A mid-Cretaceous embryonic-to-neonate snake in amber from Myanmar

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We present the first known fossilized snake embryo/neonate preserved in early Late Cretaceous (Early Cenomanian) amber from Myanmar, which at the time, was an island arc including terranes from Austral Gondwana. This unique and very tiny snake fossil is an articulated postcranial skeleton, which includes posterior precloacal, cloacal, and caudal vertebrae, and details of squamation and body shape; a second specimen preserves a fragment of shed skin interpreted as a snake. Important details of skeletal ontogeny, including the stage at which snake zygosphene-zygantral joints began to form along with the neural arch lamina, are preserved. The vertebrae show similarities to those of fossil Gondwanan snakes, suggesting a dispersal route of Gondwanan faunas to Laurasia. Finally, the new species is the first Mesozoic snake to be found in a forested environment, indicating greater ecological diversity among early snakes than previously thought.

INTRODUCTION

By the early Late Cretaceous (~100 to 95 million years (Ma) ago), snakes had achieved their initial global distribution with skeletal remains known from Africa (1), North America (2), the Middle East (3–5), South America (6–10), and Southern Europe (11), all comprising skeletal mature specimens occurring in marine and/or fluvial sediments. We report here on the first known fossilized remains of an embryonic/neonate snake, including preserved integument, from Lower Cenomanian (98.8 ± 0.6 Ma ago) (12) amber from Myanmar. A skull is not preserved, but the postcranial shows important similarities to other Cretaceous Gondwanan snakes, for example, *Najash rionegrina* and *Dinilysia patagonica* (6–8). We also describe a second amber specimen containing a large fragment of integument, possibly a piece of shed skin, considered here to be a snake and from a much larger animal. These new snake remains add a significant biological component to an already diverse fauna of rare, small-bodied vertebrate fossils from the amber deposits of northeastern Myanmar (13, 14), which includes the remains of lizards, neonate birds, and neonate nonavian dinosaurs (15–19). The new snake fossils are exceptional as one of them is clearly an embryo/neonate, while the second appears to preserve dark and light patterns in the squamation. In addition, as with the other amber fossils from Myanmar, they are part of the fauna and flora from an indubitably forested environment (13–19), thriving in an island arc system sourced from Austral Gondwana that became a part of the eastern margin of Laurasia. The new fossil snake material also indicate a greater ecological diversity and global distribution of Late Mesozoic snakes, and more specifically, Cretaceous snakes, than was previously understood. And finally, the articulated postcranial skeleton provides unprecedented data on the early ontogeny of snakes during the later part of their Mesozoic radiation.

**Systematic paleontology**

Squamata Oppel, 1811

*Serpentes* Linnaeus, 1758

*Xiaophis myanmarensis* gen. et sp. nov.

**Holotype**

DIP-S-0907 [Dexu Institute of Palaeontology (DIP)] (Figs. 1, A to C, and 2, A to K; and figs. S1 to S4A and S5, A and B), articulated postcranial skeleton (Total Length = 47.5 mm), ~97 vertebrae and ribs, and integument.

**Type locality/horizon**

Angbamo site, Tanai Township, Myitkyina District, Kachin Province, Myanmar (98.8 ± 0.6 Ma ago; earliest Cenomanian).

**Etymology**

“Xiaophis”—Xiao from the Chinese word for “dawn” and in honor of Xiao Jia, the amber specialist who donated the specimens to the DIP, Chaozhou, China; *ophis*, Greek for snake; and “myanmarensis” in recognition of Myanmar.

**Diagnosis**

Precloacal vertebral centrum roughly triangular in ventral aspect with strong ventral keels and large, paired, subcentral foramina; anterior precloacalcs have large paired fossae on posterodorsal surface of postzygapophyesal lamina; horizontal pre- and postzygapophyses with small accessory processes on prezygapophyses; elongate, posteriorly directed neural spines, present from anterior vertebrae to caudals; caudals with strongly reduced neural spines, anteriorly directed and horizontal transverse processes, and small spatulate articulating chevrons; potentially three sacral ribs/modfied cloacal ribs/lumbarjaphyses; two to three scale rows per vertebral-rib complex; and body scales small but imbricated and strongly overlapping.

