PALEONTOLOGY

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 skeletally 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 postcranium 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 indisputably 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 materials 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 precloacals have large paired fossae on posterodorsal surface of postzygapophyseal 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/modified cloacal ribs/lymphapophyses; two to three scale rows per vertebra-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).

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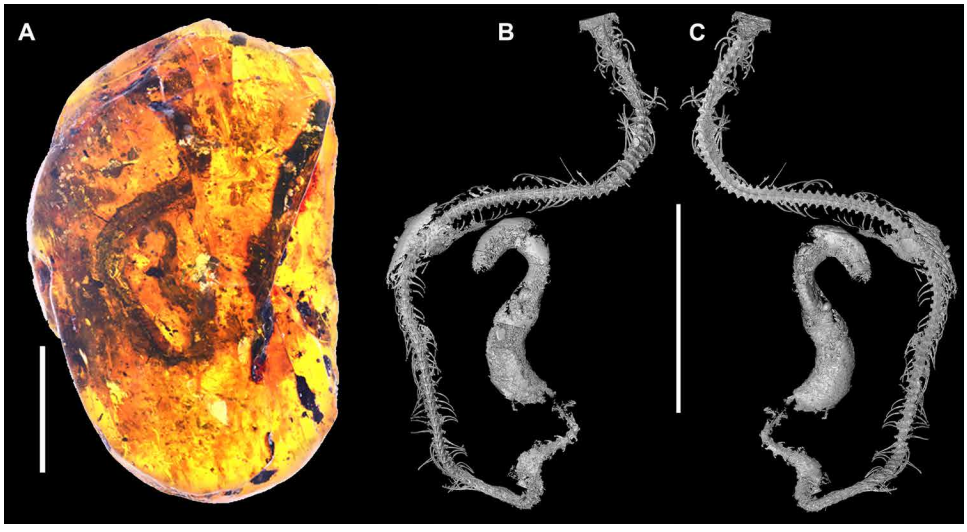

Fig. 1. Overview of amber clast with synchrotron x-ray μCT image of articulated snake skeleton (DIP-S-0907). (**A**) Amber clast with included skeletal material. (**B**) Dorsal view of skeleton, synchrotron x-ray micro–computed tomography (μCT) image. (**C**) Ventral view of skeleton, synchrotron x-ray μCT image. Scale bar, 10 mm.

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 pipe snake, *Cylindrophis ruffus* (Figs. 2, A to Q, and 3, A to D). There are 97 observable vertebrae, with the anteriormost 87 being articulated, including associated ribs, followed by 10 caudal vertebrae (Figs. 1, 2, A to K, and 3, B and D). Three radio-opaque "masses" partially obscure postcranial osteology and likely represent mineralized remnants of decayed tissues.

The large anteriormost vertebrae are likely mid-precloacal elements. The first vertebra breaches the amber surface, suggesting that many vertebrae were lost (Fig. 1, A to C, and figs. S1 to 4A and 5, A and B). Although an exact count is not possible, reference to the contemporaneous simoliophiid snake *Haasiophis terrasanctus* (155 precloacals; largest precloacal at 70th to 80th vertebra) (*5*) would suggest that DIP-S-0907 is missing 70 or more precloacal vertebrae plus the skull.

Xiaophis can be identified as a snake based on the following features. The 87 observed, and ~160 inferred, precloacal vertebrae exceed counts in all elongate squamates apart from amphisbaenians and dibamids (for example, 55 precloacal vertebrae in the legless anguid *Pseudopus apodus* and 72 in the acontine skink *Acontias meleagris*) (*20*). However, amphisbaenian and dibamid vertebrae differ from *Xiaophis* as follows: (i) complete absence of zygosphenes and zygantra (see discussion below); (ii) dorsolaterally oriented pre- and postzygapophyseal articulations (horizontal in rhineurids); (iii) fusion of diapophyses-parapophyses forming short, circular synapophyses rather than sinuous, complex articulations; (iv) prezygapophyses not connected to synapophyses; (v) ventrally flattened rather than keeled centra; (vi) subparallel rather than posteriorly converging lateral margins of centra; and (vii) neural spines absent or low (cf. *Xiaophis* and *Dinilysia* with *Amphisbaena* or *Dibamus*; fig. S4) (*21*).

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 scolecophidians (*22*) or *Coniophis* (*23*)], distinct epiphyseal pits on the neural spine tip, subhorizontal pre- and 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 costocutaneous inferior.

