

The largest lungless tetrapod: report on a second specimen of *Atretochoana eiselti* (Amphibia: Gymnophiona: Typhlonectidae) from Brazil

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The discovery is reported of a second specimen of the radically divergent lungless aquatic caecilian *Atretochoana eiselti* (Taylor), previously known only from the holotype. Aspects of the morphology of the second specimen are described and compared to the holotype, allowing a minimal evaluation of variation within this enigmatic species. With a total length of 805 mm, the second specimen is the largest known lungless tetrapod. Most of the distinctive morphological features reported for the holotype are true of the second specimen also indicating that the holotype is not a 'hopeful monster'. An important exception, from the perspective of species identification, is variation in the form of the pattern of denticulations about the cloacal disk. Although precise locality data are lacking for both the holotype and the second specimen, the latter specimen was almost certainly collected more recently and from within Brazil. This justifies increased expectation that this remarkable species is still extant and that it will be rediscovered.

KEYWORDS: *Atretochoana*, Typhlonectidae, Gymnophiona, Caecilian, lunglessness, Neotropics, Brazil.

Introduction

Taylor (1968) described *Typhlonectes eiselti* from a single specimen in the Naturhistorisches Museum, Vienna (NMW 9144) basing his diagnosis on the unusually high number of splenial teeth of this specimen. Nussbaum and Wilkinson (1995) pointed out that this species possesses a remarkable array of morphological features that set it apart from other species of *Typhlonectes* and from all other caecilians. These include lunglessness, sealed choanae, lack of pulmonary arteries and veins, a novel cranial architecture and a unique stapedial muscle. In recognition of this morphological disparity they established a new genus, *Atretochoana*, to receive this species. Wilkinson and Nussbaum (1997) described the comparative morphology of

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this radically divergent caecilian in more detail and discussed its phylogenetic relationships and evolution. Until now *A. eiselti* was known only from the holotype, a specimen from 'South America' with no precise data on its provenance or date of collection.

During a visit by the senior author to the Departamento de Ciências Fisiológicas, Universidade de Brasília, which is a centre for research on the caeciliid *Siphonops paulensis* Boettger, we identified an additional specimen of *Atretochoana eiselti* (As-1754), in the department's small collection of preserved caecilians. Given the apparent rarity of this form and its highly unusual morphology we here provide descriptive data for this second known specimen, henceforth referred to as the 'Brasília specimen', compare it with the holotype, and consider the significance of this discovery for the understanding and the status of this species.

Materials and methods

Observations were performed with the aid of a binocular dissecting microscope. Total length was measured to the nearest millimetre by stretching the specimen along a metre rule. Circumferences were measured to the nearest mm by wrapping cotton thread around the body and then stretching the thread along a ruler. All other measurements were made with dial callipers to the nearest 0.1 mm. Osteological examinations of the second specimen were made from radiographs, and limited dissection. The circulatory system was examined by gross dissection. Sex was determined by examination of gonads. Numbers of nuchal and postcloacal vertebrae were determined from radiographs following the method of Wilkinson (1989).

Results

The Brasília specimen of *Atretochoana eiselti* is an alcohol preserved, mature female with no precise locality data or other information on its collection. The specimen is in good condition except for incisions made during our examination, and the probability that the specimen was in a poor physiological state at the time of preservation (see below). Morphometric data for this specimen and comparative data for the holotype are summarized in table 1.

External morphology

The head of the Brasília specimen (figure 1) is similar to that of the holotype and agrees in all qualitative respects with those features of the holotype considered unique characteristics of the genus within the *Gymnophiona* by Wilkinson and Nussbaum (1997). Thus the head is highly dorsoventrally compressed; the eyes are dorsal, rather than dorsolateral, and lie in a shallow but distinctive ocular depression; the nares are strongly countersunk, and the cheek region is strongly curved with the lower jaws strongly countersunk laterally.

The most striking differences between the holotype and the Brasília specimen is in body proportions and the development of the dorsal 'fin' (figure 2). Taylor (1968) noted that the holotype was the largest typhlonectid he had examined and even included large size in his diagnosis of the species. With a total length of 805 mm the Brasília specimen is some 65 mm (almost 10%) longer than the holotype and has the greatest length reported for any typhlonectid and for any lungless tetrapod. Despite its greater length, the new specimen is much less robust than the holotype particularly in the posteriormost 500 mm. At midbody, the holotype has a width of 24.5 mm and circumference of 90 mm compared to only 15.3 mm and 53 mm respectively in the

Table 1. Morphometric and meristic data for the holotype and the *Brasilia* specimen of *Atretochoana eiselti*. All measurements in mm.

