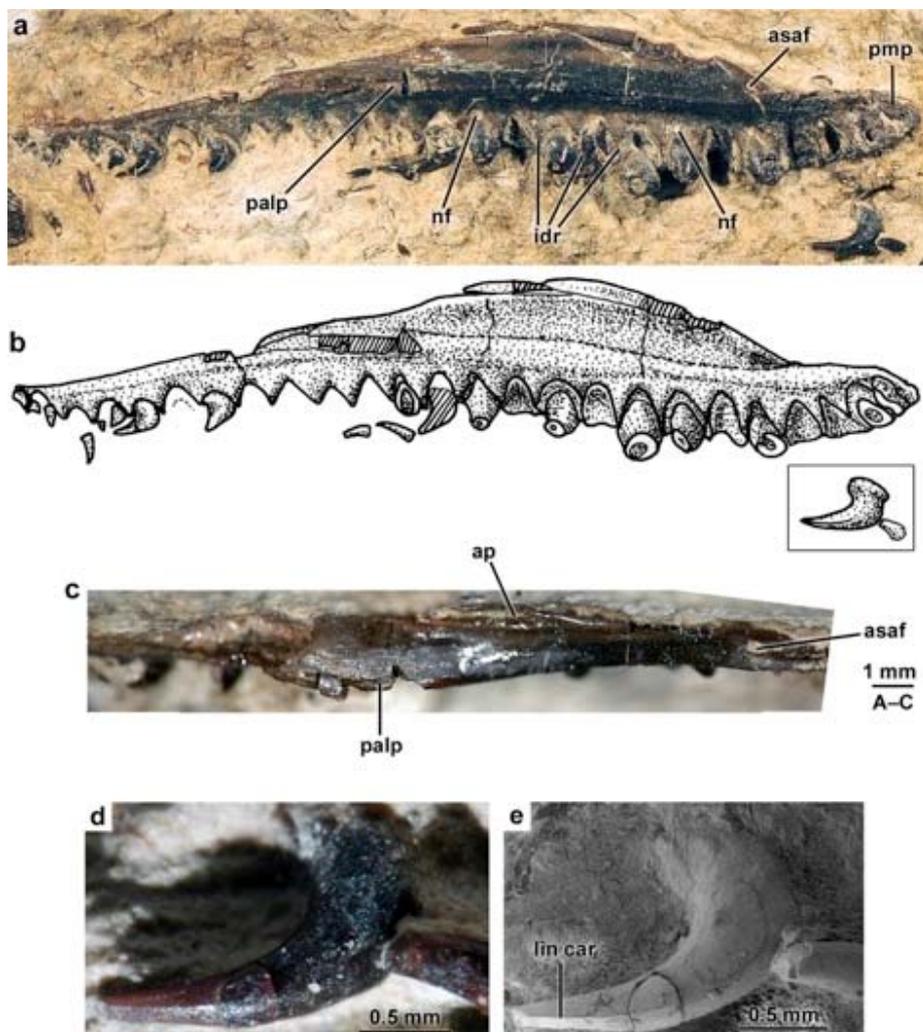
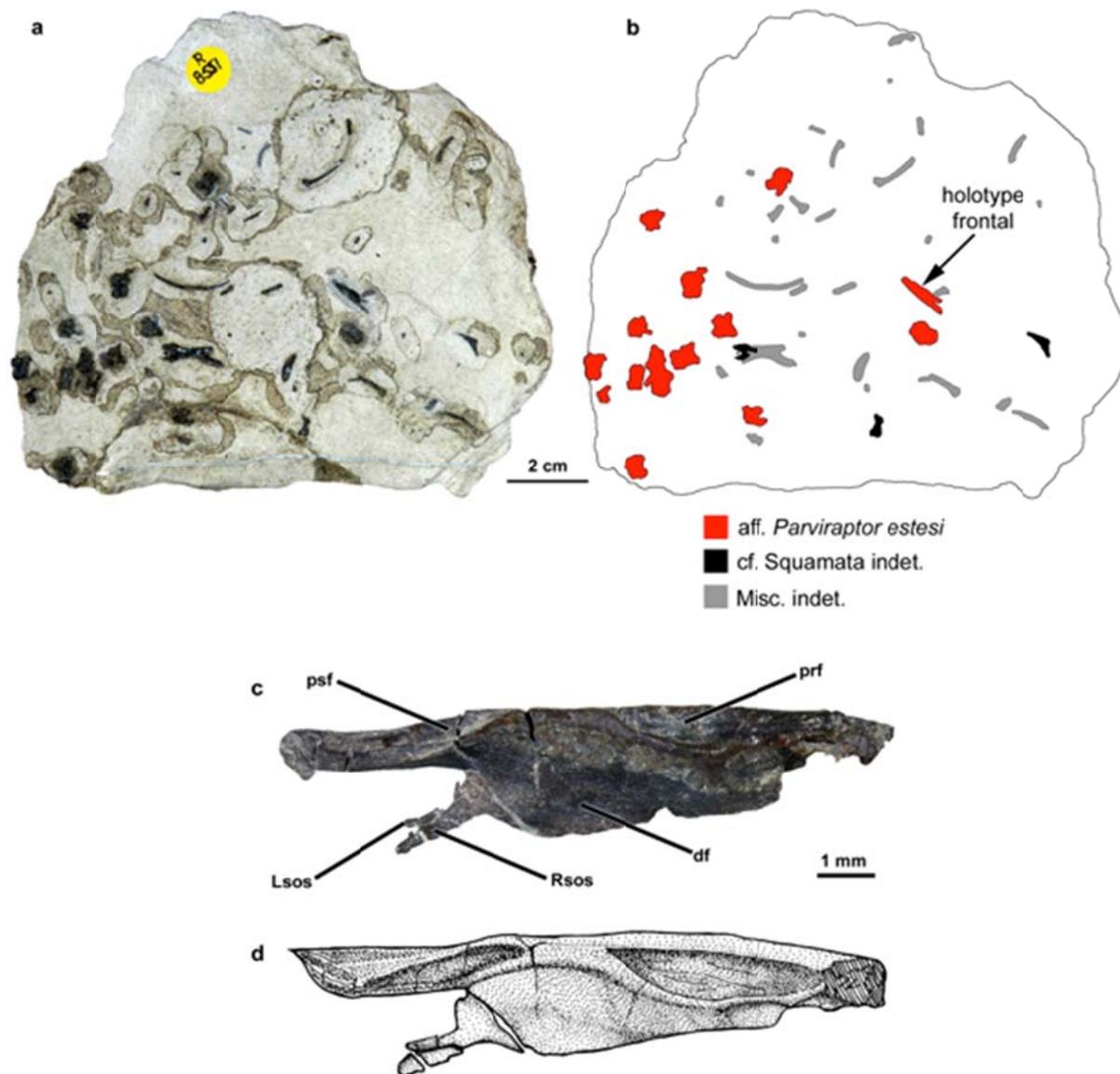


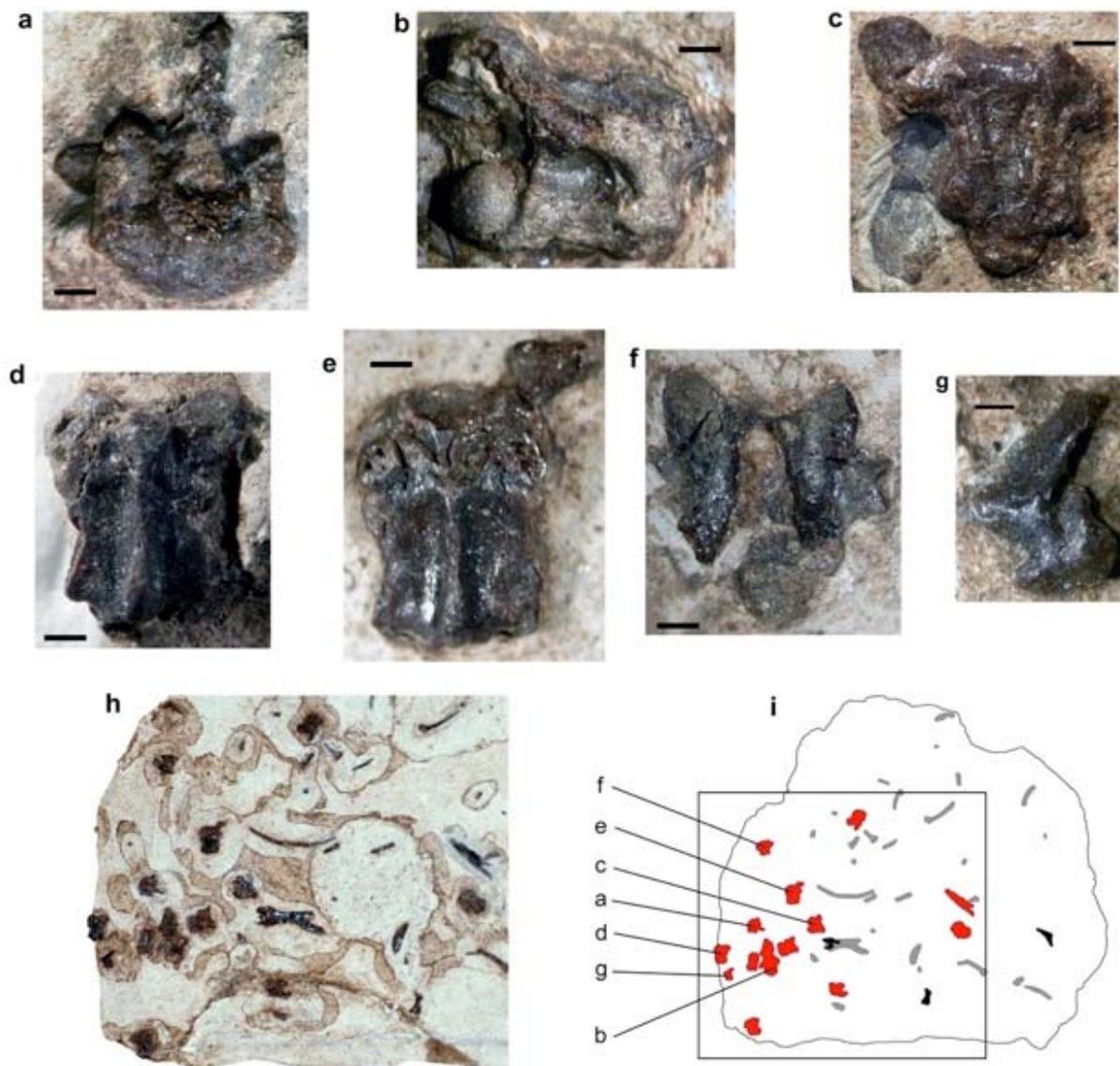
**Supplementary Figure 1. *Parviraptor estesi*.** (top) NHMUK 48388 - Type block. (bottom) Color-coded silhouettes (bottom) indicating updated taxonomic interpretation of the isolated elements. Scale bar equals 1 cm. The type left maxilla and other specimens originally referred to *Parviraptor* are isolated elements on a small block from the Purbeck Limestone Formation, Durlston Bay, Swanage, Dorset, England (Upper Jurassic; Tithonian/Lower Cretaceous; Berriasian). The block also contains isolated elements from non-squamate taxa as well as isolated elements that appear to be squamate, but so distinctly non-ophidian they are removed from *Parviraptor estesi*.



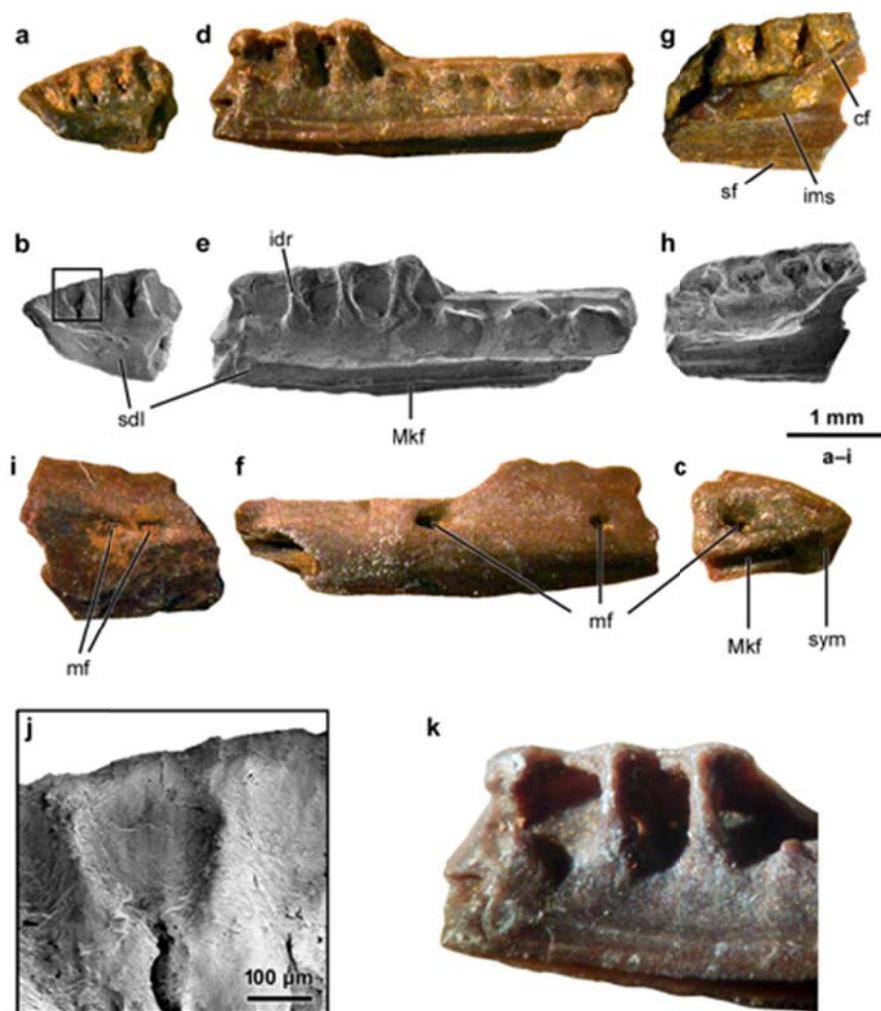
**Supplementary Figure 2. Holotype left maxilla and details of dissociated maxillary tooth of *Parviraptor estesi* (NHMUK 48388 - part).** (a) photograph of medial view. (b) Illustration of same (box indicates area detailed in d and e. (c) dorsal view. (d) Medial view of isolated tooth (position 3 or 4) of *Parviraptor estesi* (NHMUK 48388- part). (e) SEM of isolated tooth. (f) Detail of carina along medial edge of tooth. Abbreviations: ap, ascending process; asaf, anterior superior alveolar foramen; idr, interdental ridges; lin car, lingual carina; nf, nutrient foramen; pmxp, premaxillary process; Pl-pr, palatine process.



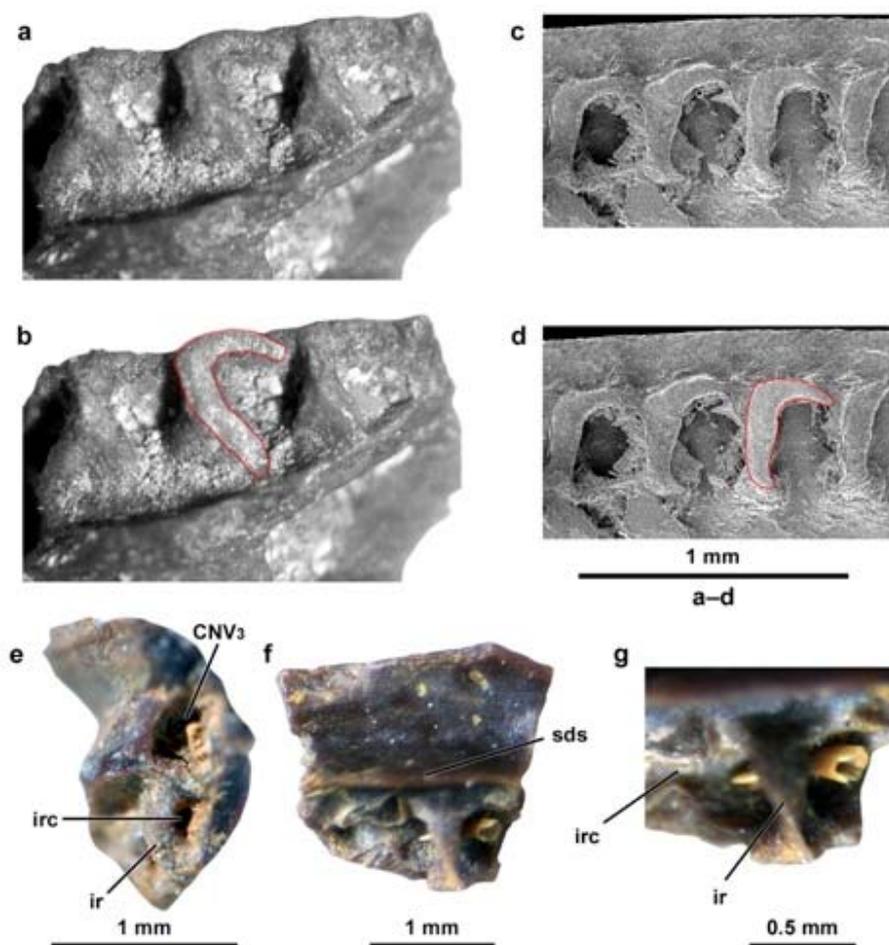
**Supplementary Figure 3. Block with frontal and vertebrae referred to *aff. Parviraptor estesi* (NHMUK R8551).** (a) photograph of block, NHMUK R8551). (b) Color-coded silhouettes indicating updated taxonomic interpretation of the isolated elements. (c) NHMUK R8551 (part). (d) Pen and ink illustration of same from slightly more dorsal view. Abbreviations: df, decensus frontalis; Lsop, left suboptic shelf; psf, postfrontal facet; prf, prefrontal facet; Rsop right suboptic shelf.



