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SNAKES OF THE SIWALIK GROUP (MIOCENE OF PAKISTAN): SYSTEMATICS AND RELATIONSHIP TO ENVIRONMENTAL CHANGE

Jason J. Head

ABSTRACT

The lower and middle Siwalik Group of the Potwar Plateau, Pakistan (Miocene, approximately 18 to 3.5 Ma) is a continuous fluvial sequence that preserves a dense fossil record of snakes. The record consists of approximately 1,500 vertebrae derived from surface-collection and screen-washing of bulk matrix. This record represents 12 identifiable taxa and morphotypes, including *Python* sp., *Acrochordus dehmi*, *Gansophis potwarensis* gen. et sp. nov., *Bungarus* sp., *Chotaophis padhriensis*, gen. et sp. nov., and *Sivaophis downsi* gen. et sp. nov. The record is dominated by *Acrochordus dehmi*, a fully-aquatic taxon, but diversity increases among terrestrial and semi-aquatic taxa beginning at approximately 10 Ma, roughly coeval with proxy data indicating the inception of the Asian monsoons and increasing seasonality on the Potwar Plateau. Taxonomic differences between the Siwalik Group and coeval European faunas indicate that South Asia was a distinct biogeographic theater from Europe by the middle Miocene. Differences between the Siwalik Group and extant snake faunas indicate significant environmental changes on the Plateau after the last fossil snake occurrences in the Siwalik section.

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INTRODUCTION

The lower and middle Siwalik Group of the Potwar Plateau (Miocene, approximately 18 to 3.5 Ma), Pakistan is an extensive, continuous fluvial sequence derived from the Himalaya foredeep that preserves a rich vertebrate fossil record and evi-

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dence of climatic and environmental transitions reflected in sedimentary and chemical records. These characteristics combined with fine chronostratigraphic control have allowed for precise studies of the relationship between vertebrate faunal evolution and environmental change through time within a geographically restricted study area (approximately 2,500 km^2; Badgley and Behrensmeyer 1995). These studies have recorded patterns of immigration and diversity change that reflect both continental-scale biogeographic histories and more localized changes in feeding ecology and diversity in response to floral transitions and increasing seasonality and aridity through time driven by the inception of the Asian monsoonal precipitation system (e.g., Flynn and Jacobs 1982; Barry et al. 1991; Badgley and Behrensmeyer 1995 and references therein; Barry et al. 2002). All of this research has focused on the fossil mammal record, and no attempts have been made to examine the Siwalik Group reptile record in terms of either rigorous systematics or relationship to environmental change. In this analysis, I describe the snakes from the Siwalik Group, examine changes in composition of the snake record through time, and compare the record to environmental histories recorded in the Siwalik Group.

PREVIOUS RESEARCH ON SIWALIK GROUP SNAKES

Only two snake taxa from the Siwalik Group were previously described. Lydekker (1885) identified four isolated, incomplete vertebrae as *Python* cf. *P. molurus* from the Siwalik Group of the Punjab. Examination of this material (BMNH R 614) demonstrates that reference to *Python* is incorrect, and all specimens are referable to *Acrochordus dehmi*. Hoffstetter (1964) described *Acrochordus dehmi* and *Python* sp. from Siwalik sediments of the Potwar Plateau. The hypodigm of *A. dehmi*, as reported by Hoffstetter (1964), consists of 156 specimens recovered from 16 localities from the Chinji, Nagri, and Dhok Pathan formations during surveys of the Potwar Plateau led by Richard Dehm in 1955-56. West et al. (1991) reported *A. dehmi* from the Siwalik section of Nepal, and Rage et al. (2001) recorded the taxon from the upper-middle Siwalik Group of Jammu, India. Hoffstetter (1964) concluded that the Siwalik Group represented primarily aquatic environments based on the size of the *A. dehmi* sample, assumptions of ecological similarity between *A. dehmi* and extant *Acrochordus*, and the lack of any additional demonstrably terrestrial snake taxa aside from *Python* from the Siwalik Group. Employing the same fundamental assumption of ecological similarity, and based on the high frequency of *A. dehmi* specimens in the Siwalik record, Head (1998) concluded that *A. dehmi* possessed the derived, low-energy physiology of extant *Acrochordus*, which is expressed ecologically by high population densities (Shine 1986a).

With the exception of a single reference to Colubroidea indeterminate (Rage in Pilbeam et al. 1979), no other snake taxa have been described from the Siwalik Group on the Potwar Plateau, and no attempt has been made to examine the relationship between Siwalik Group snake faunas and environmental change, despite collecting efforts by researchers from multiple countries spanning a time period of over 150 years.

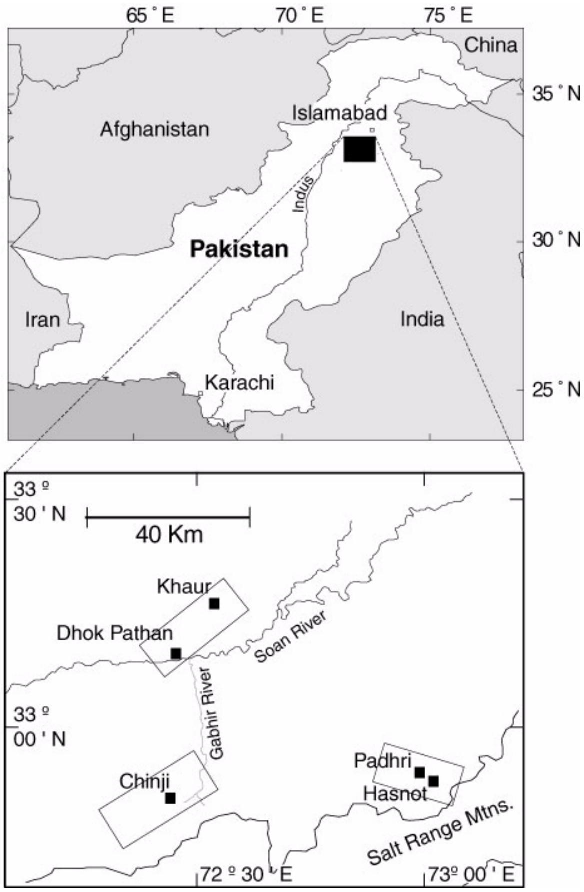


Figure 1. Map of Pakistan showing study areas of the Siwalik Group (rectangles) on the Potwar Plateau (after Barry et al. 2002). Black squares and names identify villages and towns. The Southwest study area samples primarily the Kamlial and Chinji formations, the Northern study area samples primarily the Nagri and Dhok Pathan formations, and the Southeast area samples primarily the Dhok Pathan Formation.

MATERIALS AND METHODS

This study is based on 1,579 fossil snake specimens from 139 localities on the Potwar Plateau of north-central Pakistan (Figure 1), spanning a temporal range of approximately 18 to 6 Ma (e.g., Badgley and Behrensmeyer 1995, and references therein). This dataset is the result of intensive, systematic surface-collection and screen-washing of over 1,000 fossil localities through collaborative fieldwork by representatives of the Geological Survey of Pakistan and multiple institutions from the United States, including Yale University, Harvard University, the University of Arizona, the University of Michigan, Dartmouth College, the Smithsonian Institution, University of Illinois at Chicago, and Southern Methodist University. Screen-washing efforts have been led by E.H. Lindsay and students, and especially by W.R. Downs III. Additionally, the record examined by Hoffstetter (1964) and housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich was examined.

Methods used for systematic identifications in this study differ from the majority of analyses of fossil snakes using vertebral morphology. It is common in most studies for general morphological similarity and geographic and temporal parsimony to be invoked in taxonomic assignments of snake vertebrae. However, these methods make implicit assumptions about relationships between extant and fossil faunas, and introduce circularity in biogeographic reconstructions (Bell et al. 2004). This study bases systematic hypotheses on apomorphic characters. As a result, for several taxa in this study, morphotypic, as opposed to taxonomic, assignments are used, based on characters that are taxonomically ambiguous, but consistently subdivide the Siwalik Group sample. Consequently, this study minimizes taxonomic and systematic claims relative to other analyses (e.g., Szyndlar 1984; Parmley and Holman 1995), limiting the ability to make comparisons of diversity and species richness. Finally, it should be noted that vertebral morphology for the vast majority of snake species remains undescribed. Consequently, diagnostic characters used to erect the three new colubroids described here may instead be characteristic of extant species. Therefore, systematic assignments may change dramatically when vertebral morphology of snakes is better documented.

Anatomical terminology follows Rage (1984) and Holman (2000), unless specifically cited, and Figure 2 labels anatomy unique to snakes.

INSTITUTIONAL ABBREVIATIONS

BMNH, Natural History Museum, London; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. DP, Dartmouth College–Peshawar University, H-GSP, Harvard-Geological Survey of Pakistan; Y, Yale University.

Stratigraphic abbreviation

KL, Khaur level

SYSTEMATIC PALEONTOLOGY

Ophidia Brongniart, 1800
Alethinophidia Nopcsa, 1923
Pythoninae Boulenger, 1890
Python Daudin, 1803
Species indeterminate
Figure 2

Referred specimens. H-GSP 13959, 13961-3, 13965, 13968, 14633, 17631, 17720, 19707, 19799, 21005, 21031, 21914, 22078, 22304, 22306, 22309, 23295, 23345, 23723, 24154, 24229, 24350, 24363, 24364, 26723, 27098, 27252, 27719, 27806, 31166, 31318, 31320, 32557, 40204, 40701, 40906, 41161, 41288, 41632, 42267, 46054, 46102, 46184, 46185, 46228, 46420, 46796, 47282, 47381, 47580, 49895-7, 49899, 50044, 50149, 50295, 50425, 50429, 50517, 51109, 51123, 53114, 53115, 53125, 53126, 53178, 53297, 53298, isolated precloacal vertebrae.

Localities and ages. Y-802 (16.80 Ma), Y-642 (15.20 Ma), Y-478 (14 Ma), Y-650 (13.05 Ma), Y-882 (13 Ma), Y-698 (12.94 Ma), Y-849 (12.81 Ma), Y-750 (12.7), Y-496 (12.30 Ma), Y-634 (12.20 Ma), Y-883 (11.98 Ma), Y-499 (11.95 Ma), Y-515 (11.95 Ma), Y-498 (11.55 Ma), Y-504 (11.52 Ma), Y-061 (11.46 Ma), Y-809 (11.40 Ma), Y-773 (11.34 Ma), Y-076 (11.31 Ma), Y- 311 (10.00 Ma), Y-262 (9.49 Ma), Y-633 (9.27 Ma), Y-1001 (9.25 Ma), Y-327 (9.18 Ma), Y-401 (8.89 Ma), Y-024 (8.14 Ma), Y-547 (7.93 Ma), Y-946 (7.76 Ma), Y-457 (7.30 Ma), Y-856 (7.28 Ma), Y-921 (7.24 Ma), Y-370 (7.13 Ma), Y-910 (6.98 Ma), Y-908 (6.78 Ma).

Description. Vertebrae assigned to *Python* are large and block-shaped, and include elements from all recognizable regions of the precloacal vertebrate column. In anterior view (Figure 2A.1), the cotyle has a strongly subequal ventral margin that is continuous with the haemal keel, resulting in a slightly pointed cotylar ventral apex. There is no indication of paracotylar foramina on any recovered specimens assigned to *Python*. Dorsal to the

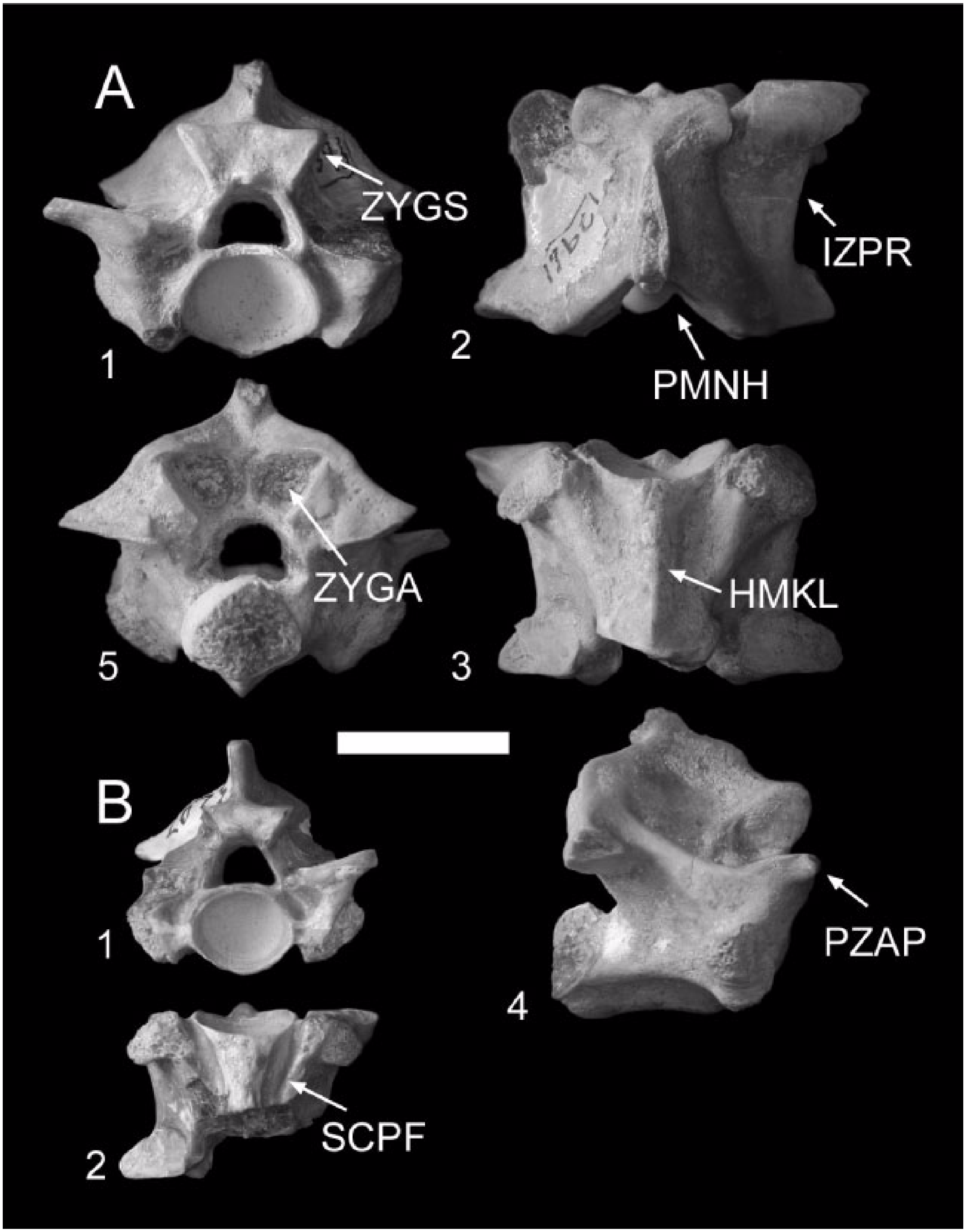


Figure 2. A. Siwalik Group *Python* precloacal vertebra (H-GSP 13961) in anterior (1), dorsal (2), ventral (3), right lateral (4), and posterior (5) views. **B.** Siwalik Group *Python* posterior precloacal vertebra (H-GSP 53297) in anterior (1), and ventral (2) views. Scale equals 10 mm. Anatomical abbreviations: HMKL, haemal keel; IZPR, Interzygapophyseal ridge; PMNH, posterior median notch; PZAP, prezygapophyseal accessory process; SCPF, subcentral paralymphatic fossae; ZYGA, zygantrum; ZYGS, zygosphene.

cotyle, the neural canal is triangular and capped by a prominent zygosphene. The zygosphene is tall, with large, high-angled articular facets. Medially, a pronounced, rounded tuberosity is present on the anterior face of the zygosphene along the dorsal margin of the neural canal. Lateral to the cotyle, the prezygapophyses are low-slung and dorsoventrally thin.

In dorsal view (Figure 2A.2), the interzygapophyseal ridge possesses a straight lateral margin that is posteromedially angled between the pre- and postzygapophyses. The posterior median notch of the neural arch is deep with straight margins, exposing the posteromedial margins of the zygantral articular facets in dorsal view. The prezygapophyseal articular facets are ovate, with straight, transversely oriented anterior margins. Small, pointed accessory processes are visible at the anterolateral margins of the prezygapophyses.

