

## The skeleton of a juvenile *Lanthanotus* (Varanoidea)

Olivier Rieppel

Dept. of Geology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, USA

**Abstract.** The cleared and stained skeleton of a juvenile *Lanthanotus borneensis* provides additional evidence for the “cervicalization” of an anterior dorsal vertebra, resulting in the 9 cervical vertebrae thought to be diagnostic of the Varanidae. *Lanthanotus* shows two complete sternal ribs associated with the vertebral segments 10 and 11, and an incomplete sternal rib associated with the 9th segment; *Varanus* shows three complete sternal ribs associated with the vertebral segments 10, 11 and 12. The loss of a sternal rib associated with the 12th segment is autapomorphic for *Lanthanotus*. Nine cervical vertebrae may be diagnostic for the genus *Varanus* only, since *Lanthanotus* preserves a rudimentary sternal rib associated with the 9th vertebral segment, at least at some stage of its ontogeny. A free carpal “intermedium” is absent (or variably present) in *Lanthanotus*. The pattern of epiphyseal calcification in the carpus and tarsus of *Lanthanotus* is described and compared to *Varanus*.

### Introduction

*Lanthanotus borneensis* has become known as one of the crucial taxa in the assessment of phylogenetic relationships at higher levels of squamate taxonomy (McDowell and Bogert, 1954; Rieppel, 1988). Its interpretation ranges from a “living fossil” to a snake ancestor (McDowell, 1972). Due to the scarcity of material, only adult skeletal material of this varanoid lizard has been available for study until now (McDowell and Bogert, 1954; Rieppel, 1980a, 1983). This is unfortunate in view of the crucial importance of ontogeny for character polarization and phylogeny reconstruction (see Rieppel, 1990, for a discussion and references). The following contribution presents observations on the skeleton of a juvenile specimen which differ from, or emend, the earlier descriptions of adult material (Rieppel, 1980a). The limited ontogenetic information thus made available bears on character conceptualization in the cladistic analysis of varanoid lizards, adding evidence to the hypothesized status of *Lanthanotus* as sister-taxon (subfamily Lanthanotinae) to varanid lizards (Varaninae) within a monophyletic Varanidae, itself sister-taxon to the Helodermatidae within a monophyletic Varanoidea (Pregill, Gauthier and Greene, 1986).

## Material and methods

The Field Museum of Natural History, Chicago (FMNH), keeps a juvenile specimen of *Lanthanotus borneensis* (FMNH 130981) with a snout-vent length of 64.5 mm prior to preparation for clearing and staining. Cartilage was stained with Alcian Blue, bone with Alizarin Red, the specimen cleared by Trypsin digestion (Dingerkus and Uhler, 1977). The specimen was compared to cleared and stained juvenile specimens of *Varanus* (*Varanus bengalensis* FMNH 182533, snout-vent length 12.9 mm; *Varanus exanthematicus* FMNH uncatalogued, snout-vent length 11.3 mm; *Varanus griseus* FMNH 11071, snout-vent length 10.6 mm; *Varanus salvator* FMNH 152229, snout-vent length 11.5 mm).

Additional skeletal material used for comparison includes the following. Anguillidae: *Diploglossus costatus* (FMNH 13254); *Diploglossus millepunctatus* (FMNH 19248); *Gerrhonotus liocephalus infernalis* (FMNH 22452); *Gerrhonotus validus* (FMNH 215858). Xenosauridae: *Shinisaurus crocodilurus* (FMNH 234242; a cleared and stained juvenile specimen). Helodermatidae: *Heloderma horridum* (FMNH 22038); *Heloderma suspectum* (FMNH 98774, 22249). Varanidae: *Varanus acanthurus* (FMNH 218083); *Varanus bengalensis nebulosus* (FMNH 22495); *Varanus dumerilii* (FMNH 223194); *Varanus exanthematicus microstictus* (FMNH 22354); *Varanus gouldi* (FMNH 51706); *Varanus griseus* (FMNH 51705); *Varanus prasinus* (FMNH 229966); *Varanus salvator* (FMNH 211938, 31320, 31358).

