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Contents

1. Systematic Paleontology

SYSTEMATIC PALEONTOLOGY

Squamata Oppel 1811
Ophidia Brongniart, 1800
Coniophidae Hoffstetter 1955
Coniophis Marsh 1892
C. precedens Marsh 1892

Holotype.

USNM (United States National Museum of Natural History, Washington) 2143.

Referred material.

UCMP V-5711, Bushy Tailed Blowout: AMNH 22846, 22850, 22851, maxillae; AMNH 14598, 15621, 15622, 22840-22845, 22847-22849, 22940, 25220, 25261, 26817-26819, 26821-26824, 26827-26834, 26999, 27000, vertebrae. UCMP 49859, 53930-53934, 53936-53944, 73044, vertebrae.

UCMP V-5620, Lull 2: UCMP 45940, 46060, 46070, 50001-50014, 53924-53929, 54219, vertebrae; UCMP 53935, 49998, 49999 maxilla; UCMP 49997, 50000, dentaries.

UCMP V-5815, Hatcher 2: UCMP 53556-53561, vertebrae.

Lance Formation, Unknown Locality: YPM-PU (Yale Peabody Museum, Princeton University Collection) 16845, vertebra.

(Estes, 1964; NRL pers. obs. 2011 of AMNH and YPM material and UCMP cranial material).

Notes. One dentary, UCMP 50020, was referred to *Coniophis* by Estes but lacks interdental ridges and therefore represents a non-snake squamate, most likely *Parasaniwa wyomingensis*. Some specimens, notably UCMP 49998 and 49997, could not be located during our study of collections and appear to be lost; we therefore cannot verify their referral to *Coniophis precedens*.

Horizon and Locality.

All specimens come from the Late Maastrichtian (Lancian), Lance Formation, Powder River Basin, eastern Wyoming.

Revised diagnosis.

Coniophis precedens is diagnosed by three apomorphies: deep, obovate, paracotylar fossae, enlarged mental foramen at the back of the maxilla, and a distinct groove on the facial process of the maxilla for articulation with the nasal.

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In addition, *Coniophis* is differentiated by the following combination of features: maxilla with well-developed facial process bearing a medial fossa for the nasal capsule, prominent vomerine process, supradental shelf, short palatine process, well-developed articulation with premaxilla and jugal, nine or more mental foramina. Dentary with subdental ridge that is deep anteriorly but shallow posteriorly; posterior of jaw does not wrap underneath surangular. Teeth isodont, moderately elongate and recurved, with mediolaterally expanded bases. Teeth separated by interdental ridges; alveoli shallow and open medially. Trunk vertebrae with a rudimentary neural spine forming a faint ridge on the posterior half of the neural arch that terminates in a tubercle caudally. Neural spine flanked by low moundlike processes on posterior of the neural arch. Neural arch not notched caudally. Prezygapophyses lacking accessory processes; synapophyses are small, single-headed, and do not project beyond prezygapophyses; paracotylar and parazygantral foramina absent. Subcentral ridges rudimentary. Condyle flattened in posterior vertebrae.

cf. *Coniophis precedens*

Material.

YPM-PU 16773 and 16774, vertebrae.

Horizon and Locality.

Middle Paleocene (Torrejonian), Tongue River Formation, Southeast Montana.

Discussion.

Vertebrae from the middle Paleocene Tongue River Formation of Montana (Estes, 1976) resemble *Coniophis precedens* in size and in all aspects of their morphology; in particular they exhibit the deep, obovate, paracotylar fossae diagnostic of this species. Given the stratigraphic separation between the two, and the absence of any cranial material, we are hesitant to definitively refer this material to *C*. *precedens*, but they do document the survival of a *Coniophis*-like snake into the Palaeocene. Some of these vertebrae (YPM-PU 16774) have previously been referred to *Dunnophis* (Estes, 1976) but examination of the type of *Dunnophis* (NRL, pers. obs.) does not support that conclusion; instead they are indistinguishable from *Coniophis*.

2. Referral of Material to *Coniophis precedens*

Assignment of fossils to *Coniophis* is a complicated problem, because the fossils are not associated, and because three snakes are present in the Late Maastrichtian of North America: (1) *Coniophis*, (2) a madtsoiid-grade snake from the Hell Creek Formation of Montana (UCMP 130696), here referred to as the "Hell Creek Snake" and (3) a small alethinophidian snake from the Lance Formation of Wyoming (AMNH 28457), here referred to as the "Lance Snake".