In ventral view (Figure 2A.3), the centrum is wide with a thin, poorly defined haemal keel in all specimens. In vertebrae from the anterior section of the vertebral column, the hypapophysis originates just anterior to the cotyle. Hypapophyses are robust and ovoid in cross section. The synapophyses are moderately developed, with robust, laterally oriented parapophyses and smaller, posteromedially oriented diapophyses. In vertebrae from the posterior region of the precloacal column, the paralymphatic channels and subcentral paralymphatic fossae are well developed and deeply excavated into the ventral surface (Figure 2B.2).

In lateral view (Figure 2A.4), the interzygapophyseal ridge possesses swollen lateral margins, and is elevated between the pre- and postzygapophyses. In posterior view (Figure 2A.5), the lateral margins of the neural arch are strongly sigmoid in outline. The posterior surface of the arch at the level of the zygantrum is rugose and pitted for attachment of intervertebral ligaments. The zygantrum is deep, with a prominent medial ridge.

Discussion. The following character combination diagnoses referred specimens to Pythoninae: zygapophyseal bridge straight and posteromedially angled; triangular neural canal; presence of a zygosphenal tuberosity; absence of paracotylar foramina. Individually, none of these characters are unique to pythonines (see discussions in Kluge 1988; Szyndlar and Rage 2003), but their combined presence is unique to the lineage. Hoffstetter (1964) recognized *Python* from the Siwalik Group based on a single specimen. Generic assignment was based on overall similarity with extant *Python*, and Hoffstetter (1964) recognized a specific-level distinction based on the following characters: relatively elongate centrum (compared to neural arch width and vertebral height), longitudinal ridge along the haemal keel, and thick zygosphenal base. There is no indication that a separate longitudinal ridge can be differentiated from the haemal keel in the Siwalik specimens, and the morphology of the keel is indistinguishable from that of other pythonines. A thick zygosphenal base is present in the majority of other pythonines. The relative length of the centrum varies in the column of all snakes, including pythonines (Hoffstetter and Gasc 1969; Polly et al. 2001), and is not considered diagnostic. Hoffstetter did not name his specimen as a new species due to limited sample size and the incomplete nature of the specimen. Based on the generic-level taxonomy of Kluge (1993b) and large sizes of specimens, this study also assigns all pythonine specimens to the genus *Python*. Because the characters used by Hoffstetter (1964) to recognize the Siwalik *Python* as a new taxon are present in extant taxa, or are variable throughout the vertebral column, I do not make a species-level assignment.

The Neogene pythonine fossil record includes occurrences in the early Miocene of Africa, Arabia, Asia, Australoasia, and Europe (Hoffstetter 1964; Rage 1976, 2003; Thomas et al. 1981; Underwood and Stimson 1990; Ivanov 2000). Geographic distributions do not exceed the current zoogeography of pythonines (Underwood and Stimson 1990), with the exceptions of a questionable taxon from the Miocene of Sardinia (Portis 1901), *P. euboicus* from the early Miocene of Greece (Szyndlar and Rage 2003), and *Python europaeus* from the middle Miocene of France (Ivanov 2000; Szyndlar and Rage 2003). The earliest occurrences of *Python* in the Siwalik section are from localities in the Kamlial Formation dated at approximately 18 Ma. This record is approximately coeval with the oldest African and European records, minimally constraining the timing of pythonine dispersal into mainland Asia and Africa (Kluge 1993b) to no younger than earliest Neogene.

Boidae? Gray, 1825
Genus et species indeterminate
Figure 3A

Referred specimens. H-GSP 24402, an isolated precloacal vertebra.

Locality and age. Y-039 (approximately 13.5 Ma).

Description. The single precloacal element questionably referred to Boidae indeterminate is incomplete (Figure 3A). The zygosphene, left side of the zygantrum, posterior neural arch, and the distal portions of both synapophyses are not preserved.

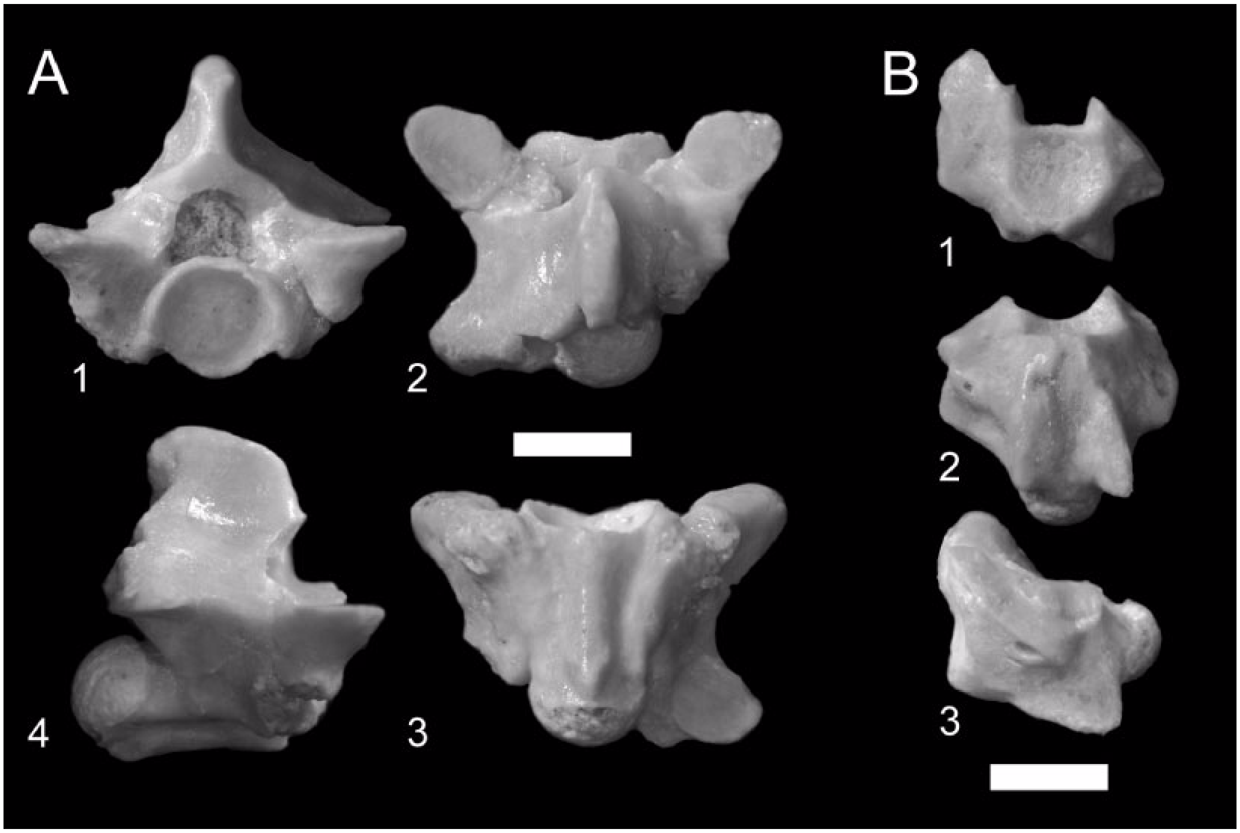


Figure 3. A. Siwalik Group Boidae indeterminate precloacal vertebra (H-GSP 24402) in anterior (1), dorsal (2), ventral (3), and right lateral (4) views. Scale equals 2.5 mm. **B.** Siwalik Group Erycinae indeterminate caudal vertebra (H-GSP 53417) in anterior (1), ventral (2), and left lateral (3) views. Scale equals 1 mm.

In all views, the vertebra is short and robust. In anterior view (Figure 3A1), the prezygapophyses are thin and elongate with low-angled articular surfaces. The prezygapophyseal accessory processes are reduced and do not extend laterally beyond the articular facets. The margins of the cotyle are subequal, with the ventral margin partially eroded. Paracotylar foramina are absent. The preserved portions of the neural canal indicate that it was subtriangular in outline, with the dorsal margin rounded and wide. In dorsal view (Figure 3A.2), the neural spine is anteroposteriorly elongate and transversely thick with a tapered anterior margin. The preserved portions of the posterior median notch indicate that it was well developed. The prezygapophyses extend farther laterally than the postzygapophyses. The interzygapophyseal ridges (Johnson 1955) are strongly concave, with the apex of the concavity anterior to the postzygapophyses. In ventral view (Figure 3A.3), a prominent medial prominence extends along the length of the centrum and is defined by deep paralymphatic fossae (LaDuke 1991). A small haemal keel that includes a small, pointed posterior margin just anterior to the condyle caps the prominence. The paralymphatic fossae extend from the ventrolateral margins of the cotyle anteriorly to the condyle posteriorly. In lateral view (Figure 3A.4), the spinous process is moderately tall and anteriorly sloped. The posterior region of the neural arch is moderately elevated with the lateroventral margin of the neural arch straight and anteroventrally angled with respect to the cotyle.

Discussion. Well-developed paralymphatic fossae indicate that the element is from the posterior region of the precloacal vertebral column (LaDuke 1991). Questionable assignment to Boidae *sensu lato* is based on the absence of caenophidian characters, including well-developed prezygapophyseal accessory processes and paracotylar foramina. The overall dimensions of the element are additionally similar to those in boines and pythonines. Among fossil taxa, H-GSP 24402 is most similar in general shape to species of the purported boine genus *Bavarioboa* from the late Paleogene and early Neogene of Europe (Szyndlar and Rage 2003). However, *Bavarioboa* is not diagnosed by unambiguous apomorphies (Szyndlar and Rage 2003, p. 21), and there are no known postcranial apomorphies that diagnose Boinae *sensu stricto*.

Similarly, cranial characters used to refer *Bavarioboa* specimens to Boinae (e.g., a posteriorly angled palatine process [Szyndlar 1994, figure 3, V, W]) are either not diagnostic for the clade (Kluge 1991, 1993a, 1993b), or consistently distributed within it (Underwood 1976, figure 4). As a result, there is no definitive fossil record of Boinae in Europe, despite referral of a large number of fossils (e.g., Szyndlar and Rage 2003).

cf. Erycinae Bonaparte, 1831
Figure 3B

Referred specimens. H-GSP 53417, isolated caudal vertebra.

Locality and age. Y641 (13.55 Ma).

Description. The caudal element is poorly preserved, lacking the majority of the neural arch and pleurapophyses (Figure 3B). Broken edges are worn on the specimen, indicating postmortem hydrologic transport and weathering. In anterior view (Figure 3B.1), the cotyle is circular with equal margins. The lateral margins of the element are partially preserved and are elevated and robust. In ventral view (Figure 3B.2), the bases of the pleurapophyses are preserved on the ventral margin of the lateral body. The pleurapophyses are more laterally offset from the centrum than seen in most taxa. In lateral view (Figure 3B.3), the haemapophyses are triangular in outline with vertical posterior margins anterior to the condyle.

Discussion. Tentative comparison of H-GSP 53417 to Erycinae is based on the presence of highly derived, posterior caudal vertebrae in the clade. Although poorly preserved, the element includes laterally offset pleurapophyses and a robust lateral body without a normally positioned prezygapophysis. These characteristics are not found in the caudal region of the vertebral column in most snakes, but are present in erycines (Sood 1941; Szyndlar 1987). Old World fossil erycines include the genera *Albaneryx*, *Bransateryx*, *Ogmophis*, and *Calamagras* (Rage 1984; Szyndlar and Rage 2003). The overall shape of H-GSP 53417 is more reminiscent of the comparatively simple caudal elements of *Calamagras gallicus* (Rage 1977) and *Albaneryx* (Hoffstetter and Rage 1972) than of the more complex vertebrae of *Bransateryx* (e.g., Szyndlar 1987).

Booidea (*sensu lato*) indeterminate

Referred specimens. H-GSP 24381, 24412, 27095, 27103, 27206, 27307, 46027, 46075, 53330, 53334, 53349, 53363, 53386, 53393, 53411, isolated, incomplete precloacal vertebrae.

Localities and ages. Y-747 (18 Ma), Y-641 (13.55 Ma), Y-668 (13.3 Ma), Y-690 (13.04 Ma), Y-825 (12.55 Ma), Y-504 (11.52 Ma), Y-076 (11.31 Ma), Y-797 (11.09 Ma), Y-450 (10.16 Ma), Y-410 (9.29 Ma), Y-024 (8.14 Ma), Y-906 (7.80 Ma), Y-931 (7.24 Ma).

Description. Specimens assigned to Booidea *sensu lato* (boines, erycines, pythonines) indeterminate consist of fragmentary vertebral centra that lack neural processes. All included elements are small, less than 0.5 cm in length. In ventral view, centra are stout and lack significant ventrolateral cotylar processes in specimens where the cotylar margin is preserved. Ventromedian processes on all specimens consist of poorly defined haemal keels that lack distinct lateral margins and are transversely wider than anteroposteriorly long.

Discussion. Assignment to Booidea is based on the presence of a poorly defined haemal keel, robust vertebral centrum, and absence of ventrolateral cotylar processes. The incomplete nature of specimens considered Booidea indeterminate prohibit refined diagnosis, but they may represent a more extensive record of erycines than can be recognized in this study, as well as neonatal to subadult *Python* specimens. It is also possible that additional boid or boine taxa are present in the Siwalik sample; however, evaluation of the Old World fossil record of boines does not support such an assignment, as noted above.

Caenophidia Hoffstetter, 1939
Acrochordus Hornstedt, 1787
Acrochordus dehmi Hoffstetter, 1964
Figures 4, 5

Referred specimens. 1289 vertebrae and ribs representing all regions of the axial skeleton.

Localities and ages. Lower and middle Siwalik Group of the Potwar Plateau, Pakistan, as well as middle Siwalik Group of Nepal and middle-upper Siwalik Group of Jammu, India (West et al. 1991; Rage et al. 2001).

Revised diagnosis. Large snake assigned to the genus *Acrochordus* based on the following characters (Hoffstetter 1964; Hoffstetter and Gayrard 1965; McDowell 1979): presence of parazygosphenal foramina, accessory processes consisting of vertically oriented blades with convex lateral margins, absence of tuberae costae on ribs, presence of small pterapophyses, synapophyses low-slung and ventrally elongate. Differs from all other members of the genus in larger size, possession of lymphapophyseal foramen, and tall neural spines with straight dorsal margins.

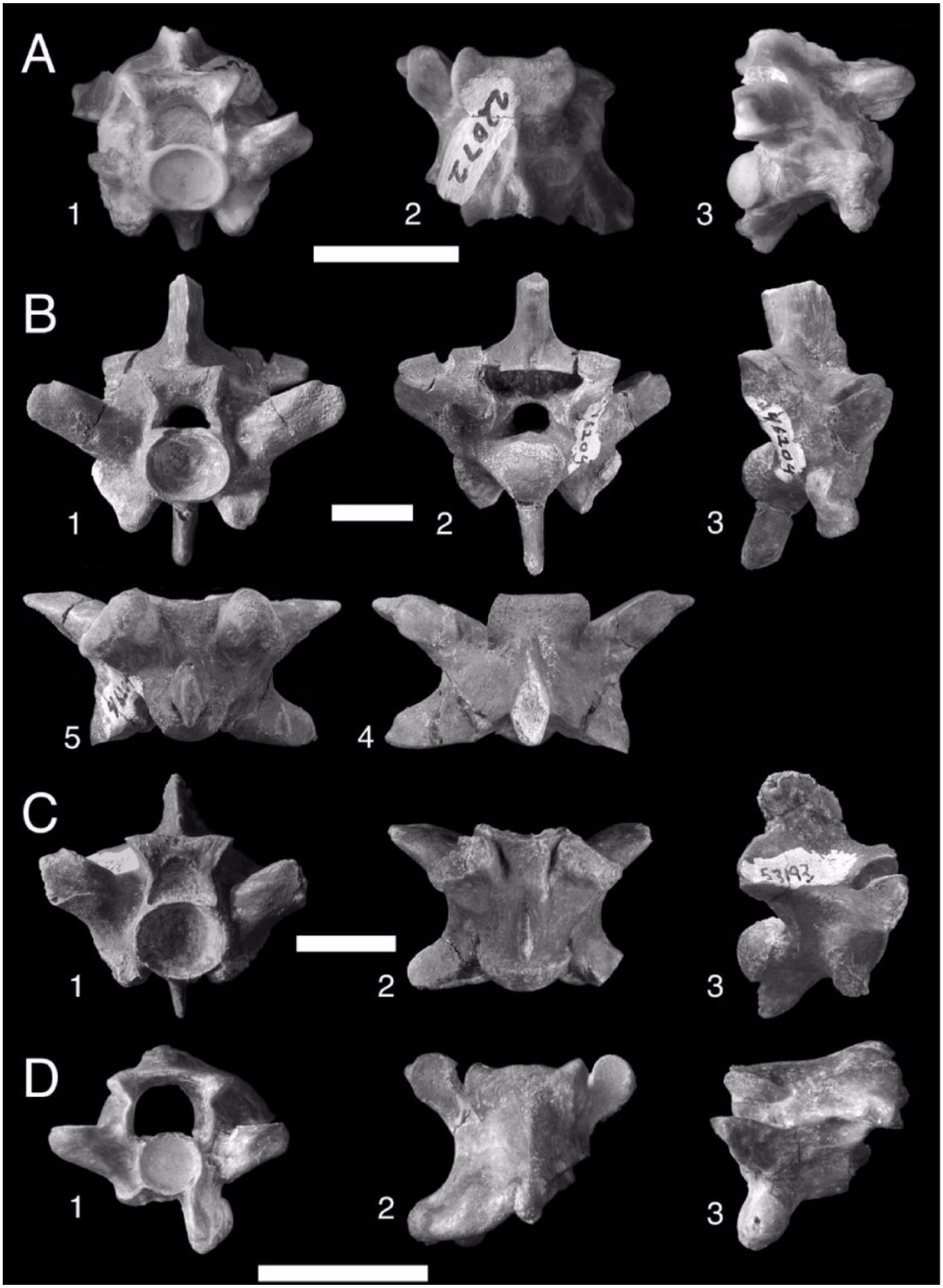


Figure 4. *Acrochordus dehmi* precloacal vertebrae. **A.** anterior precloacal vertebra (H-GSP 22072) in anterior (1), dorsal (2), and right lateral (3) views. **B.** precloacal vertebra (H-GSP 46204) in anterior (1), posterior (2), right lateral (3), dorsal (4), and ventral (5) views. **C.** posterior precloacal vertebra (H-GSP 53193) in anterior (1), ventral (2), and right lateral (3) views. **D.** neonatal precloacal vertebra (H-GSP 53319) in anterior (1), dorsal (2), and left lateral (3) views. Scales equal 10 mm for A-C, 5 mm for D.