In the dorsolateral view (fig. S3) within the second trunk mass, anterior to the first caudal vertebrae, there are two to three straight, stout, nonarticulating "ribs" or transverse processes, the last of which bears a spatulate distal tip similar to the one recognized sacral rib of *Pachyrhachis problematicus* (*3*). The fossil snake *N. rionegrina* (*6*, *8*) has shorter, stouter sacral ribs than *X. myanmarensis*; however, their ribs both display fusion to the corresponding vertebra as transverse processes (*6*, *8*). These two, possibly three, unusual transverse processes define the cloacal/pelvic region; girdle or limb elements are not evident. In modern limbless anguids or skinks (*20*), the sacral region is defined by two large and tuberculate transverse processes, unlike the gracile processes in *Xiaophis*.

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)

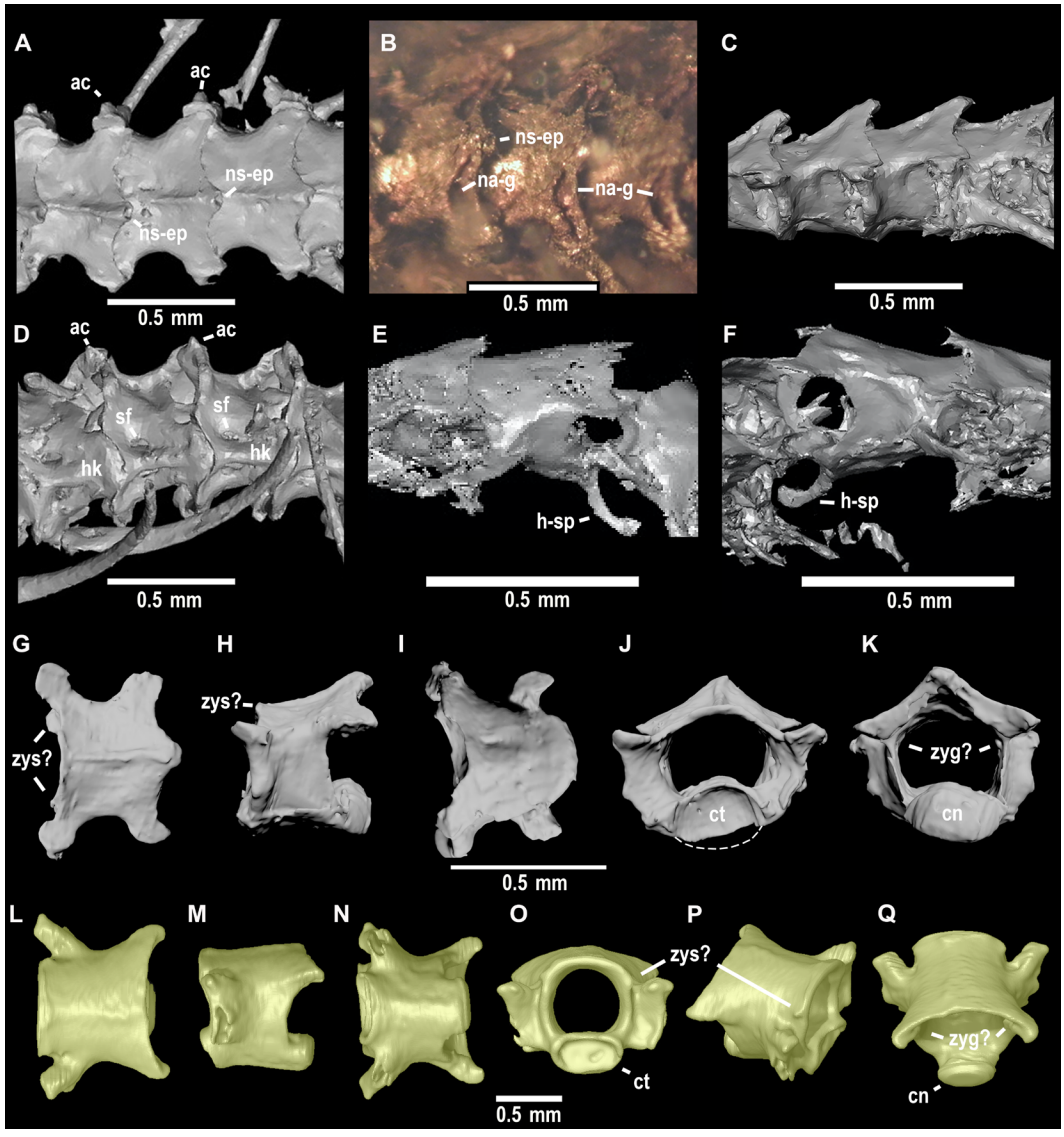

Fig. 2. Details of skeletal elements of *Xiaophis myanmarensis* (DIP-S-0907) and vertebral element of neonate of extant *Cylindrophis ruffus* (colorized light yellow for contrast with fossil material in gray). (**A** to **K**) *X. myanmarensis*. (**L** to **Q**) *C. ruffus*. (A) CT image of dorsal view of mid-precloacal vertebrae, anterior to left. (A) Light photograph of the dorsal view of mid-precloacal vertebrae, anterior to left. (C) CT image of left lateral view of mid-precloacal vertebrae, anterior to left. (D) CT image of the ventral view of mid-precloacal