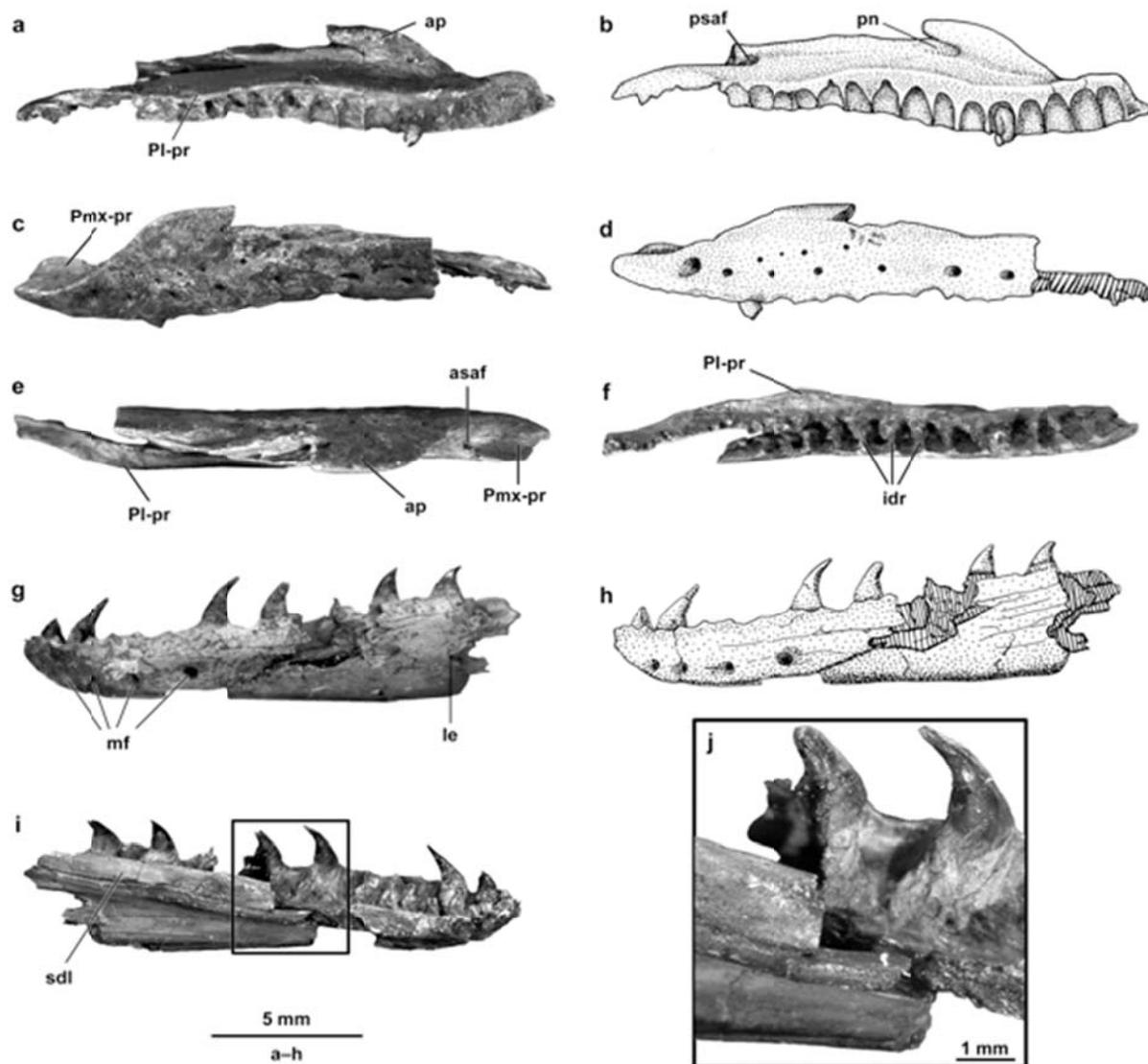
**Supplementary Figure 4. Vertebrae from block NHMUK R8551 (Swanage), aff. *Parviraptor estesi*.** In (a) posterior, (b) right lateral, (c) ventral, (d) dorsal, (e) dorsal (neural arch missing), (f) dorsal views, (g) left atlas neural arch in lateral view, (h) detail of block NHMUK R8551, (i) line drawing of block NHMUK R8551 indicating position of specimens. (a–g) Box indicates area of detail in (h). Red indicates specimens, aff. *Parviraptor estesi*. All scale bars equal 1 mm.



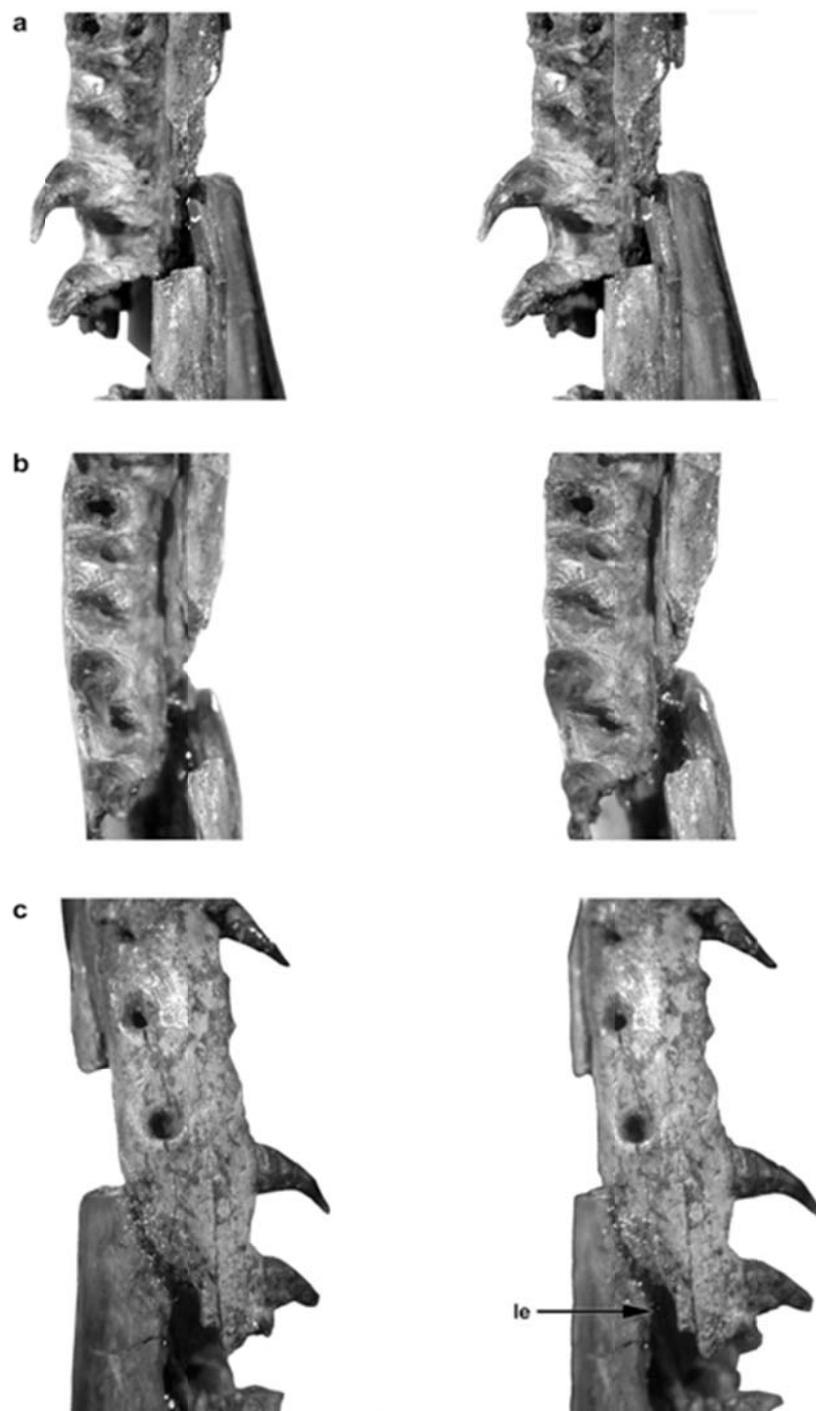
**Supplementary Figure 5.** *Eophis underwoodi*, composite illustration of right dentary specimens from Forest Marble, Kirtlington, England, Late Jurassic (Bathonian). (a–c), holotype, NHMUK R12355: (a) Photograph of medial view. (b) SEM of same (box indicates area of detail in i); and (c) photograph of ventrolateral view. (d–f) Paratype NHMUK R12354, mid-portion: (d) Photograph of medial view. (e) SEM of same. (f) Photograph of lateral view. (g–i) NHMUK R 12370, referred posterior portion: (g) Photograph of medial view. (h) SEM of same. (i) Photograph of lateral view. (j) Detail of second alveolus of NHMUK R12354. (k) Detail of alveoli of NHMUK R12354 showing light passing through the interdental ridge canals. Abbreviations: cf, coronoid articulation facet; idr, interdental lamina; ims, intermandibular septum; mf, mental foramina; Mkf, Meckelian fossa; sdl, subdental lamina; sf, splenial articulation facet; sym, symphysis.



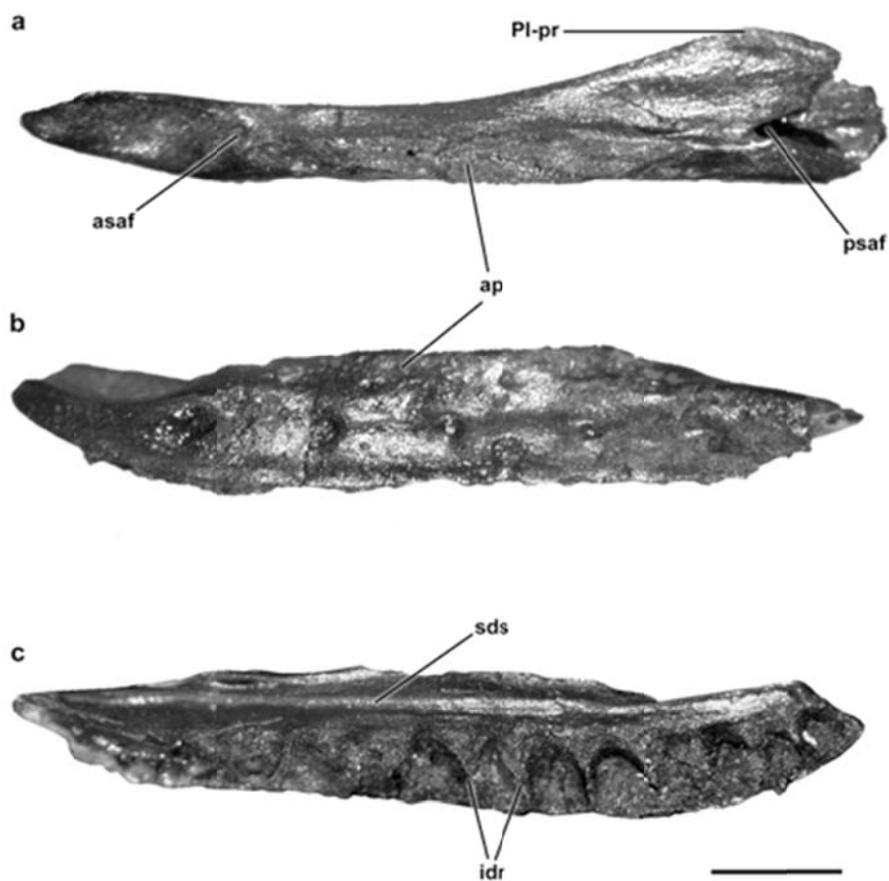
**Supplementary Figure 6. Comparison of the alveoli of *Eophis underwoodi* and *Xenopeltis unicolor*, and details of possible maxillary fragment of cf. *E. underwoodi*.** (a–b) Microphotograph of posterior portion of right dentary of *Eophis underwoodi* NHMUK R12370 (posterior portion of right dentary). (c–d) SEM image of left maxilla of *Xenopeltis unicolor* FMNH 287277. (e) Rostral view of NHMUK 12370, posterior portion of right dentary. (f–g) NHMUK R12352, fragment of left maxilla referred to *Eophis underwoodi* in (f) medial view and (g) detail of tooth imbedded in interdental ridge canal. Abbreviations: ir, interdental ridge; irc, interdental ridge canal; sds, supradental shelf; CNV<sub>3</sub>, canal for mandibular division of trigeminal nerve and associated vascular bundle. Note: J-shaped boundaries of alveoli are shown in red in (b) and (d). Scale bar equals 1 mm.



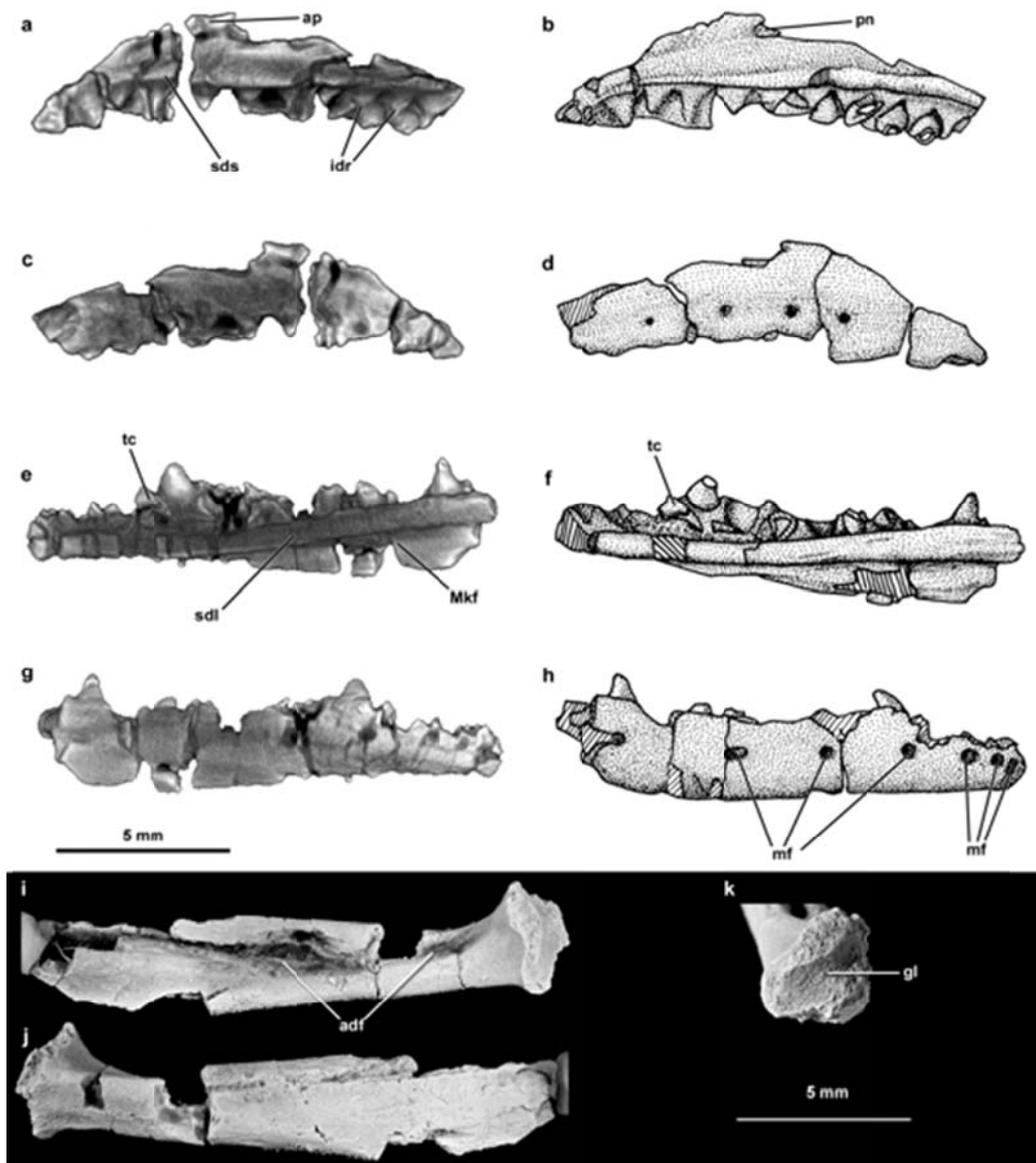
**Supplementary Figure 7. *Portugalophis lignites*, new taxon, Guimarota, Portugal (Kimmeridgian).** (a–f) Holotype left maxilla (MG-LNEG 28091): (a) Photograph in medial view. (b) Pen and ink drawing of same. (c) Photograph of dorsolateral view. (d) Pen and ink drawing of lateral view. (e) Photograph of dorsal view. (f) Photograph of occlusal view. (g–i) Paratype left dentary (MG-LNEG 28094): (g) Photograph of lateral view. (h) Pen and ink drawing of same. (i) Photograph of medial view (box indicates area of detail in j). (j) Detail of teeth and alveoli. Abbreviations: ap, ascending process; asaf, anterior superior alveolar foramen; idr, interdental ridges; le, lateral emargination; mf, mental foramina; Pl-pr, palatine process; pn, posterior notch of ascending process; psaf, posterior superior alveolar foramen; Pmx-pr, premaxillary process; sdl, subdental lamina.



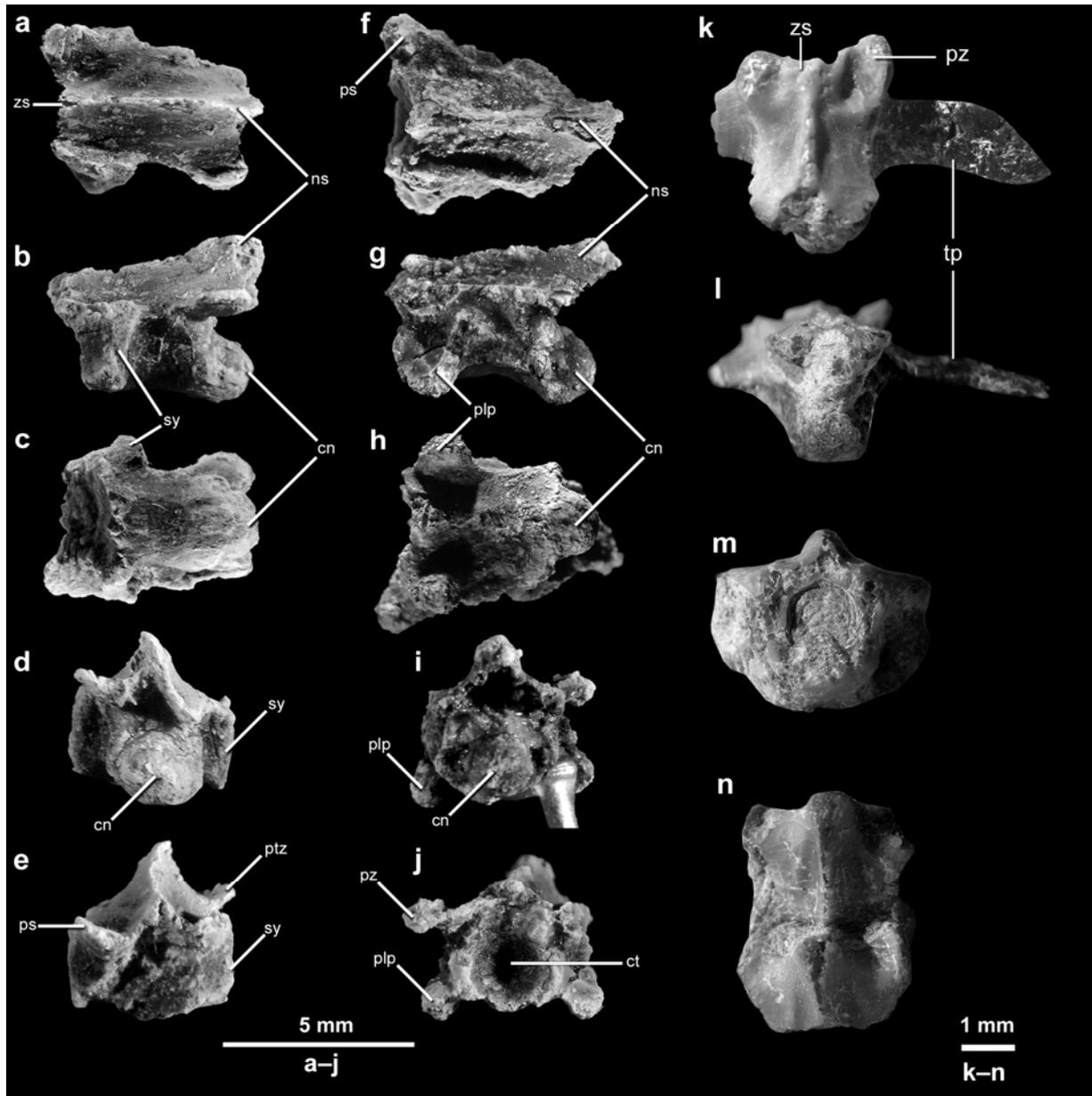
**Supplementary Figure 8. *Portugalophis lignites*, new taxon, Guimarota, Portugal (Kimmeridgian), stereopairs of paratype left dentary (MG-LNEG 28094). (a) Medial view. (b) Superior view. (c) Lateral view. Abbreviation: le, lateral emargination. Scale bar equals 1 mm.**



