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THE OCCIPITO-VERTEBRAL JOINT IN THE BURROWING SNAKES OF THE FAMILY UROPELTIDAE

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In 1939, R. Hoffstetter described an amazing condition of the head joint in the peculiar burrowing snakes of South India and Ceylon — the Uropeltidae. Quite in contrast with the condition found in all other amniotes, the first vertebral centrum was said to be fused with the occipital condyle, while the second vertebral centrum was unmodified and procoelous like those behind it. According to Hoffstetter, also, the atlas neural arches, united ventrally by a ligament, embraced the neck of the occipital condyle. The species he personally examined was *Rhinophis blythii.*

The head joint of *Rhinophis planiceps* (= *R. philippinus*), as Hoffstetter was well aware, had previously been described by Baumeister (1908, pp. 499-502, fig. 22). He, like Hoffstetter, had found the first vertebral centrum (= odontoid process) to be absent as a distinct structure. His account differed, however, from that given more than thirty years later by Hoffstetter in one very important detail. He did not find the atlas embracing the neck of the occipital condyle; instead it was in its normal place posterior to and articulating with the head of the condyle. Baumeister also interpreted the situation very differently, believing the first vertebral centrum to have been reduced and for the most part fused with and forming the major element in the anterior articular surface of the second vertebral centrum.

Whether as described by Hoffstetter or by Baumeister, it is sufficiently evident that the head joint in the uropeltids examined by them is profoundly different from the head joint in any other amniotes. In the course, therefore, of a general study of the head joint in reptiles I have found it necessary to give

special attention to this feature in this family and in related groups. The simple anatomy of the articulation needed to be carefully restudied, its taxonomic incidence established, and its morphological interpretation reassessed.

Since a detailed discussion of these points would be a lengthy digression in any more general paper, I publish this account separately.

Skeletons of the following members of the family Uropeltidae have been specifically prepared for this study. In each case the head joint was examined at the moment of separation of head and vertebral column and before further preparation.

Melanophidium wyandense
Platypletrurus madurensis
Plectrurus perroteti
Pseudotyphlops philippinus
Rhinophis blythii
philippinus
sanguineus
Teretrurus rhodogaster
Uropeltis ceylanicus
ocellatus
pulneyensis
rubrolineatus

This list includes at least one member of every genus currently recognized in the family and several species of two of these genera, including both the species for which the head joint has previously been described.

In this suite of specimens differences of a specific or generic character are indeed observable, but they involve only minor details. The general pattern is remarkably uniform.

In every case the second vertebra articulates directly and by a simple concavity with the ball-like convexity of the occipital condyle. *There is no intervening odontoid process.* The condylar articular surface is never notched dorsally or indented medially.

An atlas neural arch is always present. It is never placed over the neck of the condyle, as reported by Hoffstetter (Fig. 1B), but instead is, as Baumeister stated, always in articulation posteriorly with the neural arch of the second vertebra, and ventroanteriorly with the ball-like convexity of the occipital

condyle. In its articulation with the occipital condyle it furnishes a dorsolateral supplementary rim to the cup-like anterior concavity of the centrum of the second vertebra.

An atlas ventral arch may or may not be present. It is present as a distinct element only in *Uropeltis pulneyensis* (Figs. 3A and B). In some of the forms examined it may have been fused

