from potential predators. With a straight beak that was less spatulate than that of *Presbyornis*, dendrocygnids and modern anatids, *Conflicto* probably fed more by picking items from the ground than by filtering. *Presbyornis* shares a similar brain shape and nerve development with *Conflicto*, but possesses a more spatulated beak, which has been associated with filter-feeding behaviour. However, Zelenkov & Stidham [48] proposed an alternative mechanism for filter feeding in *Presbyornis*, suggesting that it lacked the anatomical structures required for the piston-like tongue movements used to filter small particles and may have instead employed downward movements of the lower jaw to filter larger fragments. The brain morphology of *Presbyornis* suggests that a less-specialized form of filter-feeding could be performed without major neural adaptations. Moreover, differences in the relative size of the trigeminal nerve between anatids and dendrocygnids suggest a divergence in filter-feeding specialization, with anatids exhibiting larger

trigeminal nerve branches, reflecting a greater reliance on tactile particle detection compared with dendrocygnids.

Inner ear main functions include determining position and movement of the head in space (via the semicircular canals and vestibular organ) and hearing (via the cochlear organ). Hypothetically, the shape and size of the semicircular canals are indirectly related to agility and modes of locomotion in many groups, including birds, since they are involved with gaze stabilization via the vestibulo-ocular and vestibulo-cochlear reflexes. *A priori*, it could be suspected that longer and more curved semicircular canals have greater amount of endolymphatic fluid in movement, and this could potentially be related to better manoeuvrability. Nevertheless, Benson *et al.* [26] challenge this assumption with two observations: (i) that both larger and more agile birds possess long semicircular canals, but none of the variations in the shape of the labyrinth appear to be related to the way a bird flies, and (ii) most of the variation in shape of the inner ear would be linked to the large size of the eyeballs and the small size of the braincase which reduces the space available for the labyrinth. The angles formed by the canals in *Conflicto* can be interpreted as a proxy for their curvature and as noted above, may be associated with the size of the cranial cavity and the eyes. In any case, the morphology of the inner ear of *Conflicto* supports a trend observed in other groups, such as Sphenisciformes, where stem taxa show a markedly stouter inner ear [28]. These data align with the hypothesis that evolutionary modifications of the endosseous labyrinth involve a general stylization and thinning of the semicircular canals that occurred convergently between Anseriformes and Neognathae that includes a decreasing relationship between inner ear and brain volume between crown and stem taxa.

Our aim here was not to establish a general pattern of hearing abilities, but rather to provide an initial approximation of the potential capabilities of the analysed extinct species. As is well known, a broad auditory range offers various adaptive advantages, including enhanced detection of critical environmental signals, such as those related to danger or intraspecific communication, as well as improved adaptation to acoustically complex environments. This would be particularly beneficial for organisms that rely on hearing to detect prey or predators. Walsh *et al.* [49] show that maximum endosseous cochlear duct (ECD) length is indeed predictive of best hearing range and particularly of mean hearing frequency. The upper frequency limit in birds is 12 kHz [50]. Although the inferred range is quite similar to that of the modern Anseriformes sampled, our estimates suggest that *Conflicto*, like *Presbyornis*, had a wide hearing range, tuned for intermediate frequency sounds, though higher than in most Neoaves. This is highly contrasting with the much lower values estimated for dromornithids enabled for acoustic communication over long distances and in closed vegetated environments [51]. Nevertheless, all these results have to be taken carefully, as hearing capabilities estimation has proven to be debatable [52], since metric assumption of equality between the cochlear length and the sensory basilar papilla is not exactly the same.

Although the biological significance of this condition is difficult to determine, we propose that a broad hearing range would enable detection of a wider variety of acoustic signals, thereby facilitating communication and environmental awareness in acoustically complex settings [53]. Low frequency sounds propagate more effectively in open environments or across media of varying density, making them especially advantageous for long-distance communication. This interpretation aligns with palaeoenviromental reconstructions of the López de Bertodano Formation, where the only known specimen of *Conflicto* was exhumed, which suggest non-marine settings, probably near freshwater bodies such as rivers or lakes, surrounded by dense vegetation [1].

2.1. Conclusions and future directions

The most peculiar aspect of the brain of *Conflicto*, is not its hyper-inflated appearance or the ventrally displaced optic lobes, but rather the absence of Wulsts, a condition shared with the Eocene *Presbyornis*, and considered primitive for Neornithes.