	Brasilia specimen	Holotype
Total length	805	738
Primary annuli	100	102
Vertebrae	118	115
Post-cloacal vertebrae	5	5
Nuchal vertebrae	5 or 6	5
Head length (snout tip to first nuchal groove)	27.1	28.2
Head length (snout tip to angle of the jaws)	23.9	24.5
Width of head at jaw angle	21.1	23.3
Height of head at jaw angle	10.2	12.0
Length of lower jaw	18.5	19.0
Snout projection beyond mouth	5.5	6.2
Inter-ocular distance	13.4	12.7
Inter-narial distance	8.5	8.5
Snout tip to eye level	11.6	11.2
Eye-tentacle distance	7.4	6.2
Eye-naris distance	9.0	8.6
Naris-tentacle distance	2.7	2.5
Premaxillary-maxillary teeth	51	54
Vomeropalatine teeth	40	39
Dentary teeth	51	45
Splential teeth	37	37
Width of cloacal disk	6.1	6.6
Length of cloacal disk	12.0	11.1
Distance of vent from posterior of cloacal disk	3.6	4.3
Distance of vent from terminus	9.5	12.3
Width at midbody	15.3	24.5
Ratio of total length/midbody width	52.6	30.1
Height at midbody	16.1	28.0
Circumference at midbody	53	90
Fin height at midbody	1.1	3.7
Width at vent	6.9	8.9
Height at vent	10.3	16.6
Circumference at vent	30	58
Fin height at vent	3.1	9.8

Brasilia specimen. The ratio of total length to midbody width, which has often been used in caecilian taxonomy (e.g. Taylor, 1968), of the *Brasilia* specimen is almost twice that of the holotype. The *Brasilia* specimen is also less laterally compressed than the holotype except close to the vent.

The skin of the *Brasilia* specimen is wrinkled in places, but lacks the loose baggy appearance of the holotype. A dorsal 'fin' is well developed along the entire length of the holotype behind the nuchal collars, whereas the 'fin' of the *Brasilia* specimen is more poorly expressed and is well developed only directly behind the collars and posteriorly close to the vent. At midbody, the skin of the *Brasilia* specimen is loose enough for a small (1.1 mm) 'fin' to be created by pinching the skin dorsal to the vertebral column but without this manipulation it is not apparent over much of the body. Observations of other aquatic typhlonectids indicate that fins are variably expressed both in life and in preservative (Wilkinson, 1988; 1996a) and this would seem to be true for *Atretochoana eiselti* also. A possible explanation of the great