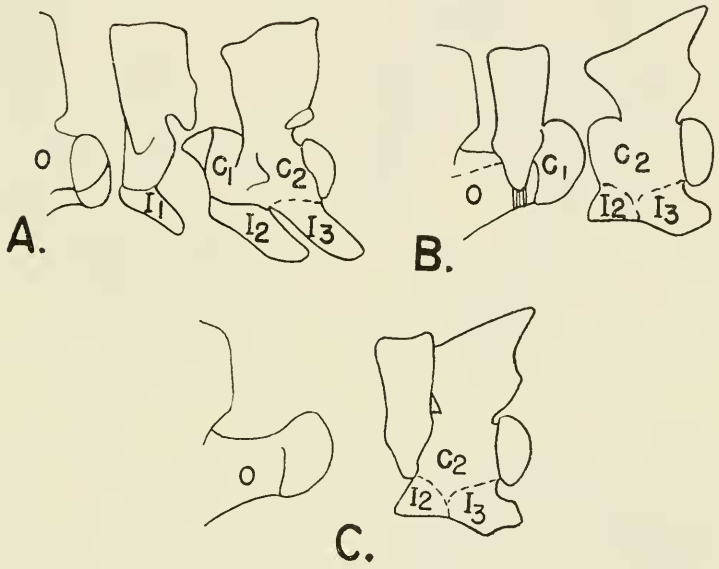

Fig. 1 A. Head joint of *Typhlops steinhausi* (after Hoffstetter). B. Head joint of *Rhinophis blythii* (after Hoffstetter). C. Real condition of the head joint of *Rhinophis blythii*. *Abbreviations:* C_1 = centrum 1, the odontoid; C_2 = centrum 2, the axis centrum. I_2 = second intercentrum; I_3 = third intercentrum. O = occiput.

into the ventral margin of the anterior concavity of the second centrum. The presence of a slight anteroventral projection — absent in *U. pulneyensis* — is suggestive of this (Figs. 2B and D; Fig. 3D).

The contribution of the pedicels of the atlas neural arch-halves or of the ventral arch (when present) to the concavity which receives the occipital condyle, is in all cases minor. The

major articular surface is always provided by the second centrum.

The uropeltid head joint may be usefully contrasted with that of a more primitive snake, *Cylindrophis rufus*, which is quite typical of the more usual squamate condition.

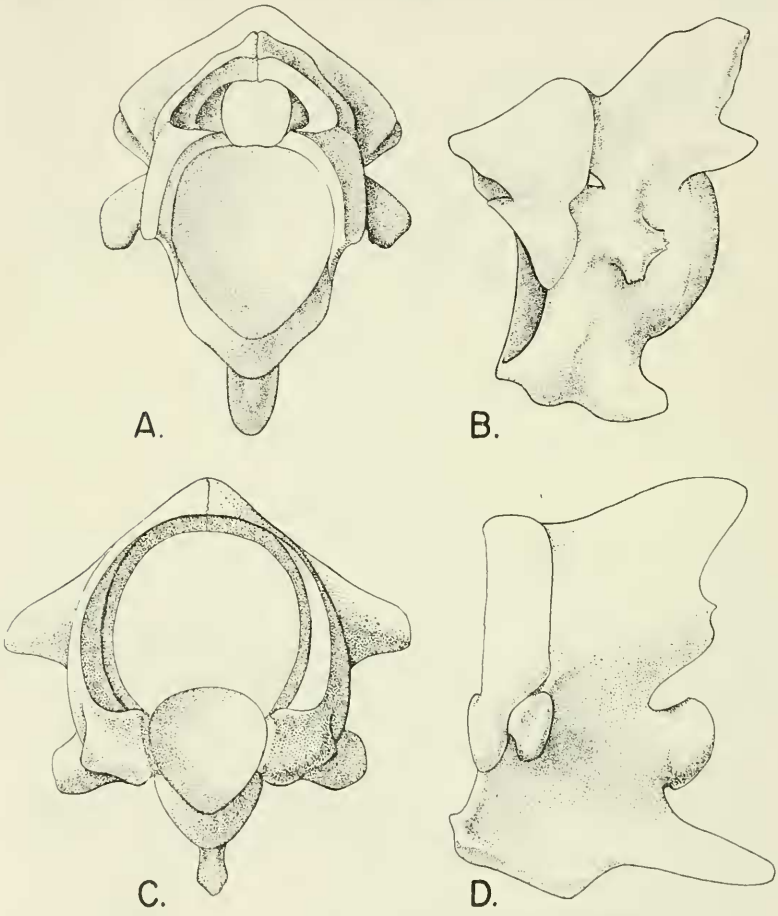

Fig. 2 A. Anterior view, atlas and axis of *Rhinophis sanguineus*. B. Side view, atlas and axis of *Rhinophis sanguineus*. C. Anterior view, atlas and axis of *Platyplectrurus madurensis*. D. Side view, atlas and axis of *Platyplectrurus madurensis*.