vertebrae, anterior to left. (E) CT image of the left lateral view showing the articulating haemal spine. (F) CT image of the right lateral view of caudal vertebrae showing the articulating haemal spine. (G to K) CT renderings of isolated precloacal vertebrae of *X. myanmarensis* (DIP-S-0907) in dorsal view (G), left lateral view (H), ventral view (I), anterior view (J), and posterior view (K). (L to Q) CT renderings of isolated precloacal vertebrae of neonate *C. ruffus*. (L) Dorsal view. (M) Left lateral view. (N) Ventral view. (O) Anterior view. (P) Right dorsolateral view. (Q) Posterodorsal view. ac, accessory process; cn, condyle; ct, cotyle; hk, haemal keel; h-sp, haemal spine; na-g, neural arch groove; ns-ep, neural spine epiphyseal pit; sf, subcentral formina; zyg?, incipient zygantrum; zys?, incipient zygosphene.

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* 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 zygosphenial 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

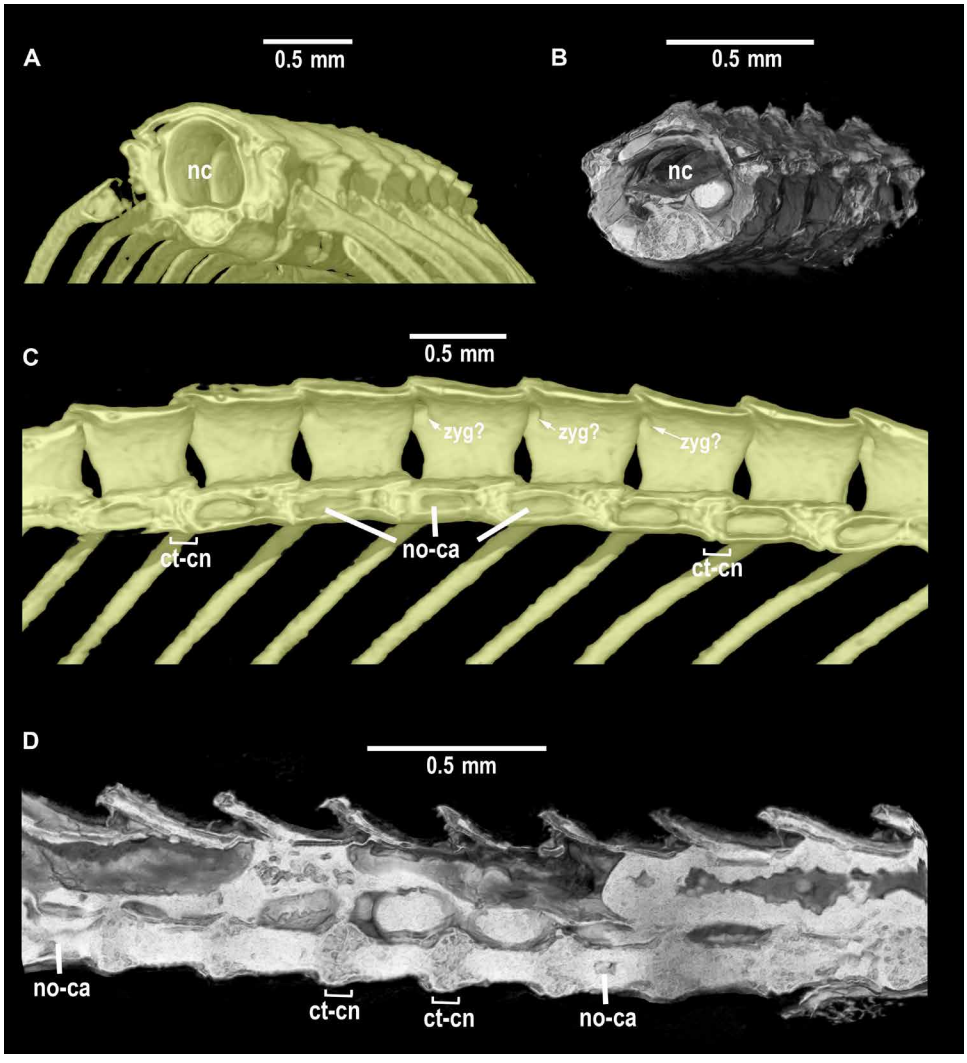

Fig. 3. High-definition CT images of neonate vertebral column of *C. ruffus* (colorized light yellow for contrast with fossil material in gray) compared to *X. myanmarensis*. Cross-sectional views through precloacal vertebrae of (**A**) *C. ruffus*, anterolateral view (note the incipient formation of zygosphenial 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 zygosphene 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)].