## Morphological description

### *The skull and hyobranchial skeleton*

In dorsal view the skull shows some juvenile characteristics such as paired, i.e. as yet unfused nasal processes of the premaxilla and paired nasal bones. The posterior portion of the external naris, between nasal and prefrontal, is wider than in adult specimens, suggesting that the posterior elongation of the external naris in varanoid lizards and snakes is a paedomorphic feature (on related phenomena see Irish, 1989; the same holds also for the independent posterior elongation of the external naris in chamaeleons: Rieppel, in prep.). The parietal is fully fused, leaving no indication of a parietal foramen, but the fronto-parietal suture is not yet fully closed, and the parietal is still notched at the midline of its anterior margin. The parietal does, however, overlap the frontal bone with anterolateral articular lappets (also described for *Varanus*: Rieppel, 1979), thus allowing functional mesokinesis. The prefrontal already contacts the “postorbitofrontal” along the posterodorsal margin of the orbit. The “postorbitofrontal”, bracing the fronto-parietal suture laterally, appears as a single ossification. There is no indication of fusion of an originally separate postfrontal and postorbital except for a distinct bifurcation of the posterior tip of the bone, absent in the adult.

As would be expected in a juvenile the skull discloses, in ventral view, a weak contact between vomer and palatine bones on the one hand, between palatine and pterygoid bones on the other hand (see Irish, 1989). In *Lanthanotus*, the opening of Jacobson’s organ is separated from the choana by a deep dorsolateral process of the vomer which is present, but appears only weakly ossified, in the juvenile. If this is an expression of a temporal sequence of ossification, it would indicate that the

neochonate follows the palaeochonate condition in development, corroborating the derived condition of the former type of palate. In an earlier contribution I cautiously suggested that the skull of *Lanthanotus* might be platybasic (Rieppel, 1983). The cleared and stained specimen shows that the trabeculae do indeed remain separate for some considerable distance between the parasphenoid-basisphenoid and the frontal downgrowths (another pedomorphic feature), but fuse to form a trabecula communis before entering between the frontal downgrowths. The skull, therefore, is technically tropibasic. While details of the chondrocranium were difficult to determine, a taenia marginalis—lacking in snakes—is present; a pila antotica, however, seems to absent as it also is in *Varanus* (Shrivastava, 1964).

The bony elements of the braincase are all unfused. A large fontanelle persists between the basisphenoid and the basioccipital ossifications, representing the fenestra basicranialis of the embryonic basal plate. The supraoccipital bears a cartilaginous ascending process meeting the posterior edge of the parietal.

The epipterygoid is well ossified, capped dorsally and ventrally by cartilage. Its dorsal head relates to the taenia marginalis which follows the lateral downgrowth of the parietal. The quadrate, again, is capped dorsally and ventrally by cartilage. Meckel's cartilage can be followed from the lower jaw symphysis back to the cartilage covering the articular ossification. The distal end of the ossified stapes relates to an elaborate cartilaginous extracolumella, accommodated in the posterior concavity of the quadrate. This observation lays to rest the controversy surrounding the question as to whether the stapes of *Lanthanotus* abuts against the shaft of the quadrate or not (see McDowell, 1967, and Rieppel, 1980b). The extracolumella bears a distinct internal process right distal to its juncture with the bony shaft of the stapes.

The hyobranchial skeleton is closely comparable to the condition described for the adult (Rieppel, 1981, fig. 1A). The transversely orientated basihyal bears an anterior entoglossal process and anterolateral hypohyals, articulating with ceratohyals. All of these elements are cartilaginous. The ossified first ceratobranchials articulate with the posterolateral corners of the basihyal and bear short, cartilaginous epibranchials. A feature not recorded for the adult is a distinct, forked lateral process halfway along the ceratohyal, loosely wrapping around the posterior tip of the retroarticular process. A similar, but smaller process was observed on the ceratohyals of juvenile varanids.