In *Cylindrophis rufus* the occipital condyle bears definite traces, in well-marked grooves, of its origin by the union of three bones and is not hemispherical but distinctly indented on its dorsal surface. This indentation is the *fovea dentis* (Gaupp, 1908, p. 518), and is the place of attachment of the *ligamentum apicis dentis*. In many forms this ligament chondrifies or ossifies in whole or in part as a small conical projection from the odontoid process which it is then convenient to call an *apex dentis* (new term). In *C. rufus* the apex dentis is a small cartilage cone.

The occipital condyle is received into a concavity formed by the ventral portions of the atlas ring, the lateral margins of which are formed by large articular surfaces on the pedicels of the atlas neural arch-halves and the articular surface of the ventral arch.

The dorsal margin of the concavity is furnished by the *ligamentum transversum atlantis*, while the outer portion of the bottom of the cup is the *septum interarticulare* (Gaupp, 1908, p. 528). Beneath the ligamentum transversum atlantis and perforating the *septum interarticulare* by means of the *foramen septi* the apex dentis projects forward into the *fovea dentis* of the condyle.

The contact of the occipital condyle in *C. rufus* is thus primarily with the atlas ring and its associated ligaments, only to a minor degree with the odontoid process, mostly by its apex dentis, and not at all with the centrum of the second vertebra.

The atlas ring in *C. rufus*, as in other typical squamates, forms posteriorly a cup for the reception of the odontoid process, entirely similar to that described for the occipital condyle. The same parts participate in a substantially similar way.

The odontoid process in *C. rufus* projects forward from the second vertebra. It is not a conical, distinctly tooth-shaped process, as in most mammals. In *C. rufus* it is an essentially wedge-shaped element, flat dorsally, posteriorly with a flat surface that is suturally united with the true centrum of the second vertebra. Its anterior surface slopes sharply backward. Medially, just below the point of juncture of anterior and dorsal surfaces the small cartilaginous cone that is the apex dentis arises so abruptly as to seem a separate element; it has frequently, though probably incorrectly, been regarded as representing the vestigial centrum of a proatlantic vertebra.

Ventral and somewhat posterior to the odontoid process is the second or axis intercentrum, an element much larger than the odontoid process; it is suturally united to the ventroanterior surface of the true centrum of the second vertebra and projects