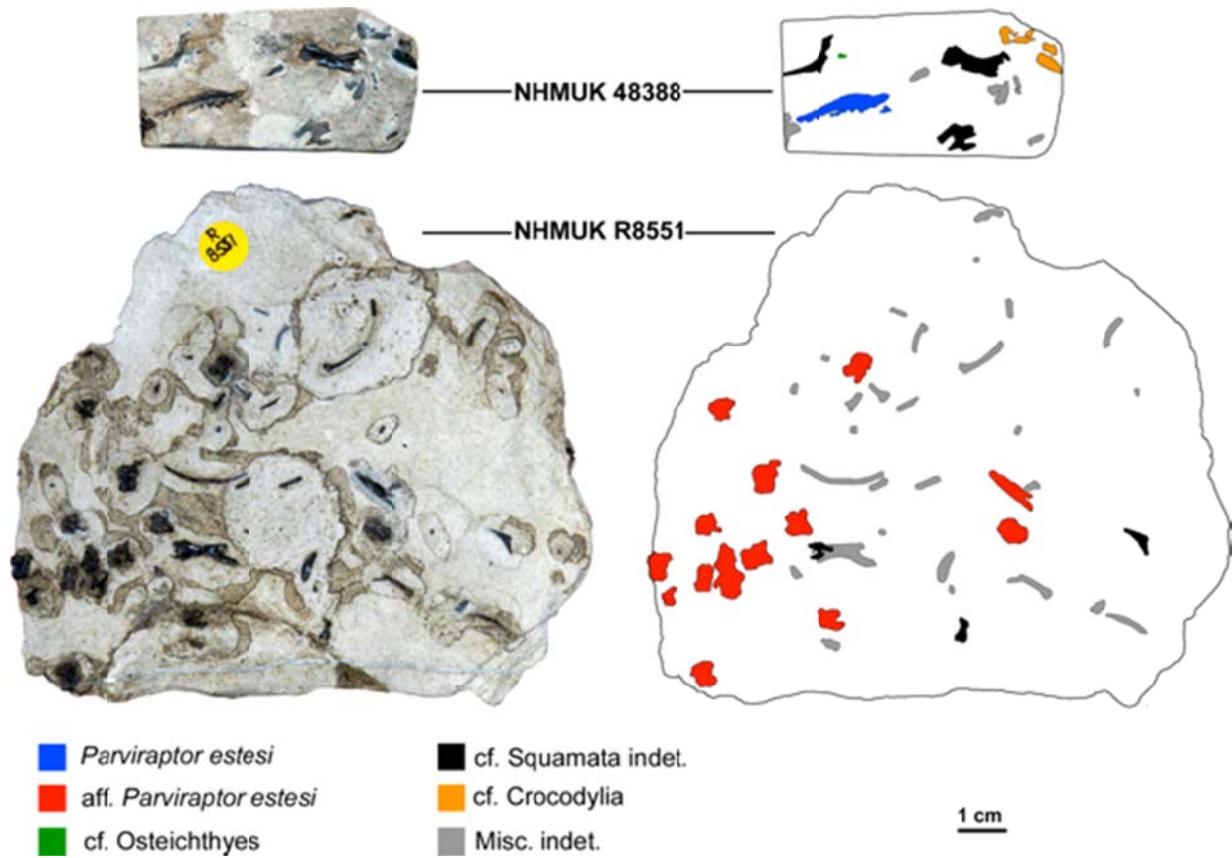
**Supplementary Figure 9. *Portugalophis lignites*, new taxon, Guimarota, Portugal (Kimmeridgian), referred left maxilla (MG-LNEG 28100).** (a) Dorsal view. (b) Lateral view. (c) Medial view. Abbreviations: ap, ascending process; asaf, anterior superior alveolar foramen; idr, interdental ridges; Pl-pr, palatine process; psaf, posterior superior alveolar foramen; sds, supradental shelf. Scale bar equals 1 mm.



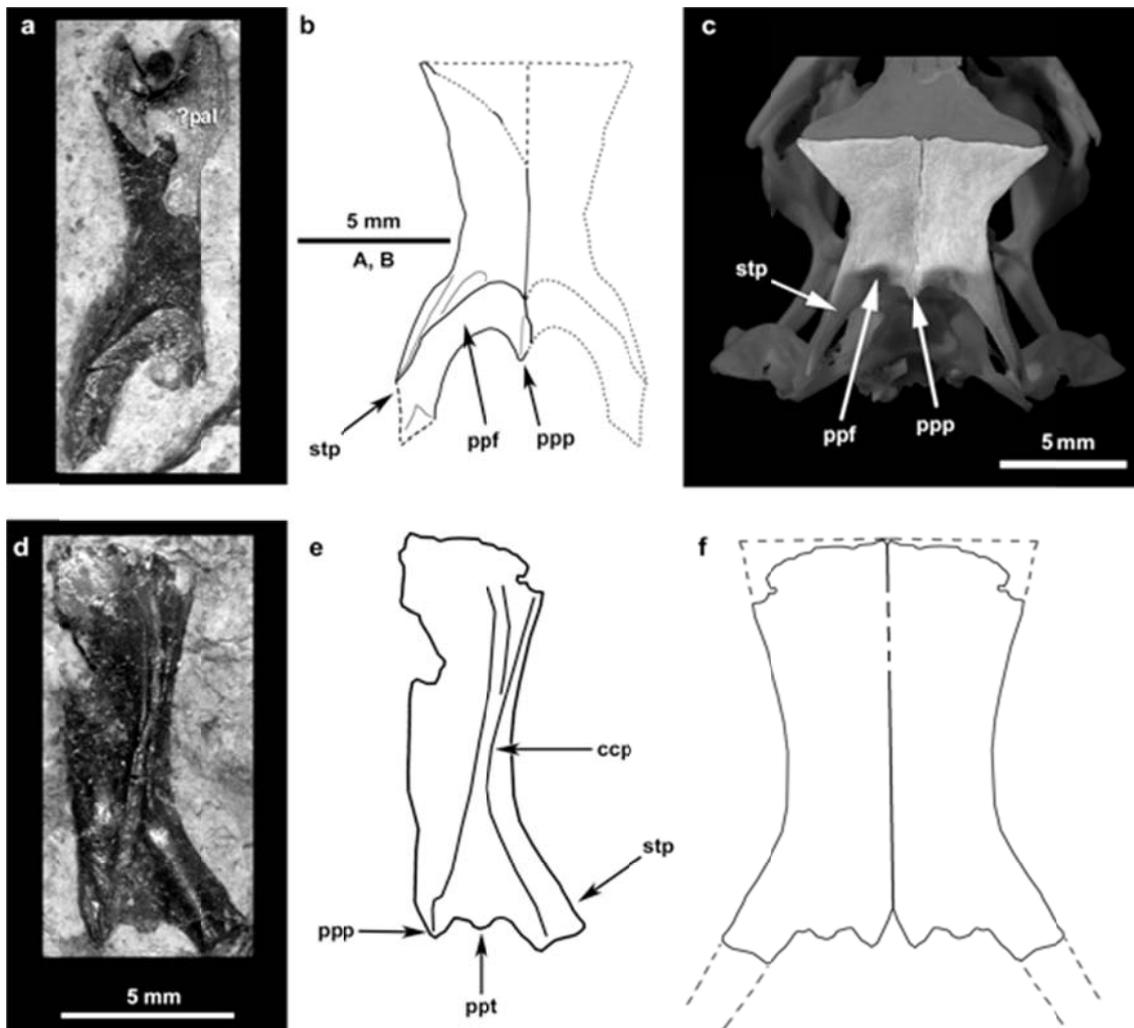
**Supplementary Figure 10.** *Diablolphis gilmorei* LACM 4684/140572 (part), holotype specimens. (a–h) Holotype right maxilla, and (i–k), holotype right surangular: (a) Photograph in medial view. (b) Pen and ink drawing of same. (c) Photograph in lateral view. (d) Pen and ink drawing of lateral. (e–h) Holotype right dentary: (e) Photograph in medial view. (f) Pen and ink drawing of same. (g) Photograph in lateral view. (h) Pen and ink drawing of lateral view. (i) Right surangular, medial view. (j) Right surangular, lateral view. (k) Detail of surangular portion of glenoid surface. Abbreviations: adf, adductor fossa; ap, ascending process; gl, glenoid fossa; idr, interdental ridges; mf, mental foramina; Mkf, Mecklian fossa; pn, posterior notch of ascending process; sdl, subdental lamina; sds, supradental shelf. Scale bar equals 5 mm.



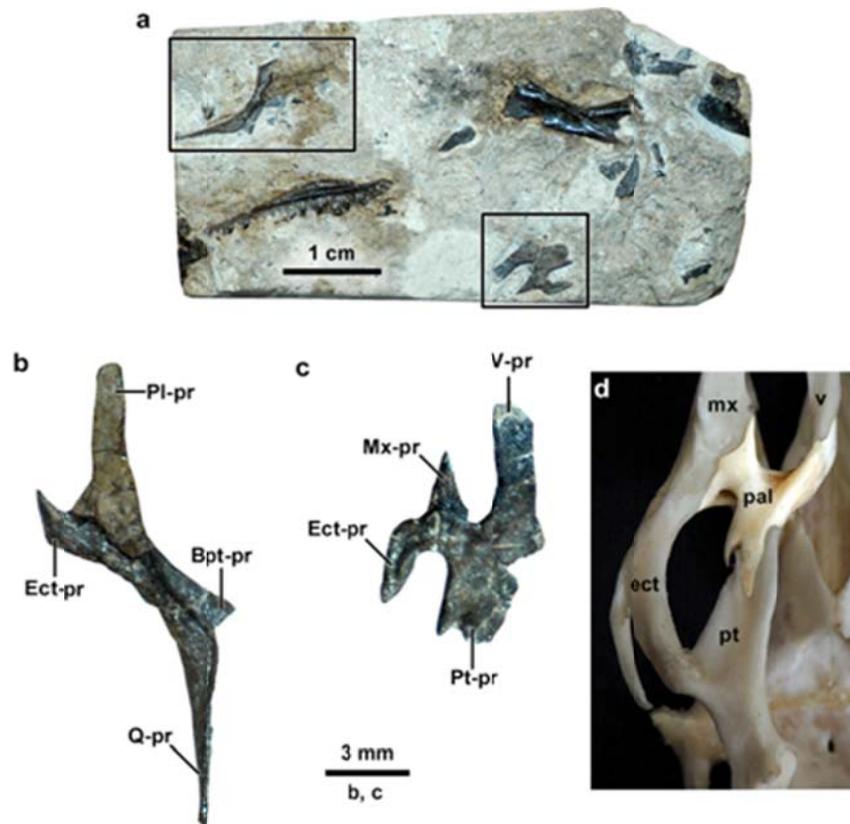
**Supplementary Figure 11. *Diablophis gilmorei*, referred vertebrae from LACM 4684/140572. (a–j) and LACM 4684/120472 (k–n). (a–e) preloacal vertebra in dorsal, lateral, ventral, posterior, and anterior views, respectively. (f–j) caudal vertebra in dorsal, lateral, ventral, posterior, and anterior views, respectively. (k–l) possible sacral in dorsal and posterior views, respectively. (m–n) two partial preloacal vertebrae in articulation in anterior and dorsal views, respectively. Abbreviations: cn, condyle; ct, cotyle; ns, neural spine; ptz, postzygapophysis; pz, prezygapophysis; plp, pleuropophysis; sy, synapophysis; tp, transverse process; zs, zygosphenes.**



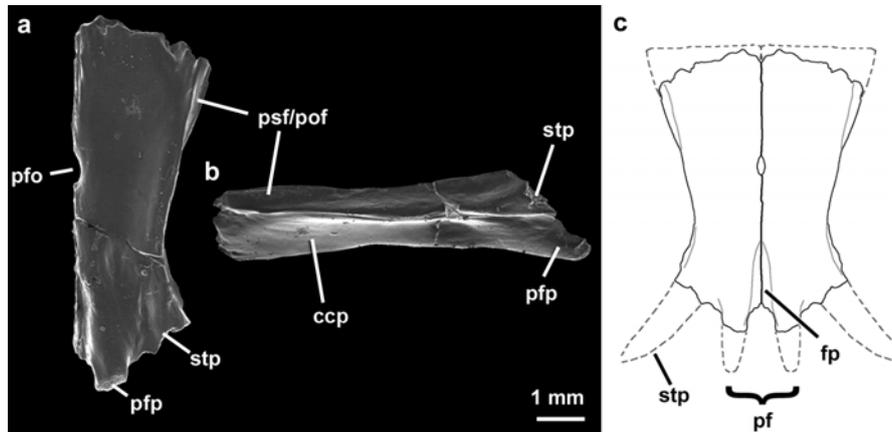
**Supplementary Figure 12.** Type blocks for *Parviraptor estesi*. NHMUK R48388 (top) and aff. *Parviraptor estesi* NHMUK R8551 (bottom) from Swanage, Dorset, England, with color-coded silhouettes indicating revised taxonomic identifications of isolated elements.



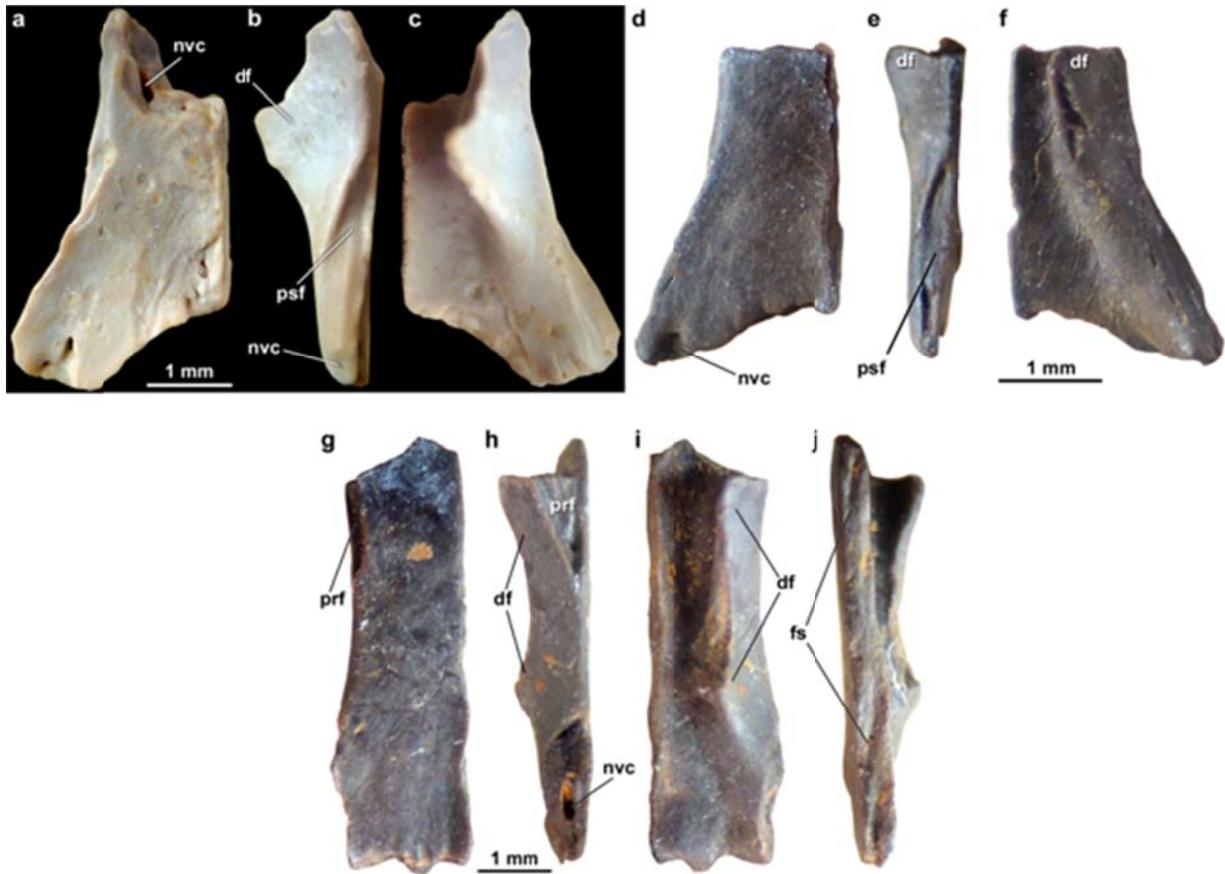
**Supplementary Figure 13. Left ‘parietal’ from NHMUK R8551 and NHMUK R48388 and comparable paired parietals of *Gekko gecko*.** (a) Photograph of NHMUK R8551 in dorsal view. (b) reconstruction of parietal table. (c) *Gekko gecko* with parietals highlighted. (d) Left parietal from NHMUK R48388 in ventral view. (e) Line drawing of same. (f) Reconstruction of parietal table. abbreviations: ccp, crista cranii parietalis; ?pal, possible palatine; ppf, posterior parietal fossa; ppp, posterior parietal process; ppt, posterior parietal tab; stp, supratemporal process.



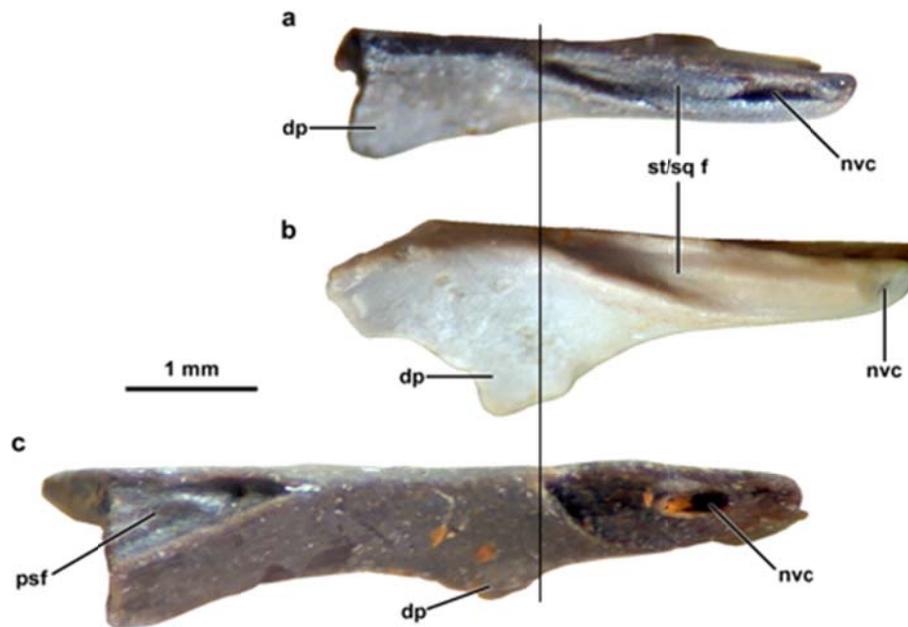
**Supplementary Figure 14. Right pterygoid and right ?palatine from NHMUK R48388.** (a) Block with boxes around the pterygoid (upper left) and ?palatine (lower right). (b) Right pterygoid in ventral view. (c) Right ?palatine in ventral view. (d) Left palatal region of *Varanus* sp. in ventral view. Abbreviations: Bpt-pr; basipterygoid process; ect, ectopterygoid; Ect-pr, ectopterygoid process; mx, maxilla; Mx-pr, maxillary process; pal, palatine; Pl-pr, palatine process; pt, pterygoid; Pt-pr; pterygoid process; Q-pr, quadrate process; v, vomer; V-pr, vomerine process. Scale bar for (a) equals 1 cm, scale bars for (b) and (c) equal 1 mm.



