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Unveiling the elusive: X-rays bring scolecophidian snakes out of the dark

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Abstract

Scolecophidian snakes have long posed challenges for scholars interested in elucidating their anatomy. The importance, and relative paucity, of high-quality anatomical data pertaining to scolecophidians was brought into sharp focus in the late 20th century as part of a controversy over the phylogeny and ecological origin of snakes. The basal position of scolecophidians in the phylogeny of snakes makes their anatomy, behavior, ecology, and evolution especially important for such considerations. The depauperate fossil record for the group meant that advances in understanding their evolutionary history were necessarily tied to biogeographic distributions and anatomical interpretations of extant taxa. Osteological data, especially data pertaining to the skull and mandible, assumed a dominant role in shaping historical and modern perspectives of the evolution of scolecophidians. Traditional approaches to the exploration of the anatomy of these snakes relied heavily upon serial-sectioned specimens and cleared-and-stained specimens. The application of X-ray computed tomography (CT) to the study of scolecophidians revolutionized our understanding of the osteology of the group, and now, via diffusible iodine-based contrast-enhanced computed tomography (diceCT), is yielding data sets on internal soft anatomical features as well. CT data sets replicate many aspects of traditional anatomical preparations, are readily shared with a global community of scholars, and now are available for unique holotype and other rare specimens. The increasing prevalence and relevance of CT data sets is a strong incentive for the establishment and maintenance of permanent repositories for digital data.

KEYWORDS
blind snake, CT scan, diceCT, osteology

1 | COMMENTARY

Scolecophidian snakes have long been recognized as a distinct assemblage of slender, fossorial snakes, characterized by a cylindrical body form and distinctive anatomical features. As a group they have a wide geographic distribution in tropical and subtropical regions, with limited range into temperate areas in North America and Europe (Cundall & Irish, 2008; Haas, 1930). Classifications of squamate reptiles in recent decades generally recognized them as one of two major clades of extant snakes (Scolecophidia and Alethinophidia), with at least three major lineages accepted—the Leptotyphlopidae, Typhlopidae, and Anomalepididae (the last treated as a distinctive group within Typhlopidae in earlier classifications). Monophyly of the Scolecophidia often was recovered in phylogenetic analyses over the last three decades, but a more recent perspective from Miralles et al. (2018) is that the Anomalepididae may be more closely related to Alethinophidia than to Leptotyphlopidae and Typhlopidae (now also taxonomically recognized as three distinct clades within a monophyletic Typhlopoidea, the Gerrhopilidae and Xenotyphlopidae encompassing some of the species traditionally classified within Typhlopidae; see Vidal et al., 2010). A controversy emerged during the last decade of the 20th century that centered in large part on new discoveries and interpretations of late Mesozoic fossil snakes with limbs and the implications of their anatomy for both the phylogeny and ecological origin of snakes (Caldwell & Lee, 1997; Lee & Caldwell, 1998, 2000; Lee, 1998; Zaher & Rieppel, 1999; Rage & Escuillié, 2000; Tchernov, Rieppel, Zaher, Polcyn, & Jacobs, 2000; see also Rieppel, Zaher, Tchernov, & Polcyn, 2003; Rieppel & Head, 2004; Apesteguía & Zaher, 2006; Caldwell, 2007; Zaher & Scanferla, 2012; Caldwell, 2020; Head, de Queiroz, & Greene, 2020). As the arguments unfolded, the necessity of accurate data pertaining to, and reliable interpretation of, the skeletal system of extinct and extant snakes was brought into sharp focus, as was the relative paucity of detailed data pertaining to the osteology of scolecophidian snakes, and a completely inadequate understanding of their ancient history.