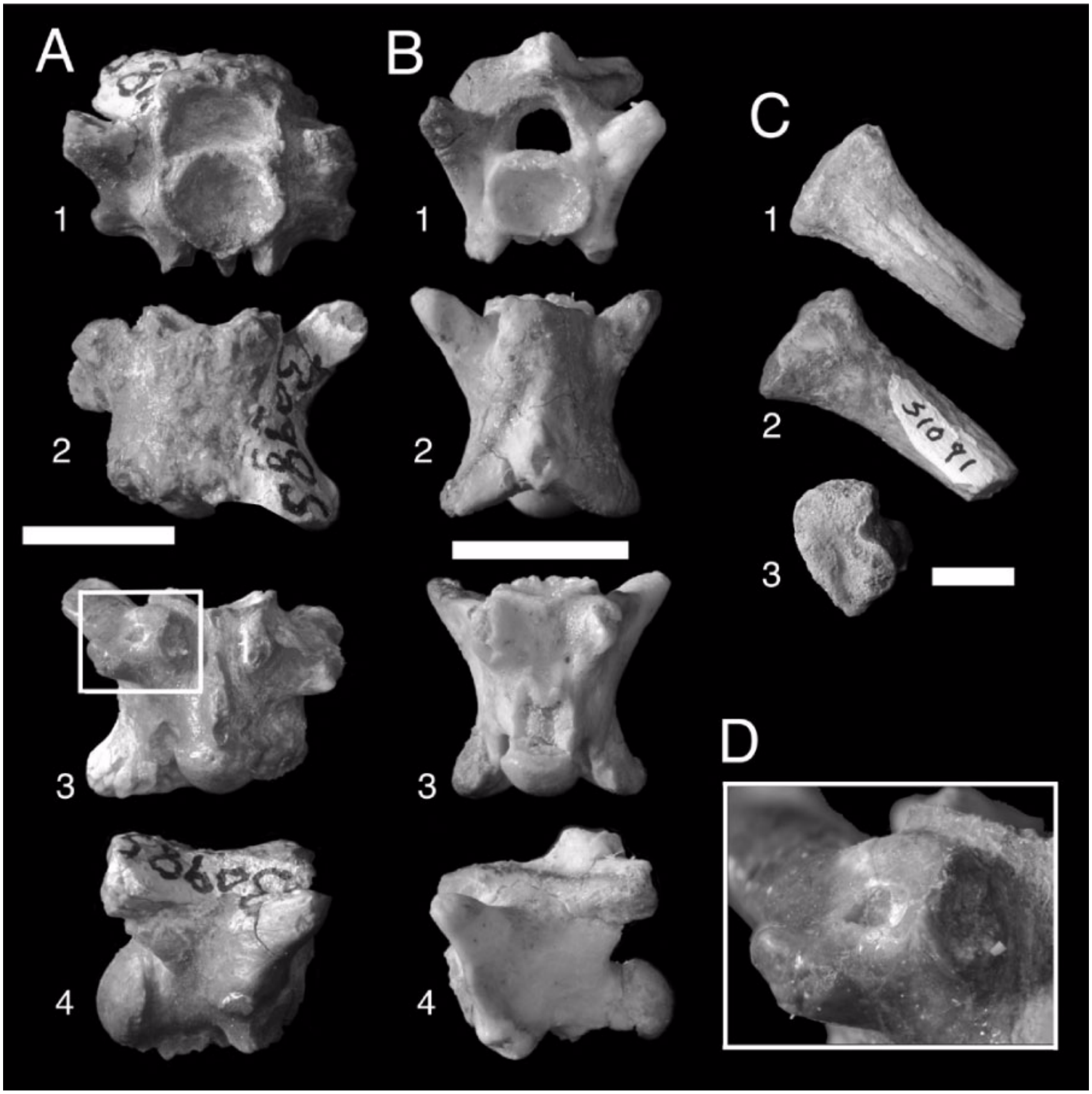


Figure 5. *Acrochordus dehmi* cloacal, postcloacal and costal elements. **A.** cloacal vertebra (HGSP 30985) in anterior (1), dorsal (2), ventral (3), and right lateral (4) views. **B.** caudal vertebra (H-GSP 46070) in anterior (1), dorsal (2), ventral (3), and left lateral (4) views. **C.** left rib (HGSP 51091) in posterodorsal (1), anteroventral (2), and dorsal (3) views. **D.** close up of cloacal vertebra in ventral view (from A) demonstrating lymphapophyseal foramen. Scales equal 5 mm.

Description. *Acrochordus dehmi* is represented by vertebrae from all regions of the column and by fragmentary ribs. No identifiable cranial elements have been recovered from the Pakistan Siwalik Group, but a distal quadrate was described from Nepal (West et al. 1991). Precloacal vertebrae from all post-embryonic ontogenetic stages were recovered from Pakistan. This description augments that of Hoffstetter (1964) and describes cloacal, postcloacal, and costal morphology, and subadult ontogenetic stages.

Precloacal vertebrae (Figure 4). In anterior view, the cotyle is approximately circular in outline. Two to three paracotylar foramina are present on either side of the cotyle. Small, paired ventrolateral cotylar processes are present below the ventral margin of the cotyle, forming a thin paralymphatic channel in most specimens. In posterior precloacal vertebrae, the ventrolateral processes are greatly reduced, and the paralymphatic channels extend along the medial surface of the synapophysis and extend onto the ventrolateral margins of the cotyle

(Figure 4C.1, 2). The prezygapophyses are robust and diverge from the body of the element at a high angle. The prezygapophyseal accessory processes are strongly rounded in outline and slightly discontinuous with the ventral angle of the prezygapophyses. The synapophyses are low slung, with anteroposteriorly wide and anteriorly angled parapophyses. The neural canal is relatively smaller than in more derived snakes, with smoothly curved lateral and dorsal margins. The zygosphene is robust and dorsoventrally tall. Parazygosphenal foramina are present at the bases of the zygosphenal articular facets. Small pterapophyses are present on the dorsal margin of the postzygapophyses (Figure 4A, B).

In posterior view, the zygantrum is wide with thick margins and divided by the posterior median notch to the base of the neural spine. Within the zygosphene, large, paired endozygantral foramina are located at the ventromedial surfaces of the articular facets. The anterior margins of spinal accessory nerve fenestrae are present at the posterior margin of the neural canal.

In lateral view, the neural spine originates just behind the zygosphene and is posteriorly angled. In more posterior vertebrae (Figure 4C.3), the dorsal margins of the neural spine are rounded and the anterior margin is depressed, as in *Acrochordus javanicus* (Hoffstetter and Gayrard 1965). In vertebrae from the middle portion of the trunk, however, the spine is robust and tall with squared dorsal edges (Figure 4B.3). A shallow fossa is present on the lateral surface of the neural arch in the same position as the lateral foramen of other taxa. Minute lateral foramina are present at the posteroventral margin of the fossa. The synapophyseal articular surface consists of distinct diapophyseal and parapophyseal facets that are strongly angled relative to each other. Ventrally, the hypapophysis is thin and elongate. It is ventrally deflected, but does not extend posteriorly beyond the condyle.

In ventral view (Figure 4B.5, C.2), the centrum is triangular in outline. The hypapophysis is ovoid and elongate in cross section. The relatively small, osseous paralymphatic channels are present at the medial margins of the synapophyses. In dorsal view (Figure 4A.2, B.4), the interzygapophyseal ridge is concave with a smoothly curving margin. The pre-and postzygapophyses are elongate and diverge from the main body of the element at high angles. Prezygapophyseal articular facets are ovoid and anterolaterally angled, becoming more laterally than anteriorly angled in vertebrae from the middle to posterior regions of the column. The accessory processes are anteroposteriorly compressed and are laterally angled with respect to the articular facets. The lateral margins of the zygosphene are curved, but the anterior margin is straight. The spinous process is transversely wide in cross section with a rounded posterior pillar tapering anteriorly to a thin lamina. The neural spine is relatively short anteroposteriorly in vertebrae from the anterior region of the column (Figure 4A.1, A.3).

Several incomplete specimens reveal internal vertebral morphology, including the patterns of communication between vertebral foramina. The internal structure of vertebrae in *A. dehmi* consists of a series of interconnected marrow cavities throughout the neural arch and processes, and bisecting the vertebral centrum. The cavities are paired and symmetrical around the sagittal plane of the element, with a main chamber within the neural arch, dorsal to the centrum body. Extensions radiate out from the main chamber to the base of the prezygapophyses and the synapophyses anteriorly and through the central body posteriorly, where they are connected. This connection possesses the same general shape as the primary lacuna described for *Python* by Hoffstetter and Gasc (1969), but is slightly more posterior. Both the paracotylar and parazygosphenal foramina communicate with the main chamber anteriorly. Posterodorsally, the endozygantral foramina (zygantral foramina, Rage 2001) communicate with the main chamber, and a smaller, medial channel branches off from the base of the foramina to form a dorsal communication between the two sides of the element. This channel has a small anteriorly directed vacuity at the base of the neural spine. The pattern of placement and communication between marrow cavities in *Acrochordus dehmi* is generally similar to that described for *Pterosphenus* (Hutchison 1985), but is more extensive than that described for other taxa (Sood 1948).

Subadults (Figure 4D). Precloacal vertebrae of subadult *Acrochordus dehmi* were recovered from 14 screen-washed localities throughout the Siwalik sequence. Subadult stages possess characters that typify juvenile growth stages in snakes (e.g., LaDuke 1991). These include an enlarged neural canal (canal diameter exceeds cotylar diameter), relatively small prezygapophyses, synapophyses with poorly differentiated para- and diapophyses that are relatively large and more ventrally deflected than in adult specimens, and a neural spine that consists only of a small posterodorsally angled process extending from the posterior margin of the neural canal. Despite these differences from adult specimens, generic assignment can be based on the possession of vertical, blade-like accessory processes and multiple pairs of paracotylar foramina. Additionally, the ventral deflection of the synapophyses characteristic of *Acrochordus* is greater than seen in adults.

Cloacal vertebrae (Figure 5A, D). A single element referable to the cloacal region of the vertebral column was recovered. It is comparatively shorter and wider than precloacal and caudal vertebrae, as in extant snakes (Hoffstetter and Gayrard 1965; Thireau 1967), and possesses the diagnostic prezygapophyseal accessory processes of *Acrochordus*. In anterior view (Figure 5A.1), bases of the dorsal and ventral lymphapophyseal processes are preserved and are separated by a wide, concave arc. Well-developed osseous paralymphatic channels are present medial to the ventral lymphapophyseal bases. In dorsal view (Figure 5A.2), the prezygapophysis is proportionally smaller relative to the neural arch than in precloacal elements. The neural spine is restricted to the posterior margin of the neural arch and is triangular in cross section. In ventral view (Figure 5A.3), the hypapophysis extends nearly the length of the centrum. The lymphapophyseal bases are transversely wide, and a large foramen is present on the anteroventral face of the lymphapophysis between the two bases (Figure 5A.3, D). The foramen is well developed, rounded, and symmetrically present on both lymphapophyses (Figure 5D). In lateral view (Figure 5A.4), the neural spine is reduced, with a gradually sloping anterodorsal margin. The spine does not extend beyond the posterior margin of the neural arch.

Caudal vertebrae (Figure 5B). Seventeen caudal vertebrae of *Acrochordus dehmi* were recovered. In anterior view (Figure 5B.1), the cotyle is relatively wider than in precloacal and cloacal elements. The prezygapophyses diverge at a steep angle and extend to the dorsal margin of the zygosphene. Prezygapophyseal accessory processes are smaller than in precloacal elements. Ventrally angled, pillar-like pleurapophyseal bases diverge from the centrum on either side of the cotyle. The zygosphene is small with weakly developed articular facets. In dorsal view (Figure 5B.2), caudal vertebrae are elongate, with a sharply convex zygosphenal ridge. The neural spine is ovoid in cross section and restricted to the posterior margin of the neural arch. In ventral view (Figure 5B.3), preserved portions of the haemapophyses indicate that they were restricted to just anterior of the condyle. The haemapophyses are divided at their contact with the central body, as in *A. javanicus* but unlike *A. granulatus*, in which the haemapophyses are only distally forked (Hoffstetter and Gayrard 1965). In lateral view (Figure 5B.4), caudal vertebrae are tall and broad with a deeper body and shorter neural arch than in precloacal vertebrae. The neural spine is low with a sloping anterior margin.

Ribs (Figure 5C). Articulated and associated ribs were recovered from a single locality (Y-935). Ribs of *Acrochordus dehmi* are robust and relatively thicker than in *A. javanicus* or *A. granulatus* (Hoffstetter and Gasc 1969). In posterodorsal and anteroventral views, the proximal end is unexpanded relative to other snakes, and there is no evidence of a pseudotuberculum process. In articular view, the capitular and tubercular articular surfaces are continuous and differentiated only by a pronounced recess for the attachment of costal ligaments on the anteroventral margin of the element. This gives the element a pronounced “C” shape in articular view (Figure 5C.3), corresponding to the recurved synapophyseal articular facets of precloacal vertebrae.

Discussion. Hoffstetter’s (1964) specific diagnosis of *A. dehmi* was based on the following characters in comparison with *A. javanicus*: large size; relatively taller, less inclined, and rounder cotyle; dorsoventrally elongate synapophyses with robust parapophyseal facets, synapophyses closely appressed in anterior view; and thickened margins of zygosphene and zygantrum. The use of body size as a diagnostic character for taxa possessing indeterminate growth is tenuous, and previous attempts using vertebral size to differentiate fossil snake species have been falsified (Christman 1975; Prange and Christman 1976). Nevertheless, the vast majority of the *A. dehmi* hypodigm consists of specimens that are considerably larger than reported for living *Acrochordus* (Hoffstetter 1964; Hoffstetter and Gayrard 1965; Shine 1986a, 1986b). The more rounded cotyle and smaller parapophyseal processes of *A. dehmi* are highly variable in both the Siwalik collection and in *A. javanicus*. They are not considered diagnostic in this study. The increased thickness of both the zygosphene and zygantral margins in *A. dehmi* appear consistent in the Siwalik sample; however, these characters were determined to be ontogenetically variable in other taxa (Auffenberg 1963). In comparison with *A. javanicus*, the majority of characters used previously to diagnose *A. dehmi* are either highly variable or are size dependent. The sample of this study allows for a survey of all regions in the vertebral column, and two characters here are used to diagnose *Acrochordus dehmi*, the presence of a lymphatic foramen on cloacal vertebrae and neural spines of nonposterior precloacal vertebrae with straight anterodorsal margins.