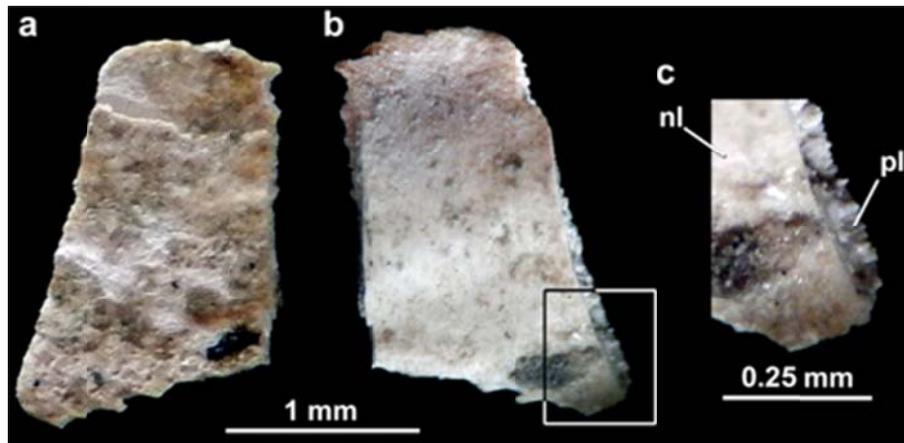
**Supplementary Figure 15. NHMUK R12353, partial left parietal reassigned to *Scincomorpha indet.*** (a) SEM in ventral view. (b) SEM in lateral view. (c) Reconstruction of paired parietals. Abbreviations: ccp, crista cranii parietalis; fp, fossa parietalis; pf, parietal fork; pfp, parietal fork process; pfo, pineal foramen; pof, postorbital facet; psf, postfrontal facet; stp, supratemporal process.



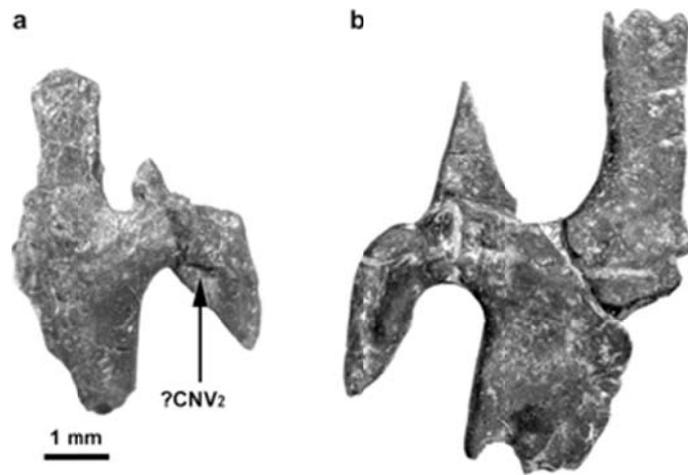
**Supplementary Figure 16. Squamate frontals from Kirtlington Quarry Assemblage (Bathonian, Middle Jurassic) assigned to *squamata incertae sedis*.** (a–c) NHMUK R12356, partial left parietal in: (a) Dorsal view. (b) Lateral view. (c) Ventral view. (d–f) NHMUK R12357, partial left parietal in: (d) Dorsal view. (e) Lateral view. (f) Ventral view. (g–j) NHMUK R12359, partial left parietal in: (g) Dorsal view. (h) Lateral view. (i) Ventral view. (j) Medial view. Abbreviations: df, descensus frontalis; fs, interfrontal suture; nvc, neurovascular canal; prf, prefrontal articular facet; psf, postfrontal facet.



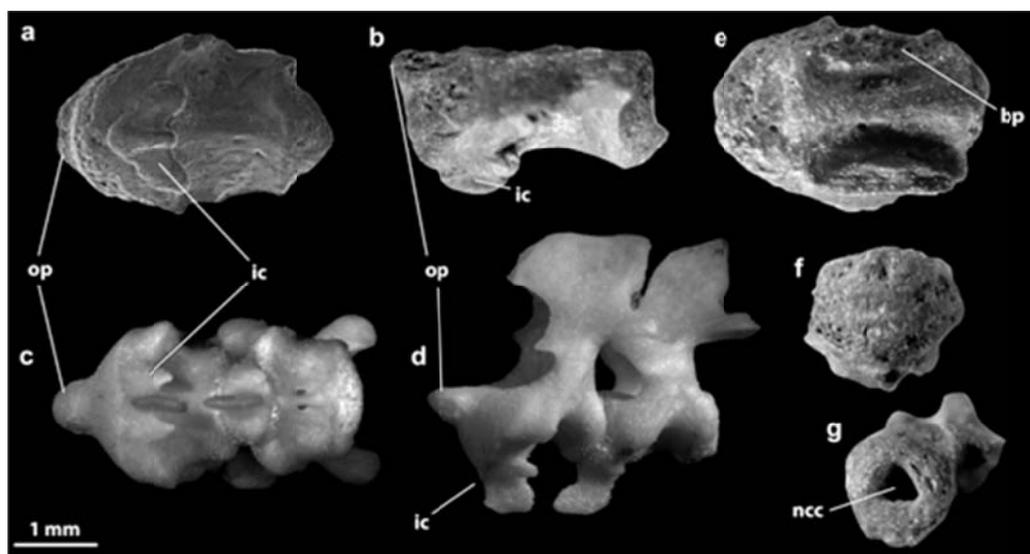
**Supplementary Figure 17. Left lateral view comparison of frontals (*Squamata indet.*) from the Old Cement Works Quarry, Kirtlington. (a) NHMUK R12357. (b) NHMUK R12356. (c) NHMUK R12359. Abbreviations: df, decensus frontalis; nvc, neurovascular canal; prf, prefrontal articular facet; psf, postfrontal facet. Black line indicates the anteriormost extent of the postfrontal articular facet in all three specimens.**



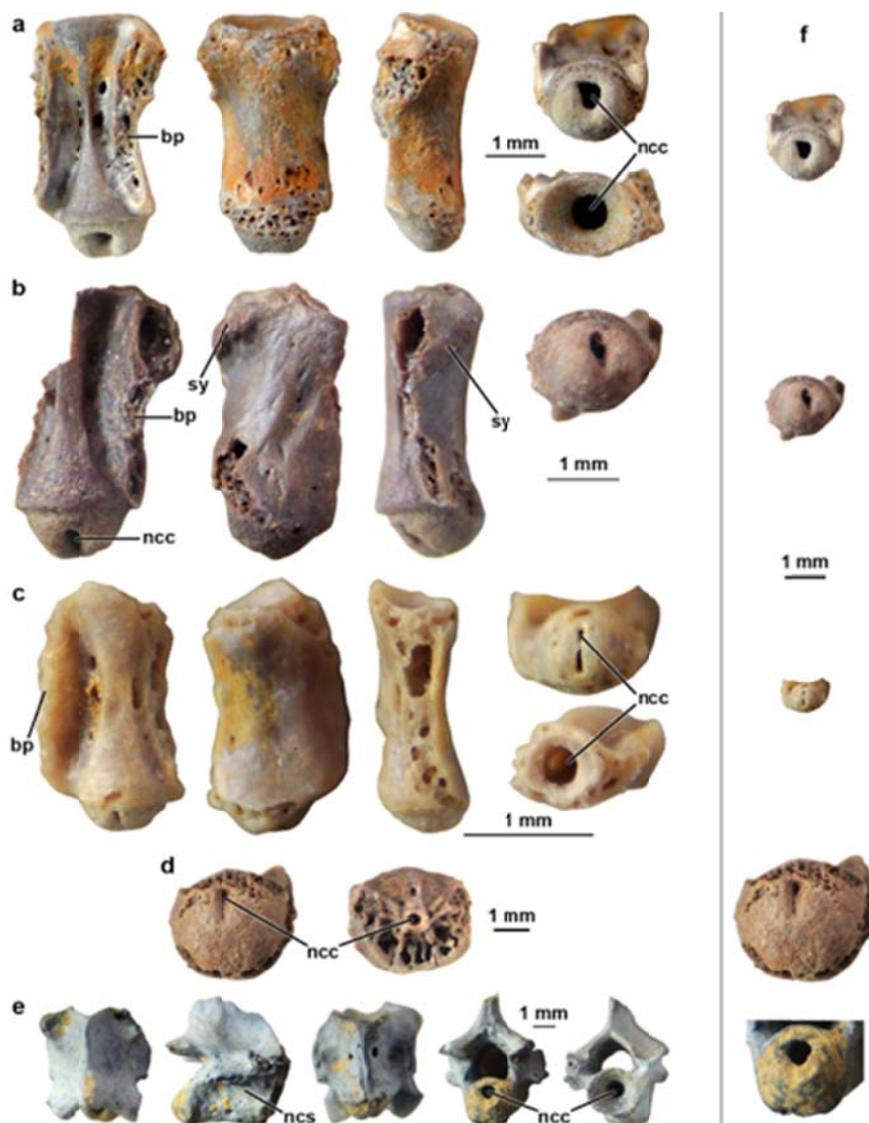
**Supplementary Figure 18. NHMUK R12358, reidentified as a mollusk shell fragment (originally identified as a partial frontal of a juvenile). (a) External view. (b) Internal view. (c) Detail of broken margin indicted in box in (b). Abbreviations: nl, nacre layer; pl, prismatic layer.**



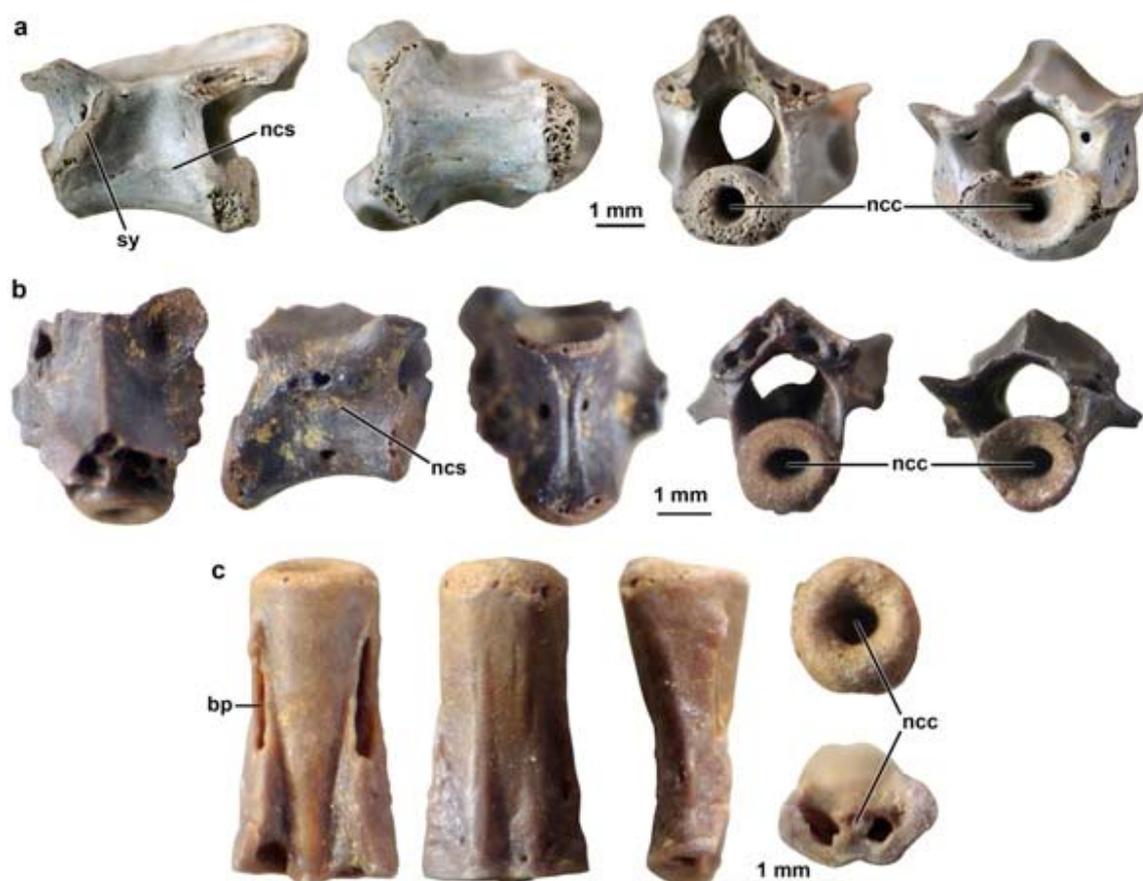
**Supplementary Figure 19. ?Palatines from Purbeck Limestone. (a) ?Palatine from NHMUK R8551. (b) ?Palatine from NHMUK R48388. Abbreviation: ?CNV2, possible channel for mandibular branch of trigeminal nerve. Scale bare equals 1 mm.**



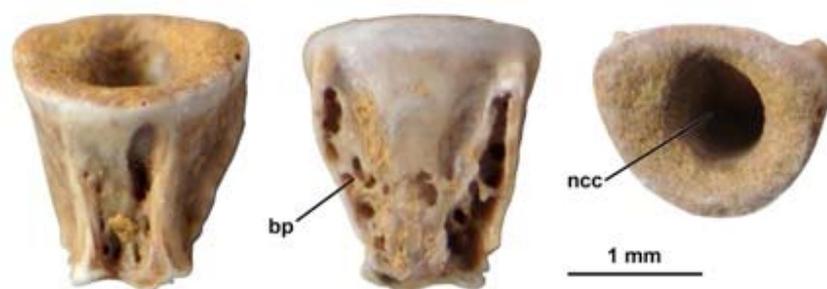
**Supplementary Figure 20. Comparison between the axis (C2) of NHMUK R12360, cf. *Gekkota taxon incertae sedis A*, and that of *Gekko gecko*.** (a, b, e–g) NHMUK R12360 in (a) ventral (SEM). (b) Left lateral. (e) Dorsal. (f) Anterior. (g) Caudal views (assuming procoely). (c, d) C2–C3 of *Gekko gecko* in (c) ventral. (d) Left lateral views. Abbreviations: bp, broken pedicle; ic, intercentrum; ncc, notochord canal; op, odontoid process.



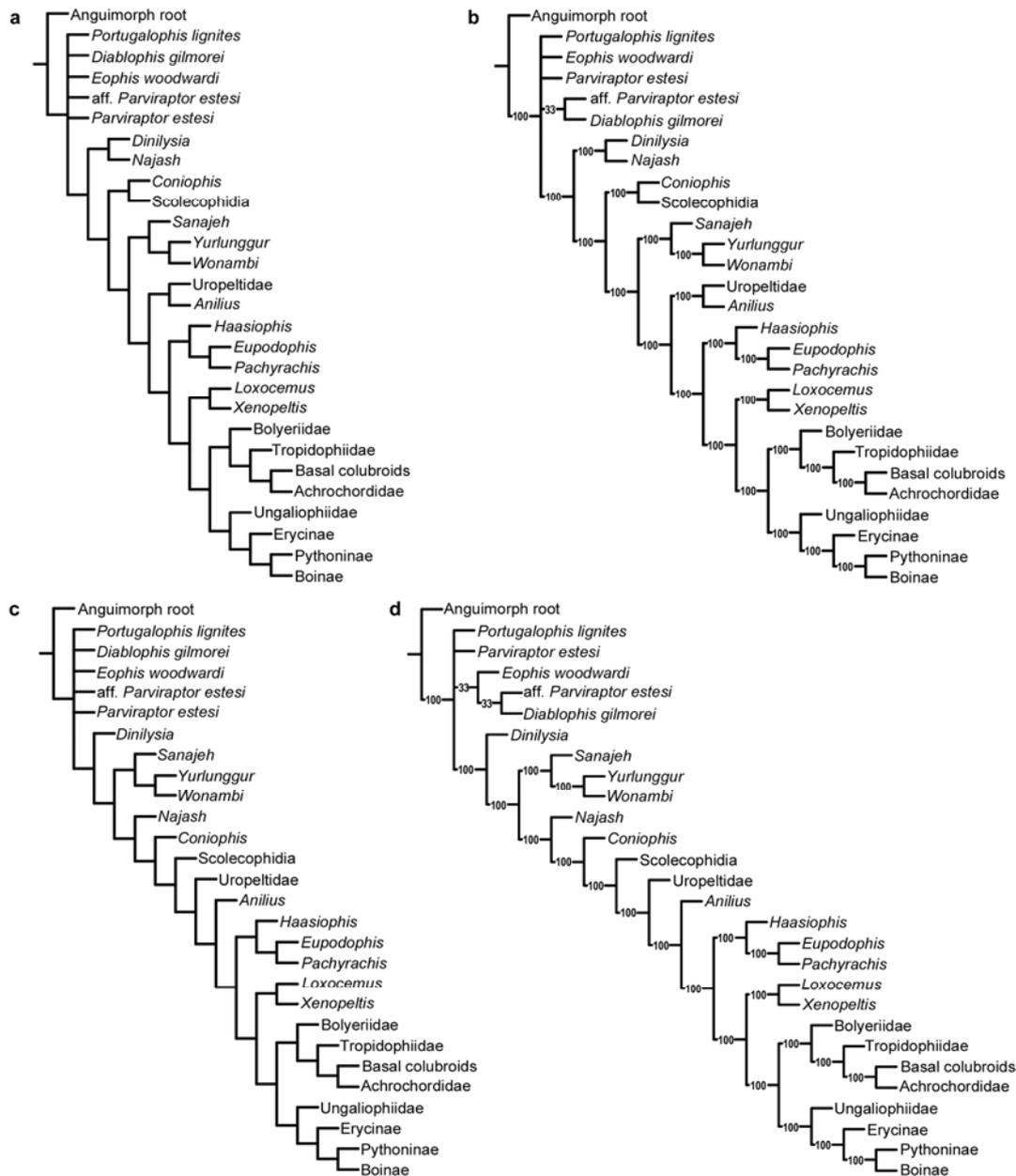
**Supplementary Figure 21. Fragmentary vertebrae from Kirtlington Quarry, Oxfordshire, England, previously assigned to *Parviraptor cf. estesi* assigned here to *cf. Gekkota taxon incertae sedis A*.** (a) NHMUK R12361, in (from left to right, top to bottom) dorsal, ventral, left lateral, caudal, and cranial views (assuming procoely). (b) NHMUK R12362, in (from left to right) dorsal, oblique ventral, left lateral and caudal views (assuming procoely). (c) NHMUK R12363, in (from left to right, top to bottom) dorsal, ventral, left lateral, caudal, cranial views (assuming procoely). (d) NHMUK R12364, in (from left to right) caudal view and cross section in cranial view. (e) NHMUK R12366, vertebra of *cf. Gekkota taxon incertae sedis A* in (from left to right) dorsal, right lateral, ventral, caudal, and cranial views. (f) posterior of view of specimens at the same scale for comparison of relative sizes. Abbreviations: bp, broken pedicle; ncc, notochord canal; ncs, neurocentral suture; sy, synapophyses.