We concede that it is impossible to be absolutely certain that all of the material described here does belong to *Coniophis precedens* as suggested by Estes (Estes, 1964). However, we emphasize that this assignment represents an hypothesis that is consistent with all available evidence, and one which can be tested by future fossil finds. Several lines of evidence lead us to assign the material described here to *Coniophis precedens*.

1. *Co-occurrence*. For the specimens to represent a single species, they should occur in the same place and time. The Cretaceous specimens described here all come from exposures of the Lance Formation in eastern Wyoming. Jaw material comes from two sites, UCMP V-5711 and UCMP V-5620, which also contain vertebrae referred to *Coniophis*. The Hell Creek snake is not known from these localities, although the Lance Snake comes from UCMP V-5711.
2. *Size*. Specimens should exhibit a similar range in size. Material referred to *Coniophis* all comes from relatively small snakes, similar in size to extant *Cylindrophis*. The Hell Creek snake, by contrast, represents a significantly larger animal, comparable in size to large *Boa constrictor*, and thus the jaw material is unlikely to come from the Hell Creek snake. The Lance snake is, however, similar to *Coniophis* in size.
3. *Shared features*. Different elements from the same species can share unique combinations of apomorphies and plesiomorphies. For instance, upper and lower jaws referred to *Coniophis* have similar tooth crown morphology, tooth implantation, and isodont teeth, consistent with the hypothesis that they represent a single taxon. Likewise, anterior, middle, and posterior trunk vertebrae referred to *Coniophis* are united by having a reduced neural spine, low neural arch, and prominent paracotylar fossae. Thus, we can be reasonably confident that the jaw material belongs to a single taxon. We can likewise be confident that the vertebrae referred to *Coniophis precedens* also belong to a single taxon. However this particular line of evidence does not allow us to determine whether the jaws and vertebrae in fact go together.

4. *Relative abundance.* Relative abundance of elements provides information about the likelihood that different elements belong to a single taxon. UCMP V-5711 has produced scores of *Coniophis* vertebrae but we have identified only a single vertebra from the Lance snake. It is not impossible that the relatively common maxillae belong to one of the rarest squamates in the assemblage, however, it is extremely unlikely.
5. *Phylogenetic congruence.* If the fossils represent the same species, then when considered separately they are expected to occupy a similar place in the phylogeny. That is the case here, as, the maxillae and dentaries both lie basal to Serpentes in the phylogeny (see SI 2). Similarly, *Coniophis* vertebrae occupy a basal position within snakes (SI 2). The Lance Snake is an alethinophidian, however, perhaps related to the Macrostomata (SI 2); in particular the well-defined condyle represents of a synapomorphy of the Madtsoiidae + crown Alethinophidia clade and the double-headed synapophyses are more derived than the single-headed synapophyses of *Coniophis*. The Hell Creek snake is a stem alethinophidian (SI 2), perhaps related to (or a member of) the Madtsoiidae; the well-defined condyle, broad neural arch, and well-developed dorsolateral ridges are all consistent with a madtsoiid identification. Although it is not impossible that the plesiomorphic jaws described here could come from a snake with derived vertebrae, the simplest explanation is that the plesiomorphic jaws belong to the same species as the plesiomorphic vertebrae (i.e. to *Coniophis precedens*), rather than to the vertebrae exhibiting alethinophidian features.
6. *"Fit".* In short, do the elements match and or/articulate such that they can be assembled into a functionally plausible animal? The upper and lower jaws referred to *Coniophis precedens* are of similar size and proportions such that they could function together in a jaw apparatus. Similarly, vertebrae referred to *Coniophis* are similar enough in the proportions of the condyles, zygapophyses and zygosphene-zygantrum that a series of these elements could potentially be articulated to form a single spinal column.

In summary, referral of these various fossils to *Coniophis precedens* is consistent with 1-6. Referral of the jaws described here to the Hell Creek snake can be rejected on the basis of 1) distribution, 2) size, and 5) phylogeny. Referral of the jaws to the Lance Snake can be rejected on the basis of 4) relative abundance and 5) phylogeny.