The fossil record of scolecophidians is heavily biased towards Neogene and younger deposits and consists entirely of vertebral elements, usually found in isolation from each other as well as from other skeletal elements. The earliest reported fossils of the group were until recently restricted to the Paleogene with records reported from the Paleocene in Europe (Folie, 2007), Paleocene-Eocene boundary in north Africa (Augé & Rage, 2006), and possibly the Paleocene (Schiebout, Rigsby, Rapp, Hartnell, & Standhardt, 1987) and certainly the Oligocene (Mead, 2013) in North America. A recent report of a large-bodied scolecophidian, *Boipeba tayasuensis*, from the Cretaceous of Brazil pushes the material record of scolecophidians back into the late Mesozoic and suggests that the relatively small body size of extant scolecophidians is a derived condition (Fachini et al., 2020). This new record is consistent with recent genomic-scale data, which estimate the node containing Typhlopoidea, Anomalepididae, and Alethinophidia in the Cretaceous (Burbrink et al., 2020).

Because of the limited nature of the fossil record, inferences on the evolutionary history of the scolecophidians depended upon analysis of patterns of biogeographic distribution of the extant taxa, and of their anatomical features including, to a limited extent, myology and other "soft" anatomical systems (Haas, 1930, 1931, 1962; Martins, Silva, & Gonzalez, 2020; Mosauer, 1935; Robb, 1960; Robb & Smith, 1966), but more importantly their osteology, especially of the skull and mandible (Cundall & Irish, 2008; McDowell, 2008; McDowell Jr. & Bogert, 1954). Clear understanding of the three-dimensional architecture of the scolecophidian skull remained an elusive goal for nearly two centuries. The diminutive size of many species of scolecophidians posed numerous challenges for scholars interested in exploring their cranial anatomy (see Thomas (1976) for an illustration of the skull of *Antillotyphlops granti*, one of the smallest reptile skulls ever illustrated). Traditional methods applied to the study of larger snakes often are of limited value in the study of many scolecophidians. Delicate structures of the skull are easily broken or lost during specimen preparation and handling (Dunn, 1941); even skinning a specimen can result in loss of data (List, 1966), and this is exacerbated in the case of burrowing snakes because some elements are attached to the skull only by ligamentous joints. Standard "dry" skeletal preparations that rely upon dermestid beetles are feasible only if the preparator selects and uses the smallest instars of the insects; even then, thin and delicate bones can be destroyed or damaged, and small skeletal elements are easily lost among the shed exuvia and other insect waste products (pers. obs.). Furthermore, drying in the skeletonization process almost certainly leads to shrinkage of tissues between bones and may cause deformations that lead to misleading views of bone-to-bone relationships (McDowell, 1967). Maceration in water will yield clean bones, but they are disarticulated and also may be easily lost during preparation (pers. obs.).

Among the earliest utilized methods of skeletal preparation of scolecophidians was the time-consuming and intricately delicate task of direct manual dissection from fluid-preserved specimens. This was the method used by Müller (1831) to extract and illustrate a skull of *Typhlops lumbricalis*, and he noted the delicate nature of the skull, the effort required for its preparation, and the scientific yield resulting from his patience—the revelation of anatomical details not otherwise visible in museum preparations of other specimens (Müller, 1831, pp. 240–241). Some later practitioners followed his lead (Evans, 1955; Rieppel, 1979; Waite, 1918), but by far the most productive approaches were those involving serial sections (Haas, 1964, 1968) or clearing and staining of heads to reveal and distinguish cartilaginous and ossified elements of the skull. By 1932, cleared-and-stained preparations were yielding new data on the skull (e.g., the existence of paired parietals, the distribution of which among scolecophidians is still not entirely documented; see

Mookerjee & Das, 1932; Broadley, 2004) and those preparations dominated the field for decades. The most comprehensive investigation of the scolecophidian skull (in terms of species examined) was based upon cleared-and-stained material (List, 1966—the published version of a dissertation completed 10 years earlier; see McDowell, 1967), as were the studies by Haas (1930), Mahendra (1936), Dunn (1941), Dunn and Tihen (1944), Tihen (1945), Evans (1955), List (1958), Thomas (1989), Abdeen, Abo-Taira, and Zaher (1991a, 1991b, 1991c, 1992), Zaher, Abo-Taira, and Abdeen (1992), Iordansky (1997), and Broadley and Broadley (1999). The ready differentiation of different tissues involved in the architecture of the head yielded many new anatomical insights, especially about internal anatomical features not visible in an articulated skull (Brock, 1932; Haas, 1930, 1959, 1962, 1964, 1968; Rieppel, 1979, 1980; Smit, 1949).