**Supplementary Figure 22. Vertebrae from Kirtlington Quarry, Oxfordshire, England, previously assigned to *Parviraptor cf. estesi* assigned here to *cf. Gekkota taxon incertae sedis B*.** (a) NHMUK R12367 in (from left to right) left lateral, ventral, posterior, and anterior views. (b) NHMUK R12365, in (from left to right) dorsal, right lateral, ventral, posterior, and anterior views. (c) NHMUK R12369, in (from left to right, top to bottom) dorsal, ventral, left lateral, posterior and anterior cross sectional views (orientation of d and e assuming procoely). Abbreviations: bp, broken pedicle; ncc, notochordal canal; ncs, neurocentral suture (closed and fused); sy, synapophyses.



**Supplementary Figure 23. NHMUK R12368, partial vertebra of an indeterminate taxon.** Views from left to right are ventral, dorsal, and anterior. Abbreviations: bp, broken pedicle; ncc, notochord canal.



**Supplementary Figure 24. Phylogeny of oldest known snakes and other fossil and living snakes derived from TNT 1.1 analyses of the data set. (a, b),** resulting Strict consensus (a) and Frequency Distribution (b) trees from ‘Traditional’ analysis (100 random seed Wagner trees and 100 replications; recovered 18 trees of length 513). (c, d), resulting Strict consensus (c) and Frequency Distribution (d) trees from Drift (New Technology) analysis (default assumptions used; resulted in three trees of length 513).



**Supplementary Figure 25. Strict Consensus Tree of 108,981 shortest trees (using TNT 1.1), illustrating overall phylogeny of squamates<sup>9</sup> including *Parviraptor*, *Diablophis*, and *Portugalophis*. All three taxa are nested within a polytomy comprised of Mesozoic snakes (*Dinilyisia*, *Pachyrhachis*, *Haasiophis*, etc.), scolecophidians, and alethinophidians, with *Najash* as the basal most snake.**

## Supplementary Note 1

### SYSTEMATIC PALEONTOLOGY OF NON-SNAKE MATERIALS

#### Identity of non-snake specimens originally referred to *Parviraptor*

##### **Identity of non-snake remains originally referred to *Parviraptor estesi***

The fossils from the Purbeck Marble (Tithonian–Berriasian), Durlston Bay, Swanage, Dorset, England originally referred to *Parviraptor estesi*<sup>1</sup> comprise a series of disarticulated and disassociated cranial and postcranial remains that are co-preserved on two limestone blocks (Supplementary Fig. 12) collected from the Purbeck Marble (*Parviraptor estesi*), Swanage, Dorset. Most of the elements on the blocks from Dorset were assigned to *Parviraptor estesi*<sup>1</sup> represents an assembling of these elements. Based on our examination of the blocks from Dorset we have come to a more conservative conclusion regarding which of the exposed elements can be referred to the snake *Parviraptor estesi*. In addition to the type maxilla of *P. estesi* there are also crocodylian, fish, and indeterminate vertebrate remains on block NHMUK 48388. Since the type maxilla of *P. estesi* is clearly that of a snake and with the exception of the non-hypertrophied palatine process, has no discernable residual lacertilian features we expect any other elements of the same taxon to be similarly “snake-like” in morphology. Three other elements, a pterygoid, a parietal, and a possible palatine, on the same block were referred to *P. estesi*<sup>1</sup>. Of these the pterygoid is almost certainly that of a squamate (palatine process is missing, but its impression remains on the block), but of lacertilian-, not ophidian-grade. The parietal is also referable to Squamata, but of uncertain affinity. Other specimens include an indeterminate

squamate, a crocodylian, and several elements that are too poorly preserved or lacking in distinguishing morphological characteristics for confident referral to any group (Supplementary Fig. 12).

We have also established above that the frontal and the vertebrae of NHMUK R8551 belong to a snake with probable affinities to aff. *Parviraptor estesi*. The other squamate specimens compare more favorably with non-ophidian taxa or are indeterminate. The following is a review of the non-jaw specimens associated with the *Parviraptor* material from England.

#### **A. Parietal (NHMUK R8551, part) (Supplementary Fig. 13a–b)**

The isolated left ‘parietal’ from block NHMUK R8551 was the primary specimen among the three parietals identified<sup>1</sup> for the original reconstruction of the skull of *Parviraptor estesi*. Among squamates paired parietals are limited to most xantusiids, pygopodids, and non-eublepharid geckos<sup>2</sup>. The identification of this element as a parietal is questionable since its structure is unlike that of any squamate parietal (particularly any snake) for which we are aware. Notably, the structures identified as supratemporal processes are semicircular and have a deep, subcircular fossa bounded by a prominent ridge. For all squamates that possess supratemporal processes on the parietal the processes are straight, not curved, and typically taper to a point as they project posterolaterally from the parietal table. Additionally, the anterior (or frontal) margin of this ‘parietal’ courses anterolaterally, not transversely. However, due to the ‘palatine’ overlying the ‘parietal’ we are unable to determine if this margin is natural or a broken edge. If it is natural this shape of the anterior margin is generally similar with that of many crown group snakes, but in these taxa the parietal has anterolateral processes that clasp the frontal and not a V-

shaped contact with the frontal. While identification as a parietal is problematic, we do agree that the general outline of the specimen suggests no reasonable alternative identification<sup>1</sup> and reconstructed the element here as a parietal (Supplementary Fig. 13a–b). In the reconstruction there are some noteworthy anatomical features. There is a small posterior parietal process in line with the main axis of the sagittal margin. It is possible that there was a complementary process on the right parietal, but the sagittal margin deviates to the right and we have reconstructed a single posterior parietal process similar to that in *Gekko gekko* (Supplementary Fig. 13c). A similar process is also present on the fossil gekkonomorph AMNH 21444 from the Early Cretaceous of Mongolia<sup>3</sup> (which also has paired parietals). There is no convincing evidence for or against the presence of a pineal foramen along the visible portion of the sagittal margin of the ‘parietal’ and our reconstruction is commensurately vague in this regard. The supratemporal process is broken distally and its full length and degree of articular relationships are not known.

**B. Parietal (NHMUK R48388, part) (Supplementary Fig. 13d–f).**

A second left parietal from Swanage is on the block NHMUK R48388 (Supplementary Fig. 13d–f). This specimen is preserved in ventral view and has a well-defined, but low crista cranii parietalis. The sagittal margin relatively straight, but is damaged near the anterior end of the element. The anterior margin is also damaged and the nature of the frontal articulation is unknown. Posteriorly there are three processes that extend from the parietal table. Laterally there is the heavily built base of the broken supratemporal process. Just medial to the supratemporal process there is a short posterior parietal tab that projects into the supratemporal fossa. At the medial edge of the parietal is a small posterior parietal process that project

posterolaterally from near the end of the sagittal margin. This posterior parietal process diverges sufficiently from the sagittal margin that we have reconstructed the complete parietal complex as having paired posterior parietal projections. These projections are too short to be considered parietal forks as is seen in NHMUK R12353 from Kirtlington (see below).

It is clear that this parietal is from a different taxon than that of the ‘parietal’ from NHMUK R8551. The structure of this parietal is also sufficiently different than that of any known snakes that it is not referred to aff. *Parviraptor estesi*, but rather is considered as an indeterminate lacertilian-grade squamate.

#### **C. Pterygoid (NHMUK R48388, part) (Supplementary Fig. 14a, b)**

Another specimen from block NHMUK R48388 that is referable to Squamata is a right pterygoid (Supplementary Fig. 14a, b). The specimen is long and gracile. An impression in the limestone preserves the shape of the dorsal surface of the missing palatine process and associated portion of the body. The exact morphology of the palatine articulation (e.g., overlapping vs. interdigitating) cannot be determined from the impression. The ectopterygoid process is short and directed anterolaterally. The quadrate process is long, narrow, and bears a thin crest along the ventromedial surface. The posteriormost portion of the quadrate process was removed when the block was cut and the exact length of the element is unknown. At the anterior end of the quadrate process is a well-developed basipterygoid process with a posteromedially facing articulation facet.

#### **D. ?Palatine (NHMUK R48388, part) (Supplementary Fig. 14c, d)**

The large, complex element opposite of the parietal on NHMUK R48388 was originally identified<sup>1</sup> as a left palatine based on its similarity to the palatine of varanid lizards. We agree that this is the closest comparison and tentatively follow this identification. One difference in this interpretation is that based the relatively flat appearance of the exposed surface we believe that this is more likely a right palatine in ventral view. Based on this tentative identification the element has a long and broad vomerine process, a short and broad pterygoid process, a triangular maxillary process and a semicircular ectopterygoid process. Together these processes form an H-shaped element similar to that of *Varanus* (Supplementary Fig. 14d). Unlike *Varanus* the vomer process of the fossil specimen is turned nearly 90° relative to the same process in *Varanus* (Supplementary Fig. 14c, d). With the dorsal surface embedded in the limestone it is not possible to confirm the presence or absence of the typical choanal and prefrontal processes, but there is no apparent arching of the palatine between the medial and lateral sides. The specimen has suffered one obvious fracture across the body of the element that resulted in the posterior displacement of the vomerine process (corrected in Supplementary Fig. 14c).

### **Review of specimens previously referred to *Parviraptor* cf. *P. estesi***

The Mammal Bed horizon of the Old Cement Works Quarry, Forest Marble (Bathonian), Kirtlington, Oxfordshire, England, has produced a remarkable and diverse microvertebrate fauna that has been recovered through hand quarrying and screen wash concentration. The almost 50 known taxa<sup>4</sup> recovered to date from this fauna include amphibians<sup>5-7</sup>, turtles<sup>8</sup>, choristoderes<sup>9,10</sup>, mammals<sup>4,11-14</sup>, sphenodontians<sup>4</sup>, and lizards<sup>1,15</sup> and now also a snake. The specimens are all isolated elements (i.e., jaws, cranial elements, vertebrae) making their referral to any single taxon

difficult. Under such circumstances any such associations are potential chimaeras and should be regarded carefully prior to utilizing the “taxon” for systematic and taxonomic studies. In the original erection of *Parviraptor*<sup>1</sup> multiple specimens from the Old Cement Works Quarry were assigned to either *P. estesi* or *Parviraptor* cf. *P. estesi*. We have removed the jaw elements (NHMUK R12352, R12354–12356) from *Parviraptor* cf. *P. estesi* and reassigned them to the snake *Eophis underwoodi*. Below is a summary of the other specimens with updated interpretations based on detailed review of each element.

**A. Parietal (NHMUK R12353) (Supplementary Fig. 15a–c)**

This specimen is a partial left parietal with broken processes for the supratemporal-parietal fork. Referral to *Eophis underwoodi* is unlikely. Based on the broken stubs of the processes it is clear that this parietal had a very well developed parietal fork as well as a supratemporal process (Supplementary Fig. 15). The presence of a well-developed parietal fork (= bifid supraoccipital process) also occurs in some scincids (e.g., *Amphiglossus*, *Brachymeles*, *Chalcides*, *Eumeces*, *Sphenomorphus*) cordylids (e.g., *Angolosaurus*, *Cordylus*), and gerrhosaurids (e.g., *Cordylosaurus*, *Gerrhosaurus*, *Tracheloptychus*, *Zonosaurus*). Based on the presence of a parietal fork we refer this specimen to Scincoidea<sup>2</sup> incertae sedis.

**B. Frontals (NHMUK R12356; 12357; 12359) (Supplementary Figs 16a–j; 17a–c)**

These three specimens (Supplementary Fig. 16a–j) were originally identified as paired frontals of *Parviraptor* cf. *P. estesi* from Kirtlington<sup>1</sup>. This identification was based on the presence of a ventral bony process interpreted to be a decensus frontalis similar to that of the

frontal on the Purbeck specimen NHMUK R8551 that articulates with suboptic shelves (see above). Referral of these frontal specimens to a specific taxon is more problematic. As shown herein, the various specimens from Kirtlington originally referred to *Parviraptor* cf. *P. estesi* is actually a mix of lepidosauromorphan and non-lepidosauromorphan taxa. While we agree that these specimens are likely partial frontals it is not clear whether they are referable to the early snake *Eophis underwoodi*, the indeterminate scincomorphan represented by the isolated parietal, the gekkotan represented by the atlas vertebra, or to an hitherto unrecognized squamate in the fauna. Paired frontals are present throughout Squamata ([Gauthier et al., 2012: character 36(1)], while development of a decensus frontalis is less common ([Gauthier et al., 2012: character 38(1, 2, 3)]). The combination of these two characters is most commonly found in gekkonids and some amphisbaenids, although unlike the Kirtlington frontals, the decensus frontalis in gekkonids and amphisbaenids meet at the midline and enclose the olfactory tracts. In the skink *Sphenomorphus* the frontals are paired and the decensus frontalis are developed similarly to those in the Kirtlington specimens. Evans<sup>1</sup> was of the opinion that the Kirtlington specimens she referred to *Parviraptor* cf. *P. estesi* represented juvenile forms. While possible, it seems unlikely that all of the frontals (and vertebrae; see below) recovered would be from a single age class, while no definitive adult forms are present. Pending the recovery of more complete material we feel a referral to Squamata incertae sedis is more appropriate for the isolated frontals from Kirtlington.

### C. “Frontal” (NHMUK R12358) (Supplementary Fig. 18a–c)

This specimen (Supplementary Fig. 18a–c) has a trapezoidal shape characteristic of the other specimens of “frontals” and was originally identified as a left frontal from a juvenile of

*Parviraptor* cf. *P. estesi*<sup>1</sup>. The specimen lacks any of the processes or facets noted for the isolated frontals discussed above. High magnification microscopic examination of the specimen reveals an internal prismatic organization of large, presumably CaCO<sub>3</sub> crystals between two thin nacre layers. This specimen is a fragment of a mollusk shell (Supplementary Fig. 18a–c). Mollusk shells are known to be a common component in the Mammal Bed horizon of the Forest Marble<sup>16</sup>.

#### **D. “Palatine” (NHMUK R8551) (Supplementary Fig. 19a)**

Lying on the surface of the purported parietal on NHMUK R8551 is a small complex element that was originally identified<sup>1</sup> as a left palatine in ventral view. If the specimen is indeed a palatine (see discussion above for specimen from NHMUK R48388), the arched portion exposed indicates that it is more likely to be a right palatine in dorsal view (Supplementary Fig. 19a). The ?palatine from NHMUK R8551 is approximately  $\frac{3}{4}$  of the size of the similar element from NHMUK R48388 (Supplementary Figs 14c, 19b). Aside from size the primary difference between the two specimens is the clear presence of an arching dorsal surface typical of squamate palatines and the presence of a small channel near the anterior end of the ectopterygoid process that, assuming the element is a palatine, would have conducted the neurovascular bundle associated with the maxillary branch of the trigeminal nerve.

#### **E. Vertebrae (Supplementary Figs 20, 21, 22, 23)**

There are 10 vertebral specimens from Kirtlington that Evans referred to *Parviraptor* cf. *P. estesi*. All of these vertebrae share the presence of a notochordal canal in the centrum.

Evans<sup>1</sup> concluded that the presence of the notochordal canal indicated that all of these specimens were from juveniles of *Parviraptor* cf. *P. estesi*. While it is known that an open notochordal canal has been demonstrated to be present in hatchling *Anguis* and *Natrix*, these close soon after hatching<sup>17</sup>. In none of the Kirtlington vertebrae originally referred to *Parviraptor* cf. *P. estesi* are there any centra with closed notochordal canals. To assess the relative ontogenetic age of the vertebrae from Kirtlington we used the timing of the terminal fusion of the neurocentral suture<sup>18</sup> where it was found that in nearly all lizards (with the exception of xantusiids) the neurocentral suture closes near or at the same time as sexual maturity. In all of the vertebral specimens from Kirtlington for which complete or partial pedicles are present—R12364 (Supplementary Fig. 21d) is only a condyle and does not preserve the rest of the centrum—all of the neurocentral sutures appear to be closed and fused. In most of the vertebrae with missing neural arches the bases of the pedicles are fractured exposing cancellous bone indicating that the neurocentral sutures were fused and remodeled. NHMUK R12363 has a clearly broken pedicle, but the bone is so thin that it lacks a cancellous portion (Supplementary Fig. 21c). We interpret this evidence as indicating that these vertebrae are from adult/nearly adult individuals.

Comparison of the condylar portions of the vertebrae (Supplementary Fig. 21f; no condyle is preserved on specimen NHMUK R12368) it appears that there are likely two taxa represented by the vertebral specimens from Kirtlington. In many of the vertebrae the notochord canal at the condyle is displaced dorsally and constricted appreciably (NHMUK R12361, R12362, R12366) or nearly completely closed and present as a narrow slit or foramen (NHMUK R12360, R12363, R12364). The latter morphology does not appear to indicate a stage of closure since these vertebrae include the some of the smallest and as well as largest specimens

(Supplementary Fig. 21f). A similar morphology was common in the procoelus vertebrae of eublapharine geckos<sup>19</sup>, a group considered to be the most primitive of the living gekkotans; recent molecular-based<sup>20–23</sup> and morphology-based<sup>3</sup> phylogenetic analyses support a sister taxon relationship of eublepharids to gekkonids + sphaerodactylids among the living taxa. The difference in the state of closure of the notochordal canals in these specimens may be related to positional differences along the vertebral column and, pending the recovery of more informative specimens we choose to recognize both as likely grades within a single taxon. A closer comparison of these vertebrae is to the eublepharid gekkos (e.g., procoely, notochord canal present throughout centrum) rather than to juvenile anguimorphans or snakes. We reassign these specimens as follows below.

## Supplementary Note 2

### Systematic Paleontology of Reassigned Vertebral Specimens

Squamata Oppel, 1811

Cf. Gekkota Cuvier, 1807

Taxon incertae sedis A

(Supplementary Figs 20a, b e–g; 21a–c)

**Materials.** NHMUK R12360–R12364, R12366; isolated vertebrae. All specimens recovered from the Mammal Bed horizon of the Old Cement Works Quarry, Forest Marble, Kirtlington, England; Late Jurassic (Bathonian).

**Description.** Notochord canal present throughout ontogeny, notochord canal restricted to small opening at dorsal surface of condyle. Specimen specific descriptions as follows:

**NHMUK R12360**—partial atlas vertebra (Supplementary Fig. 20a, b, e–g). The centrum is short, the odontoid process projects from the dorsal aspect of the centrum and preserves a small foramen for a restricted notochord. The opening for the notochord canal on the condylar end is restricted dorsally such that the overall outline of the opening is triangular. There is a fused intercentrum at the anterior end of the centrum with two posterolateral projections and a short hypapophysis centrally. Dorsally the broken bases of the pedicles expose cancellous bone indicating that the neurocentral suture was closed and fused.