We also note that although the range of variation among the trunk vertebrae in *Coniophis precedens* exceeds that seen in crown alethinophidians, this is not unexpected, given that other lizards, including scolecophidian snakes, exhibit a relatively high degree of variation along the spine; note, for example, the condition in *Typhlops*, where the neural arches of anterior trunk vertebrae are proportionately short and broad and posterior trunk vertebrae are long and slender. A lack of differentiation in trunk vertebrae is a derived feature, and so a stem snake is expected to show a higher range of variation than a modern snake.

3. Other reports of *Coniophis*.

Over the years, a wide range of small, primitive snakes have been referred to the genus *Coniophis* (Table S1). We emphasize that referral of these specimens to *Coniophis* is not supported by apomorphies, and suggest that the only specimens which we are justified in referring to *Coniophis* are the Maastrichtian specimens from the Lance, and the middle Paleocene specimens from the Tongue River. Some of these fossils, notably the vertebrae reported from the Albian-Cenomanian of Utah by Gardner and Cifelli (1999), are strikingly *Coniophis*-like and the possibility that they represent a related taxon deserves closer scrutiny. In other cases, notably "*Coniophis*" *cosgriffi*, the vertebrae are so different in morphology that referral that referral to the genus seems to be unwarranted.

Although it is conceivable that the various snakes referred to *Coniophis* represent a single, long-lived, and widely dispersed clade, it seems just as likely that "*Coniophis*", as previously applied, represents either a paraphyletic grade of basal snakes or a polyphyletic assemblage of small, fossorial snakes, as proposed by Rage and Augé (2010). A revision of the systematics of these ophidians is required, but beyond the scope of this study.

Table S1. Reports of *Coniophis*.

Identification	Age	Locality	Reference
Coniophis precedens	late Maastrichtian	USA	Marsh (1892)
Coniophis cosgriffi	late Campanian	USA	Armstrong-Ziegler (1978)
Coniophis cf. *precedens*	late Santonian/early Campanian	Canada	Fox (1975)
Coniophis sp.	latest Albian/earliest Cenomanian	USA	Gardner and Cifelli (1999)
Coniophis precedens	middle Paleocene	USA	Estes (1976)
Coniophis platycarinatus	middle Eocene	USA	McGrew et al. (1959)
Coniophis carinatus	Middle Eocene	USA	McGrew et al. (1959)
Coniophis dabiebus	Cenomanian	Sudan	Rage and Werner (1999)
Coniophis sp.	Paleocene	Morocco	Augé and Rage (2006)
Coniophis sp.	Eocene	Morocco	Augé and Rage (2006)
Coniophis sp.	Maastrichtian	India	Rage et al. (2004)
Coniophis sp.	Paleocene	Brazil	Albino (1991)
Coniophis sp.	Eocene	France	Rage (1988)