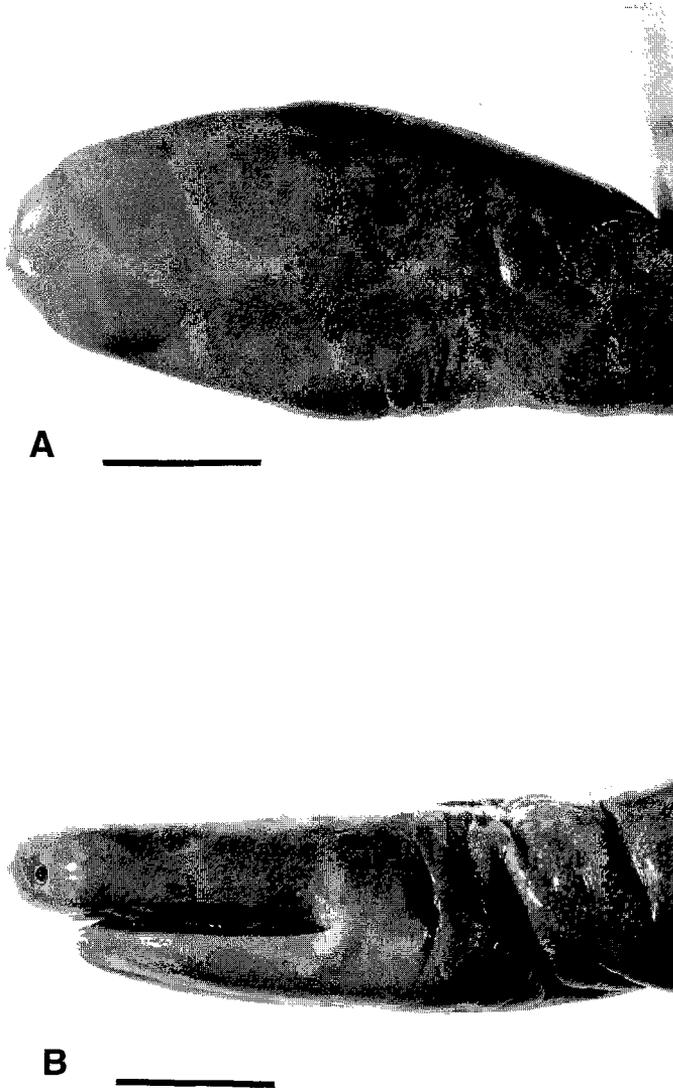


FIG. 1. Head of the Brasilia specimen of *Atretochoana eiselti*: (A) dorsal; and (B) ventral views. Scale bar = 10 mm.

differences in proportions of the holotype and the Brasilia specimen is that the Brasilia specimen was in a much poorer physiological condition at the time of preservation. This is also suggested by the fact that the vertebral column of the Brasilia specimen can be felt through the skin and seen in relief in those regions where the 'fin' is poorly developed. This is a highly unusual characteristic and probably not typical of healthy individuals.

As in the holotype, the body of the Brasilia specimen narrows considerably over the last quarter of its length. The holotype also has some loose skin ventrally, anterior to the cloacal disk which Wilkinson and Nussbaum (1997) considered might

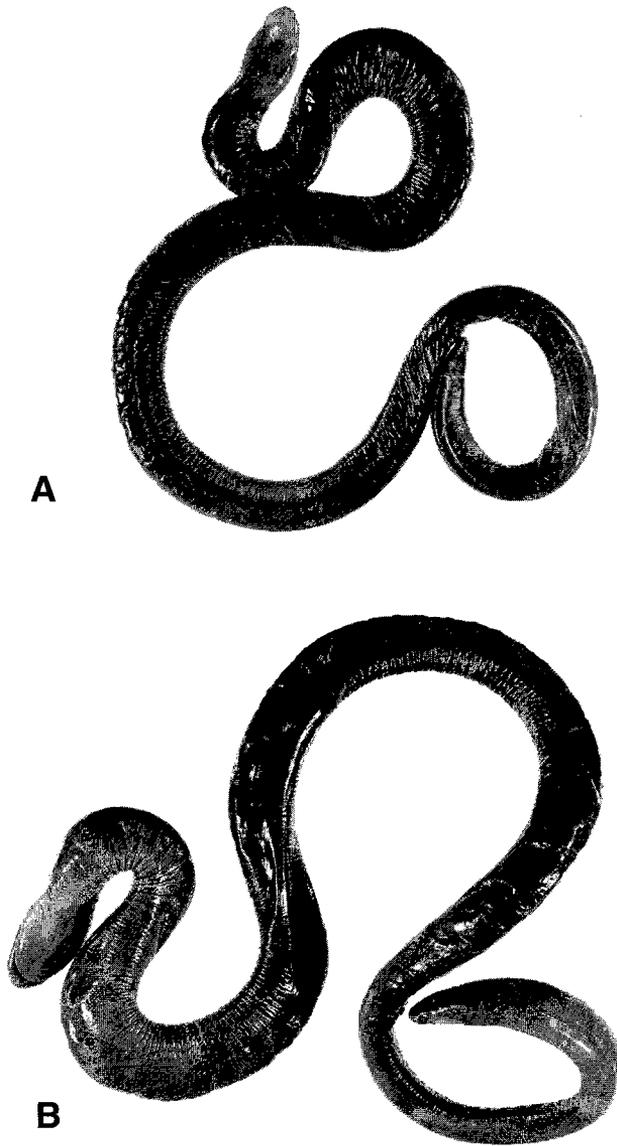


FIG. 2. Brasilia specimen of *Atretochoana eiselti*: (A) dorsal; and (B) ventral views. Total length = 805 mm.