Acrochordus dehmi is one of the few snake taxa whose species level interrelationships can be determined by vertebral characters. Similarities between *A. dehmi* and *A. javanicus* were noted (Hoffstetter 1964; Rage 1987), and the presence of parazygosphenal foramina unambiguously unites the two as sister taxa to the exclusion of *A. granulatus* and potentially *A. arafurae* (McDowell 1979). Greatly reduced lateral foramina in *A. dehmi* are also similar to the condition in *A. javanicus*, where well-developed foramina are absent (Hoffstetter and Gayrard 1965). The complete bifurcation of caudal haemapophyses in *A. dehmi* and *A. javanicus* relative to the limited bifurcation in *A. granulatus* supports this hypothesis, but the polarity of this character has not been determined.

Acrochordus dehmi is the most abundant Siwalik reptile taxon, and is represented by 1,289 specimens from 113 localities throughout the entire temporal interval represented by the lower and middle Siwalik Group. Hoffstetter (1964) suggested that that *Acrochordus* in the Siwalik record may represent anagenetic evolution, with a second, younger species replacing *A. dehmi* in the Dhok Pathan Formation, but was unable to test this hypothesis due to sample size limitations. Rage (1987) echoed Hoffstetter (1964) in stating that two species of *Acrochordus* are present- *A. dehmi* in the lower and middle Siwalik Group, and a second taxon closely related to *A. javanicus* in the middle and upper Siwalik Group. Examination of the *Acrochordus* record from the Potwar Plateau does not reveal differences between younger and older samples that can be separated from intracolumnar variability. Thus, all specimens are referred to *Acrochordus dehmi* in this study.

Despite a wide geographic distribution of extant species throughout southern Asia to Australia (e.g., McDowell 1979), there is only a single definitive fossil record of *Acrochordus* within its current geographic range, from the early Miocene of Thailand (Rage and Ginsburg 1997). Reports of *Acrochordus* from the Pliocene of northern Australia (Smith and Plane 1985) now represent an elapid (Scanlon et al. 2003). As a result, fossil distributions suggest an Asian origin of the genus with subsequent dispersal through Indonesia to northern Australia. The absence of *Acrochordus* from any Australian Miocene fossil localities, despite intense study of the snake record, suggests that immigration did not occur prior to the Pliocene. The minimum divergence timing for *Acrochordus* can be constrained as no younger than the first occurrence of its sister taxon Colubroidea in the early Eocene (e.g., Rage et al. 2003; Head et al. 2005). The fossil record of *Acrochordus dehmi* extends throughout the lower and middle Siwalik Group, and the timing of extinction for the taxon can only be limited to younger than 6.35 Ma.

Colubroidea Oppel, 1811
Genus et species indeterminate
Colubroid morphotype A
Figure 6

Referred specimens. H-GSP 26722, isolated precloacal vertebra; H-GSP 26666, incomplete, associated, and partially articulated postcranial skeleton.

Localities and ages. Y-726 (13.01 Ma), Y-698 (12.94 Ma).

Description. Colubroid morphotype A consists of approximately 106 partially associated and articulated vertebrae and ribs representing a single animal from locality Y-726, and an isolated precloacal vertebra from locality Y-698. The partially articulated specimen consists of precloacal and a single caudal vertebra embedded in calcareous siltstone (Figure 6A). In ventral view, precloacal elements are elongate (Figure 6B). Hypapophyses are present on all elements. They originate anteriorly at the level of the parapophyses and are elongate and posteriorly angled. Well-developed prezygapophyseal accessory processes are present, and are anteroposteriorly swollen with sharply pointed distal margins. Prominent ventrolateral cotylar processes are present on all specimens.

In lateral view (Figure 6C), the zygosphene is low with anteroposteriorly elongate articular facets. Ventrally, elongate, pointed parapophyseal processes occur on all vertebrae. The hypapophysis is low and blade-like. It extends to the posterior margin of the condyle where it terminates in a sharp point. Dorsally, the posterior median notch is well developed with straight margins. The neural spine extends anterior to the dorsal margin of the zygosphene. The spine is tall and uniformly thick. In anterior view (Figure 6E), the neural canal is rounded in outline and is capped by a small zygosphene. The prezygapophyseal accessory facet is slightly dorsolaterally angled. The accessory process is approximately horizontal. There are no accessory-process foramina.

The single caudal vertebra is exposed in ventral view (Figure 6D). The pleurapophyses are elongate and ventrally deflected. Their posterior margins extend to the condyle, giving the element a triangular appearance. Large subcentral foramina are present on the ventrolateral margins of the centrum. Anteriorly, the cotylar ventral margin is flush with the prominence, and posteriorly, the condyle is small and unexpanded. Preserved cos-

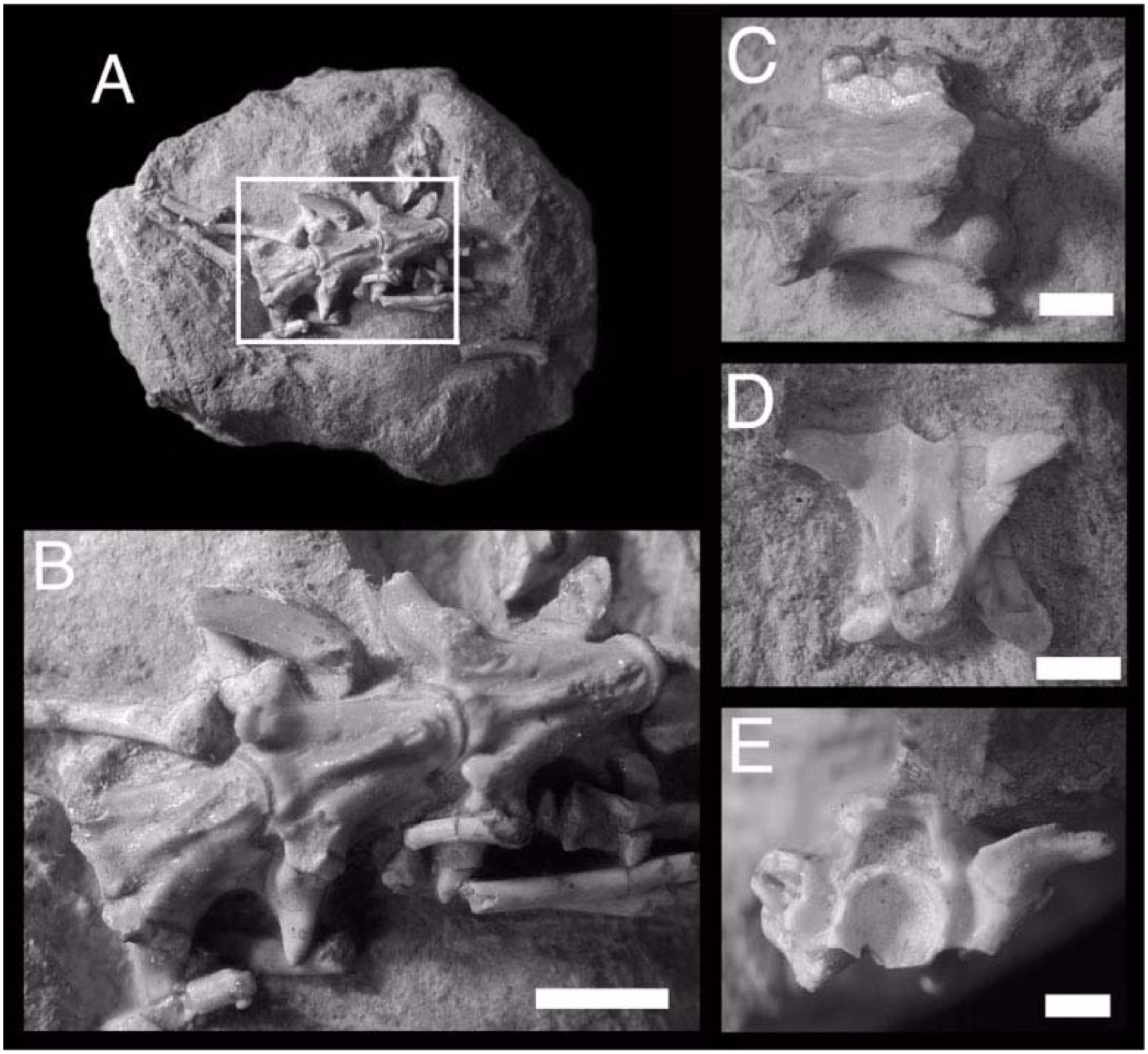


Figure 6. Siwalik Group colubroid morphotype A (H-GSP 26666). **A.** articulated precloacal vertebrae and ribs in ventral view. **B.** detail of articulated precloacal elements. **C.** isolated precloacal vertebra in left lateral view. **D.** isolated caudal vertebra in ventral view. E. isolated precloacal vertebra in anterior view. Scale equals 5 mm for B, 2 mm for C-E.

tal elements consist of elongate, thin proximal and mid-shaft regions. No complete ribs were recovered. Proximal regions of the ribs are elongate and thin, and include a well-developed pseudotuberculum (Figure 6B).

Genus et species indeterminate
Colubroid morphotype B
Figure 7A

Referred specimens. H-GSP 13970, 24343, 24350, 24352, 24354, 24355, 24356, 24368, 24386, 24418, 24421, 24423, 27061, 27162, 27173, 27177, 50264, 51121, 53305, 53306, 53307, 53308, 53310, 53369, 53370, isolated precloacal vertebrae.

Localities and ages. Y-367 (8.95 Ma), Y-024 (8.14 Ma), Y-547 (7.93 Ma), Y-457 (7.30 Ma), Y581 (6.97 Ma), Y-908 (6.78 Ma).

Description. Specimens referred to as colubroid morphotype B are small, relatively stout elements, all of which possess well-developed hypapophyses and prezygapophyseal accessory processes. In anterior view (Figure 7A.1), the neural canal is rounded in outline and is capped by a zygosphene that possesses a flat dorsal margin. The cotyle is circular and includes large ventrolateral processes. A large paracotylar foramen is present on either side of the cotyle. The parapophyseal process is large with a rounded anterior margin. The prezygapophyseal articular facets are low and horizontal.

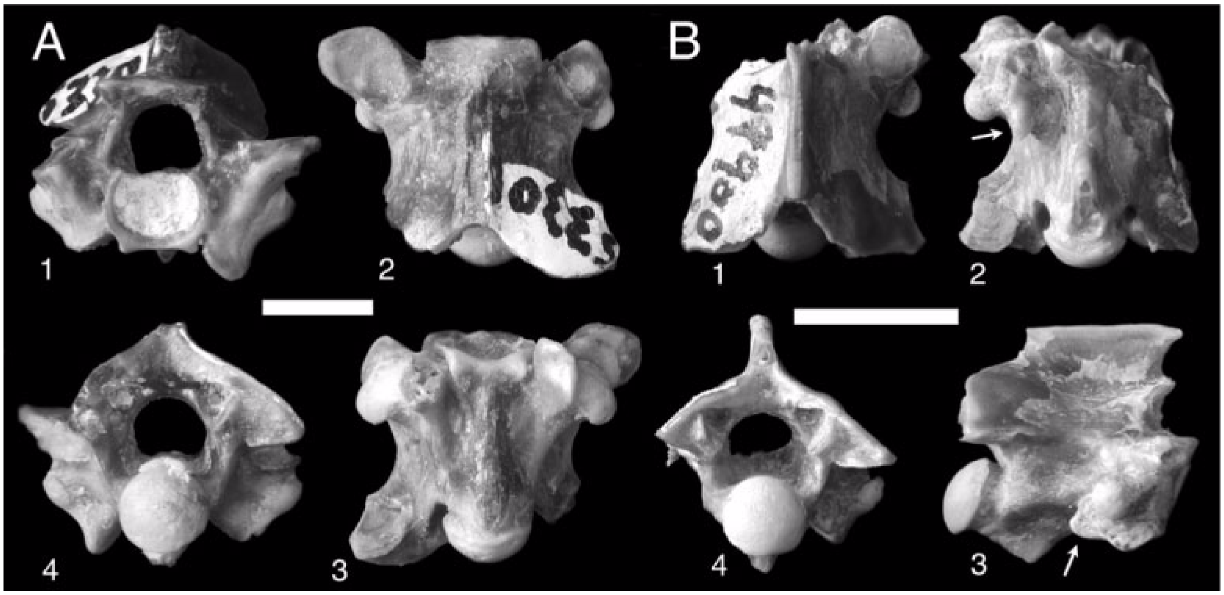


Figure 7. A. Siwalik Group colubroid morphotype B (H-GSP 53306) in anterior (1), dorsal (2), ventral (3), and posterior (4) views. **B.** *Gansophis potwarensis* gen. et sp. nov. (H-GSP 49900, holotype) in dorsal (1), ventral (2), right lateral (3), and posterior (4) views. Arrows point to parapophyseal accessory process. Scales equal 2 mm.

Where preserved, the prezygapophyseal accessory processes are elongate and distally pointed. A large accessory process foramen is present at the base of the process. In dorsal view (Figure 7A.2), the interzygapophyseal ridge is smoothly concave. The prezygapophyseal articular facet is anteroposteriorly wide and approximately subtriangular with an anteromedially angled apex. The base of the neural spine is elongate and extends onto the zygosphene. The anterior margin of the zygosphene is approximately straight to slightly concave. The margins of the posterior median notch are smoothly convex. In ventral view (Figure 7A.3), the centrum is relatively stout with large subcentral foramina. Anteriorly the parapophyseal process is rounded. Hypapophyseal bases indicate an elongate, posteriorly angled hypapophysis. In posterior view (Figure 7A.4), the dorsal margin of the neural arch is slightly convex with a relatively steep angle compared to other Siwalik Group taxa. The posterior margin of the arch is smooth. There is no indication of epizygapophyseal spines or parazygosphenal foramina. The parapophysis is elongate and thin in posterior view.

Gansophis gen. nov.

Type species. *Gansophis potwarensis* sp. nov.

Etymology. Gans + Ophis (Gr. Masc), “snake.” “Gans’ snake,” generic nomen in honor of Dr. Carl Gans for his many contributions to herpetology.

Diagnosis. Colubroid snake of indeterminate status recognized by a posteriorly projecting accessory parapophyseal process that forms an elongate articular surface for the costal tubera.

Gansophis potwarensis gen. et sp. nov.
Figure 7B

Holotype. H-GSP 49900, isolated precloacal vertebra.

Type locality and age. Y-908 (6.78 Ma).

Diagnosis. As for genus.

Etymology. Specific name from the Potwar Plateau in north-central Pakistan.

Description. The single vertebra assigned to *Gansophis* is incomplete, missing most of the zygosphene, left prezygapophysis and synapophysis, right prezygapophyseal accessory process, distal portion of the hypapophysis, most of the cotyle, and the posterior margin of the neural spine.

In dorsal view (Figure 7B.1), the diapophyseal articular facet extends beyond the base of the synapophysis. The dorsal margin of the neural spine is laterally expanded with a shallow median groove, producing a slightly bilobate anterodorsal margin to the spine. Posteriorly, the margins of the posterior median notch are crenulate. In ventral view (Figure 7B.2), the parapophyseal accessory process is triangular in outline and is laterally recurved. The ventral and medial portions of the process are covered by smooth periosteum that is continuous with the rest of the element and forms an ovoid, elongate articular surface for the costal tubera. Anteriorly, a single, well-developed ventrolateral cotylar process is preserved along the right ventral margin of the cotyle.

In lateral view (Figure 7B.3), the neural spine is elongate, and the anterior margin of the spine overhangs the zygosphene. The posterior margin of the neural arch is elevated, and the posterior margin of the neural spine is shorter than the anterior margin. The synapophysis is well developed, with a prominent, laterally extended diapophyseal process. The parapophyseal process is expanded to include a small, posteriorly oriented accessory process. The process is triangular in lateral view, and its lateral margin consists of a costal articular facet continuous with the main body of the synapophysis. The anteroventral margin of the hypapophysis is steeply angled, and the distance between the margin and the cotyle indicates that the hypapophysis was broad.

In posterior view (Figure 7B.4), the lateral margins of the neural arch are straight and slightly angled at the level of the dorsolateral margin of the zygantrum. A small prominence is present at the lateral margin of the postzygapophysis, but it is considerably smaller than the epizygapophyseal spines of other colubroid taxa. The posterior surface of the neural arch lacks parazygantral foramina.

Discussion. Of the three indeterminate colubroids, only *Gansophis* can be diagnosed by an apomorphic character, the presence of the posterior accessory parapophyseal process. The process is not described for any other snake (e.g., Rochebrune 1881; Dowling and Duellman 1978; Rage 1984; Holman 2000). It is possible that the accessory process represents a teratological or pathological abnormality, conditions that are known to occur in the vertebral column of snakes (e.g., Albrecht 1883). Examination of the process does not demonstrate irregular or abnormal bone growth. Instead, it is smoothly continuous with the rest of the parapophysis, suggesting functional articulation with an expanded costal tuberculum. Among the other two taxa, colubroid morphotype A is unique in the Siwalik Group record in the absence of large foramina at the anteroventral margins of the prezygapophyseal articular facets. Colubroid morphotype B can be distinguished by a comparatively short centrum among colubroid specimens.