3. Supplementary Figures of *Coniophis precedens* material

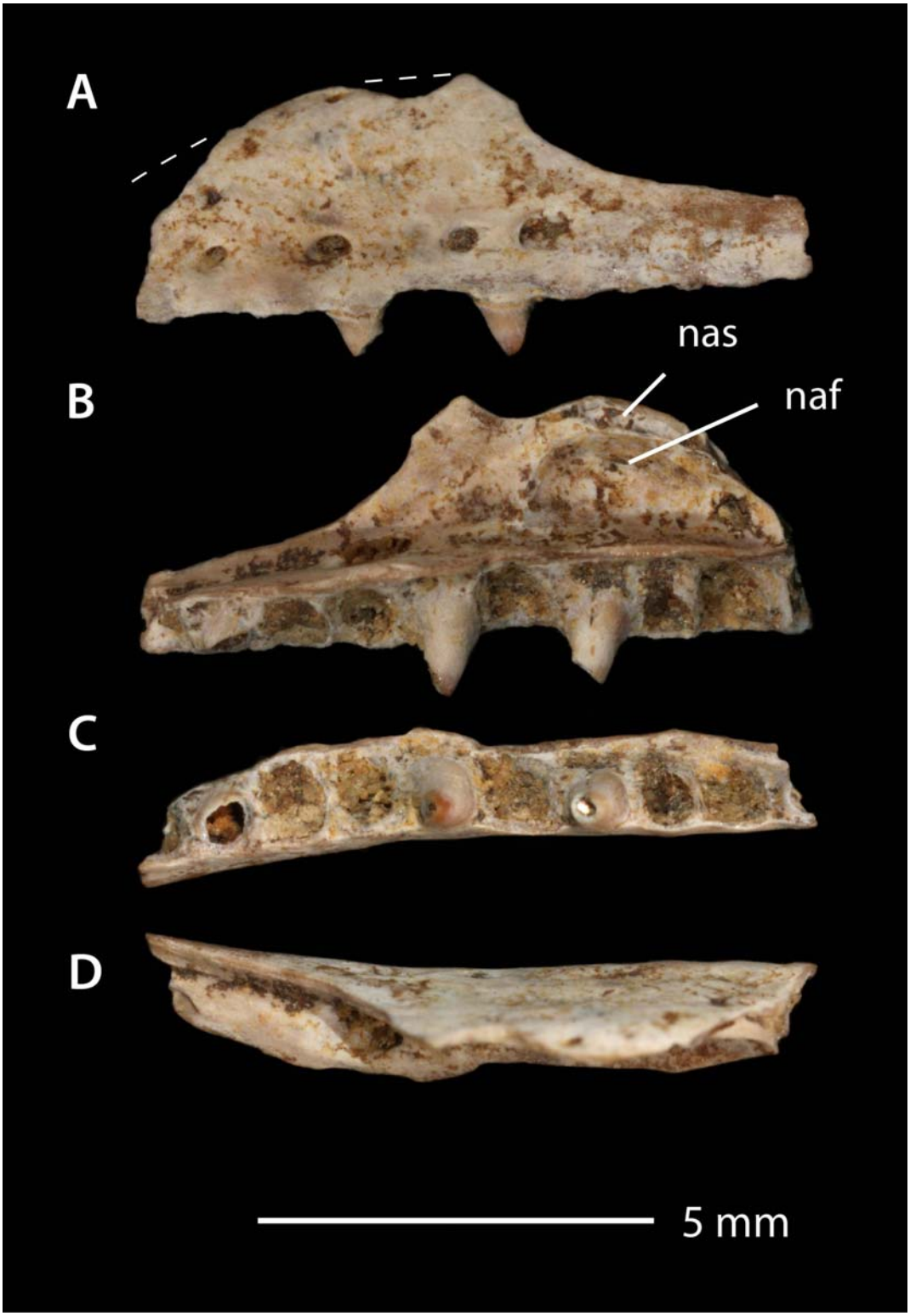

Fig. S1 *Coniophis precedens* left maxilla, AMNH 22413,in **a**, lateral, **b**, medial, **c**, ventral; **d**, dorsal views. Abbreviations: naf, nasal fossa; nas, slot for nasal.