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

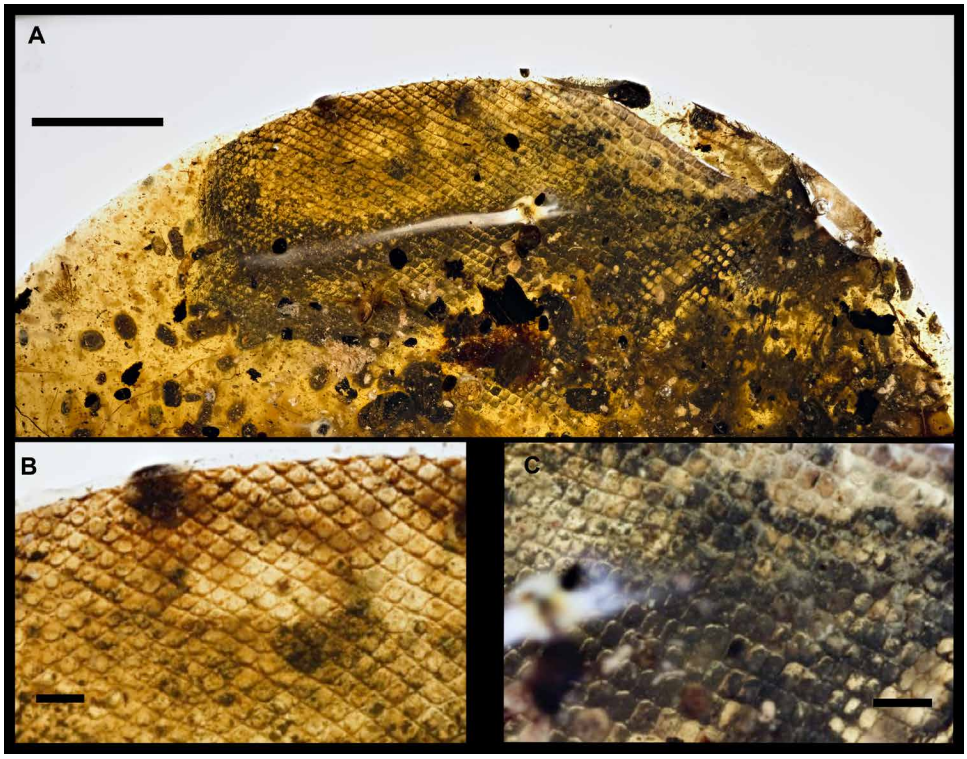

Fig. 4. Light photographs of probable snake shed skin (DIP-V-15104). (**A**) Overall view of the complete specimen. Scale bar, 5 mm. (**B**) Close-up of the left portion of the specimen showing converging scale rows (center top). Scale bar, 1 mm. (**C**) Close-up of the right mid-region of the specimen. Scale bar, 1 mm.

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). Adding *X. myanmarensis* to a phylogenetic analysis of early snakes (*26*) reconstructs it between basal Gondwanan taxa, such as *Najash*, *Dinilysia*, and *Sanajeh*, and modern (crown) snakes (fig. S8). The morphological resemblance of *Xiaophis* to these basal Gondwanan fossil snakes (*6*–*9*, *27*–*29*), coupled with its position between the latter snakes and crown snakes, is consistent with a Gondwanan ancestry for crown snakes. Osteological similarities between *Xiaophis* and Gondawanan snakes also expand our knowledge of Cretaceous madtsoiid-like snake distributions. This is particularly important because southeast Asian exotic terranes were sourced from northern Australia during the Late Triassic to Late Jurassic (fig. S7; see also the Supplementary Materials) (*30*). 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 volcaniclastic 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 loaned from the Western Australian Museum (WAM R49553) and scanned with a SkyScan 1076 (Bruker MicroCT) at Adelaide Microscopy, University of Adelaide, Australia. The scan settings were 65 kV, 153 μA, no filter, and an isotropic voxel size of 8.7 μm. The reconstruction was carried out using the software NRecon (Bruker MicroCT), and the volume renderings were created in the software Avizo 9.0 (Thermo Fisher Scientific).

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

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

Supplementary Text

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 represented on a map of Cenomanian arrangement of land masses.

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

Data file S1. Data matrix for phylogenetic analysis: Nexus file format.

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