indicate the presence of a short ventral fin in life. This feature is not apparent in the second specimen. As in the holotype, the annuli and nuchal collars of the Brasilia specimen are very poorly marked with the annular grooves complete ventrally but not crossing the dorsum. Our count of 100 annuli for the Brasilia specimen, like the similar count for the holotype (102), is approximate because of the indistinctness of the annular grooves of both specimens. In both specimens, no annuli are discernible at the level of the vent or posterior to it but there is no clearly defined unsegmented terminal shield. The colour of the Brasilia specimen is a light bluish-grey above, slightly lighter ventrally, with numerous irregular lighter lines created

by concentrations of dermal glands. The holotype is similar but a little lighter and less bluish. The colour of caecilians may fade in preservative and the colour in life is expected to be somewhat darker. The holotype and Brasilia specimen share a creamy white patch on the ventral surface of the head between the mandibles that extends posteriorly across the nuchal region and narrows onto the anterior annuli. The tip of the snout and the areas bordering the mouth are a more olive-grey.

Both the holotype and the Brasilia specimen have an egg-shaped cloacal disk, with the narrow apex anterior. The disk is recessed and bordered by fleshy flaps of skin in the holotype. The lack of these features in the Brasilia specimen is probably correlated with its poor condition. Patterns of cloacal disk denticulations vary between species of aquatic caecilians (*Atretochoana*, *Typhlonectes* and *Potomotyphlus*) and have been recommended as useful for discriminating species (Wilkinson, 1996b). The disk of the holotype (figure 3A) has a regular geometric pattern of denticulations surrounding the vent with six anterior and six posterior and with the two posteromedial denticulations incompletely separated proximal to the vent. Other species of aquatic caecilians have five posterior, and either four or five anterior denticulations. However, the Brasilia specimen (figure 3B) differs from the holotype in having the more typical aquatic caecilian pattern of five posterior denticulations with a single undivided posteromedial denticulation. The number of anterior denticulations is the same as in the holotype, but the denticulations are irregular with poorly marked boundaries between the anterolateral and anteromedial denticulations.

In both the holotype and the Brasilia specimen the grooves separating the denticulations extend from close to the margin of the disk to the vent posteriorly.

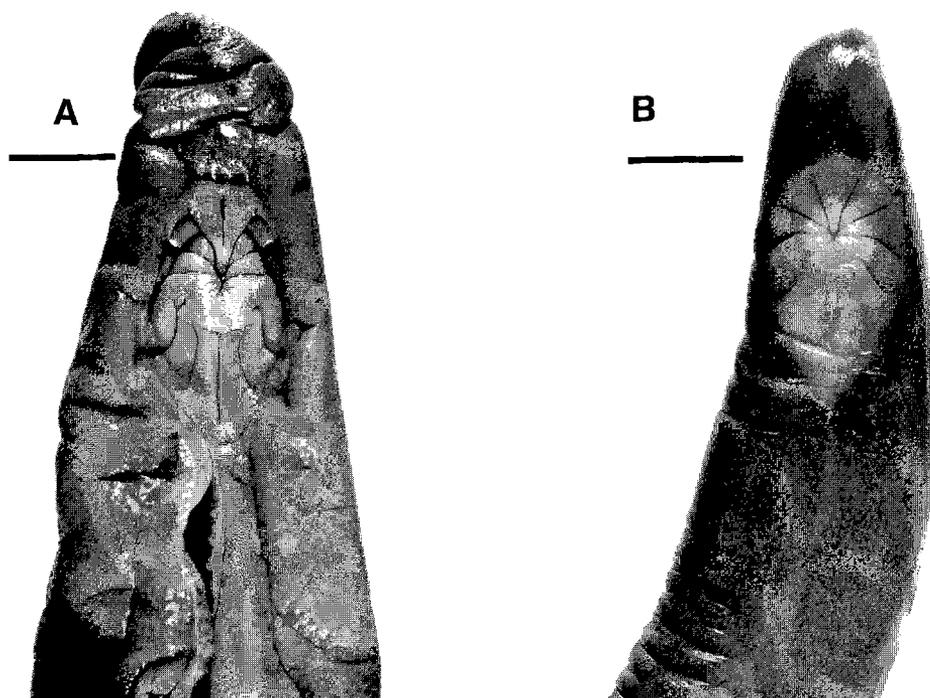


FIG. 3. Cloacal disks of *Atretochoana eiselti*: (A) holotype, and (B) Brasilia specimen. Scale bar = 5 mm.