This specimen is very similar in morphology to the atlas of a gekkonid (Supplementary Fig. 20c, d). The unusual trifold second intercentrum is also found in gekkonids<sup>24</sup>. A similar

horizontally broad intercentrum (Supplementary Fig. 20a) has been described for some species of the eublepharine genus *Coleonyx*<sup>25</sup>. Additionally the presence of a notochord canal in the axis that is closed at the odontoid process, but open posteriorly is a recognized gekkonid trait<sup>3, 19</sup> and is illustrated here in *Gecko gecko* (Supplementary Fig. 20c). Referral to Gekkonidae incertae sedis is more consistent with the morphology of this vertebra.

**NHMUK R12361**—partial vertebra (Supplementary Fig. 21a). Similar to NHMUK R12360, this specimen possesses a notochord canal. Note the cancellous bone exposed in the broken pedicles (Supplementary Fig. 21a). The opening of the notochord canal on the condyle is displaced dorsally, but lacks the restriction present on NHMUK R12363 and R12364.

**NHMUK R12362**—partial vertebra (Supplementary Fig. 21b). Similar to NHMUK R12361 in the condition of the notochordal canal at the condyle. Note again (Supplementary Fig. 21b) the cancellous bone exposed in the broken pedicles. There is a partially preserved synapophysis near the anterior end of the better preserved right side.

**NHMUK R12363**—partial vertebra (Supplementary Fig. 21c). Similar to NHMUK R12360 in the condition of the notochordal canal at the condyle. The opening of the notochord canal at the cotyle is large, circular, and centrally located. The broken pedicle is very thin and preserves only cortical bone (Supplementary Fig. 21c), but the neurocentral suture is clearly closed and fused.

**NHMUK R12364**—partial vertebra preserving only the condylar portion (Supplementary Fig. 21d). Similar to NHMUK R12363 in the position and degree of restriction of the opening of the notochordal canal at the condyle.

**NHMUK R12366**—nearly complete vertebra (Supplementary Fig. 21e). Neural spine moderately tall with posteriorly displaced apex (broken); pre- and postzygapophyses short; transverse processes broken; cotyle and condyle circular, opening for notochordal canal central in cotyle and displaced dorsally in condyle and only slightly smaller than opening at cotyle (similar to NHMUK R12361).

Taxon incertae sedis B

(Supplementary Fig. 22a–c)

**Materials.** NHMUK R12365, R12367, R12369; isolated vertebrae. All referred specimens recovered from the Mammal Bed horizon of the Old Cement Works Quarry, Forest Marble, Kirtlington, England; Late Jurassic (Bathonian).

**Description.** Vertebrae with complete notochordal canals, condylar opening of notochord canal central and unobstructed. Neurocentral and neural (determined only for NHMUK R12365 and R12367) sutures closed and fused. Neural spines short, condyle ventrally displaced relative to cotyle. Specimen specific descriptions below.

**Discussion.** These vertebrae differ from the gekkonid vertebrae in condylar opening of the notochord canal being circular and located at the center of the condyle. Additionally the condyle is ventral to the cotyle. The closed and fused neurocentral and neural sutures indicates an age at or near sexual maturity<sup>17, 18</sup>. The specimens are referred to Squamata based on the presence of procoely and referred tentatively to Gekkota based on the presence of a complete notochordal canal late into ontogeny. NHMUK R12369 is tentatively included based on the centrally located and circular condylar opening of the notochordal canal. These specimens are not included with the vertebrate in cf. Gekkota taxon incertae sedis A, based on the differences in

the position and shape of the condylar opening of the notochord canal and differences in the relative positions of the condyle and cotyle.

**NHMUK R12365**—nearly complete presacral vertebra (Supplementary Fig. 22a). Neural spine low; prezygapophyses short; postzygapophyses missing; synapophyses well developed; cotyle and condyle circular, opening for notochordal canal central and unobstructed in both cotyle and condyle.

**NHMUK R12367**—nearly complete caudal vertebra (Supplementary Fig. 22b). Neural spine low; prezygapophyses excavated for articulation with postzygapophyses; postzygapophyses missing; transverse processes central, broken; centrum with ventral groove and large subcentral foramina; cotyle and condyle circular, condyle weakly projecting posteriorly; opening for notochordal canal central and unobstructed in both cotyle and condyle.

**NHMUK R12369**—partial ?caudal vertebra (Supplementary Fig. 22c). Condyle circular with centrally placed circular opening for notochordal canal; notochord canal greatly narrowed at mid centrum. Centrum with ventral groove, but lacking subcentral foramina; neural arch and cotyle missing.

## Vertebrata

### Taxon incertae sedis

(Supplementary Fig. 23a–c)

**Materials.** NHMUK R12368, partial vertebrae. Recovered from Mammal Bed horizon of Old Cement Works Quarry, Forest Marble, Kirtlington, England; Late Jurassic (Bathonian).

**Description.** Articular surface platy-amphicoelus, circular, and with centrally placed circular opening for notochordal canal; notochord canal greatly narrowed at mid centrum.

**Discussion.** Based on the relatively flat articular surface it is possible that this specimen is of a sphenodontian, but the lack of preserved diagnostic morphology makes referral to Osteichthyes, Lissamphibia, or even Choristodera possible.

**NHMUK R12368**—partial vertebra (Supplementary Fig. 38). Centrum tightly restricted centrally and with ventral groove, but lacking subcentral foramina (on preserved portion); neural arch, cotyle, transverse processes missing.

## Supplementary Methods

### Materials examined

The extant snake species examined in collections include: *Anomalepis aspinosus* MCZ 14785 (cleared and stained); *Anomalepis flavapices* AMNH R-6966 (CT-scanned specimen); *Leptotyphlops dulcis* AMNH R-160152; *Leptotyphlops humilis* AMNH R-73716, USNM 222795; *Leptotyphlops scutifrons* MCZ 54515 (cleared and stained), MCZ 68781 (cleared and stained); *Rhamphotyphlops braminus* USNM 509423; *Rhamphotyphlops subocularis* MCZ 65993, MCZ 65997, MCZ 72084; *Rhinotyphlops schlegeli* MCZ 29174 (cleared and stained), MCZ 70064 (cleared and stained), MCZ 38551; *Typhlops angolensis* AMNH R-11633; *Typhlops diardi* NHML 1930-5-8-3; *Typhlops lineolatus* MCZ 48063; *Typhlops punctatus* MCZ 7293, MCZ 2249, NHML 1911-6-9-2, NHML 1975-567, SNHM 320704; *Typhlops reticulatus* AMNH R-3001; *Anilius scytale* MCZ 19537, MCZ 2984, MCZ 17645, NHML 58-8-23-48; *Cylindrophis maculatus* NHML 1930-5-8-50; *Cylindrophis ruffus* AMNH R-85647, NHML 1930-5-8-47, USNM 297456; *Rhinophis planiceps* NHML 1930-5-8-69; *Rhinophis sanguineus* NHML 1930-5-8-62; *Uropeltis ocellatus* MCZ 3873; *Uropeltis pulneyensis* MCZ 3870; *Uropeltis rubrolineatus* MCZ 47101; *Loxocemus bicolor* AMNH R-110151, AMNH R-44902, AMNH R-19393, NHML 82-8-17-16; *Xenopeltis unicolor* AMNH R-29969, AMNH R-71531, NHML 1947-1-1-10, NHML 1947-1-1-12, USNM 287277; *Tropidophis canus* AMNH R-45839, AMNH R-73066; *Tropidophis pardalis* FMNH 233; *Ungaliophis panamensis* AMNH R-58845, AMNH R-62639, MCZ 56051; *Boa constrictor* ZFMK 21661, ZFMK 54844; *Calabaria reinhardtii* ZFMK 89190, AMNH R-10092, NHML 1911-10-28-17, UAZM R937 (dissected); *Charina*

*bottae* FMNH 1218, FMNH 22348, FMNH 31300; *Corallus caninus* AMNH R-57788, AMNH R-63587, AMNH R-73347, AMNH R-155263; *Eryx colubrinus* ZFMK 50246; *Eryx conicus* NHML 1930-5-8-14; *Eryx jaculus* FMNH 19624; *Eryx johni* NHML 1930-5-8-34; *Eunectes murinus* AMNH R-54158, AMNH R-29349, AMNH R-29350, AMNH R-57474; *Messelophis variatus* SMF ME-1828; *Messelophis ermannorum* SMF ME-759; *Liasis albertisi* ZFMK 5165, ZFMK 70427; *Morelia spilota* AMNH R-59880, AMNH R-79043, FMNH 22234, FMNH 22380, ZFMK 84282; *Palaeopython fisheri* SMF ME-1002; *Python breitensteini* UAZM R938 (dissected); *Python molurus* NHML 1972-21-78, ZFMK 5161, ZFMK 83431; *Python reticulatus* FMNH 15678, FMNH 51631, NHML 1972-2169, ZFMK 5175, ZFMK 70207; *Acrochordus javanicus* AMNH R-46251, AMNH R-140814, AMNH R-155254; *Pareas carinatus* NHML 1964-1092, NHML 1964-1094, NHML 1964-1098; *Xenodermus javanicus* FMNH 67427; *Atractaspis aterrima* NHML 95-5-3-58, AMNH R-12352 (CT-scanned specimen); *Atractaspis bibroni* AMNH R-82071; *Atractaspis corpulenta* MCZ 4826; *Atractaspis irregularis* FMNH 142994, MCZ 53534, AMNH R-12355; *Atractaspis microlepidota* FMNH 58397; *Homoroselaps lacteus* FMNH 187420, FMNH 187421, FMNH 204893, FMNH 206416; *Agkistrodon piscivorus* ZFMK 21724, AMNH R-81544, AMNH R-57801; *Azemiops feae* FMNH 218628; *Causus rhombeatus* FMNH 2268, FMNH 51692, FMNH 51693, FMNH 164744; *Bitis gabonica* ZFMK 21718, AMNH R-64518, AMNH R-57792, AMNH R-137177; *Cerastes cerastes* ZFMK 53537, ZFMK 5181; *Vipera russelli* AMNH R-75739, AMNH R-74818, ZFMK 5187; *Bungarus fasciatus* AMNH R-56198, AMNH R-76574; *Laticauda colubrina* FMNH 236242, FMNH 234147, FMNH 234149, FMNH 236242, FMNH 236243; *Micrurus fulvius* FMNH 34282, FMMNH 229600; *Micrurus nigrocintus* FMNH 210092; *Naja naja* AMNH R-57807, AMNH R-

74833, ZFMK 21704, ZFMK 21705; *Pelamis platurus* FMNH 171628, FMNH 171632, FMNH 216510; MCZ 7084, MCZ 131501; *Cerberus rhynchops* NHML 58-9-21-3, NHML 1964-10-20; *Homalopsis buccata* NHML 111-18-1-e, NHML 1930-5-8-630, NHML 1930-5-8-631, NHML 1964-11-25; *Coluber caspius* ZFMK 5221; *Coluber viridiflavus* AMNH R-67896; *Dasypeltis scabra* MCZ 30208, MCZ 54894; *Heterodon platyrhinos* AMNH R-63590, AMNH R-69647, AMNH R-155313; *Lampropeltis getulus* AMNH R-70097, AMNH R-75539, AMNH R-128202, ZFMK 54259, ZFMK 5205; *Malpolon monspessulanus* ZFMK 5197; *Natrix natrix* ZFMK 42502; *Oxyrhabdium modestum* FMNH 96532; *Pseudoxenodon macrops* NHML 1930-5-8-271, NHML 1930-5-8-273, NHML 1930-5-8-274; *Thamnophis sirtalis* AMNH R-74849, AMNH R-148084; *Thamnophis validus* AMNH R-62287. Information concerning the cranial osteology of Scolecophidia was complemented by reference to three previous studies<sup>26-28</sup>.

#### Phylogenetic analysis

The following list details the character codings for the maxillae of *Parviraptor*, *Portugalophis* and *Diablophis*; the original character<sup>29</sup> precedes the fossil snake taxon and the state assigned for that character. The remainder of the matrix remained coded as in the original study<sup>29</sup> and is not reproduced here. Analysis of this large matrix resulted in 108,981 shortest trees with the followings supporting statistics: Tree Length [TL] 5290; Consistency Index [CI] = 0.1841; Homoplasy Index [HI] = 0.8159; Retention Index [RI] = 0.7934; Bootstrap support for clade Ophidia: 85 (calculated using TNT).

CH. 5: Premaxillary-maxillary fenestra: (0) absent; (1) present. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (?).

CH. 9: Premaxilla-maxilla suture: (0) firm; (1) loose. *Parviraptor* (1), *Portugalophis* (?), *Diablophis* (?).

- CH. 20: Nasal-maxilla suture: (0) present; (1) absent. *Parviraptor* (1), *Portugalophis* (1), *Diablophis* (?).
- CH 112: Maxilla premaxillary process dorsal surface grooved (often enclosed) for passage of a deeper and more internally placed ramus of the subnarial artery: (0) absent; (1) present. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (0).
- CH. 115: Maxilla facial process height: (0) tall, to skull roof; (1) reduced ; (2) absent; (3) columnar process received in longitudinal concavity on anterior face of prefrontal. *Parviraptor* (1), *Portugalophis* (1), *Diablophis* (1).
- CH 118: Maxilla narial margin rises at: (0) high angle; (1) low angle. *Parviraptor* (1), *Portugalophis* (1), *Diablophis* (1).
- CH 119: Maxilla firmly sutured to palatine: (0) present; (1) prominent palatine process of maxilla; (2) loosely ligamentous connection via projecting palatine process of maxilla and distinct maxillary process of palatine, with the former lying anterior to the latter; (3) maxilla free of palatine, suspended from prefrontal; (4) maxilla rotates to erect fang. *Parviraptor* (?), *Portugalophis* (1), *Diablophis* (?).
- CH 121: Maxilla suborbital process width ventral to ectopterygoid: (0) tapers posteriorly; (1) widens below articulation (i.e., ectopterygoid flange). *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (?).
- CH 123: Maxilla suborbital process tip shape at jugal articulation: (0) suborbital margin slopes smoothly to tip; (1) with distinct step or V-shaped notch distally at jugal articulation. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (?).
- CH 125: Maxilla, intramaxillary joint: (0) absent; (1) present. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (0).
- CH 135: Prefrontal-maxilla articulation: (0) prefrontal posteroventromedial corner narrowly (or not at all) in contact with maxilla lateral to palatine; (1) prefrontal broadly contacts maxilla supradental shelf lateral to palatine; (2) prefrontal has mobile contact with maxilla; (3) rod-like prefrontal arched dorsally, bifid at each end, with mobile joints at maxilla and frontal (prefrontal functionally part of upper jaw). *Parviraptor* (2), *Portugalophis* (2), *Diablophis* (2).
- CH 417: Maxilla, enlarged teeth (fangs) (relative to adjacent teeth): (0) absent; (1) present on anterior maxilla; (2) present on posterior maxilla. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (?).
- CH 420: Maxillary tooth count: (0) 0; (1) 2-5; (2) 7-15; (3) 16-27; (4) 31 or more. *Parviraptor* (3), *Portugalophis* (3), *Diablophis* (?).
- CH 423: Position of marginal teeth relative to tooth-bearing element: (0) on medial side of tooth-bearing element; (1) near/on apical margin of tooth-bearing element. *Parviraptor* (1), *Portugalophis* (1), *Diablophis* (1).
- CH 424: Fusion of marginal teeth: (0) unfused to each other; (1) fused to each other. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (0).
- CH 430: Tooth replacement: (0) present; (1) absent. *Parviraptor* (0), *Portugalophis* (0), *Diablophis* (0).

Character descriptions adapted from recent matrix<sup>30</sup> for ingroup analysis of snakes

The following characters and character states have been adapted and re-evaluated from a previous data<sup>30</sup> that was itself derived from a number of existing data sets<sup>31-36</sup>. Characters bearing an “\*” were recoded for one of more taxa, and most importantly, and noted as such, based on our restudy of the specimens used to create the terminal taxon chimaera for *Coniophis precedens* given in a recent study<sup>30</sup>. We took a much more conservative approach to defining our “*Coniophis*” terminal taxon. For the purposes of this study we used the vertebral assemblage assigned to *C. precedens*<sup>30</sup>, and the right dentary (UCMP 50000) and left maxilla (UCMP 53935) as we agree that these elements belong to some kind of snake even if we question their assignment<sup>30</sup> to *C. precedens* (a vertebral form taxon). It remains possible, and beyond the scope of this study, that these unassociated vertebrae and jaw fragments may represent a second or even third snake in the Lance Formation fauna similar to the multiple snake taxa known from the equivalent and nearby Hell Creek Formation fauna<sup>30</sup>. We also followed the more restrictive concept of *Najash*<sup>31</sup> in coding that taxon as was recently suggested in a conservative revision of the materials assigned to the type of that taxon<sup>32</sup>.

The Traditional Search analysis resulted in 3 trees of length 518 (Supplementary Fig. 24a, b). The main difference between this analysis and PAUP are the positions of *Dinilysia* and *Najash* (sister taxa at base of tree above basal polytomy) and *Coniophis* (sister taxon to *Scolecophidia*). The Parviraptoridae were again placed in an unresolved basal polytomy with weak support in the Frequency Distribution tree (Supplementary Fig. 24b) for a sister taxon relationship between aff. *Parviraptor estesi* and *Diablophis*. The result of the Drift search was three trees of length 515. The Strict consensus tree (Supplementary Fig. 24c) of this analysis has

the same topology as that of the PAUP analysis. The Frequency Distribution tree (Supplementary Fig. 24d) reconstructs a weakly supported resolution of the relationships of *Eophis*, aff. *Parviraptor estesi*, and *Diablophis*. We converted the language of the character descriptions given below into telegraphic language, and reorganized some sentences for both clarity and brevity. The scores for the five new fossil taxa added to this matrix are also given for each scoreable character.

#### Dentition

- \*1. Tooth implantation on dentary: pleurodont (0); Alethinophidian (1). *This character is extremely problematic as “Alethinophidian”<sup>38</sup> is not an anatomical feature and thus does not define a homolog statement of any recognizable kind. We interpret the condition of “Alethinophidian” following the recently defined histological characteristics defined<sup>39-41</sup> for snake alveoli. We rescored Najash, Scolecophidia, and Coniophis as state “1” as none of these snakes show a pleurodont form of attachment – the original coding<sup>30</sup> is contra its own claims that the “interdental” plates are definitive snake morphology and has the effect of forcing Coniophis, Najash and Scolecophidia to the base of the tree. We also note that this character is uninformative but have left it in the analysis for consistency with the earlier study<sup>30</sup>. Parviraptor, Portugalophis, Diablophis and Eophis were scored as “1” for this state based on the possession of alveoli forming “interdental” plates on three sides of the tooth (similar to Xenopeltis, Dinilyisia, Python, etc. [Figs 1a–l; 2a–p; see Supplementary Figs 2, 7]).*
- \*2. Plicidentine: present (0); absent (1). *This character is uninformative, but is retained in this analysis for consistency with an earlier study<sup>30</sup>. All snakes, including Parviraptor, Portugalophis, Diablophis and Eophis, are coded as absent following our observations and utilizing recent definitions and arguments on plicidentine<sup>39-41</sup>.*
- \*3. Maxillary and dentary teeth: relatively short conical, upright (0); robust, recurved (1); elongate needle-shaped, distinctly recurved (2). *Parviraptor, Portugalophis, and Diablophis are the only parviraptorids that possess teeth and are coded as possessing state “2” (Figs 1a–l; 2a–r; Supplementary Figs 2d, e; 7). Scolecophidia was recoded as polymorphic (1&2) to accurately reflect the recurved teeth in the maxilla of Typhlops, and less elongate teeth in the dentary and maxilla of Liotyphlops. Our Coniophis code reflects the teeth as preserved in the maxilla (UCMP 53935) and dentary (UCMP 50000) that we consider to show snake characteristics.*
4. Premaxillary dentition: present (0); absent (1).
5. Alveoli and base of teeth: not expanded transversely (0); wider transversely than anteroposteriorly (1). *Parviraptor, Portugalophis, Diablophis and Eophis were scored as “1” for this state based on the assessment of both the alveoli as preserved, and the attached and isolated teeth (Figs 1a–l; 2a–r).*
6. Pterygoid teeth: absent (0); present (1).