Large olfactory bulbs could indicate certain olfactory capabilities absent in most modern bird lineages as enlarged olfactory bulbs are typical of basal birds but also in species living in semi-aquatic environments [54]. An olfactory-based combined with a visually guided foraging strategy is assumed due to the enlarged olfactory bulbs and the proportionally large size of the orbits and the upward orientation (this last condition is observed in some shorebirds such as certain scolopacids and charadriids that possess small olfactory bulbs, reduced Wulsts, but enlarged optic lobes and trigeminal systems [55]), although brain specializations related to visual feeding like a large optic lobe and/or Wulst are absent in *Conflicto*. Its somatosensory system based on the trigeminal nerve is less developed than in modern anatids, but closer to that of dendrocygnids, anhimids and Galliformes. Its

relatively enhanced olfaction may have played a role in its feeding strategy, perhaps compensating for the absence of these brain and nerve specializations. Based on neuroanatomy, if *Conflicto* were filter feeding, its tactile capabilities were markedly less than those of modern anatids and dendrocygnids. Moreover, the presence of a straight beak that was less spatulate than in *Presbyornis*, dendrocygnids and anatids, together with the brain features mentioned above as well as the presence of long legs (as in *Presbyornis*), seems to indicate that *Conflicto* probably fed more by picking items from the ground than by filtering.

The neuroanatomy of *Conflicto* comprises a step forward for understanding the evolution of the major avian lineages, revealing a mosaic evolution of skull and brain anatomy across Anseriformes (and Neornithes in general), retaining primitive brain features, but derived skull characteristics, like a broad (though not-spatulate) beak. If *Conflicto* and *Presbyornis* had an incipient filter-feeding strategy, their nervous system lacked the adaptations seen in modern dendrocygnids and anatids. Moreover, *Conflicto*'s brain morphology suggests that several features and feeding strategies evolved convergently across Neornithes.

3. Material and methods

3.1. Anatomical nomenclature

Except when noted, endocasts are referred to as brain models or simply as brains. The description of the endocasts modelled follows the brain anatomical terminology for the central nervous system primarily proposed by Breazile & Kuenzel [56] and Reiner *et al.* [57]. Osteological terminology follows [58].

3.2. Computed tomographic scanning and visualization

MicroCT scans of the skull of *Conflicto* skull (holotype MLP 07-III-1-1 from López de Bertodano Formation, Seymour Island, Maastrichtian-Danian, 64-61.1–63.8-65.5 Myr) were taken in Y-TEC, Berisso, Buenos Aires Province, Argentina. Virtual models of the brain and inner ear endocasts of MLP 07-III-1-1 were generated by segmentation using Avizo 7.1 (Thermo Fisher Scientific, Waltham, MA, USA). For comparative purposes, we rendered endocasts from the skulls of fossil (*Presbyornis pervetus*) and living Anseriformes (*Chauna torquata*, *Cygnus melancoryphus*, *Dendrocygna viduata* and *Lophonetta specularioides*), and Galliformes (*Crax fasciolata*). Endocasts of *Anseranas semipalmata* and Dromornithidae were obtained from [18]. Details on the specimen list and CT scan data can be found in the electronic supplementary material.

3.3. Metrics

Measurements follow [27] and [59]. Surface measurements of the brain portions were obtained using Geomagic Wrap software (Artec3d). Length measurements were taken on the three-dimensional models in millimetres on a surface (a single dimension in a straight line), using the 'measure' tool of the software Avizo 7.1. Surface measurements were taken over a two-dimensional area in mm^2, covering the relevant structures of interest in the avian brain. For this purpose, endocranial models of STL format were used in the Geomagic Wrap software which allows the measurement of areas with the 'calculate area' tool from the 'Analysis' menu. Ear measurements follow [60]. Diameters of the semicircular canals were measured in two directions of each of the semicircular canals as an expression of the thickness of each. To estimate mean hearing range (range of audibility) of *Conflicto*, we applied the method proposed by Zelenkov & Stidham [48], using scaled and transformed cochlear duct lengths.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data can be provided by F.J.D. pending scientific review and a completed material transfer agreement. Requests for the data should be submitted to: Dr. Federico Javier Degrange, fjdino@gmail.com.

Supplementary material is available online [61].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. F.J.D.: conceptualization, data curation, investigation, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review and editing; R.S.D.M.: conceptualization, investigation, methodology, validation, writing—original draft, writing—review and editing; M.T.E.: formal analysis, investigation, methodology, writing—review and editing; M.M.D.F.: investigation, methodology, writing—review and editing; L.W.: data curation, resources, visualization, writing—review and editing; C.P.T.: conceptualization, funding acquisition, investigation, project administration, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. PIP-CONICET 2021, PICT 2019-0771, PUE 2016 - CONICET – CICTERRA, NSF IOB-0517257, NSF IOS-1050154, NSF IOS-1456503, Swedish Research Council (2021-02973).

Acknowledgements. For assistance with CT scanning and data management, we thank Ariel Salomón and Emanuel Restelli (Hospital Nacional de Clínicas, Córdoba), María Bernarda Epele (Y-Tec, Berisso) and Germán A. Tirao (FaMAF, Córdoba). Chris Torres is thanked for sharing Vegavis endocast model, and Trevor Worthy is thanked for his kind contributions to an earlier version of this manuscript. H.S. Druetta is thanked for *Conflicto*'s life restoration shown in figure 1. We would like to thank the two anonymous reviewers and editors Laura Porro and Peter Haynes for their kind comments and suggestions.

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