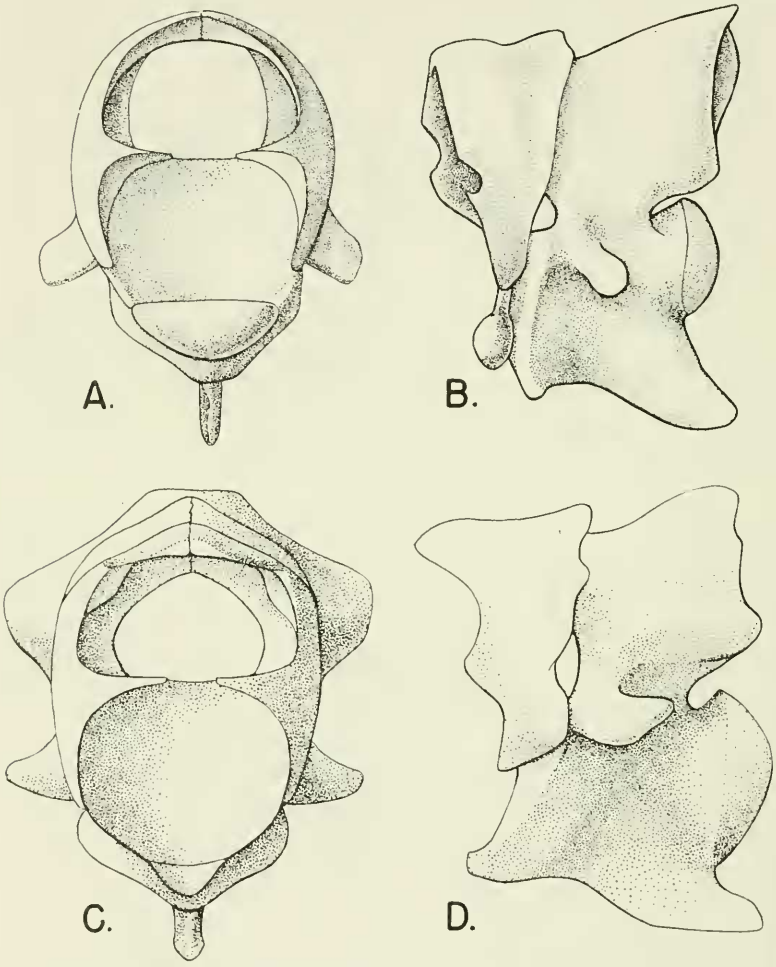

Fig. 3 A. Anterior view, atlas and axis of *Uropeltis pulneyensis*. B. Side view, atlas and axis of *U. pulneyensis*. C. Anterior view, atlas and axis of *Uropeltis ocellatus*. D. Side view, atlas and axis of *U. ocellatus*.

obliquely backward as the first of two ventral spines on the axis vertebra. Anteriorly this element articulates with the ventral arch of the atlas.

With minor differences in details of shape and size this description would serve for the head joint of any typical squamate or of *Sphenodon* (cf. *Typhlops,* Fig. 1A), and with no serious modifications except in regard to relative size of the odontoid process and second intercentrum, it will serve for any crocodile or most turtles.

The essential differences between the uropeltid head joint and that typified by *Cylindrophis rufus* are:

1. The condyle of the uropeltids lacks a fovea dentis.
2. There is neither a ligamentum apicis dentis nor an apex dentis.
3. The articular surfaces on the atlas neural arch pedicels are reduced.
4. The atlas ventral arch is reduced as a whole or more frequently has disappeared altogether as a distinct element.
5. There is no odontoid process.

Somewhat aberrant among squamates is the head joint of *Cylindrophis maculatus* of Ceylon (Fig. 4). The occipital condyle is not notched dorsally, nor indented medially. The grooves indicating the place of union of the three participating bones, are, however, present. There was apparently no ligamentum apicis dentis or apex dentis. The basal portions of the atlas ring — including the neural arch pedicels, but especially the ventral arch — are highly developed. The two neural arch pedicels almost meet mid-dorsally, reducing the ligamentum transversum atlantis to an extremely short connection between the two. The area which could have been filled by a septum interarticulare is very small; perhaps there was none. The odontoid process itself seems somewhat reduced and truncate in front.

In certain ways in which uropeltids differ from typical squamates, *C. maculatus* appears to be modified in a direction opposite to that seen in the uropeltids. The basal parts of the atlas are enlarged in *C. maculatus,* reduced in uropeltids.

In certain other ways *C. maculatus* approaches the uropeltids: in the absence of the fovea dentis and of the correlated ligamentum apicis dentis or apex dentis.

Even the enlargement of the atlas basal elements can, however, be interpreted as tending in the direction of the uropeltids. The typical squamate and other reptilian condition is complex, essentially two joints, one within the other. On the outside there is a major condylar convexity fitting into an atlantal cup; inside this is a joint oriented in the opposite direction — a convexity arising from the odontoid (atlas centrum), fitting into a small concavity within the condyle. See diagram Figure 5A.

The uropeltids and *C. maculatus* have simplified this arrangement by abolishing the internal odontoid joint and perfecting a