**RESULTS**

The articulated snake postcranial skeleton is 47.5 mm in total length (Figs. 1, A to C, and 2, A to K; and figs. S1 to S4A and S5, A and B).
Individual vertebrae are extremely small (anterior precloacals, ~0.5 mm in centrum length; caudals, ~0.35 mm in total length), comparable in size and morphology to those of a neonate Asian ~0.5 mm in centrum length; caudals, ~0.35 mm in total length). Individual vertebrae are extremely small (anterior precloacals, (~0.5 mm in centrum length; caudals, (~0.35 mm in total length).)

In the dorsal view, precloacals appear shorter than wide (Fig. 2, A and B, and figs. S1 and S2), with a tall and steep posterior angle to the neural spine (differentiating Xiaophis from other extremely small-bodied snakes, such as scolecodiids (22) or Coniophis (23)), distinct epiphyseal pits on the neural spine tip, subhorizontal pre-

postzygapophyses, small prezygapophyseal accessory processes (similar to Dinilysia (7, 9)), and wide fossae on the posterior margins of the postzygapophyses (Figs. 2, A to K, and 3, B and D). In the lateral view, the paradiapophyses are ventrally directed, with paired superior and inferior facets, connected to the base of the prezygapophysis by a crest or ridge; the pre- and postzygapophyses appear connected by a short crest; large lateral foramina are observed on many vertebrae. The cotyles/condyles are round in outline. Observations of individual vertebrae indicate that the neural arch lamina does not display fully developed zygosphenes (Fig. 2, A to K). However, in some vertebrae, small projections on the lateral margins of the lamina are interpreted here as partially formed zygosphenes (21). In the ventral view, the centra are triangular, with prominent ventral keels, ventrally directed paradiapophyses, and large subcentral foramina. Rib heads are complex with a double-headed facet and tubercles for intercostal musculature (Figs. 2, A to K, and 3, B and D); distal rib ends bear a distinct facet, interpreted here as the origin of the musculus costocutaneus inferior.

Within and posterior to the second trunk mass (Fig. 1 and figs. S1 to 4A and S5, A and B) are ~10 preserved caudal vertebrae (Fig. 2, E and F). They are small (~0.3 to 0.4 mm) with short neural spines, flattened neural arches, and no zygosphenes and zygantra (21). The transverse processes are anteriorly directed, and there are short, spatulate haemal spines or chevrons preserved on two vertebrae (Fig. 2, E and F) (5, 6, 8). A large debris mass (~10 mm in length).
that is covered in poorly preserved scales obscures the posteriormost part of the body.

**DISCUSSION**
The anatomy of DIP-S-0907 shows similarities to extant embryonic-to-neonate snakes such as the neonate of a southeast Asian pipe snake *C. ruffus* (Figs. 2, A to Q, and 3, A to D) or the embryos (head length, 5 mm) and neonates (head length, 8.0 mm) of the colubroid *Natrix natrix* (21): (i) The neural canal is at least twice as large as the centrum body (Figs. 2, A to Q, and 3, A to D); (ii) some vertebral centra in *Xiaophis myanmarensis* display a notochordal canal that is present but undergoing endochondral ossification similar to *Cylindrophis* (Fig. 3, A to D) and *Natrix* (21). A relatively large neural canal coupled with the presence of a notochordal canal can also be observed in juveniles of the typhlopoid *Anilios (Rhamphotyplops) bicolor* and the python *Antaresia stimsoni* (fig. S6); (iii) absent or weak ossification of the zygosphenes and zygantral joint (zygosphene + zygantrum) is consistent with embryonic-to-neonate extant snakes [facets absent in embryonic *Cylindrophis* (Figs. 2, A to Q, and 3, A to D) but just forming, along with zygapophyses, in neonate *Natrix* (21)]. Coupled with extremely small size (estimated ≤8.0 cm in total...
body length), these features indicate that DIP-S-0907 is the first known fossil embryonic-to-neonate snake. *Xiaophis* provides direct evidence that many aspects of snake vertebral ontogeny have remained conservative for nearly 100 Ma, such as delayed development of the zygosphene-zygantra system and late closure of the notochordal canal.