The higher order systematic relationships of these specimens within Colubroidea cannot be precisely resolved. Morphotypes A and B can be definitively excluded from Colubrinae and Viperidae on the basis of hypapophyseal morphology, but could be included in a wide range of colubroid higher-order lineages. Because *Gansophis* is represented by only a single incomplete specimen, its systematic relationships within Colubroidea are more poorly constrained.

Colubroidea indeterminate

Referred specimens. H-GSP 24181, 24342, 24344, 24347, 24349, 24353, 24355, 24366, 24369- 71, 24375, 24376, 24379, 24380, 24386, 24387, 24388, 24390, 24393, 24395, 24397, 24398, 24407, 24420, 24421, 24424, 24425, 26220, 26223, 26245, 26248, 27058, 27060, 27062, 27064, 27074, 27077, 27079, 27080, 27082-6, 27088, 27099, 27100, 27104, 27105, 27150, 27152, 27157, 27160, 27161, 27163, 27165, 27167, 27168, 27172, 27174-6, 27179-85, 27200, 27202, 27204, 27216, 27217, 27219, 27220, 27222, 27233, 27303, 27321, 27322, 46699, 53295, 53311- 4, 53329, 53331, 53337, 53340, 53344, 53348, 53351, 53353-6, 53358-60, 53364-8, 53371, 53373-5, 53381-4, 53387-9, 53399, 53404, 53406, 53415, isolated precloacal and caudal vertebrae.

Localities and ages. Y-747 (18 Ma), Y-680 (14.10 Ma), Y-491 (13.77 Ma), Y-641 (13.55 Ma), Y-640 (13.55 Ma), Y-668 (13.30 Ma), Y-690 (13.04 Ma), Y-504 (11.52 Ma), Y-809 (11.4 Ma), Y-076 (11.31 Ma), Y-450 (10.16 Ma), Y-311 (10.00 Ma), Y-182 (9.16 Ma), Y-367 (8.95 Ma), Y-388 (8.68 Ma), Y-387 (8.64 Ma), Y-024 (8.14 Ma), Y-547 (7.93 Ma), Y-906 (7.80 Ma), Y-866 (7.33 Ma), Y-457 (7.30 Ma), Y-931 (7.24 Ma), Y-581 (6.97 Ma).

Description and Discussion. Indeterminate colubroid specimens consist of fragmentary precloacal and caudal elements that possess some combination of the following characters: well-developed prezygapophyseal accessory processes and accessory-process foramina; large ventrolateral cotylar processes; paracotylar foramina; strongly differentiated diapophyseal and parapophyseal articular facets of the synapophyses; prominent hypapophyses; elongate centra; subcentral paralymphatic fossae; elongate pleurapophyses and haemapophyses on caudal elements. Indeterminate colubroid remains have been recovered from screen-washed localities throughout the Siwalik Group and undoubtedly include multiple taxa.

Elapidae Boié, 1827
Bungarus Daudin, 1803
Species indeterminate

Referred specimens. H-GSP 05071, 24365, 24374, 24391; 24396; 27078, 27224, 53026, incomplete precloacal vertebrae.

Localities and ages. Y-450 (10.16 Ma), Y-310 (9.26 Ma), Y-182 (9.16 Ma), Y-388 (8.68 Ma),

Y-024 (8.14 Ma), Y-898 (7.77 Ma).

Description and Discussion. All listed specimens are referred to *Bungarus* on the basis of possessing the elongate, expanded prezygapophyseal accessory processes that are diagnostic for the genus (Hoffstetter and Gasc 1969). Within the genus, all Siwalik specimens are allocated to the polytomy of species more derived than *B. flaviceps* and *B. bungaroides* (McDowell 1970; Slowinski 1994).

The first occurrence of *Bungarus* in the Siwalik Group occurs at approximately 10.2 Ma, and the taxon persists upsection. Implications of Siwalik Group *Bungarus* for estimating elapid divergence timing and biogeography will be examined elsewhere (Head, in prep).

Elapidae? indeterminate
Figure 8A

Referred specimens. H-GSP 21021, 51107, 50147, incomplete precloacal vertebrae.

Localities and ages. Y-311, (10.00 Ma), Y-908 (6.78 Ma), Y-910 (6.98 Ma).

Description. Three vertebrae represent the largest colubroid specimens recovered from the Siwalik Group. All specimens are incomplete, lacking zygapophyses, the majority of the neural spine, and the majority of the zygantrum and posterior neural arch. In anterior view (Figure 8A.1), the dorsal margin of the zygosphene is flat. The cotyle is circular, and small paracotylar foramina are deeply set along its lateral margins. Small ventrolateral processes are present on the ventral margin of the cotyle, giving it a flattened appearance. Relatively small paralymphatic channels are present between the processes and the synapophyses. The synapophyses possess a low-angled articular surface for the ribs. The diapophyseal articular facet is pronounced and laterally differentiated from the synapophyseal body by a shallow trough. The parapophysis is well developed and rounded.

In ventral view (Figure 8A.2), the centrum is elongate and wide with slightly convex lateral margins. The ventral margin of the cotyle is medially embayed. The hypapophysis is prominent and extends from the cotylar lip to the base of the condyle. The synapophyses are anterolaterally angled away from the centrum. The preserved margins of the interzygapophyseal ridge indicate that it is smoothly convex. In lateral view (Figure 8A.3), the posterior margin of the neural spine is short and much more elevated than the inferred anterior margin. The dorsal margin of the spine appears gently rounded. The ventral margin of the centrum is slightly concave, and the hypapophyseal ventral margin is strongly so. The angle of the hypapophyseal margin indicates that the complete structure was angled posteriorly more than ventrally.

Discussion. Tentative inclusion in Elapidae is based on the large size of the Siwalik specimens, relatively small paralymphatic channels, and concave ventral margin of the centrum. These characters compare well with the king cobra *Ophiophagus*. A convex ventral margin of the centrum was considered diagnostic of Elapidae by Hoffstetter (1939); however, this character is difficult to assess, and comparison of elapids and other colubroids indicates considerable variability in the curvature of the ventral margin.

Although the referred specimens can be united on the basis of the characters used to compare them with *Ophiophagus*, they cannot be unambiguously diagnosed to the genus or even to Elapidae. If the specimens do belong to *Ophiophagus*, then they represent the only fossil occurrence of the genus and a northern geographic range extension. Extant *Ophiophagus* is not reported from Pakistan (Minton 1966).

Colubridae Opell, 1811
Natricinae Bonaparte 1838
Genus et species indeterminate
Figure 8B

Referred specimens. H-GSP 24351, 27164, 50293, incomplete precloacal vertebrae.

Locality and age. Y-547 (7.93 Ma); Y-457, (7.30 Ma).

Description. In anterior view (Figure 8B.1), the vertebrae are low and wide. Paracotylar foramina are present. Elongate ventrolateral cotylar processes form enlarged, circular lymphatic channels between the cotyle and the synapophyses. The parapophyses include large, elongate accessory processes that are rounded in anterior view. The diapophysis is moderately developed relative to other Siwalik taxa. In dorsal view (Figure 8B.2), the neural spine is elongate, uniformly thick, and extends the length of the neural arch. Prominent epizygapophyseal spines are present at the posterolateral margins of the postzygapophyses. The posterior median notch is well developed, with broadly concave margins. In posterior view (Figure 8B.3), the dorsal margin of the neural arch is straight and shallowly angled relative to other taxa. Large parazygantral foramina are present lateral to

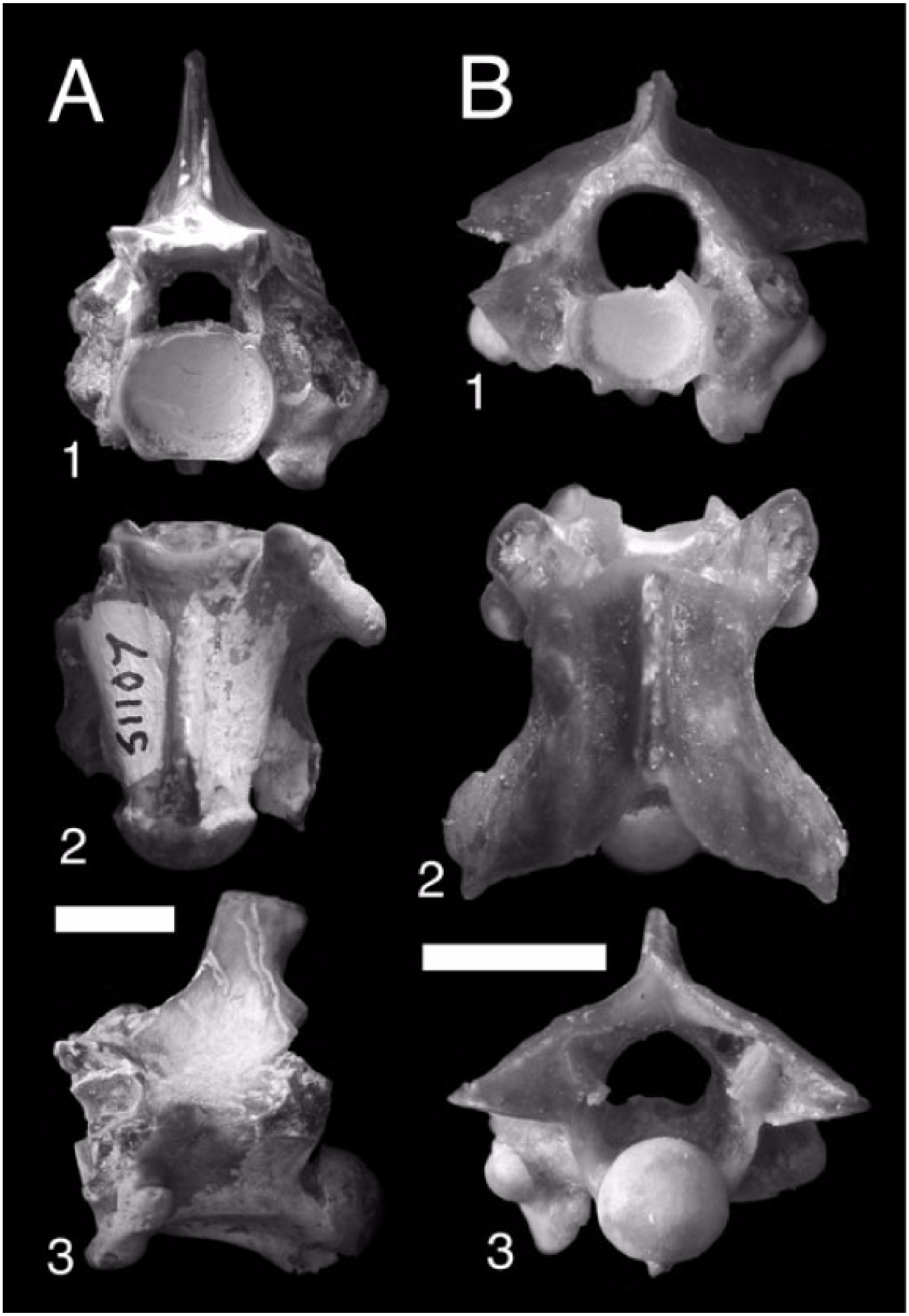


Figure 8. A. Siwalik Group Elapidae? indeterminate (H-GSP 51107) precloacal vertebra in anterior (1), ventral (2), and left lateral (3) views. **B.** Siwalik Group Natricinae indeterminate (H-GSP 50293), precloacal vertebra in anterior (1), dorsal (2), and posterior (3) views. Scale equals 5 mm for A, 2.5 mm for B.

the zygantral margins. Additional large foramina are present just below the epizygapophyseal spines.

Discussion. Assignment to Natricinae is based on the combination of epizygapophyseal spines and parazygantral foramina. The incomplete nature of Siwalik natricine specimens precludes more refined assignment. There is an extensive list of Old World fossil taxa referred to Natricinae, including *Paleonatrix lehmani*, *P. silesiaca*, *Neonatrix europaea*, *N. nova*, *Natrix longivertebrata*, and *N. sansaniensis* from the Miocene of Europe and *Mionatrix diatomeus* from the Miocene of China (Sun 1961; Mlynarski et al. 1982; Rage 1984; Szyndlar 1984; Rage and Szyndlar 1986; Szyndlar and Schleich 1993; Ivanov 2000); however, only Paleonatrix is generically diagnosable from vertebral remains by the presence of an apomorphic anteriorly expanded hypapophysis with a square anteroventral margin (Ivanov 2000). No discrete characters have been used in other generic or specific assignments, and there is no basis to allocate Siwalik specimens to previously erected taxa.

Colubrinae Opell, 1811
Chotaophis gen. nov.

Type species. *Chotaophis padhriensis* sp. nov.

Etymology. Chota (Urdu) "little" + Ophis (Gr. Masc), "snake" indicating the small size of referred specimens.

Diagnosis. Small colubrine snake possessing narrow zygapophyses, anteriorly positioned lateral foramina, transversely thin neural spine, and parazygantral foramina.

Chotaophis padhriensis sp. nov.
Figure 9

Holotype. H-GSP 24346, isolated precloacal vertebra.

Paratype. H-GSP 26246, isolated vertebra.

Type locality. Y-367 (8.95 Ma)

Locality and age. Y-457 (7.30 Ma)

Diagnosis. As for genus

Etymology. Specific nomen from Padhri, the local community at locality Y-457. Nomen translates as "little snake from Padhri."

Description. In anterior view (Figure 9.1), the vertebrae are short and narrow. The neural spine is thin. The zygosphene is transversely wide with a thin anterior margin and small articular facets. The cotyle is relatively small with ventrolateral processes represented only by a slight squaring of the ventral margin of the centrum. The prezygapophyses are low relative to the dorsal margin of the zygosphene and possess horizontal articular facets. There is no indication of elongate prezygapophyseal accessory processes, but large accessory-process foramina are present at the ventrolateral margins of the articular facets. In dorsal view (Figure 9.2), the interzygapophyseal ridge is smoothly concave. The posterior median notch has straight margins. Anteriorly, the prezygapophyseal articular facet is ovoid and elongate. The anterior margin of the zygosphene is broadly convex. The base of the neural spine is transversely uniform in width.

In ventral view (Figure 9.3), the centrum is elongate. The haemal keel is well developed and becomes progressively wider posteriorly, terminating in a blunt, triangular tip. Small subcentral foramina are present on either side of the keel toward the cotyle. The postzygapophyseal articular facet is elongate and anteroposteriorly oriented.

In lateral view (Figure 9.4), the ventral margin of the centrum is concave. The haemal keel possesses a flat ventral margin. Anteriorly, the cotyle is angled more posteroventrally than in other Siwalik taxa. Above the cotyle, the dorsal margin of the zygosphene is elevated. The neural spine extends to the anterior margin of the zygosphene. Although the majority of the spine is not preserved in either specimen, its posterior portion is gradually curved and appears to include a portion of the dorsal margin, suggesting that the spine was low. Small lateral foramina are present on the sides of the centrum. The foramina are located just posterior to the synapophyses and are more anteriorly positioned than in other taxa. In posterior view (Figure 9.5), the neural arch is steeply angled with a concave margin. The posterior margin of the arch includes prominent parazygantral foramina located lateral to the zygantrum. The postzygapophysis is not as expanded laterally as in other Siwalik taxa.

Discussion. *Chotaophis* is recognized as a distinct taxon based on the unique combination of anteriorly positioned lateral foramina, presence of parazygantral foramina, and elongate centrum. *Chotaophis* is placed with Colubrinae based on the presence of a well-formed haemal keel. The fossil record of Old World colubrines is extensive; however, vertebral morphology has been considered too ambiguous to define interrelationships and taxonomy within the clade (e.g., Szyndlar 1984, 1987). Old World fossil colubrines include multiple species of the extant genera *Coluber, Elaphe,* and *Coronella,* as well as the extinct genera *Zelceophis* and *Texasophis* (Rage 1984; Szyndlar 1984; Szyndlar and Schleich 1993; Ivanov 2000). *Chotaophis* can be differentiated from *Coluber,*

Figure 9. *Chotaophis padhriensis* gen. et sp. nov. (H-GSP 24346 holotype), precloacal vertebra in anterior (1), dorsal (2), ventral (3), left lateral (4), and posterior (5) views. Scale equals 1 mm.