## Skull

7. Premaxilla: broadly articulated with maxilla (0); loosely contacting maxilla (1).
8. Transverse processes of premaxilla: curved backwards (0); extending straight laterally or anterolaterally (1).
9. Nasal process of premaxilla: elongate, approaching or contacting frontals (0); short, divides nasals only at anterior margin or not at all (1).
10. Dorsal (horizontal) lamina of nasal: relatively broad anteriorly, with narrow gap between lateral margin and vertical flange of septomaxilla (0); dorsal lamina of nasal distinctly tapering anteriorly, leaving wide gap between lateral margin and vertical flange of septomaxilla (1).
11. Medial flanges of nasal, articulation with median frontal pillars: present (0); absent (1).
12. Anterior margin of nasals: restricted to posteromedial margins of nares (0); extend anteriorly toward tip of rostrum (1).
13. Lateral flanges of nasals: articulate with anterior margin of frontals (0); separated from frontals (1).
14. Posterolateral margin of nasal: contacts posteromedian margin of prefrontal (0); elements in contact along most of their length (1); contact between elements with interfingering of nasal and prefrontal margins (2); nasals do not contact prefrontals (3).
15. Septomaxilla posterior dorsal process of lateral vertical flange: absent (0); short (1); long (2).
16. Septomaxilla articulation with median frontal pillars: absent (0); present (1).
17. Ventral portion of posterior edge of lateral flange of septomaxilla and opening of Jacobson's organ: located at level of posterior edge or behind (0); distinctly in front (1).
18. Vomeronasal cupola: fenestrated medially (0); closed medially by a sutural contact of septomaxilla and vomer (1).
19. Septomaxilla: forms lateral margin of opening of Jacobson's organ (0); vomer extends into posterior part of lateral margin, restricting septomaxilla to anterolateral part of lateral margin of opening of Jacobson's organ (1).
20. Vomeronasal nerve: does not pierce vomer (0); exits vomer through single large foramen (1); through cluster of small foramina (2).
21. Posterior ventral (horizontal) lamina of vomer: long, parallel edged (0); short, tapering to pointed tip (1).
22. Posterior dorsal (vertical) lamina of vomer: well developed (0); reduced or absent (1).
23. Prefrontal: articulates with frontal laterally (0); anterolaterally (1). *Only aff. Parviraptor estesi can be scored for this character, and even then, only referring to the preserved prefrontal facet on the frontal (Fig. 1b; Supplementary Fig. 2s, t).*
24. Lateral margin of prefrontal: slanting anteroventrally (0); positioned vertically (1).
25. Lacrimal foramen on prefrontal: not completely enclosed (0); enclosed by prefrontal (1).
26. Lateral foot process of prefrontal: absent (0); contacts maxilla only (1); maxilla and palatine (2); palatine only (3).
27. Medial foot process of prefrontal: absent (0); present, low (1); present, high (2).
28. Anterior/lateral flange of prefrontal covering nasal gland and roofing auditus conchae: absent (0); present (1).
29. Ventral margin of lateral surface of prefrontal: articulates with dorsal surface of maxilla (0);

- retains only posterior contact (1).
30. Dorsal lamina of prefrontal: contacts or forms overlapping contact with nasal posteromedially (0); remains separate from nasal (1).
  31. Medial frontal pillars: absent (0), present (1). *Though not figured, the type specimen of aff. Parviraptor estesi, NHMUK R8551, can be examined using microscopy and there is no apparent preservation of the median frontal pillars, nor any evidence they were present. The taxon is scored as "0" for this character (Figs 1b; 2s,r; Supplementary Fig. 3).*
  32. Transverse horizontal shelf of frontal: developed and broadly overlapped by nasals (0); poorly developed and never broadly overlapped by nasals (1); absent (2).
  33. Lacrimal: present (0); absent (1).
  - \*34. Postfrontal: present (0); absent (1). *We refer to a recent study [14] for clarity on identifications of the postfrontal in snakes. Of the new taxa described herein, only aff. Parviraptor estesi can be scored for this character, and even then, only referring to the preserved postfrontal facet on the frontal (Figs 1b; 2s, t).*
  - \*35. Postorbital (JUGAL): present (0); absent (1). *We refer to a recent study<sup>39</sup> for clarity on identifications of the postorbital in snakes, and treat the codings for this character as recognizing the presence of the jugal, not the postorbital. This is a non-trivial difference, but is consistent with all tests of similarity for the identification of this element.*
  - \*36. Ventral tip of postorbital (JUGAL): remains separated by wide gap from ectopterygoid (0); contacts or closely approaches ectopterygoid, forming almost complete posterior margin of orbit (1). *Following the clarity of recent argumentation and Tests of Similarity<sup>42</sup>, we consider the "postorbital" in this character to be the JUGAL, and consider this character to further refine and support previous arguments<sup>42</sup>.*
  37. Dorsal head of postorbital: fuses or articulates with posterodorsal surface of postfrontal (0); articulates with parietal (1).
  38. Parietal: without lateral wings meeting postorbital bones (0); with lateral wings meeting postorbital bones (1).
  39. Distinct lateral ridge of parietal: extending posteriorly from anterior lateral wing up to prootic: absent (0); present (1).
  40. Frontoparietal suture: relatively straight (0); frontoparietal suture U-shaped (1).
  41. Parietal margin of optic foramen: straight (0); concave (1).
  42. Lateral margins of braincase open anterior to prootic (0); descending lateral processes of parietal enclose braincase (1).
  43. Supratemporal processes of parietal: distinctly developed (0); not distinctly developed (1).
  44. Parietal enters anterior aspect of base of basiptyergoid process: absent (0); present (1).
  45. Contact between parietal and supraoccipital: V-shaped with apex pointing anteriorly (0); straight transverse line (1); V-shaped with apex pointing posteriorly (2).
  46. Ascending process of maxilla: tall, extending to dorsal margin of prefrontal (0); short (1); absent (2). *Parviraptor, Portugalophis, and Diablophis were scored as "1" for this character (Figs 1a, c, d, g, h; 2a–c; Supplementary Figs 2; 7; 9–11).*
  47. Small horizontal shelf on medial surface of anterior end of maxilla: present (0); absent (1). *Only Parviraptor and Portugalophis were scored as "0" for this character (Figs 1c, i; 2a, c; Supplementary Figs 2; 7; 9–11), and share this feature with the purported Coniophis maxilla (UCMP 53935).*

48. Posterior end of maxilla: does not project beyond posterior margin of orbit (0); projects moderately beyond posterior margin of orbit (1); projects distinctly beyond posterior margin of orbit, with broad flat surface (2). *Only Parviraptor and Portugalophis can be confidently scored as "1" for this character as the maxilla of Diablophis is broken posterior to the palatine process (Figs 1a,g; 2a,c).*
49. Medial (palatine) process of maxilla: located in front of orbit (0); located below orbit (1). *Parviraptor, Portugalophis, and Diablophis were scored as "0" for this character (Figs 1a,g; 2a,c; Supplementary Figs 2; 7; 9–11).*
50. Medial (palatine) process of maxilla: pierced (0); not pierced (1). *Parviraptor, Portugalophis, and Diablophis were scored as "1" for this character as there is no evidence in any of the parviraptorids of a foramen in the palatine process of the maxilla (Figs 1a,g; 2a,c; Supplementary Figs 2; 7; 9–11).*
51. Anterior end of supratemporal: located behind or above posterior border of trigeminal foramen (0); anterior to posterior border of trigeminal foramen (1).
52. Supratemporal facet on opisthotic-exoccipital: flat (0); sculptured and delineated with projecting posterior rim that overhangs exoccipital (1).
53. Free-ending posterior process of supratemporal: absent (0); present (1).
54. Supratemporal: present (0); absent (1).
55. Anterior dentigerous process of palatine: absent (0); present (1).
56. Medial (choanal) process of palatine: forms extensive concave surface dorsal to ductus nasopharyngeus (0); narrows abruptly to form curved finger-like process (1); forms short horizontal lamina that does not reach vomer (2).
57. Choanal process of palatine: without expanded anterior flange articulating with vomer (0); with anterior flange (1).
58. Pterygoid contacts palatine: complex and finger-like articulations (0); tongue-in-groove joint (1); reduced to flap-overlap (2).
59. Palatine contact with ectopterygoid: present (0); absent (1).
60. Dentigerous process of palatine contact with vomer and/or septomaxilla posterolateral to opening for Jacobson's organ: present (0); absent (1).
61. Maxillary process of palatine: anterior to posterior end of palatine (0); at posterior end of palatine (1).
62. Lateral (maxillary) process of palatine and maxilla: in well-defined articulation (0); loosely overlapping medial (palatine) process of maxilla, or absent (1).
63. Maxillary branch of trigeminal nerve: pierces lateral (maxillary) process of palatine (0); passes dorsally between palatine and prefrontal (1).
64. Vomerine (choanal) process of palatine: articulates broadly with posterior end of vomer (0); meets vomer in well-defined articular facet (1); touches or abuts vomer without articulation or remains separated from vomer (2).
65. Internal articulation of palatine with pterygoid: short (0); long (1).
66. Pterygoid tooth row: anterior to basipterygoid joint (0); tooth row reaches or passes level of basipterygoid joint (1).
67. Quadrato ramus of pterygoid: robust, rounded or triangular in cross-section, but without groove (0); blade-like and with distinct longitudinal groove for protractor pterygoidei (1).
68. Transverse (lateral) process of pterygoid: forms distinct, well-defined lateral projection (0);

- gently curved lateral expansion of pterygoid, or absent (1).
69. Lateral edge of ectopterygoid straight (0); angulated at contact with maxilla (1).
  70. Anterior end of ectopterygoid: restricted to posteromedial edge of maxilla (0); invades dorsal surface of maxilla (1).
  71. Pterygoid attached to basicranium: by strong ligaments at palatobasal articulation (0); pterygoid free from basicranium in dried skulls (1).
  72. Quadrate: slender (0); broad (1).
  73. Quadrate: slanted clearly anteriorly, posterior tip of pterygoid dislocated anteriorly from mandibular condyle of quadrate (0); positioned slight anteriorly or vertically (cephalic condyle positioned behind or at same level of mandibular condyle) (1); slanted posteriorly (cephalic condyle positioned in front of mandibular condyle) (2).
  74. Cephalic condyle of quadrate: elaborated into posteriorly projecting suprastapedial process (0); suprastapedial process absent or vestigial (1).
  75. Stapedial footplate: broad and massive (0); narrow and thin (1).
  76. Stylohyal: not fused to quadrate (0); fuses to posterior tip of suprastapedial process (1); fuses to ventral aspect of reduced suprastapedial process (2); stylohyal fuses to quadrate shaft (3).
  77. Stapedial shaft: straight (0); angulated (1).
  78. Stapedial shaft: slender and longer than diameter of stapedial foot-plate (0); thick, and equal to, or shorter than diameter of stapedial foot-plate (1).
  79. Paroccipital process of otooccipital: well developed and laterally projected (0); reduced to short projection or absent (1).
  80. Juxtastapedial recess defined by crista circumfenestralis: absent (0), present but open posteriorly (1); present and closed posteriorly (2).
  81. Crista circumfenestralis: exposes most of stapedial footplate (0); converges upon stapedial footplate (1).
  82. Crista interfenestralis: does not form individualized component in ventral rim of crista circumfenestralis (0); does form individualized component in ventral rim of crista circumfenestralis (1).
  83. Jugular foramen: exposed in lateral view by crista tuberalis (0); concealed in lateral view by crista tuberalis (1).
  84. Otooccipitals: do not contact each other dorsally (0); contact each other dorsally (1).
  85. Otooccipital posterolateral processes: short and narrow, do not extend toward posterior margin of occipital condyle (0); wider than condyle and long, combine with crista tuberalis to extend to approximate posterior margin of occipital condyle (1).
  86. Supraoccipital contact with prootic: with narrow (0); broad (1).
  87. Prootic exclusion of parietal from trigeminal foramen: absent (0); present (1).
  88. Laterosphenoid: absent (0); present (1). *We note that identification of a "laterosphenoid" for Haasiophis and Eupodophis have recently been contested and revised, and are now recognized as ectopterygoids, not broken flanges underlying the laterosphenoids<sup>43</sup>. We have therefore rescored these two states as "?", not present "1", for these two taxa.*
  89. Prootic ledge underlap of posterior trigeminal foramen: absent (0); present (1).
  90. Prootic: exposed in dorsal view medial to supratemporal or to supratemporal process of parietal (0); fully concealed by supratemporal or parietal in dorsal view (1).
  91. Exit hyomandibular branch of facial nerve inside opening for mandibular branch of

- trigeminal nerve: absent (0); present (1).
92. Vidian canal: does not open intracranially (0); open intracranially (1).
93. Anterior opening of Vidian canal: single (0); divided (1).
94. Sella turcica: bordered posteriorly by well-developed dorsum sellae (0); dorsum sellae low (1); dorsum sellae not developed, sella turcica with shallow posterior margin (2).
95. 'Lateral wings of basisphenoid': absent (0); present (1).
96. Ventral surface of basisphenoid: smooth (0); with weakly developed sagittal crest from which protractor pterygoidei originates (1); with strongly projecting sagittal crest (2).
97. Basioccipital: contributes to ventral margin of foramen magnum (0); basioccipital excluded by medial contact of otooccipitals (1).
98. Basisphenoid-basioccipital suture: smooth (0); transversely crested (1).
99. Basipterygoid (= basitrabecular) processes: present (0); absent (1).
100. Crista trabeculares: short and or indistinct (0); elongate and distinct in lateral view (1).
101. Cultriform process of parabasisphenoid: does not extend anteriorly to approach posterior margin of choanae (0); approaches posterior margin of vomer (1).
102. Parabasisphenoidal rostrum behind optic foramen: narrow (0); broad (1).
103. Parabasisphenoid rostroventral surface: flat or broadly convex (0); concave (1).
104. Basioccipital meets parabasisphenoid: suture located at level of fenestra ovalis (0); located at or behind trigeminal foramen (1).
105. Parasphenoid rostrum interchoanal process: absent (0); broad (1); narrow (2).

#### MANDIBLE

106. Anteromedial margin of dentaries: symphyseal articular facet (0); no symphyseal facet (1).  
*Only Eophis is confidently scored for this character, "1", as the remaining new taxa described herein do not preserve this detail on the identified elements (Figs 1k; 2g; Supplementary Fig. 5a, b).*
107. Posterior dentigerous process of dentary: absent (0); present, short (1); present, long (2).
108. Medial margin of adductor fossa: relatively low and smoothly rounded (0); forms distinct dorsally projecting crest (1).
109. Mental foramina on lateral surface of dentary: two or more (0); one (1). *Only Portugalophis, Diabtophis and Eophis can be scored for this character, "0" and they all large, and two or more mental foramina (Figs 1e, j, l; Supplementary Figs 5c, f, i; 7g, h; 8c; 10g, h).*
110. Coronoid process of coronoid bone: high, tapering distally (0); high, with rectangular shape (1); low, not exceeding significantly coronoid process of compound bone (2).
111. Coronoid bone: present (0); absent (1).
112. Posteroventral process of coronoid: present (0); absent (1).
113. Coronoid process on lower jaw: formed by coronoid bone only (0); or by coronoid and compound bone (1); or by compound bone only (2) (i.e. coronoid absent).
114. Posdentary elements: presence of separate elements (0); fusion of surangular /articular into compound bone (1).

#### VERTEBRAE

- \*115. Chevrons: present (0); absent (1). *We have recoded Wonambi, Eupodophis and Haasiophis*

- as possessing distinct chevron bones*<sup>43</sup>.
- \*116. Hemapophyses: absent (0); present (1). *We have recoded Wonambi, Eupodophis and Haasiophis as possessing distinct hemapophyses*<sup>43</sup>.
  - 117. Hypapophyses: restricted to anterior-most preloacal vertebrae (0); present throughout preloacal skeleton (1).
  - 118. Para-diapophysis: confluent (0); separated into dorsal and ventral facet (1). *Diablophis and aff. Parviraptor estesi are coded as "1" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 119. Prezygapophyseal accessory processes: absent (0); present (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 120. Subcentral paralympathic fossae on posterior preloacal vertebrae: absent (0); present (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 121. Subcentral foramina: absent (0); present, consistently small (1); present, of variable size (2). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 122. Well-developed, consistently distributed paracotylar foramina: absent (0); present (1).
  - 123. Ventral margin of centra: smooth (0); median prominence from cotyle to condyle (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 124. Axis intercentrum: not fused to anterior region of axis centrum (0); fused (1).
  - 125. Neural spine height: well-developed process (0); low ridge or absent (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 126. Posterior margin of neural arch: shallowly concave in dorsal view (0); with deep V-shaped embayment in dorsal view (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 127. Cotyle shape of preloacal vertebrae: oval (0); circular (1). *Diablophis and aff. Parviraptor estesi are coded as "1" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 128. Parazygantral foramen: absent (0); present (1).
  - 129. Lymphapophyses: absent (0); present (1).
  - 130. Lymphapophyses: three or fewer (0); three lymphapophyses and one forked rib (1); more than three lymphapophyses and one forked rib (2).
  - 131. Sacral vertebrae: present (0); absent (1).
  - 132. Position of synapophyses in relation to lateral edge of prezygapophyses: at same level or slightly more projected laterally (0); clearly medial to edge of prezygapophyses (1). *Diablophis and aff. Parviraptor estesi are coded as "1" for this character Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 133. Pachyostotic vertebrae: absent (0); present (1). *Diablophis and aff. Parviraptor estesi are coded as "0" for this character (Fig. 3a,b; Supplementary Fig. 4a–g).*
  - 134. Preloacal vertebrae number: fewer than 100 (0); more than 100 (1).
  - 135. Caudal vertebrae number: greater than 50% of preloacal number (0); approximately 10% or less than preloacal number (1).

136. Tuber costae absent from ribs (0), tuber costae present (1).

#### HINDLIMBS

137. Pectoral girdle and forelimbs: present (0); absent (1).

138. Tibia, fibula, and hind foot: present (0); absent (1).

139. Trochanter externus: present (0); absent (1).

140. Pelvis: external to sacral-cloacal ribs (0); internal to sacral-cloacal ribs (1).

141. Ilium and pubis length: ilium longer than pubis (0); ilium and pubis of same size (1); pubis much longer than ilium (2).

142. Pelvic elements: with strongly sutured contact (0); with weak (cartilaginous) contact (1); fused together (2).

143. Pelvic elements: present (0); absent (1).

#### NEW CHARACTERS (1)

144. Medial vertical flanges of nasals: absent (0); present (1).

145. Preorbital ridge: dorsally exposed (0); overlapped by prefrontal (1).

146. Lateral foot process of prefrontal: articulates with lateral edge of maxilla via thin anteroposteriorly directed lamina (0); articulates with maxilla via large contact that runs from lateral to medial dorsal surface of maxilla (1).