#### *The axial skeleton*

The regionalization of the reptile axial skeleton is largely a matter of definition. The 1st dorsal vertebra is usually defined by the 1st sternal rib (Hoffstetter and Gasc, 1969). 9 cervical vertebrae and 2 sternal ribs were reported for the adult *Lanthanotus* (Rieppel, 1980). The juvenile specimen FMNH 130981 shows 2 complete sternal ribs, articulating with the 10th and 11th vertebrae, and meeting the sternum posteriorly and posterolaterally as in the adult (Rieppel, 1980, fig. 5). This leaves 9 cervicals as described for the adult. However, a free ending, cartilaginous sternal rib segment was

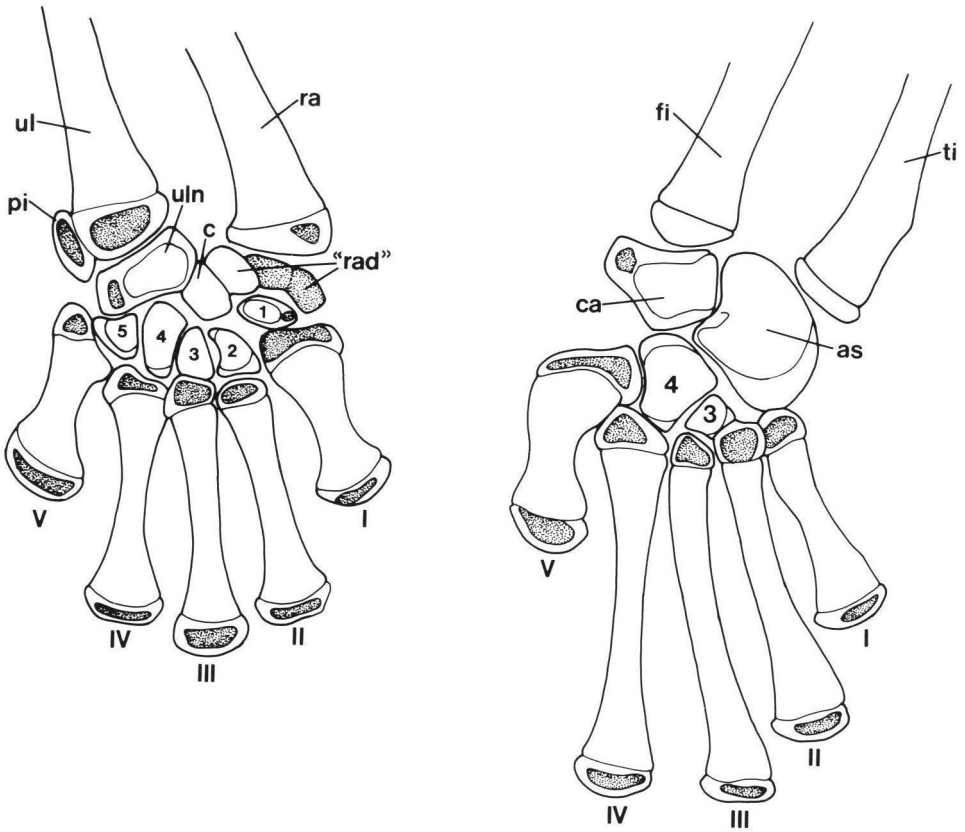
observed to articulate with the lateral edge of the roughly triangular sternum, a rib segment which has lost continuity with the ossified rib articulating with the 9th vertebra. The juvenile, cleared and stained *Varanus* all show three complete sternal ribs associated with the 10th, 11th and 12th vertebrae. The first sternal rib of varanids contacts the sternum posterolaterally, in a position comparable to the first complete sternal rib of *Lanthanotus*. The incomplete sternal rib segment of *Lanthanotus*, however, belonging to the 9th segment, relates to the sternal plate in a similar anterior and lateral position as does the anteriormost complete sternal rib associated with the 9th segment in most other lizards, and in all anguimorphs with the exception of *Varanus* (see also Lécuru, 1968a). These observations suggest, as will be further discussed below, that the 9 cervical vertebrae diagnostic for the Varanidae result from the cervicalization of an anterior dorsal element. In view of the juvenile specimen here described, there remains some ambiguity whether *Lanthanotus* should be characterized as having 8 or 9 cervicals.