Elaphe, Coronella, and *Zelceophis* by the absence of prezygapophyseal accessory processes. *Chotaophis* and *Texasophis* share relatively unexpanded prezygapophyses and reduced prezygapophyseal accessory processes. However, *Chotaophis* has more anteriorly positioned lateral foramina, and is relatively more elongate than published specimens of *Texasophis*. *Texasophis* is considered a problematic taxon, because vertebral morphology in colubrines is relatively undocumented (Szyndlar 1987), and the genus has not been diagnosed using discrete characters. As a result, there is no evidence to support referral to *Texasophis*.

Sivaophis gen. nov.

Type species. *Sivaophis downsi* sp. nov.

Etymology. “Siva” (Hindi), “God of death” + Ophis (Gr. Masc), “snake.” Generic nomen continues a secular tradition in naming Siwalik taxa and should

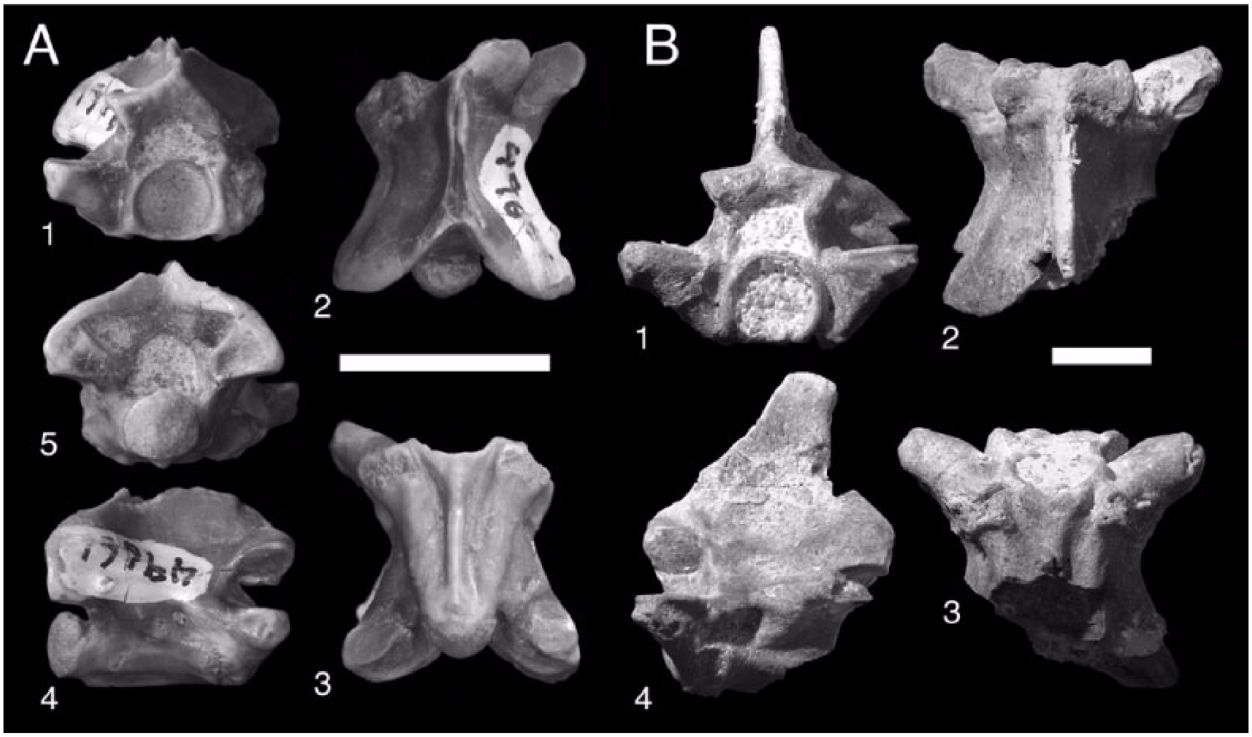


Figure 10. *Sivaophis downsi* gen. et sp. nov. **A.** H-GSP 49661 (holotype), precloacal vertebra in anterior (1), dorsal (2), ventral (3), right lateral (4), and posterior (5) views. Scale equals 10 mm. **B.** BSP 1956 II 2267 (paratype) in anterior (1), dorsal (2), ventral (3), and left lateral (4) views. Scale equals 5 mm.

not be interpreted as favoring or disparaging a particular religion.

Diagnosis. Colubrine possessing wasp-waisted interzygapophyseal ridges in dorsal and ventral view, large lateral foramina, and an extremely tall neural spine.

Sivaophis downsi sp. nov.
Figure 10

Holotype. H-GSP 49661, isolated precloacal vertebra.

Paratype. BSP 1956 II 2267, isolated precloacal vertebra.

Referred specimens. BSP 1956 II 2267, H-GSP 05063, 09764 17618, 24174, 24339, 24340, 26221, 26367, 27120, 27122, 27315, 31363, 31364, 49898, 50263, 50700, 53302, 53303, 53309, 53418, 53419, BSP 5.2.56, isolated precloacal vertebrae.

Type locality. Y-227 (9.29 Ma).

Localities and ages. Dhok Pathan Formation, Winnewala (BSP collections), Y-059 (13.60 Ma), Y-640 (13.55 Ma), Y-825 (12.55 Ma), Y-504 (11.52 Ma), Y-224 (9.29 Ma), Y-227 (9.29 Ma), Y-260 (9.19 Ma), KL-01 (9.18 Ma), Y-182 (9.16 Ma), Y-367 (8.95 Ma), Y-388 (8.67 Ma), Y-457 (7.30 Ma), Y-908 (6.78 Ma), DP-13 (6.35 Ma).

Etymology. Specific nomen translates as “Downs,” in honor of the contributions of William R. Downs III to the paleontology of the Siwalik Group. Full nomen translates to “Downs’ Siva snake.”

Description. In anterior view (Figure 10A.1, B.1), the zygosphene is thick and has a broadly convex dorsal margin. The cotyle is round with very small ventrolateral processes in all specimens. A single pair of small paracotylar foramina is present at the lateral margins of the cotyle. The prezygapophysis is low slung and approximately horizontal. Small, triangular accessory processes are present below the prezygapophyseal articular facets. The synapophyses are small with low-angled dia- and parapophyseal articular surfaces.

In lateral view (Figure 10A.4, B.4), the neural arch is tall. The zygosphenal articular facets are elevated well beyond the level of the prezygapophysis and are anterodorsally angled. The neural spine is partially preserved in only a single specimen (Figure 10B.4). The spine is wide and tall, with a convex dorsal margin. The majority of the anterior margin is not preserved in BSP 5.2.56; however, the angle of the spine at its base suggests that it was slightly angled posteriorly. The posterior margin of the neural arch is elevated with vertical to posteriorly angled margins. A large lateral foramen is present in a shallow fossa just behind the prezygapophysis. The zygosphenal ridge forms the dorsal margin of the fossa, with a sharp angle between the pre- and postzygapophyses. In posterior view (Figure 10A.5), the neural arch is elevated and strongly vaulted, with curved lateral margins. The posterior surface of the neural arch is broad, and the zygantrum is deeply recessed. Medially, the neural canal is tall and narrow.

In dorsal view (Figure 10A.2, B.2), the neural spine is elongate and terminates anteriorly between the zygosphenal articular facets. The anterior margin of the zygosphene is highly variable, ranging from straight to broadly concave to strongly crenulate (Figure 10B.2, B.3). The prezygapophyseal articular facets are relatively small, ovoid, and elongate. Between the zygapophyses, the interzygapophyseal ridge is concave and strongly angled toward the apex, giving the element a strongly wasp-waisted appearance in dorsal view. The posterior median notch is well developed and extends anteriorly toward the transverse midline of the element. The margins of the notch and the posterior neural arch are sigmoid in dorsal view from the base of the postzygapophysis to the posterior margin of the neural spine. In ventral view (Figure 10A.3, B.3), the centrum is elongate and triangular. The haemal keel is narrow and well developed, extending from the ventral margin of the cotyle to the anterior margin of the condyle, where it terminates in a blunt, unexpanded point. Deep paralymphatic channels define the keel laterally. The condyle is relatively smaller than in other Siwalik taxa. The postzygapophyseal articular facets are small and restricted to the lateral margins of the neural canal.

Discussion. *Sivaophis* is diagnosed by the presence of wasp-waisted interzygapophyseal ridges, which distinguish it from other Siwalik specimens and all other fossil and extant taxa in which vertebral morphology is described (e.g., Dowling and Duellman 1978; Rage 1984; Szyndlar 1984; Holman 2000). The neural spine in *Sivaophis* is much taller than seen in many extant and extinct colubroids (e.g., Dowling and Duellman 1978; Holman 2000), although a larger spine is present in some lineages (e.g., *Boiga*). Among Siwalik specimens, *Sivaophis* also possesses relatively larger lateral foramina. The presence of a prominent haemal keel and small but well- developed prezygapophyseal accessory processes justifies inclusion in Colubrinae.

Differences in the shape of the zygosphenal anterior margin were previously used as systematically valid characters in diagnosing fossil snakes (e.g., Auffenberg 1963), but examination of complete precloacal vertebral columns demonstrates intracolumnar variability in the shape of the margin from strongly concave to strongly convex (see also Rieppel et al. 2002). Two distinct taxa were previously considered to be present in the collection referred to as *Sivaophis* (Head 2002) based on variation in the anterior margin of the zygosphene. However, intracolumnar variation in this character prohibits such diagnoses. The original diagnosis for the genus was also based on inferences of missing morphology that have been falsified by examination of BSP 1956 II 2267. As a result, the hypodigm has been recombined, with *S. downsi* as the type and only species.

Colubrinae indet.

Referred specimens. H-GSP 27076, 27081, 27145, 27149, 27178, 27232, 27301, 30812, 53400, 53410.

Localities and ages. Y-709 (14.30 Ma), Y-641 (13.55 Ma), Y-809 (11.40 Ma), Y-450 (10.16 Ma), Y-311 (10.00 Ma), Y-388 (8.68 Ma), Y-387 (8.64 Ma), Y-547 (7.93 Ma).

Description and Discussion. Specimens referred to Colubrinae indeterminate consist of partial centra and are too incomplete to be assigned to either *Chotaophis* or *Sivaophis*, but can be recognized on the basis of the following morphology: in ventral view, the centrum is elongate and the haemal keel is well developed and wide. The keel widens posteriorly with a posterior margin that ranges from sharply pointed to spoon-shaped and rounded. In dorsal view, the posterior median notch is well developed with strongly convex medial margins. There is no indication of epizygapophyseal spines on the postzygapophyses.

THE SIWALIK GROUP SNAKE RECORD

The Siwalik Group provides a unique opportunity to examine snake faunal history due to the large sample sizes, number of localities, and precise chronostratigraphic control. In contrast, the majority of European and North American Neogene snake records consists of assemblages derived from a few large, time-averaged localities with much coarser temporal control (e.g., Szyndlar 1987; Szyndlar and Schleich 1993; Holman, 2000). The Siwalik Group additionally provides data on evolutionary histories of South Asian snakes, which are poorly known relative to European and North American taxa. Thus, examination of the Siwalik record focuses on faunal change within the

Table 1. Vertebral size and collection methods for Siwalik Group snake genera and morphotypes. Size is represented by centrum length (in mm) measured from the cotyle to the anterior margin of the condyle. Abbreviations: N, number of specimens measured for each taxon; S.D., standard deviation. Abbreviations for collection methods: B, both surface-collected and screen-washed; SC, surface-collected; SW, screen-washed.

Taxon	N	Maximum length	Minimum length	Mean length	S.D.	Collection method
Python sp.	61	13.0	5.26	8.95	2.07	B
Acrochordus	941	16.71	4.47	9.93	2.06	B
colubroid A	2	6.65	5.51	-	-	SW
colubroid B	21	4.80	1.50	3.40	0.80	SW
Bungarus	9	6.59	3.00	4.29	1.20	B
Elapidae indet.	2	12.05	11.76	-	-	SC
Natricinae indet.	3	4.75	2.25	3.57	1.26	SW
Chotaophis	2	3.50	2.40	-	-	SW
Sivaophis	16	10.44	3.25	8.16	2.05	B

local section and the implications of Siwalik snakes for understanding the larger evolution of Asian snake faunas, after accounting for changes in record quality and taphonomic biases.

The Siwalik snake assemblage consists of two separate records derived from surface-collection and screen-washing, as with the mammalian record (Badgley et al. 1995, 1998). Each method recovered specimens of different sizes. Surface-collected methods recovered specimens with centrum lengths greater than 1 cm, whereas screen-washed methods recovered specimens with centrum lengths less than 1 cm (Table 1). As a result, the records are treated separately in examining record quality and sample biases. Unlike the mammalian record, however, the two snake records sample the same fauna, because almost half of the described taxa and morphotypes were collected using both methods (Table 1). Taxa represented by single occurrences, Boidae? indeterminate (13.50 Ma), cf. Erycinae indeterminate (13.55 Ma), and *Gansophis potwarensis* (6.78 Ma), are not included in taphonomic and diversity analyses.

Record Quality, Specimens, and Localities

Figure 11 shows the numbers of specimens collected by both methods at 0.5 Ma intervals, the shortest temporal interval for which localities can be combined to produce consistently large sample sizes of specimens and localities (see Barry et al. 1995). Intervals range from 0 to .5 Ma, with the youngest age used as the reference datum for each. Several intervals between 6.5 and 18.0 Ma are either poorly represented or lack snake fossils. The dataset was culled to exclude those intervals with less than one locality for both the surface-collected and screen-washed records. Two exceptions are the 11.5 Ma and 8.5 Ma intervals, both of which possess high record quality for one of the records.

The datasets after culling are plotted in Figure 11B, D. Culling both data sets results in the absence of data for several important intervals, including 18.0 to 14.5 Ma, 10.5 Ma, 9.5 Ma, 8.0 Ma, and 6.0 Ma. The 18.0 to 14.5 Ma interval spans the Kamlial Formation in the Siwalik Group. Although this interval is crucial for determining the origin of the Siwalik snake fauna, its low record quality renders it uninformative with respect to this analysis. The younger intervals span a history of significant environmental change within the Siwalik Group, and their exclusion limits interpretation of faunal histories (see below).

Both records show a generally poor relationship between sample size (number of individual specimens) and the number of localities throughout the section. The surface-collected record shows an inverse relationship between sample size and number of localities between the14.0 Ma and 10.0 to 9.0 Ma intervals, followed by a more positive relationship between sample and locality sizes from 9.0 to 8.5 Ma. The screen-washed record demonstrates a positive relationship between sample size and number of localities from 14.0 to 12.0 Ma, followed by an inverse relationship between 11.5 and 7.0 Ma. Both records demonstrate a decrease in sample size at 6.5 Ma.

Comparing the records reveals two distinct histories of record quality. The surface-collected record shows a greater concentration of specimens relative to localities between 14.0 to 10.0 Ma, followed by a decrease in both concentration and total number of specimens from 10.0 Ma and younger. The screen-washed record demonstrates the inverse—a sharp increase in the relative concentration and overall number of specimens from 11.0 to 10.0 Ma and from 9.0 to 7.5 Ma.