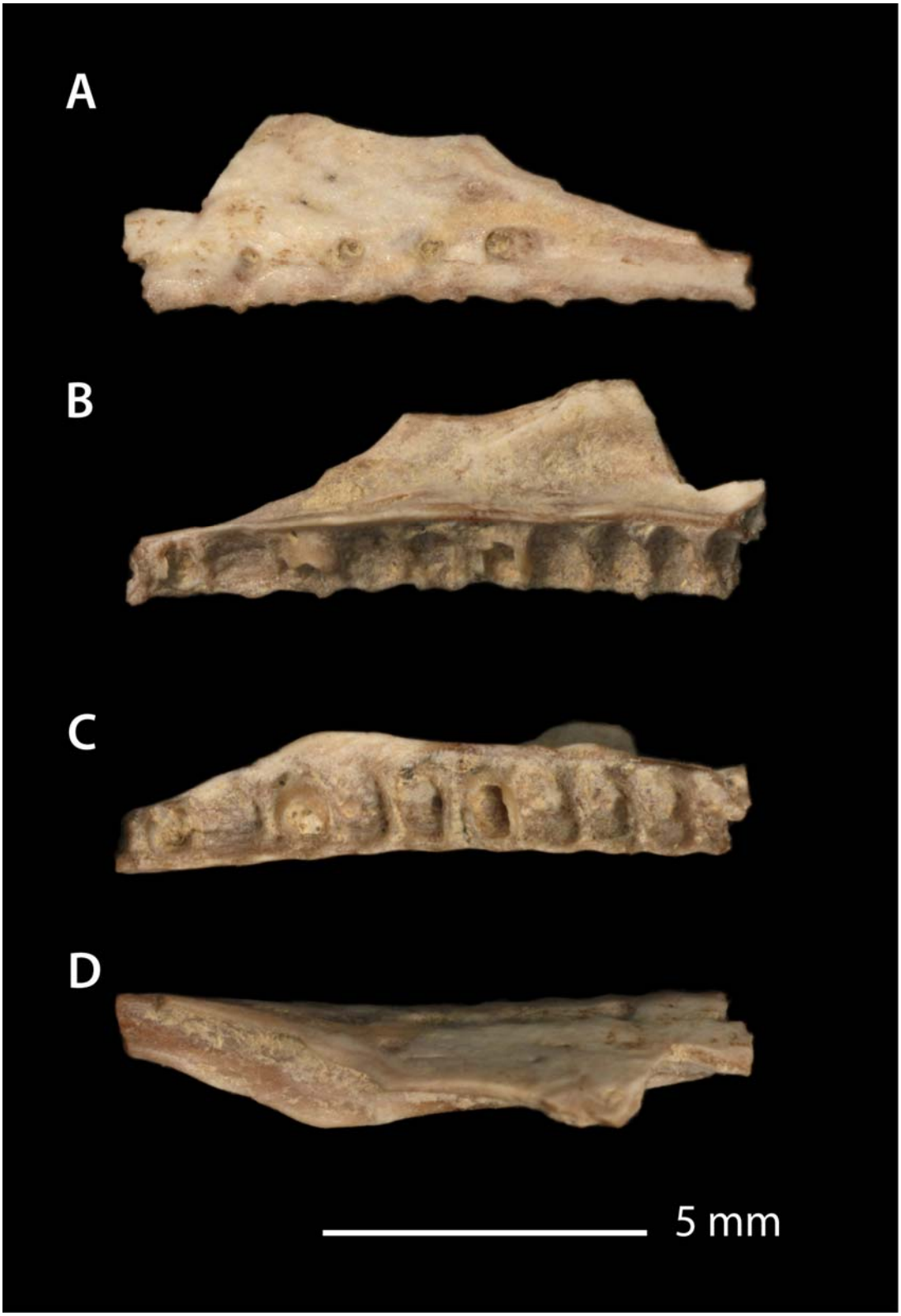

Fig. S2. AMNH 26660, left maxilla. **a**, lateral, **b**, medial, **c**, ventral, **d**, dorsal views.

References

Albino, A.M., 1991. Las serpientes de São José de Itaboraí (Edad Itaboraiense, Paleoceno medio), Brasil. Ameghiniana 27, 337-342.

Armstrong-Ziegler, J.G., 1978. An aniliid snakes and associated vertebrates from the Campanian of New Mexico. Journal of Paleontology 52, 480-483.

Augé, M., Rage, J.-C., 2006. Herpetofaunas from the Upper Paleocene and Lower Eocene of Morocco. Annales de Paléontologie 92, 235-253.

Estes, R., 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. University of California Publications, Department of Geological Sciences 49, 1-180.

Estes, R., 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, Southeastern Montana. Journal of Paleontology 50, 500-520.

Fox, R.C., 1975. Fossil snakes from the upper Milk River Formation (Upper Cretaceous), Alberta. Canadian Journal of Earth Sciences 12, 1557-1563.

Gardner, J.D., Cifelli, R.L., 1999. A primitive snake from the Cretaceous of Utah. Special Papers in Palaeontology 60, 87-100.

Marsh, O.C., 1892. Notice of new reptiles from the Laramie Formation. American Journal of Science, Series 3 43, 449-453.

McGrew, P.O., Hecht, M.K., Hummel, J.M., Simpson, G.G., Wood, A.E., 1959. The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bulletin of the American Museum of Natural History 117, 117-176.

Rage, J.-C., 1988. Le Gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertebres de l'Eocene Superieur. Palaeontographica Abteilung A 25, 3-27.

Rage, J.-C., Augé, M., 2010. Squamate reptiles from the middle Eocene of Lissieu (France). Geobios 43, 253-268.

Rage, J.-C., Prasad, G.V.R., Bajbai, S., 2004. Additional snakes from the uppermost Cretaceous (Maastrichtian) of India. Cretaceous Research 25, 425-434.

Rage, J.-C., Werner, C., 1999. Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan: the earliest snake assemblage. Palaeontologia Africana 35, 85-110.