The total vertebral count for the cervical and dorsal region is 38 in the juvenile *Lanthanotus* (FMNH 130981). There is one true lumbar vertebra with no rib; the three preceding vertebrae show ribs of distinctly smaller size as compared to more anterior ribs. There are two sacral vertebrae bearing fully fused sacral ribs (pleurapophyses). The total vertebral count for the caudal region is 65 or 66. The peduncles supporting the chevron bones are already well developed. The first chevron bone articulates with the first caudal vertebra, but it is of a rudimentary or reduced appearance, which is why it may be missing (or may have been overlooked) in the adult (Rieppel, 1980a).

#### *The appendicular skeleton*

The pectoral girdle compares well to the adult condition (see Rieppel, 1980a fig. 5) except for two details. The anterolateral and posterolateral tips of the anterior transverse expansion of the interclavicle are drawn out into delicate, tapering processes, of which the posterior ones are longer than the anterior ones. No posterior coracoid foramen is, as yet, present in the juvenile. Should it develop during later growth stages (rather than its presence being variable), its late appearance in ontogeny would corroborate its derived status.

Of some considerable interest is the pattern of carpal and tarsal ossifications (fig. 1). The carpus includes a total of 11 ossification or calcification centers respectively. There is a pisiforme, lying ventro-latero-distal to the as yet unfused epiphysis of the ulna. Distal to the ulna lies the large ulnar cartilage which incorporates two ossification or calcification centers respectively, the large medial ulnare proper and a small lateral calcification, representing an epiphysis on the ulnare. In the juvenile, cleared and stained *Varanus*, the ulnare bears a diminutive lateral calcification center (epiphysis) in *V. exanthematicus* and *V. griseus* only. Distal to and between radius and ulna lies the large intermedium which seems continuous with a "calcification" (ossification?) distal to the radius (the "radiale": see Shubin and Alberch, 1986, for



**Fig. 1.** The carpus and tarsus of *Lanthanotus borneensis* (FMNH 130981). Left: the right carpus in dorsal view; right: the right tarsus in dorsal view. Abbreviations: as, astragalus; c, centrale; ca, calcaneum; fi, fibula; pi, pisiforme; ra, radius; "rad", "radiale"; ti, tibia; ul, ulna; uln, ulnare; 1-5, distal carpals and tarsals respectively; I-V, metacarpals and metatarsals respectively.

a discussion of the homology of that bone). The juvenile *Varanus* clearly show the fusion of the intermedium with an originally separate ossification distal to the radius, which explains the suture observed on the adult radiale by Renous-Lécuru (1977: 752 and fig. 33). This is in agreement with Shubin and Alberch's (1986) scheme, according to which the reptile intermedium fuses into what has been called the radiale. The description of a separate intermedium in the adult *Lanthanotus* by Renous-Lécuru (1977) and Rieppel (1980a) may be erroneous, based on the misidentification of some sesamoid ossification, or the presence of a separate "intermedium" is variable. In fact it remains to be seen which lizards do retain a separate "intermedium" (its first description by Born, 1976, was based on *Lacerta*), and what the homology of this separate element indeed is. The carpus is completed by the centrale and the 5 distal carpals, of which the 4th is the largest (in accordance with its position on the primary axis of the limb: see Shubin and Alberch, 1986).

The tarsus of the juvenile *Lanthanotus* FMNH 130981 incorporates a total of five ossification or calcification centers respectively. Distal to the fibula lies the fibular cartilage, which incorporates a larger inner ossification center (the calcaneum) and a small outer calcification (an epiphysis on the calcaneum). The latter is lacking in all the juvenile *Varanus* examined. The astragalus is a single large ossification in the juvenile *Lanthanotus* with no signs of fusion. It lies between tibia and fibula, and expands laterally distal to the tibia. In the cleared and stained *Varanus* examined, there is a small calcification lying between the astragalus on the one hand and the metatarsal 1 (and 2nd distal tarsal) on the other, and which seems just about to fuse with the astragalus (representing an astragalar epiphysis); the astragalus bears no epiphysis in the juvenile *Lanthanotus*. The tarsus of the latter is completed by the distal tarsals 4 and 3, of which the 4th is again larger. The phalangeal formula is the same as that described for the adult, 2-3-4-4-3, with the reduction of 1 phalange in the 4th digit of manus and pes.