Anteriorly they do not reach the vent but are interrupted by a raised and undivided area. In both specimens the centre of the disk is a creamy white and the periphery pigmented. Two whitish cloacal papillae are present toward the periphery of the anterolateral denticulations. Cloacal papillae were mistakenly considered by Taylor (1968) to be present only in males. As in the holotype, the terminus of the body, behind the vent is narrow and somewhat bluntly rounded (figure 3), but more pointed than in the more terrestrial typhlonectids of the genera *Chthonerpeton* and *Nectocaecilia*.

Buccal cavity

Features of the buccal cavity of the Brasilia specimen are mostly like those of the holotype. The choanae are completely sealed by the presumed evolutionary fusion of choanal valve flaps, and the resulting soft tissue cloacal seal projects strongly into the buccal cavity. The tongue is separated from the tooth-bearing regions by a groove, and bears two large narial plugs, complementary to the choanal seal. The numbers of teeth are similar in both specimens (table 1). Many of the teeth of the Brasilia specimen are hidden (not erupted) in the gingivae. Erupted teeth frequently occur in adjacent pairs separated by a single unerupted element, suggesting, perhaps, some form of co-ordinated replacement pattern. As in the holotype, the teeth are all monocusped, pointed and recurved with only weak lateral flanges. Wilkinson and Nussbaum (1997) reported that the tooth crowns of the holotype were attached to the pedicels by a flexible region and that they could flex about this attachment almost to the horizontal plane. Although the tooth crowns of the new specimen are also flexibly attached to their pedicels, the degree of flexure is only about one half of that seen in the holotype. The different condition of the Brasilia specimen supports the view that the condition of the holotype is in part a preservation artefact caused by tissue maceration (Wilkinson and Nussbaum, 1997). In contrast, both the holotype and the Brasilia specimen have very flexible mandibular symphyses and mobile cheek regions that are unlikely to be artifactual.

Aspects of internal morphology

Given the divergent cranial, cardiovascular and pulmonary morphologies reported for the holotype of *Atretochoana eiselti*, we made limited dissections and prepared radiographs of the Brasilia specimen in order to evaluate the consistency of this morphology within the species. Radiographs (figure 4) reveal the new specimen to have 118 vertebrae, five of which are postcloacal and five or six nuchal. The count of nuchal vertebrae is approximate because of difficulty in delimiting the extent of the nuchal collars. As far as can be determined the new specimen shares the remarkable cranial modifications reported for the holotype. The jaw articulation is displaced posteriorly (figure 5) through the elongation of the squamosal and quadrate, producing a much enlarged gape. The stapes has lost its articulation with the quadrate and is rotated and extended posteriorly (figure 5A). Dissection reveals that the novel *pars stapediales* of the *m. pterygoideus* described for the holotype also is present in the Brasilia specimen, as is the strange *pars superficialis* of the *m. intermandibularis*, and the separation of the anteriormost fibres of the *m. intermandibularis* from the main body of this muscle. None of these features are known in other caecilians.

As with the holotype, there are no traces of lungs in the Brasilia specimen. A

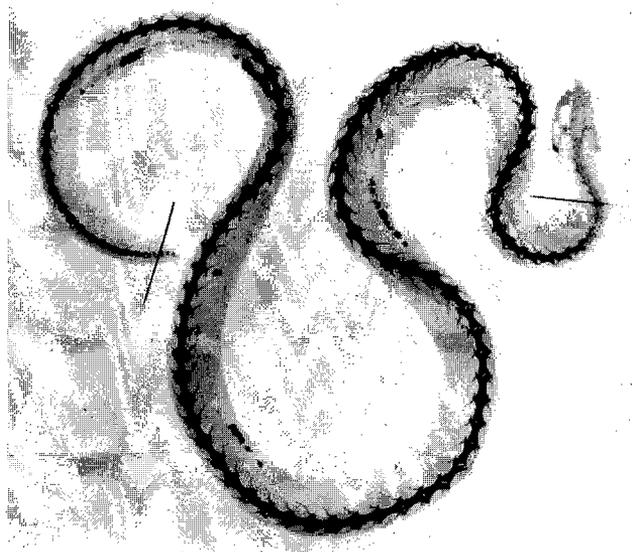


FIG. 4. X-radiograph of the Brasilia specimen of *Atretochoana eiselti*. Total Length = 805 mm. Opaque lines are the shadows of metal pins inserted at the vent and the posterior margin of the nuchal collars to enable determination of the numbers of post-cloacal and nuchal vertebrae.