The scientific yield of those studies pertaining to osteological features of the Leptotyphlopidae, Anomalepididae, and Typhlopidae were summarized by Cundall and Irish (2008) based upon an extensive review of the published literature. That summary was serendipitously timed perfectly to mark an extraordinary division between knowledge gained from traditional approaches to the study of the skull of Scolecophidia and the explosion in new knowledge following the emergence and application of new technologies.

In the last years of the 20th century, digital and other technologies opened new avenues for creative investigation of scolecophidian anatomy and biology. Those technologies included high-speed videography (Kley, 1998, 2001; Kley & Brainerd, 1999) and scanning electron microscopy (Zaher & Rieppel, 1999) that brought out high-quality visualizations to enhance understanding of functional morphology, behavior, and anatomy. Another powerful technology impacting studies of anatomy and paleontology at that same time was high-resolution X-ray computed tomography (CT). CT technology was rapidly applied to the study of squamate reptiles, but resolution of early scanners was insufficient to yield high-quality imagery of tiny specimens, and of small-scale anatomical features of interest for some questions (e.g., the position of foramina for passage of cranial nerves—a problem noted by Haas in 1930 for serial sections of the diminutive members of Leptotyphlopidae—his Glauconiidae). Although X-ray imagery was occasionally applied to the study of scolecophidian skulls before the development of CT and its widespread use outside of biomedicine (Brongersma & Helle, 1951; Haas, 1959; Joger, 1990; Thomas, 1989; Wallach & Ineich, 1996), the application of micro-CT has proven to be transformative (see Chretien, Wang-Claypool, Glaw, & Scherz, 2019; Daza & Bauer, 2015; Gauthier, Kearney, Maisano, Rieppel, & Behlke, 2012; Koch, Martins, & Schweiger, 2019; Palci, Lee, & Hutchinson, 2016; Pinto, Martins, Curcio, & de O Ramos, 2015; Rieppel, Gauthier, & Maisano, 2008; Rieppel, Kley, & Maisano, 2009; Rieppel & Maisano, 2007; Santos, 2018; Santos & Reis, 2018, 2019). The new data emerging from CT scans contribute substantially to a better understanding of anatomy and the distribution of morphological traits across a phylogeny (Figure 1).

An interesting and important aspect of micro-CT scanning is that in important ways it permits replication of many aspects of the traditional techniques. The resulting digital models allow for three-dimensional and rotational investigation similar to traditional observations of dry skulls or skeletons in hand. Digital segmentation permits disarticulation of individual cranial elements to reveal the articulation surfaces between elements as well as detailed views of interior structures comparable to those readily visualized from disarticulated dry-skeleton preparations. Traditional cleared-and-stained specimens allowed investigators to appreciate the relationships between bones and cartilages in the cranium, track patterns of ossification, and see the relationships of bones *in situ*, without the deformations and shrinkage that accompany dried skeletal preparations (McDowell, 1967). However, clearing and staining can have the opposite effects of those produced by dry skeletonization techniques because digestion causes connective tissues to relax and articulations become looser than they are in life. Results of clearing-and-staining vary depending upon the protocol used and upon the preservation history of specimens (Broadley & Broadley, 1999; Haas, 1930), and reconstructions of small elements from serial-sectioned heads may be subject to significant errors (McDowell, 1967). CT data are readily visualized as slices through a data volume, permitting visualizations similar to those generated by traditional serial sections—at least for hard-part anatomical features—and without the distortions that may occur as a result of chemical preparation and handling of specimens required in the traditional treatments. The development of other techniques such as diffusible iodine-based contrast-enhanced computed tomography (diceCT; Gignac et al., 2016) and MRI (Jackson et al., 2017) are now permitting visualization of many soft anatomical features in CT imagery that are directly comparable to traditional preparations (Figure 2).