147. Medial finger-like process of ectopterygoid articulating with medial surface of maxilla: present (0); absent (1).

148. Posterolateral corners of basisphenoid: strongly ventrolaterally projected (0); not projected (1).

149. Basioccipital: expanded laterally to form floor of recessus scalae tympani (0); excluded from floor of recessus scalae tympani by otooccipital (1).

150. Frontal subolfactory process: absent or present as simple horizontal lamina (0); present and closing tractus olfactorius medially (1). *In anterior view, the type specimen of aff. Parviraptor estesi, NHMUK R8551, can be observed as possessing state "1" as the subolfactory processes angle sharply to the midline of the element. The taxon is scored as "1" for this character (Fig. 1b; Supplementary Figs 2s-r; 3).*

151. Ectopterygoid contact with pterygoid: restricted to transverse (lateral) process of pterygoid (0); contact expanded significantly on dorsal surface of pterygoid body (1).

152. Maxillary process of palatine: main element bridging contact with maxilla and palatine in ventral view (0); covered ventrally by expanded palatine process of maxilla (1).

153. Coronoid bone contributes to anterior margin of adductor fossa: present (0); absent (1).

154. Coronoid bone: sits mostly on dorsal and dorsomedial surfaces of compound bone, being exposed in both lateral and medial views of mandible (0); applied to medial surface of compound bone (1).

#### TEETH

155. Teeth, implantation: interdental ridges absent (0); interdental ridges present (1). *This character is clearly redundant with Character 1 but is retained here for consistency with the study from which this data set was derived and is being compared to<sup>30</sup> Parviraptor, Portugalophis, Diablophis and Eophis were scored as "1" for this state based on the*

- possession of alveoli forming “interdental” plates on three sides of the tooth (similar to Xenopeltis, Dinilyisia, Python, etc. [Figs 1a–l; 2a–p; Supplementary Figs 2, S7]).*
156. Teeth, replacement: replacement teeth lie vertically (0); lie horizontally in jaws (1).
157. Teeth, replacement: single replacement tooth per tooth position (0); two or more replacement teeth per tooth position (1).
158. Teeth, attachment: ankylosed to jaws (0) teeth loosely attached by connective tissue (1). *This character is clearly redundant with Character 1 but is retained here for consistency with the study from which this data set was derived and is being compared to<sup>30</sup>. Many extant snakes possess hinged teeth, i.e., the teeth are attached by uncalcified periodontal ligaments to the margins of the alveoli, and as such this state overlaps with and is not independent of, Character 1, the “Alethinophidian” attachment condition. Parviraptor, Portugalophis, and Diablophe were scored as “0” for this state based on the possession of alveoli forming “interdental” plates on three sides of the tooth (similar Dinilyisia, Python, etc. [Figs 1a–l; 2a–p; Supplementary Figs 2, 7]).*
- \*159. Teeth, size: crowns isodont or enlarged at middle of tooth row (0) crowns large anteriorly, and decrease in size posteriorly (1); anterior teeth conspicuously elongate, length of crown significantly exceeds height of dentary at midlength (2). *We recoded our combination for “Coniophis precedens” for this character as “?” as the anterior tip of the dentary is missing and the character cannot be scored. Among the parviraptorids, only Portugalophis, was scored for this character with a state “0” [Figs 1i, j; 2k; Supplementary Figs 7, 8).*

## SKULL

160. Premaxilla: teeth borne medially on premaxilla (0); teeth absent from midline of premaxilla (1).
161. Premaxilla: ascending process transversely expanded, partly roofing external nares (0); ascending process mediolaterally compressed, blade-like or spine-like (1).
- \*162. Premaxilla: premaxilla medial to maxillae (0); located anterior to maxillae (1). *We recoded our combination for “Coniophis precedens” for this character as “?” as the anterior tip of the maxilla is missing and the character cannot be scored.*
163. Prefrontal: prefrontal socket for dorsal peg of maxilla absent (0); present (1).
164. Prefrontal extends medially across frontal for more than 75% of width of frontal: absent (0); present (1).
166. Frontal: nasal processes of frontal project between nasals (0); nasal processes absent (1).
167. Frontals: frontals taper anteriorly, distinct interorbital constriction (0); frontals broad anteriorly, interorbital region broad (1).
168. Frontal: subolfactory process abuts prefrontal in immobile articulation (0); subolfactory process articulates with prefrontal in mobile joint (1); subolfactory process with distinct lateral peg or process that clasped dorsally and ventrally by prefrontal (2).
169. Frontals and parietals: do not contact ventrally (0); descending wings of frontals and parietals contact ventrally to enclose optic foramen (1).
170. Parietal, sagittal crest: absent (0); present posteriorly but not anteriorly, and extending for no more than 50% of parietal midline length (1); present anteriorly and posteriorly, and extending more than 50% of parietal midline length (2).

171. Parietal: narrow (0); inflated (1).
173. Skull, postorbital region relative length: short, less than half (0); elongate, half or more (1).
174. Supraoccipital region of skull: nuchal crests absent (0); present (1).
175. Supratemporal: supratemporal short, does not extend posterior to paroccipital process (0); elongate, extending well beyond paroccipital process (1).
176. Maxilla: palatine process short, weakly developed (1); palatine process long, strongly projecting medially (1). *Parviraptor*, *Portugalophis*, and *Diablophis* were scored as “1” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11).
177. Maxilla: facial process (*ascending process as described in this study*) projects up strongly, caudal margin inclined steeply relative to maxilla (0); facial process weakly projecting, caudal margin of facial process lies at angle of 30° to horizontal or less (1). *Parviraptor* and *Portugalophis* were scored as “1” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). NOTE: this character strongly overlaps on Character 46, but is retained here for consistency with that previous study<sup>30</sup>.
178. Maxilla, premaxillary process: medial projection articulating with vomers present (0); premaxillary process does not contact vomers (1). *Parviraptor* and *Portugalophis* show a similar morphology to the condition as observed in the maxilla (UCMP 53935) assigned to *Coniophis*<sup>30</sup> and scored in that data matrix. While we agree that the morphology of these three elements is similar, none of them are preserved as intact skulls demonstrating empirically observable articulations. Many extant snakes (e.g., *Xenopeltis*) possess medial processes of the maxilla in the same position as those observed in *Parviraptor*, *Portugalophis* and *Coniophis*, which articulate with no other elements, though they approach the septomaxilla or premaxilla. Only in lizards, does this process contact the vomer. We have elected to score this character as “?” for these three taxa as we cannot confirm or discount a vomer contact (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11).
179. Maxilla, number of mental foramina: 5 or more (0); 4 or fewer (1). *Portugalophis* shows state “0”, while *Diablophis* shows at least state “1” with 4 preserved foramina. However, we have elected code *Diablophis* as “?” because the posterior portion of the maxilla is missing (Figs 1d, h; Supplementary Figs 7c,d; 10c,d).
- \*180. Maxilla, supradental shelf development: extending full length of maxilla (0); reduced anterior to palatine process (1). *Parviraptor*, *Portugalophis*, and *Diablophis* were scored as “0” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). *Coniophis* was rescored as “?” because UCMP 53935 preserves only the anterior portion of the maxilla.
- \*181. Maxilla: medial surface of facial process with distinct naso-lacrimal recess demarcated dorsally by anteroventrally trending ridge: (0) present; (1) absent. *Parviraptor*, *Portugalophis*, and *Diablophis* were scored as “1” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). As UCMP 53935 does not preserve the ascending/facial process, this character was scored as “?” for *Coniophis*.
- \*182. Maxilla: medial surface of facial process with well-defined fossa for lateral recess of nasal capsule: present (0); reduced and present as small fossa on back of facial process (1); absent, fossa for lateral recess developed entirely on prefrontal (2). *Parviraptor*, *Portugalophis*, and *Diablophis* were scored as “2” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). As UCMP 53935 does not preserve the ascending/facial process, this

- character was scored as “?” for Coniophis.*
- \*183. Maxilla: extensive contact of dorsal margin of maxilla with nasal (0); nasal-maxilla contact lost (1). *As UCMP 53935 does not preserve the ascending/facial process, this character was scored as “?” for Coniophis.*
  - \*184. Maxilla: maxilla overlaps prefrontal laterally in tight sutural connection (0); overlap reduced, mobile articulation (1). *As UCMP 53935 does not preserve the ascending/facial process, this character was scored as “?” for Coniophis.*
  - \*185. Maxilla: excluded from anteroventral margin of orbit by jugal (0); maxilla forms anteroventral margin of orbit (1). *Coniophis was rescored as “?” because UCMP 53935 preserves only the anterior portion of the maxilla.*
  - \*186. Maxilla: palatine process of maxilla projects medially (0); palatine process of maxilla downturned (1). *Parviraptor, Portugalophis, and Diablophis were scored as “0” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). Coniophis was rescored as “?” because UCMP 53935 preserves only the anteriormost portion of the maxilla, exclusive of the palatine process.*
  - \*187. Maxilla: superior alveolar foramen: positioned near middle of palatine process, opening posterodorsally (0); positioned near anterior margin of palatine process, opening medially (1). *Parviraptor, Portugalophis, and Diablophis were scored as “-” for this character (Figs 1a,c,d,g,h; 2a-c; Supplementary Figs 2; 7; 9–11). Coniophis was rescored as “?” because UCMP 53935 preserves only the anteriormost portion of the maxilla, exclusive of the palatine process.*
  - \*188. Maxilla, accessory foramen posterior to palatine process: absent (0); present (1). *Only Portugalophis was scored for this character, with the state assignment being “0”. Coniophis was rescored as “?” because UCMP 53935 preserves only the anteriormost portion of the maxilla, exclusive of the palatine process.*
  - \*189. Maxilla, ectopterygoid process: absent (0); present (1). *Coniophis was rescored as “?” because UCMP 53935 preserves only the anterior portion of the maxilla.*
  - \*190. Maxilla: articulates with distally expanded postorbital element to form complete postorbital bar: present (0); absent (1). *Coniophis was rescored as “?” because UCMP 53935 preserves only the anterior portion of the maxilla.*
  - \*191. Maxilla: 15 or more maxillary teeth (0); fewer than 15 maxillary teeth (1). *Coniophis was rescored as “?” because UCMP 53935 is incomplete.*
  - 192. Postfrontal: anterior and posterior processes clasping frontals and parietals (0); anterior and posterior processes present, but postfrontal abuts frontals and parietals (1); anterior and posterior processes absent (2).
  - 193. Supratemporal: free caudal end of supratemporal projects posteroventrally (0); posteriorly or posterodorsally (1).
  - 194. Quadrate, lateral conch: present (0); absent (1).
  - 195. Quadrate, maximum length relative to proximal width: quadrate elongate, maximum length at least 125% of maximum width of quadrate head (0); quadrate short, length less than 125% of width of quadrate head (1).
  - 196. Quadrate, proximal end platelike: absent (0); present (1).
  - 197. Palatine, palatine teeth small relative to lateral teeth (0); or enlarged, palatine teeth at least half diameter of posterior maxillary teeth (1).

198. Palatine, elongate lateral process projecting to lateral edge of orbit to articulate with caudal margin of prefrontal: absent (0); present (1).
199. Epipterygoid: present (0); absent (1).
200. Ectopterygoid: clasps pterygoid anteromedially (0); ectopterygoid overlaps pterygoid (1); ectopterygoid abuts pterygoid medially (2).
201. Vidian canals: enclosed in sphenoid (0); open intracranially (1).
202. Vidian canals: posterior openings symmetrical (0); asymmetrical (1).
203. Exoccipitals: separated ventral to foramen magnum (0); contact below foramen magnum (1).
204. Exoccipital-opisthotic: horizontal, winglike crista tuberalis absent (0); present (1).
205. Otoccipitals: do not project posteriorly to level of occipital condyle (0); project posteriorly to conceal occipital condyle in dorsal view (1).
206. Sclerotic ring: present (0); absent (1).

#### MANDIBLE

- \*207. Dentary, enlarged mental foramen: absent (0); present (1). *The original coding (1) had this character coded as polymorphic. Our observations of scolecophidian snakes find that all mental foramina present are in fact very large in relationship to the size of the dentary. We recoded the character to only state "1". Portugalophis, Diablophis and Eophis were scored as "1" for this character (Figs 1e, j, l; Supplementary Figs 5c,f,i; 7g,h; 8c; 10g,h).*
- \*208. Dentary, depth of Meckelian groove anteriorly: deep slot (0); shallow sulcus (1). *We recoded our combination for "Coniophis precedens" for this character as "1" as the Meckelian groove is not deep. Portugalophis, Diablophis and Eophis were scored as "0" for this character (Figs 1f, i, k; 2g-k; Supplementary Figs 5a-i; 7i, j; 10e, f).*
- \*209. Dentary, angular process shape: posteroventral margin of dentary angular process weakly wrapped around underside of jaw (0); dentary angular process projects more nearly horizontally to wrap beneath jaw (1). *We recoded our combination for "Coniophis precedens" for this character as "?" as the posterior portion of the dentary, key to the character description, is missing<sup>30</sup> and is not comparable to Dinilyisia or any other snake. Portugalophis, Diablophis and Eophis were scored as "1" for this character (Figs 1e, j, l; 2g-k; Supplementary Figs 5a-i; 7i, j; 10e, f).*
210. Dentary, angular process length relative to coronoid process: angular process distinctly shorter than coronoid process, former terminating well anterior to latter (0); subequal in length posteriorly (1).
211. Dentary, symphysis: weakly projecting medially (0); hooked inward and strongly projecting medially (1). *This character is redundant with Character 106, however for consistencies sake it is retained in this analysis. Only Eophis is scored for this character with state "0".*
- \*212. Dentary, ventral margin: unexpanded, medial margin of dentary straight in ventral view (0); expanded, medial margin crescentic in ventral view (1). *We recoded our combination for "Coniophis precedens" for this character as "?" as the posterior portion of the dentary, key to the character description, is missing. Portugalophis, Diablophis and Eophis were scored as "0" for this character (Figs 1f, i, k; 2g-k; Supplementary Figs 5a-i; 7i, j; 10e, f).*
213. Dentary, coronoid process: wraps around surangular laterally and medially (0); broad and sits atop surangular (1).

- \*214. Dentary, coronoid process with slot for medial tab of surangular: absent (0) or present (1).  
*We recoded our combination for “Coniophis precedens” for this character as “?” as the posterior portion of the dentary, key to the character description, is missing.*
- \*215. Dentary, subdental shelf: present along entire tooth row (0); present only along posterior portion of tooth row (1); absent (2). *We completely rewrote the original characters 215 and 216 as recently presented<sup>29</sup>, condensing them into our Character 215. Portugalophis, Diablophis and Eophis were scored as “0” for this character (Figs 1f, i, k; 2g–k; Supplementary Figs 5a–i; 7i, j; 10e, f).*
216. Dentary, enlarged mental foramen position: near tip of dentary (0); displaced from tip of jaw (1); displaced further to lie halfway between symphysis and surangular notch (2).
217. Surangular, dentary process with distinct triradiate cross-section: absent (0); present (1).
218. Surangular, adductor fossa: small (0); extended caudally towards jaw articulation (1).
219. Surangular: ventrolateral surface of surangular bearing distinct crest for attachment of adductor muscles: absent (0); present (1).
220. Coronoid, lateral overlap of coronoid onto dentary: absent (0); present (1).
221. Splenial attachment to dentary above Meckel’s canal: close throughout length (0); loose, with dorsal dentary suture confined to posterodorsal corner of splenial (1); (2) contact with subdental shelf reduced to small spur of bone or contact lost entirely.
222. Splenial – angular articulation: splenial overlaps angular (0); splenial abuts against angular to form hinge joint (1).
223. Splenial, size: splenial elongate, extends more than half distance from angular to dentary symphysis (0); splenial short, extends less than half distance from angular to symphysis (1).
224. Splenial, anterior mylohyoid foramen: present (0); absent (1).
225. Angular, lateral exposure (with coronoid region pointing dorsally): angular broadly exposed laterally along length (0); angular narrowly exposed laterally (1).
226. Angular, length posteriorly relative to glenoid (quadrate articulation): relatively long, extends more than half distance from anterior end of angular to glenoid; (0) relatively short, half or less of distance to glenoid (1); very short, one third or less of distance to glenoid (2).
227. Surangular, enlarged anterior surangular foramen: absent (0); or present (1).
228. Coronoid eminence: (0) well-developed; (1) weakly developed or absent.
229. Glenoid, shape: quadrate cotyle shallow (0), anteroposteriorly concave and transversely arched, ‘saddle shaped’ (1). *While we recognize a probable surangular bone amongst the Diablophis materials, we are conservative in scoring that element here for its contribution to the glenoid shape as the element does not appear to be a compound bone, but an isolated surangular. As such it either represents an early stage in snake compound bone evolution, or, it is not part of the Diablophis taxon and belongs to a contemporary lizard (Supplementary Fig. 10i–k).*
230. Retroarticular process: retroarticular process elongate (0) or shortened (1).
- \*231. Ventral projections (pedicles) of anterior preloacals: short, about 50% length of centrum (0); long, subequal to or longer than centrum (1). *We note that the “pedicles” [4] are not homologs of intercentra, but rather are the hypapophyses and potentially the fused intercentra (pedicles) as represented by snakes such as Pachyrhachis, Dinilysia, Eupodophis, and Haasiophis<sup>43</sup> where the intercentra are not fused to the hypapophyses.*
232. Vertebrae, ridgelike or bladeliike ventral keels developed posterior to pedicles: (0) absent;

- (1) present. *Diablophis* and aff. *Parviraptor estesi* were scored as “0” for this character (Fig. 3a, b; Supplementary Fig. 4a–g).
233. Vertebrae, dorsolateral ridges of neural arch: (0) absent; (1) present. *Diablophis* and aff. *Parviraptor estesi* were scored as “0” for this character (Fig. 3a, b; Supplementary Fig. 4a–g).
- \*234. Vertebrae, vertebral centrum: narrow in ventral view (0); broad and subtriangular in shape (1); broad and square (2). We added a character state “2” to this character in order to recognize a primary homology between pachyophiid/simoliophiid snakes concerning centrum shape and pachyostosis. *Diablophis* and aff. *Parviraptor estesi* were scored as “0” for this character Fig. 3a, b; Supplementary Fig. 4a–g).
235. Vertebrae, arterial grooves: absent in neural arch (0); present (1). The vertebrae of both aff. *Parviraptor estesi* and *Diablophis* appear to show this snake synapomorphy, but only *Diablophis* was assigned state “1” as the aff. *Parviraptor estesi* material is not well enough prepared. The “trefoil”<sup>29</sup> condition of the neural canal is easily observed in *Diablophis*.
236. Vertebrae, posterior condyle: confluent with centrum ventrally (0); distinctly separated from centrum by groove/constriction between centrum and condyle (1). *Diablophis* and aff. *Parviraptor estesi* were scored as “1” for this character (Fig. 3a, b; Supplementary Fig. 4a–g).
237. Vertebrae: narrow, width across zygapophyses not significantly greater than distance from prezygapophyses to postzygapophyses (0); vertebrae wide, width across zygapophyses 150% of length or more (1). *Diablophis* and aff. *Parviraptor estesi* were scored as “0” for this character (Fig. 3a, b; Supplementary Fig. 4a–g).

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