vestigial trachea was found during extensive dissections of the holotype but we were unable to locate this structure with our more limited dissections of the second specimen. One of the most surprising aspects of the anatomy of the holotype reported by Nussbaum and Wilkinson (1995) was that absence of lungs was accompanied by the loss of all traces of pulmonary veins and arteries. In other lungless tetrapods the pulmonary arch is retained and sends blood to other respiratory surfaces. We made a careful examination of the aortic arches of the second specimen and also found no traces of pulmonary arches. Examination of the heart of the Brasilia specimen revealed one additional unique feature that was not noted in examinations of the holotype. The sinuatrial aperture is displaced anteriorly compared to other caecilian species and lies approximately half way between the posterior margin and anterior apex of the atria. In other caecilians, this aperture lies on the dorsal surface of the atria close to its posterior margin and adjacent to the base of the ventricle (Wilkinson, 1992, 1996c, personal observation).

Gut contents

The gut of the second specimen contained numerous small fragments of quartz and of limonite up to 2 mm in diameter, and some fragmentary plant material (Leguminosae: indet.).

Discussion

Several aspects of the anatomy and, by inference, the habits and physiology of *Atretochoana eiselti* are very different from other caecilians. This species is the only lungless caecilian and, as the largest lungless tetrapod, *A. eiselti* should be of interest to comparative respiratory physiologists studying mechanisms of cutaneous gas exchange and size constraints on lunglessness in tetrapods. In addition, *A. eiselti*

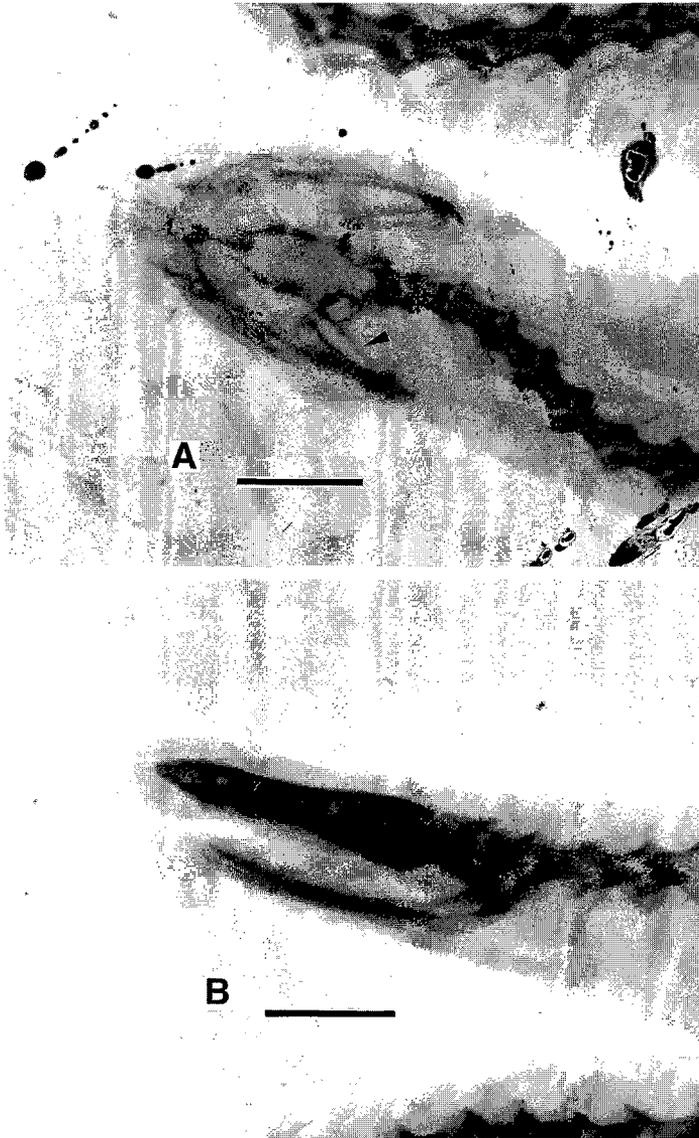


FIG. 5. X-radiographs of the head of the Brasilia specimen of *Atretochoana eiselti*: (A) horizontal; and (B) lateral. Scale bar = 10 mm. Arrowhead points at the left stapes.