The fact that all of these visualizations can be rendered of the same specimen from a single CT scan, and with minimal handling and no damage to the original specimen, makes this an especially valuable and versatile tool. Micro-CT data sets are fundamentally altering the study and understanding of scolecophidian cranial osteology and have stimulated a new wave of investigation that is adding rapidly to our knowledge of these snakes. The

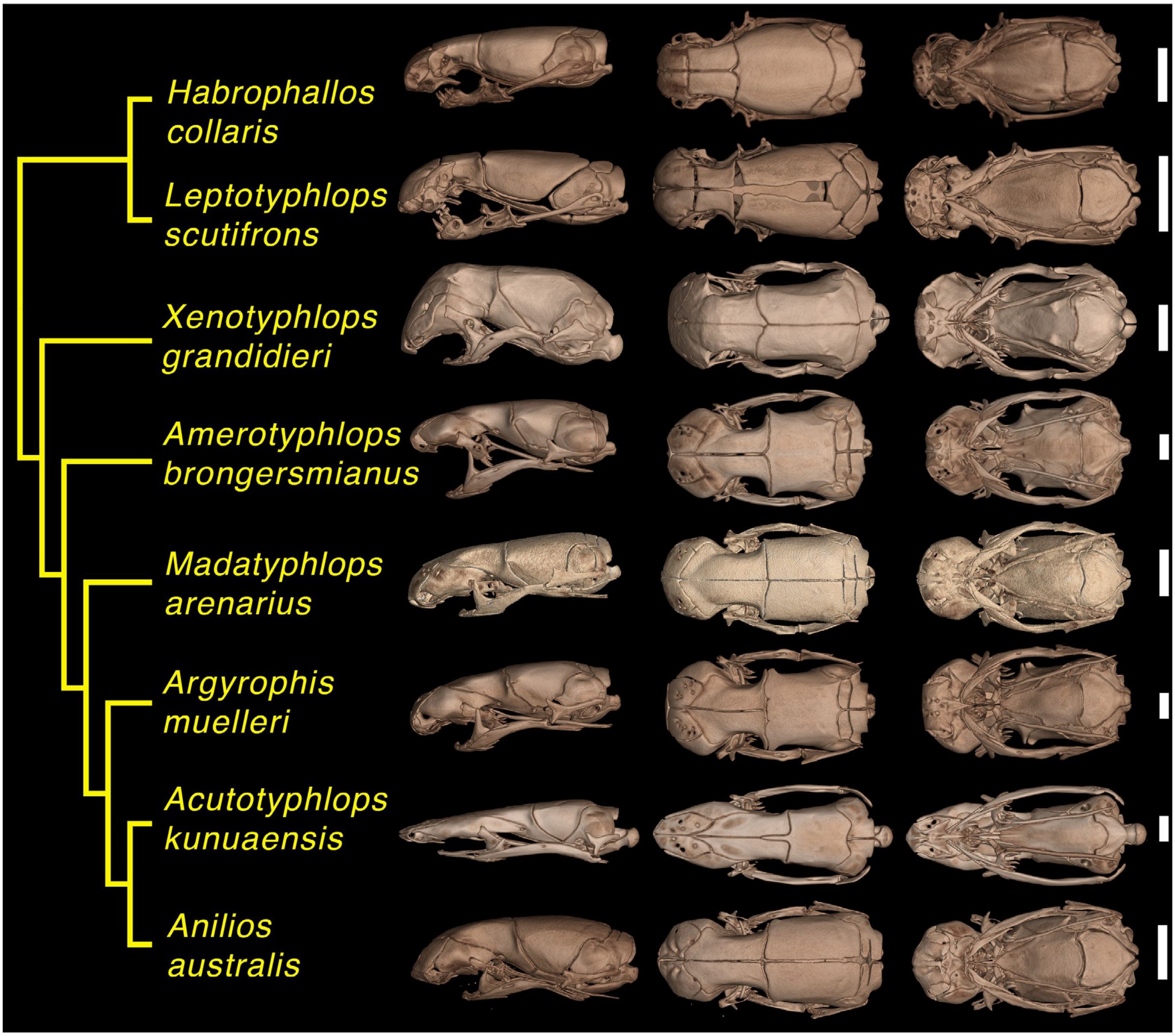

FIGURE 1 Sample of scolecophidian skulls in lateral, dorsal, and ventral views. Images derived from CT scans from the oVert (Open Exploration of Vertebrate Diversity in 3D) project from multiple contributors. CT scanned specimens and links to the raw files: *Habrophallos collaris* (MCZ-R149550, https://doi.org/10.17602/M2/M77530), *Leptotyphlops scutifrons* (UF-H-187225, https://doi.org/10.17602/M2/M120685), *Xenotyphlops grandidieri* (ZSM-22132007, https://doi.org/10.17602/M2/M79511), *Amerotyphlops brongersmianus* (FMNH-H-95928, https://doi.org/10.17602/M2/M65157), *Madatyphlops arenarius* (UMMZ-Herps-241854, https://doi.org/10.17602/M2/M70130), *Argyrophis muelleri* (FMNH-H-259200, https://doi.org/10.17602/M2/M69970), *Acutotyphlops kunuaensis* (LSUMZ-Herps-93566, https://doi.org/10.17602/M2/M78505), and *Anilios australis* (WAM-R-102717, https://doi.org/10.17602/M2/M36837). All white scale bars on the right equal 1 mm. Institutional abbreviations: FMNH, Field Museum of Natural History, Chicago IL, USA; LSUMZ, Louisiana State University Museum of Natural Science, Baton Rouge LA, USA; MCZ, Museum of Comparative Zoology, Cambridge MA, USA; UF, Florida Museum of Natural History, Gainesville FL, USA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor MI, USA; WAM, Western Australian Museum, Perth WA, Australia; ZSM, Zoologische Staatssammlung München, Munich, Germany

contributions to this special volume are a testimony to the application of this technology to this field of study: ten of the contributions include CT imagery of scolecophidians. One of the most interesting and novel consequences of micro-CT is that it has opened the door to development and documentation of detailed data on the internal anatomy even of type specimens, which otherwise have historically remained immune to internal anatomical investigations that were, of necessity, invasive and destructive. CT scans of holotype and paratype specimens of scolecophidians yielded excellent imagery in the past (Koch et al., 2019; Martins et al., 2019; Salazar-Valenzuela, Martins, Amador-Oyola, & Torres-Carvajal, 2015; Santos & Reis, 2018, 2019) and, with the publication of