Figure 12A plots the total number of Siwalik specimens for each taxon or morphotype. The record is dominated by *Acrochordus dehmi*, which constitutes approximately 80% of the entire sample. This record differs from most Neogene snake assemblages that often possess more even distributions of specimens among taxa or are domi-

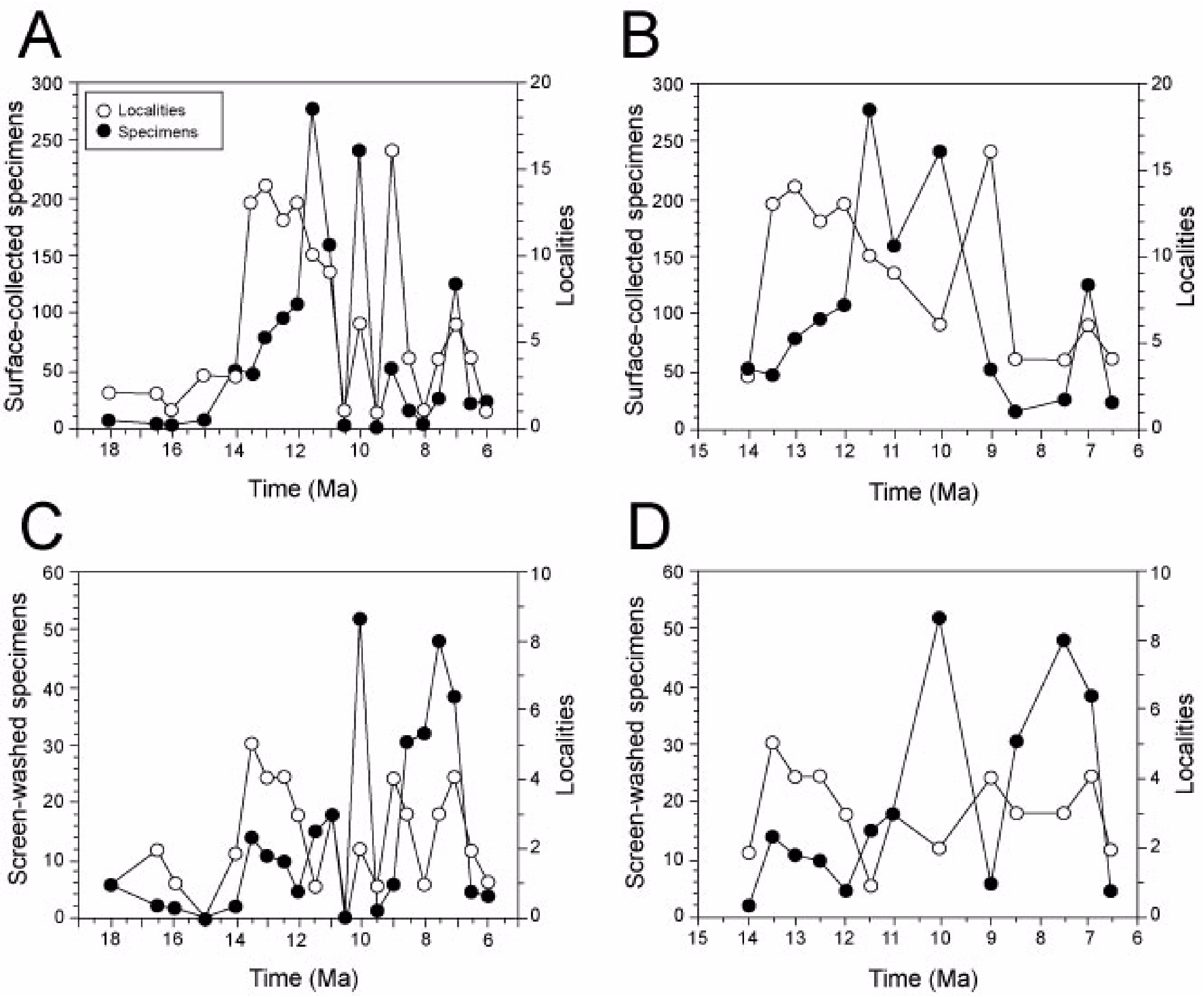


Figure 11. The Siwalik Group snake record of specimens and localities binned at 0.5 m.y. intervals. **A.** surface-collected record, all 0.5 m.y. intervals. **B.** culled surface-collected record. **C.** screen-washed record, all 0.5 m.y. intervals. **D.** culled screen-washed record.

nated by several taxa (e.g., Ivanov 2000, p. 587), and likely reflects both depositional and ecological histories within the Siwalik snake record (Head 1998, see below). The relationships between number of taxa and morphotypes and sample size for the screen-washed and surface-collected records are plotted in Figure 12B, C. Taxonomic/morphotypic diversity has a positive, significant relationship to sample size for the screen-washed record, as documented for the screen-washed mammal fauna (Badgley et al. 1998), but no significant relationship exists between diversity and sample size for the surface-collected record.

Taphonomic Comparisons

I examined the relationship of sample size to depositional and collection processes using Analysis of Variance (ANOVA) and least squares linear regression. Biases affecting sizes, distributions, and compositions of fossil assemblages are well documented for the Siwalik Group, and consist of variability in fluvial transport and depositional environment among surface-collected records, and biotic agents, namely predator accumulations, for screen-washed samples (Badgley 1986a, 1986b; Badgley et al. 1998). These factors presumably affect the composition of the snake faunas as well. Collection bias can be examined as sampling intensity for the screen-washed record (see below), but cannot be measured for the surface-collected record.

The extent to which fluvial transport determines sample size was tested using ANOVA between sample size and grain-size lithology for both surface-collected and screen-washed localities. Badgley et al. (1998) constrained the effects of fluvial transport on screen-washed mammal assemblages from the Chinji Formation using ANOVA and demonstrated that sample size was independent of lithology. For the snake record, the

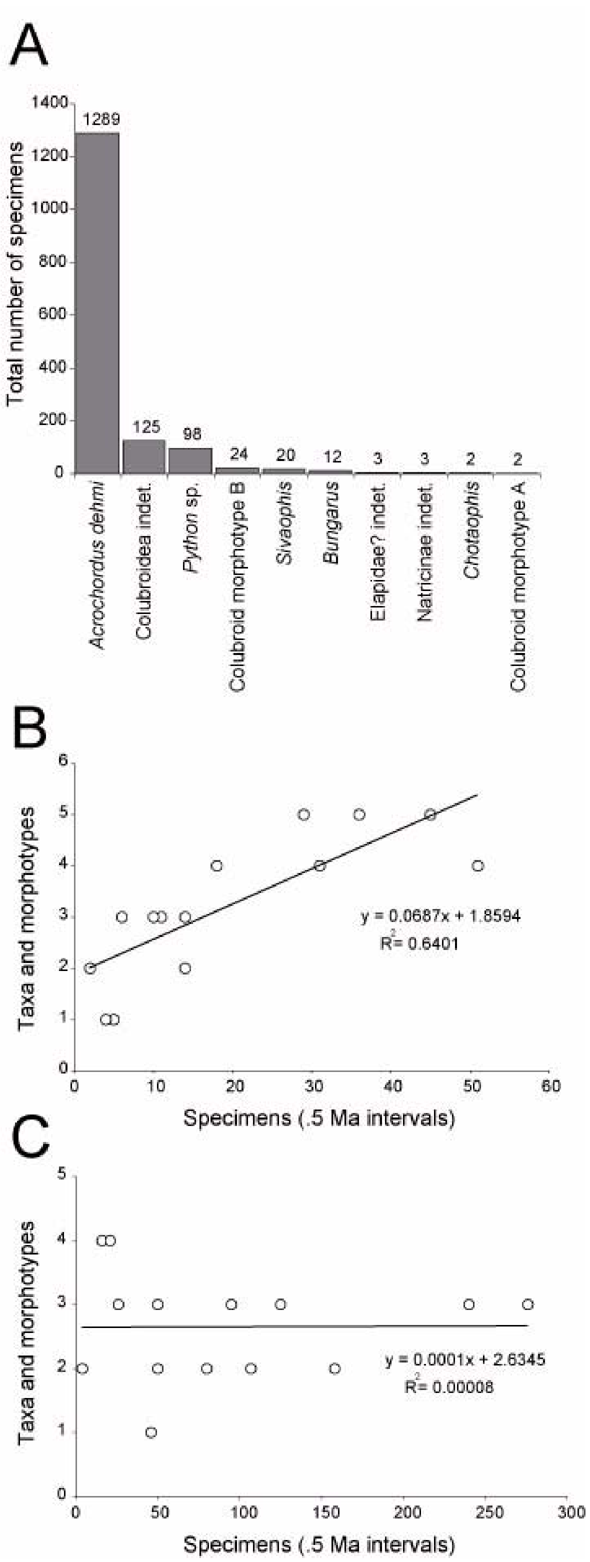


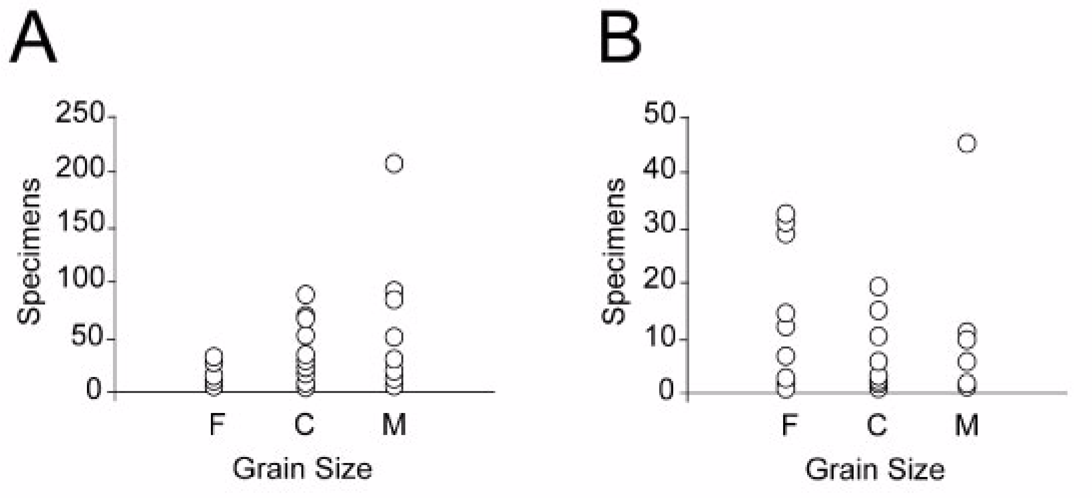
Figure 12. A. Total number of specimens for Siwalik Group snake taxa and morphotypes. **B.** Least-squares linear regression of number of taxa onto sample size for the Siwalik Group screen-washed snake record. **C.** Least-squares linear regression of number of taxa onto sample size for the Siwalik Group surface-collected snake record.

analysis demonstrates the absence of a relationship between sample size and grain size for screen-washed samples (Figure 13B), but shows a statistically significant relationship between surface-collected specimens and grain size (Figure 13A). The correlation with grain size can be explained by depositional processes but may also represent habitat specificity of autochthonous taxa.

Least-squares linear regression was used to determine the relationship of sample sizes in both records to locality temporal duration and the relationship of screen-washed sample size to collection intensity and the potential for chemical destruction. Temporal duration refers to the time span within which deposition and incorporation of fossils occurred at individual localities, and ranged from 0.02 to 0.22 m.y. for screen-washed localities, and 0.01 to 0.16 m.y. among surface-collected localities (see Barry et al. 2002 for locality durations and estimation methods). Potential biases affecting the screen-washed record include sampling intensity and productivity, chemical destruction, and biotic agents of assembly. As seen in Figure 12C, D, there is little correlation between sample size and the number of screen-washed localities per interval through the Siwalik section; however, the extent to which individual localities have been sampled could potentially explain the increase in the number of recovered specimens from screen-washed sites. screen-washed specimens were recovered from reduction of bulk matrix, and the measure of sampling intensity was the total mass of processed matrix from each locality (Badgley et al. 1998).

Comparison with the Siwalik rodent record was used to test the influence of chemical destruction because screen-washed vertebrate remains of similar size and composition should show similar patterns of changing abundance if changes in sample size through time are the result of changing chemical preservation modes. Material differences in rodent teeth and snake vertebrae somewhat limit the use of rodents as proxy data for chemical environment, because dense enamel is more resistant to destruction. However, the record provides at least a first-order approximation.

Regression of sample size onto the described taphonomic variables failed to produce significant relationships (Figure 14A-D). ANOVA results indicate that depositional bias affects the surface-collected record in the same general pattern as for other Siwalik vertebrates, with the lowest sample sizes in fine-grained deposits (Badgley et al. 1995, 1998), but no significant bias amongst the screen-washed records. The independence of screen-washed snake records from any of the examined



Sample	SSQ Between	SSQ Within	MSQ Between	MSQ Within	F - value	P-value
Surface collected	4839.19	70758.43	2419.60	589.65	4.013	0.019
Screen washed	83.97	5568.19	41.98	46.4	0.905	0.407

Figure 13. Analysis of variance of the relationship between sample size and depositional lithology. A. surface-collected specimens; B. screen-washed specimens; Degrees of freedom between lithologies= 2, within lithologies= 120, F-critical= 3.072.

sources of bias suggests an agent of accumulation other than sedimentological, chemical, or collection processes, such as predation, as proposed for Chinji Formation rodents (Badgley et al. 1998).

Taxonomic and Ecological Richness

Figure 15B plots relative frequency of taxa/morphotypes, expressed as number of identified specimens (NISP) from the combined records. Both raw richness and range-through (Cheetham and Deboo 1963) values are plotted. Overall, the number of taxa and morphotypes increases through time in the Siwalik Group: richness is comparatively low through the Chinji Formation, followed by a progressive increase through the Nagri and Dhok Pathan formations, starting between 11.0 and 10.0 Ma, with maximum richness at 7.0 Ma, and a decline at 6.5 Ma. This pattern is consistent within both the screen-washed and surface-collected records. Raw and range-through values track each other, suggesting that the increase in taxa and morphotypes is a historical event as opposed to simply a preservational bias. The pattern of increasing richness is similar to the increasing sample size within the screen-washed record (Figure 11D), reflecting (in part) the positive relationship between taxonomic/morphotypic diversity and sample size in the screen-washed record. The richness increase in the surface-collected record is concurrent with a decrease in sample size (Figure 11B, Table 2), however, indicating that sample size alone does not explain the increase.

Figure 15B plots relative frequency of taxa/morphotypes, expressed as number of individual specimens (NISP) from the combined records. Because sample sizes are extremely small for most taxa (Tables 2, 3), all colubroid taxa and morphotypes are summed as Colubroidea. Between 14.0 and 10.0 Ma, *Acrochordus dehmi* represents between 88-97% of all recovered specimens. Between 10.0-8.5 Ma, the relative frequency of *A. dehmi* decreases sharply to 28%, due to both lower sample sizes for the taxon and the influx of colubroid specimens. The spike in relative frequency of *Acrochordus* at 7.0 Ma is partially artifactual, because that interval includes a locality (Y 935) containing a large number of elements (84) that likely represent a single, associated, surface-collected skeleton.

Changes in taxonomic richness and relative frequency are coeval with changes in depositional environment, despite a poor correlation of sample size to lithology for the screen-washed record. The three Siwalik formations included between 14.0

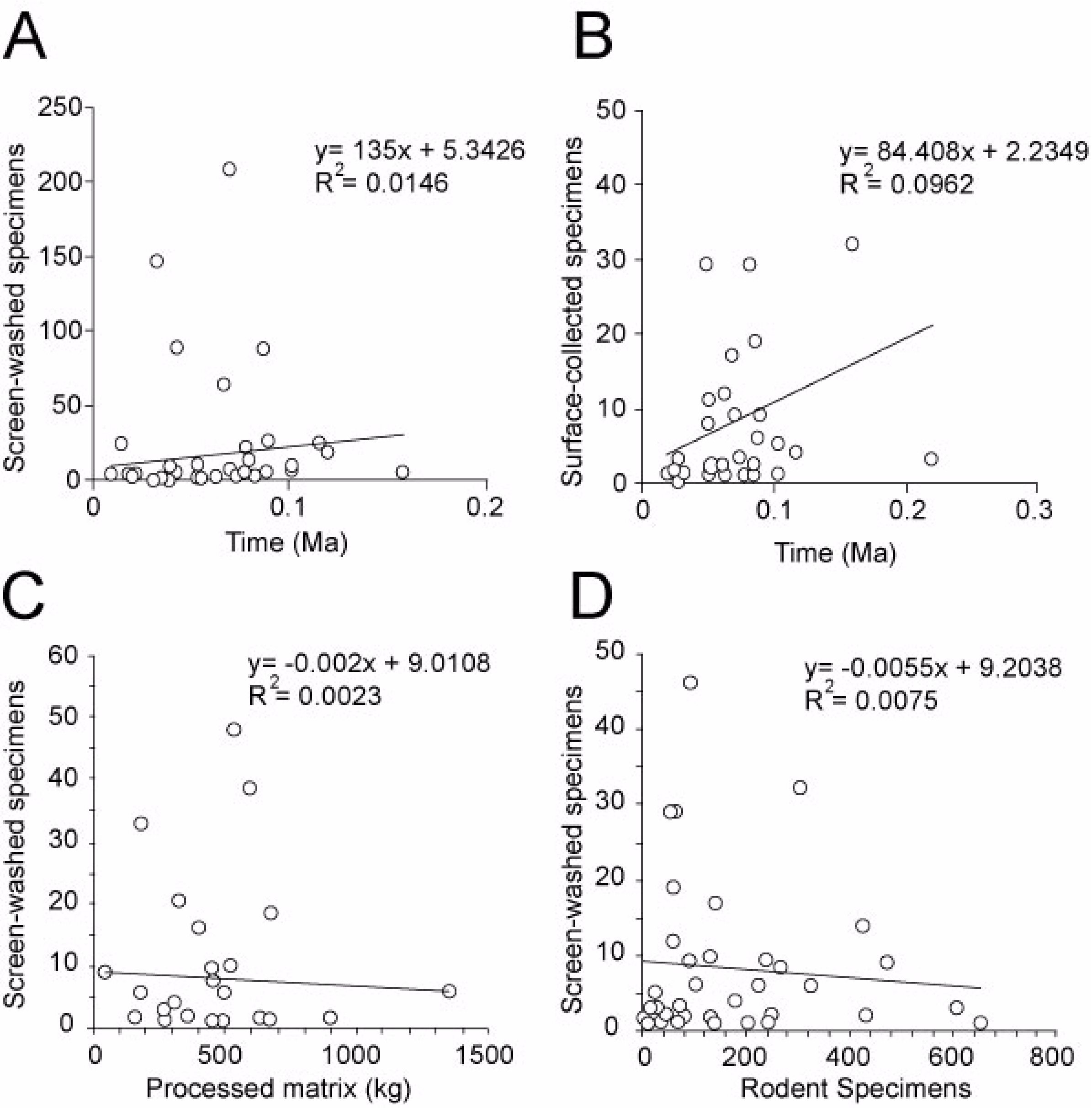


Figure 14. Least-squares linear regression of sample size of snakes (number of specimens per locality) onto taphonomic data. **A.** screen-washed specimens onto locality duration; **B.** surface-collected specimens onto locality duration; **C.** screen-washed specimens onto mass of processed matrix per locality ; D. screen-washed specimens onto rodent record size per locality. No statistically significant correlation exists between sample size and proxy data.

and 6.5 Ma represent distinct fluvial systems. The Chinji Formation (14.2 to 11.2 Ma) is primarily a fine-grained sequence representing large upland-sourced river systems, and characteristically includes regularly spaced overbank deposits. The Nagri Formation (11.2 to 9.0 Ma) is characterized by massive sandstones and represents large trunk systems. The Dhok Pathan Formation (10.1 to 3.5 Ma) is fine grained and represents smaller, upland-sourced river systems with increased avulsion and poorly drained floodplains (Willis and Behrensmeyer 1995; Barry et al. 2002). The domination by *Acrochordus* occurs through the larger river systems of the Chinji and Nagri Formations between 14.0 and 11.0 Ma, and decreases throughout the more heterogeneous Dhok Pathan Formation. The increase of taxonomic and morphotypic richness is approximately concurrent with the transition from the Nagri fluvial system to the Dhok Pathan system at approximately 10.1 Ma (Barry et al. 2002), with the oldest locality at which diversity increases dated to 10.2 Ma (Y 450).