The preserved integumentary details of DIP-S-0907 indicate that the scales are imbricated, diamond-shaped, and thin (fig. S5, A and B). Large, rectangular, ventral scales (paired or unpaired), typical of most modern snakes, are not observed, nor are the annular scales of amphisbaenians. DIP-V-15104 appears to represent a shed skin of a larger individual, but the limited material precludes referral to *Xiaophis* (Fig. 4, A to C, and fig. S5C), although it appears to be the skin of a snake. The scales of DIP-V-15104 are diamond-shaped or ovoid diamond-shaped, with deep lines formed by integument between each scale. Some rows converge as observed ventrally in extant snakes (that is, the bifurcations of the scale rows point ventrally). No enlarged ventral scales (gastrosteges) can be observed. Light and dark areas distributed across the shed skin reveal color patterning, but original color is not preserved. There is an irregular zone with circles or rings of dark patterning (Fig. 4, A to C, and fig. S5C).

The new remains of a Cenomanian-aged embryonic-to-neonate snake from the eastern margin of Laurasia, together with the skin fragment, are important new data points in our understanding of the patterns and processes of ancient snake evolution, ontogeny, radiation, and diversification (fig. S7; see also the Supplementary Materials). As with other vertebrate fossils from Myanmar amber (15–19), the quality of preservation of such a small individual, as represented by

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**Fig. 3.** High-definition CT images of neonate vertebral column of *C. ruffus* (colorized light yellow for contrast with fossil material in gray) compared to *X. myanmarensis*. Cross-sectional views through precloacal vertebrae of (A) *C. ruffus*, anterolateral view (note the incipient formation of zygosphenal joint as small nubs on neural arch lamina facing into small facets of posterior arch portion of more anterior vertebra in partial section) and (B) *X. myanmarensis* at level of zygosphenal tectum, anterolateral view. Sagittal sections through precloacal vertebral series of (C) *C. ruffus*, anterior to right (note the presence of soft but distinct zygantral facets on posterior and internal surface of neural arch, and open notochordal canals (no-ca) and distinct ossification of cotyle-condyle (ct-cn) portions of bony centra at joints) and (D) *X. myanmarensis*, anterior to right (note that neural canal (nc) and notochordal canals are infilled with permineralized material of similar density, although spaces are obvious in both canals; density and histology of bone at cotyle-condyle joints differs from permineralized infilling material; cotyle-condyle bone–forming joints are similar to that observed in neonate of *C. ruffus* (C)).
this snake skeletal specimen, provides unique osteological and soft tissue data on a previously unseen stage of ancient snake ontogeny that compares well to ontogenetic stages in modern snakes. Both the skeletal and shed-skin specimens, from the amber clasts they are preserved in, present new data on a formerly unknown ancient snake ecology—a terrestrial (possibly arboreal) ecosystem marginal to inland and coastal fluvial environments (24). The amber inclusions provide taphonomic support for a forested ecosystem, as both DIP-S-0907 and DIP-V-15104 contain abundant insects, carbonized insect feces, and fragmentary plant materials, which are usually associated with “litter amber” or resin produced near the forest floor (25). Almost all other known Cenomanian snakes show aquatic adaptations (3–5) or are found in fluvially deposited sediments (2) and cannot be conclusively linked to terrestrial habits [cf. oldest known snakes (26)]. The only exception is *N. rionegrina* from mesic-xeric ecosystems in the Cenomanian of Gondwanan Argentina (6, 8).

*X. myanmarensis* (DIP-S-0907) and DIP-V-15104 are a new and important data point in the Mesozoic fossil record of eastern Laurasian snakes (excluding Gondwanan India, which became a part of Eurasia only in the Cenozoic) and demonstrate that snakes had achieved a circumglobal distribution at least 100 Ma ago (fig. S7; see also the Supplementary Materials). A complex series of paleobiogeographic scenarios arise from these new data. As an example, one hypothesis, among many, could be that the Myanmar amber faunal and floral elements, including *Xiaophis*, were dispersed from Austral-Gondwana to Laurasia as relicts carried on this island arc for tens of millions of years (30). It is also possible that many of these faunal elements were sourced from Laurasia only when the terranes and island arc were in some proximity to eastern Laurasia; a future step for other faunal and floral elements is to link them to their sister taxa within Laurasian or Gondwanan clades (15–19). An alternative scenario, specific to *Xiaophis*, is that its kind descended from aquatic or amphibious snakes that had secondarily colonized terrestrial environments on the islands of these allochthonous terranes; the broad distribution and surprising diversity of Cenomanian-aged marine snakes found throughout the Tethys (3–5) and most recently in the Cenomanian of South America (10) hint at unexpected snake diversity in both terrestrial and aquatic realms (fig. S7; see also the Supplementary Materials). Finally, *X. myanmarensis* offers unprecedented opportunities to observe aspects of skeletal ontogeny in a fossil snake, providing exceptional and unexpected insights into the evolution of one of nature’s most successful and iconic animal groups.