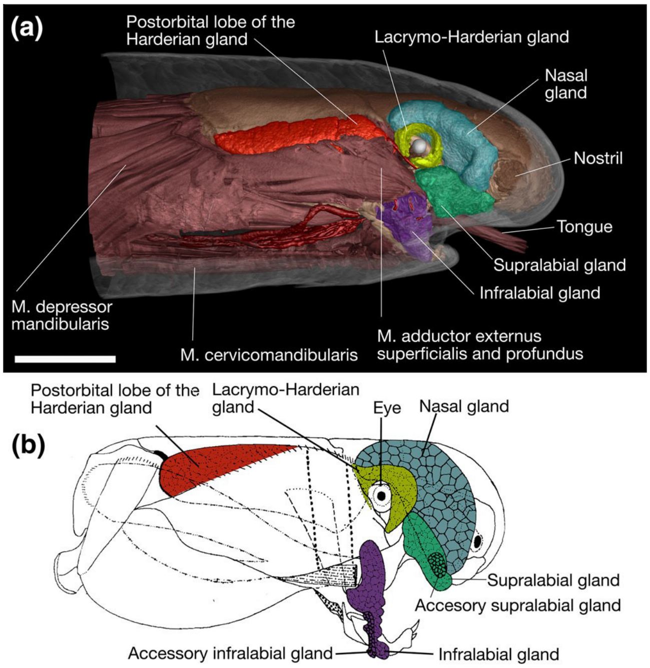

FIGURE 2 Two perspectives of the cephalic glands in *Liotyphlops*. (a) DiceCT image of *Liotyphlops* cf. *albirostris* (available at https://doi.org/10.17602/M2/M379372). (See Linares-Vargas, this volume). (b) *Liotyphlops albirostris*, modified from figure 5 of Haas (1964, p. 14). Scale bar equals 1 mm. The diceCT data set provides a different perspective of the extent and size of the cephalic glands; the accessory supralabial and infralabial glands recognized by Haas are not differentiated in the diceCT data set

CT data from 12 type specimens (seven holotypes, two paratypes, and one each of lectotype, neotype, and syntype) in this special volume, may now be considered almost *routine*! Furthermore, this volume includes micro-CT images, and in most cases detailed osteological descriptions, for the skulls of eight type species (13 if counting those in this article), contributing significantly to a broader understanding of basic skull morphology for eight genera of scolecophidian snakes.

Published images derived from CT data are not free of anatomical bias. The person doing the image processing selects grayscale values and digital filtering that impact the visualization of skeletal elements and other anatomical features, and may impact visualization of extremely thin bones. Digital disarticulation may under some circumstances be subjected to individual bias about where element boundaries are located, particularly if those elements are associated with complex sutures or partial fusion. Detailed reporting of image-processing protocols and archival storage of unprocessed CT data and the image-processed files, however, allow for relative ease of replication of original work, and exploration of the impacts of different protocols on resultant images. CT data are now readily shared among a global community of researchers, and as of yet, have not been demonstrated to suffer the "shelf-life" deterioration that has impacted the quality of some historical serial sections. The open Vertebrate (oVert) Thematic Collections Network is an initiative funded by the National Science Foundation to share—via the online 3D-data repository MorphoSource.org—high-quality 3D data of at least one species of every vertebrate genus found in natural history collections within the United States. Over the past three years, that project has generated 30,000 CT data sets from over 10,000 vertebrate specimens. MorphoSource.org now houses CT data sets of 37 species of scolecophidians, representing four families and 24 genera. Although there is still room for researchers to improve their data sharing practices (Hipsley & Sherrat, 2019) online resources are growing rapidly, and greatly facilitate comparative studies through collaborative efforts from multiple institutions around the world. In our opinion morphologists, and journal editors, need to assume the responsibility for ensuring that datasets are shared in much the same way genetic data are required to be made available. The long-term relevance and impact of CT data sets will be dependent upon establishment of permanent digital repositories for the data, and the continued existence of the hardware and software necessary to view and manipulate them. That challenge is ongoing, but it is abundantly clear that X-rays—a portion of the spectrum that eludes our visual system—may truly be said to have shed *new light* upon the study of scolecophidians, shattering long-standing barriers that posed significant challenges to understanding a phylogenetically and biologically important group of snakes.

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Christopher Bell: Conceptualization, Investigation-Equal, Methodology-Equal, Project administration-Equal, Supervision-Equal, Validation-Equal, Writing-original draft, Writing-review & editing. Juan Daza: Conceptualization-Equal, Funding acquisition-Equal, Visualization-Equal, Writing-original draft-Equal, Writing-review & editing-Equal. Edward Stanley: Funding acquisition, Software-Equal, Visualization, Writing-original draft. Rebecca Laver: Conceptualization, Writing-original draft.

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