Changes in relation to depositional environment are consistent with inferred ecology. *Acrochordus dehmi*, *Python* sp., and Colubroidea can be broadly characterized for habitat and prey pref-

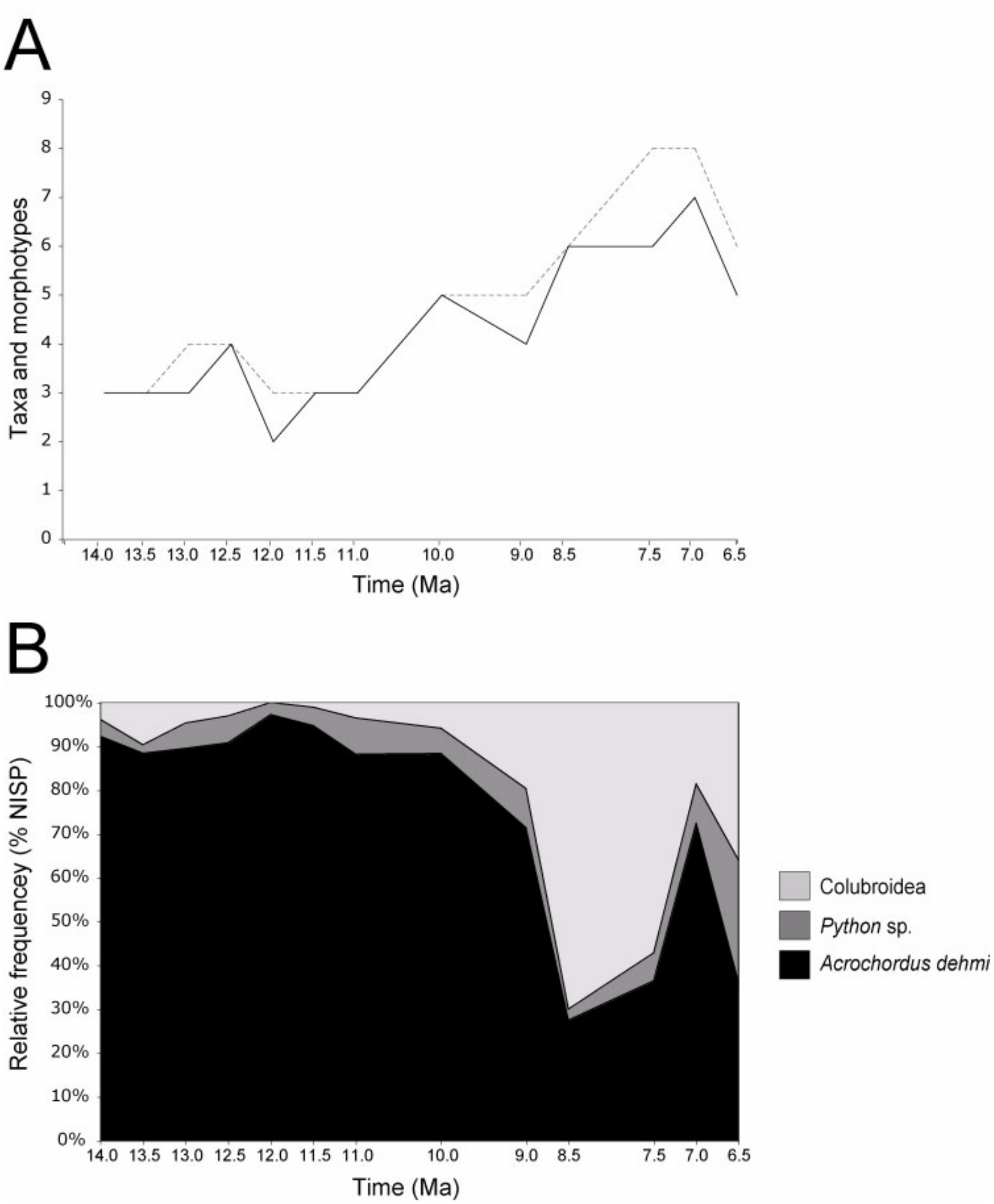


Figure 15. A. Taxonomic and morphotypic richness of Siwalik Group snakes from 14.0 to 6.5 Ma. Dark line records raw richness, light, dashed line records range-through estimates of richness. **B.** relative frequency of Siwalik Group snakes by number of identified specimens (NISP).

erence via phylogenetic constraint and comparison with extant sister taxa. *Acrochordus* represents a fully-aquatic piscivore (Shine 1986a, 1986b). *Python* represents a terrestrial predator of large vertebrates (Murphy and Henderson 1997). Colubroidea represent a wide range of semi-aquatic to fully terrestrial small carnivores (e. g., Mushinsky 1987). Within this context, the snake fauna of the Chinji and Nagri formations are predominately aquatic, and the Dhok Pathan record includes increasing representation of both large and small semi-aquatic and terrestrial taxa. *Python* is present in low abundance as a large vertebrate predator throughout the entire Siwalik sequence, and likely represents an allochthonous component of most depositional environments.

Table 2. Siwalik Group surface-collected snake specimens per 0.5 m.y. intervals.

Temporal Interval (m.y.)	*Python* **sp.**	*Acrochordus dehmi*	*Bungarus* **sp.**	**Elapidae? Indet.**	*Sivaophis downsi*
14	2	48	0	0	0
13.5	0	46	0	0	0
13	3	77	0	0	0
12.5	5	88	0	0	2
12	3	104	0	0	0
11.5	11	264	0	0	1
11	11	147	0	0	0
10	14	225	0	1	0
9	4	40	0	0	6
8.5	2	10	1	0	4
7.5	3	22	1	0	0
7	12	111	0	0	2
6.5	7	9	0	2	3

DISCUSSION

Correlation of Faunal Change with Environmental Factors

The two major environmental changes recorded in the Siwalik Group, the older inception of the Asian monsoonal precipitation system and the younger transition from C3 floras to C4 grasses, are broadly concurrent with the increase in richness and evenness in the snake record, but precise correlations are problematic. The timing of monsoonal inception is controversial: uplift of the Tibetan Plateau drives the Asian monsoons, but the timing of the uplift is not precisely constrained, with different lines of proxy data providing age estimates from 7.0 to 8.0 Ma (Molnar et al. 1993) to 9.0 to 11.0 Ma (Kroon et al. 1991). Oxygen-18 isotopic studies have demonstrated the onset of monsoonal precipitation patterns in the Siwalik Group of Nepal beginning by 10.7 Ma (Dettman et al. 2001), and δ^{18}O values consistent with seasonal precipitation patterns began on the Potwar Plateau at approximately 9.15 Ma (Quade and Cerling 1995 [dates refined in Barry et al. 2002]). Thus, the majority of data generally constrains the inception of the monsoons to between 11.0 and 9.0 Ma, but does not unanimously provide a more refined estimate.

The inferred monsoonal precipitation pattern is a progressive environmental event that generally corresponds with the pattern of diversity increase in the Siwalik snake record. However, temporal correlation is relatively weak within the 500-Kyr intervals. The beginning of diversity increase among Siwalik snakes at 10.2 Ma (Y-450) precedes consistent oxygen isotopic evidence for seasonality on the Potwar Plateau. This may represent faunal response to increasing aridity prior to the onset of seasonal evaporation in the western Siwalik Group. Conversely, isolated δ^{18}O values from the Potwar Plateau at 10.7 to 10.5 Ma are consistent with coeval values indicating seasonal evaporation from Nepal (Dettman et al. 2001; Barry et al. 2002), and may represent an earlier increase in seasonality than previously recorded.

The transition from C3-dominated to C4-dominated vegetation is temporally well constrained at approximately 8.1 Ma, with fully C4 floras present by 7.4 Ma and the last occurrence of C3 floras at 7.0 Ma (Barry et al. 2002). This transition had a marked effect on mammalian feeding ecology (e.g., Flynn and Jacobs 1982) and is generally concurrent with increasing diversity in the snake record. More precise comparisons between the floral shift and the snake record are hampered by decreasing sample sizes from localities within the 6.5 Ma interval and younger, however.

Changes in richness and frequency in the Siwalik Group snake fauna are coeval with both increasing seasonality and the occurrence of the Dhok Pathan depositional environment, which are related and in turn ultimately driven by uplift histories of the Himalaya and Tibetan Plateau. Both events (and the subsequent evolution of C4 grasslands) would have increased the range of habitats within the area of the modern Potwar Plateau, which would have allowed an increasing diversity of taxa and habits within the Siwalik Group snake fauna.

Comparisons with Other Fossil Snake Faunas and the Evolution of the South Asian Biogeographic Theater

The Siwalik Group is unique among Neogene fossil snake assemblages in its domination by a single taxon (compare with Szyndlar and Schleich 1993; Ivanov 2000) and in the absence of several taxa. There is no definitive occurrence of viperids within the Siwalik record, despite their extensive Neogene record throughout Europe (Szyndlar and Rage 1999), North America (Holman 2000), and other Asian localities (Rage and Ginsburg 1997;

Table 3. Siwalik Group screen-washed snake specimens per 0.5 m.y. intervals.

Temporal interval (m.y.)	**Boidae indet.**	*Acrochordus dehmi*	**Colubroid morphotype A**	**Colubroid morphotype B**	*Bungarus* **sp.**
14	0	0	0	0	0
13.5	1	0	0	0	0
13	2	0	1	0	0
12.5	1	1	1	0	0
12	0	2	0	0	0
11.5	1	5	0	0	0
11	0	0	0	0	0
10	3	3	0	0	0
9	2	18	0	0	1
8.5	0	1	0	3	0
7.5	1	1	0	3	0
7	2	2	0	12	0

Ivanov 1999), and their presence in extant South Asian faunas (Minton 1966; Armed Forces Medical Intelligence Center, 1991). Their absence from the Siwalik section results from either taphonomic or ecological bias: the considerable sample of indeterminate colubroid specimens may include viperids, or viperids may not have actively inhabited the Siwalik environments proximal to depositional settings. Similarly, the absence of scolecophidians in the Siwalik Group is inconsistent with their presence in other Neogene strata (e.g., Szyndlar 1985, 1987, 1991). Scolecophidians are extremely small and fossorial to cryptic in habit. Their absence from the record likely reflects poor sampling of this habitat, an inference reinforced by the limited representation of similarly cryptic erycines in the Siwalik record, despite their abundance throughout the Neogene (Rage 1984; Holman 2000).

Extant European and South Asian snake faunas represent distinct biogeographic theaters (Boulenger 1913; Pope 1935; Minton 1966). The evolution of European snake faunas has been intensely studied (e.g., Ivanov 2000; Szyndlar and Rage 2003), but the Siwalik record is the only extensive fauna known for the Neogene of South Asia. Comparisons between the Siwalik fauna and approximately coeval faunas of Europe (Rage 1984; Szyndlar 1984, 1987; Ivanov 2000) demonstrate shared higher-order clades including Natricinae, Colubrinae, and possibly Erycinae, all of which were cosmopolitan by the end of the Paleogene (Rage 1984; Holman 2000). At more exclusive systematic levels, only a single genus, *Python*, is shared between Asia and Europe, a distribution that was achieved by the end of the Paleogene (Szyndlar and Rage 2003, this study). The rest of the Siwalik snake fauna is either endemic to the section or is singularly Asian. The fossil record of *Acrochordus* is only known from the Siwalik Group of South Asia and the Miocene of Thailand. Occurrence in Thailand indicates that the more eastern range of the genus was established early in its history, with physiographic barriers limiting the western distribution beyond Pakistan established by the onset of Siwalik sedimentation no later than 18 mya. The fossil record of *Bungarus* is also restricted to the Siwalik Group, which is geographically equivalent to the western margin of its extant distribution (Smith 1943; Minton 1966). That this very diagnostic taxon has not been recovered from the European record suggests that its past western distribution also did not extend beyond Pakistan, and the first occurrence of *Bungarus*, along with *Chotaophis*, *Gansophis*, and *Sivaophis* indicates that biogeographic barriers for derived snakes between South Asia and Europe were present by approximately 10.0 Ma.

The Siwalik snake record is different from the extant fauna of the Potwar Plateau. The modern snake fauna consists exclusively of colubroids, and only *Bungarus* is shared between the two intervals (western distributions of extant *Python* are just east of central Pakistan, Murphy and Henderson 1997). *Acrochordus* persists throughout the entire section, but *A. dehmi* is extinct, and there are no definitive historical records of extant species at the latitudes of Pakistan. Additionally, extant *Acrochordus* is not distributed as far inland as the Siwalik Group at any point in its current range. Extinction of *A. dehmi* on the Potwar Plateau is constrained as no older than 6.35 Ma and likely resulted from the draining of the Siwalik fluvial system off the plateau during the Pleistocene.

CONCLUSIONS

The Siwalik Group snake fauna includes eight diagnosable taxa consisting of Python sp, cf. Erycinae indeterminate, Acrochordus dehmi, Gansophis potwarensis gen. et sp. nov., the first fossil record of Bungarus, Natricinae indeterminate, Chotaophis padhriensis gen. et sp. nov., and Sivaophis downsi gen. et sp. nov, as well as Boidae? indeter-

Table 3 (continued).

Natricinae Indet.	Chotaophis padhriensis	*Sivaophis downsi*/ Colubrinae indet.	Colubroidea indet.
0	0	1	2
0	0	3	5
0	0	0	4
0	0	0	1
0	0	0	0
0	0	2	2
0	0	0	6
0	0	0	15
0	1	6	5
1	0	1	23
2	1	2	35
0	0	0	27

minate, Elapidae? indeterminate, and two recognizable but unnamed morphotypes. The record is dominated by *Acrochordus* in terms of frequency of specimens, but demonstrates increasing taxonomic/morphotypic diversity starting between 10.0 and 9.0 mya that is concurrent with the inferred development of the Asian monsoonal system and the deposition of the Dhok Pathan Formation. These two events, driven by the uplift of the Tibetan Plateau, likely provided an increasing range of potential habitats for a greater diversity of taxa.

The Siwalik Group snake fauna was highly endemic, and exclusivity of *Acrochordus*, *Bungarus*, and new taxa described here to the Siwalik sequence suggests that partition of European and South Asian biogeographic theaters occurred no later than middle Miocene. The snake fauna of the Siwalik Group is markedly different from the extant fauna of the Potwar Plateau, with only *Bungarus* occurring in both. These differences are present at the youngest Siwalik snake localities indicating that the pronounced faunal changes occurred after 6.35 Ma, likely concurrent with the draining of the Siwalik fluvial system off of the Plateau during the Quaternary.

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