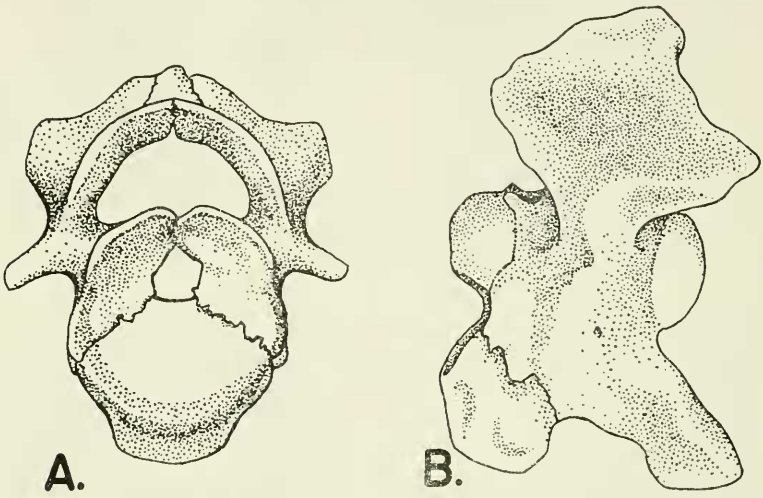

Fig. 4. *Cylindrophis maculatus*. A. Anterior view of atlas. B. Side view of axis.

ball and socket joint entirely comparable to the joints between vertebrae, posteriorly. (Fig. 5B.)

If this be the correct interpretation of the results achieved by the uropeltid – *C. maculatus* modification, it may reasonably be wondered why the extreme uropeltid condition was found adaptively necessary. *C. maculatus* has achieved a reasonably good ball and socket joint without losing the odontoid process entirely. A hypothesis may be offered here, for future mechanical and functional analysis to test. The axis of *C. maculatus* even with some reduction of the odontoid is much longer than

the vertebrae behind it. The uropeltid axis on the contrary is *as short or shorter than* the vertebrae behind it. We may assume that in the still unanalyzed functioning of the uropeltid head joint this shortening of the axis[1] has been mechanically and thus selectively valuable. That this shortening has been accomplished by reduction of the odontoid to essential nullity we may believe to have been an accident of evolution in this specialized group — or we may see in it the culmination of a trend begun in an ancestral form which must have been similar to *C. maculatus*.

It must be explained that although *C. maculatus* occurs in the same area as the uropeltids, shows in several respects special morphological resemblances to them, and may well have had a long history independent of other members of the group, part of the resemblances between *maculatus* and the uropeltids may well

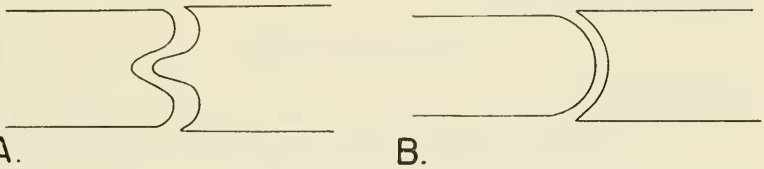

Fig. 5. Diagrammatic horizontal section of the head joint region. A. in most reptiles. B. in uropeltids.

be parallelism. At least, as Bellairs and Underwood (1951, p. 231) have indicated, the presence of two ventral transverse scale rows to each body segment in uropeltids rather than one as in *Cylindrophis* is possibly primitive and prompts the inference that the uropeltids have not been directly derived from *Cylindrophis* or its immediate relatives.

Thus, while it is interesting to suggest that the uropeltid head joint may in the course of its evolution have gone through a stage directly comparable to that in *C. maculatus* — a stage in which the basal parts of the atlas were enlarged rather than reduced — there is no compelling reason derived from any demonstrated direct phyletic relation of *C. maculatus* to the uropeltids to accept such a stage as a necessary intermediate. It would appear

[1] Most uropeltids have also elongated the pedicel of the occipital condyle, but this is not true in *Melanophidium* which seems in skull and scutellation the most primitive member of the family.

simpler to suppose that in the uropeltids the modification of the head joint was accomplished from the first by strong reduction of the ventral parts of the atlantal ring and of the odontoid simultaneously. The question is one, however, on which critical evidence is unavailable.

If the course of evolution of the uropeltid head joint is likely to remain for some time unknown, more hope may be offered that its ontogeny can be examined. The uropeltids are ovoviviparous; it will therefore be worthwhile to examine the collections already in existence for pregnant females. Though this would be unlikely to provide a stage by stage view of the ontogeny of the head joint region, in the present state of our knowledge *any* glimpse of the development (as of the function or the evolution) of this region in uropeltids would put us substantially farther ahead.

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