**MATERIALS AND METHODS**

**Material and photography**

Two specimens were obtained from an amber deposit in the Angbamo area, Tanai Village, Hukawng Valley of Myanmar. Age was estimated...
at 99 Ma ago (98.8 ± 0.6 Ma ago; earliest Cenomanian) based on U-Pb dating of zircons from the volcanioclastic matrix containing the amber (12). Two specimens were cataloged as DIP-V-15104 and DIP-S-0907. DIP-V-15104 was 44.5 by 46.8 mm and 8.61 g in weight; DIP-S-0907 was 17.1 by 24.8 by 39.0 mm and 9.30 g in weight. The original specimens are housed in the DIP, Chaozhou, China.

The pieces of amber were examined with a Leica MZ 12.5 dissecting microscope with a drawing tube attachment. Photographs were taken using a Canon digital camera (5D Mark III, MP-E 65mm f/2.8 1-5X) fitted to a macro rail (Cognisys) and processed in Helicon Focus 5.1. Final figures were prepared with Photoshop CS5 (Adobe) and Illustrator CS5 (Adobe).

**µCT scanning and three-dimensional reconstruction**

Specimen DIP-S-0907 was scanned with a MicroXCT 400 (Carl Zeiss X-ray Microscopy Inc.) at the Institute of Zoology, Chinese Academy of Sciences. The entire animal (Fig. 1) was divided into seven scans that were combined to create a single model, and the scans were conducted with a beam strength of 60 kV, 8 W, and absorption contrast and a spatial resolution of 2.5464 μm. In addition, specimen DIP-S-0907 was imaged using propagation phase-contrast synchrotron radiation microtomography on the beamline 13W at the Shanghai Synchrotron Radiation Facility. The isotropic voxel size was 2.25 μm.

On the basis of the obtained image stacks, structures of the specimen were reconstructed and separated with Amira 5.4 (Visage Imaging). The subsequent volume rendering was performed with Avizo 9.0 (Thermo Fisher Scientific) and VG StudioMax 2.1 (Volume Graphics). The neonate C. ruffus was scanned at 65 kV, 153 μA, and an isotropic voxel size of 8.7 μm.

**Phylogenetic analysis**

The phylogenetic relationships of *X. myanmarensis* were tested using a previously published data matrix of extant and fossil snake species (26). *X. myanmarensis* could be scored for 17 of 237 characters (see the Supplemental Materials for details), and the data set was analyzed in PAUP* 4.0b (31) using parsimony optimization, heuristic search, 1000 random addition replicates, tree-bisection-reconnection branch swapping, and characters unordered and with equal weights. Bootstrap support values were obtained in the phylogenetic program TNT v.1.5 (32) using 10,000 replicates and default settings.

**SUPPLEMENTARY MATERIALS**

Supplemental material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/7/eaat5042/DC1

**Fig. S1.** High-definition x-ray µCT image of holotype skeleton (DIP-S-0907).

**Fig. S2.** High-definition x-ray µCT images of holotype skeleton (DIP-S-0907).

**Fig. S3.** Probable sacral ribs, right dorsolateral view, x-ray µCT image of holotype.

**Fig. S4.** Precloacal vertebrae of *X. myanmarensis* and other snakes.

**Fig. S5.** Scales of and second-scale specimen.

**Fig. S6.** Mid-sagittal sections through posterior precloacal vertebrae of two juvenile snakes.

**Fig. S7.** Distribution of Late Jurassic (Barremian)–Late Cretaceous (Maastrichtian) snakes (Squamata: Ophidia) from the Cenomanian of Northern South America. Peer. J. evo2017 (2017).

**Fig. S8.** Strict consensus of 2040 equally parsimonious trees.

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