has a highly kinetic skull and associated modifications of the suspensorium and cranial musculature that require biomechanical investigation. The combination of these features in a single caecilian species imply an enhanced rate of morphological evolution and suggest possible correlated evolution of the feeding and respiratory systems (Wilkinson and Nussbaum, 1997). Thus the discovery of the radically divergent morphology of *Atretochoana* raises many intriguing functional and evolutionary questions. However, research on *Atretochoana* is hampered by a lack of specimens and by a dearth of information on its ecology and distribution.

Until the discovery of the Brasilia specimen, *Atretochoana eiselti* was known only from the holotype. Other than 'South America', the holotype lacks locality and

collection data. Although the date of collection of the holotype is uncertain, the lack of data suggests that it was collected sometime prior to 1945 (some records of the NMW having been destroyed or lost during World War II). Further, its condition and the data associated with other South American caecilians in the NMW suggest that it was probably collected more than 100 years ago. With no other specimens known to have been collected in the interim and with the extent of habitat destruction in the Neotropics, Nussbaum and Wilkinson (1995) expressed concern over the status of the species and noted that it may be extinct. Unfortunately, the Brasilia specimen also lacks locality and collection data. However, the Universidade de Brasilia was founded in 1961 suggesting collection after or not much before that time. It is also likely that the Brasilia specimen was collected in Brazil, as the collection contains few specimens from other countries. Thus the discovery of the Brasilia specimen provides a slightly more focused locality for the species, and also raises our expectation that populations of *A. eiselti* remain to be discovered. It also raises the expectation that additional specimens, and thus far elusive locality data, may exist in other collections in Brazil.

Gut contents of the Brasilia specimen do not shed much light on its biology or provenance. Wilkinson and Nussbaum (1997) argued that the large size of the holotype combined with its reliance upon cutaneous respiration implied an upland environment in cold fast moving waters. The presence of fairly large quartz crystals in the gut of the Brasilia specimen and absence of much smaller particles does not provide strong evidence, but is consistent with this ecological reconstruction. Caecilians are carnivorous and the plant and mineral materials found in the gut of the Brasilia specimen are presumed to have been ingested accidentally.

Discovery of the Brasilia specimen also allows some minimal assessment of variation within *Atretochoana eiselti*. Importantly, the similarity of the holotype and Brasilia specimen in all major features that set *Atretochoana* apart from other caecilians allows the possibility that the holotype was some kind of unique 'hopeful monster' or teratology to be discounted. Differences between the holotype and the Brasilia specimen are mostly minor or reflect differences in condition of the specimens (table 1). Thus the more flexible teeth of the holotype reflect its greater maceration, and the narrow body and poorly developed 'fin' of the Brasilia specimen probably reflects poor physiological condition at the time of preservation. The most surprising difference between the holotype and Brasilia specimen is in the patterns of denticulations about the cloacal disk. This pattern is more or less constant and species specific in aquatic caecilians, and provides a readily accessible key character for discriminating species that are otherwise notoriously difficult to identify (Wilkinson, 1991; 1996a). However, occasional variants are encountered in which there is partial fusion or supernumerary division of the denticulations. Such deviations from the norm usually produce asymmetric patterns so that deviant specimens are readily recognised as such. With a sample of only two, we cannot characterise a norm for the cloacal disk pattern of *A. eiselti*. Both specimens have six anterior denticulations, but these are highly irregular in the Brasilia specimen. The difference in the posterior denticulations (five or six) is dramatic, and suggests that this feature should be used cautiously and not relied upon too heavily in species identifications at least with respect to *A. eiselti*. However, *A. eiselti* is the only aquatic caecilian known that ever has more than five anterior or more than five posterior regular cloacal denticulations and aquatic caecilians with one or both of these features should be compared to *A. eiselti* leading to investigation of dental (many splenial teeth) and buccal (sealed choanae) characters that are readily accessible and unique to this enigmatic taxon.

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