## Discussion

The study of a juvenile specimen does not alter the phylogenetic position of *Lanthanotus*, the sister-taxon of *Varanus*. It does, however, result in the re-interpretation of a number of characters.

The Varanidae have been diagnosed, *inter alia*, by 9 cervical vertebral elements, the highest count among tetrapod squamates. The majority of lizards shows 8 cervical vertebrae (Hoffstetter and Gasc, 1969), the first sternal rib being associated with the lateral edges of the sternum. This is also the condition observed in all anguimorphs examined (see the section on Material and methods), except the Varanidae. All of the non-varanid anguimorphs share 4 (5; 1 of which xiphisternal, in the anguioids) complete sternal ribs, associated to the vertebrae 9 through 12 (13). The lack, in the Varanidae, of a sternal rib associated with the 9th segment, and articulating with the lateral edge of the sternum, suggests that the increase in the number of cervical vertebrae (by one element) resulted from the "cervicalization" of an anterior dorsal vertebra. That the pectoral girdle has shifted posteriorly in the Varanidae was indicated by the observation of Lécure (1968b), who showed that the first root of the brachial plexus derives from the spinal nerve which passes between the 6th and the 7th vertebrae in *Varanus* and *Lanthanotus*, but between the 5th and the 6th vertebrae in *Heloderma* and most other lizards. Further support for this hypothesis is provided by the juvenile specimen of *Lanthanotus* here described, which shows a rudimentary and cartilaginous sternal rib segment, articulating with the lateral edge of the sternum, but having lost continuity with the rib related to the 9th segment which would correspond to the anteriormost sternal rib in other lizards. This indicates that the posterior displacement of the pectoral girdle by one segment resulted in the loss of the anteriormost sternal rib in the Varanidae, a hypothesis which requires further testing by more complete developmental data. At the same time some ambiguity remains as to whether

*Lanthanotus* should be characterised by 8 cervical vertebrae since it preserves that sternal rib rudiment at some stage during its ontogeny, leaving 9 cervicals as being diagnostic of the genus *Varanus*.

That an anterior dorsal vertebra is incorporated into the cervical series in the Varanidae is also indicated by vertebral morphology. The cervical vertebrae of the Varanidae are diagnostic in that hypapophyses are sutured to distinct peduncles formed by the vertebral centrum (the axis bears two hypapophyses) (Hoffstetter and Gasc, 1968). In *Lanthanotus*, the 6th cervical vertebra is the last one to carry a hypapophysis; the 7th bears a ventral keel, the 8th and the 9th show a flat ventral surface (Rieppel, 1980a). In the *Varanus* here examined (see the section on Material and methods), it is the 7th (sometimes the 8th) cervical which carries the last hypapophysis; the 8th (9th) cervical vertebra carries a ventral keel, and the lower surface of the 9th cervical vertebra is flat. The only exception is *Varanus bengalensis nebulosus* (FMNH 22495), which carries a small hypapophysis on a ventral keel on the 9th cervical vertebra. This shows that although the 9th cervical vertebra is indistinguishable, on morphological grounds, from succeeding dorsal ones in most Varanidae, "cervicalization" may effect the morphology of this element.

All anguimorphs here examined, except *Lanthanotus*, show a posterior sternal rib (the posteriormost in the Varanoidea) associated with the 12th vertebral segment; its absence must therefore be an autapomorphy of *Lanthanotus*. *Lanthanotus* and *Varanus* also differ in the pattern of epiphysis formation in the carpus and tarsus. The loss of the "intermedium" in the carpus is not autapomorphic for *Varanus*, but shared by *Lanthanotus* (the question of homology of the free "intermedium" in the lizard carpus is addressed above). In addition, the juvenile *Varanus* here described document the calcification of a distal epiphysis on the astragalus. The amniote (and, by implication, the reptilian) astragalus has been identified as a fusion of the amphibian tibiale, intermedium, and proximal distale (Peabody, 1951; Romer, 1956; Gauthier, Kluge and Rowe, 1988). Neither the juvenile *Lanthanotus*, nor the cleared and stained *Varanus* specimens here described, show any sign of fusion of originally separate ossifications in the formation of the astragalus. However, Romer (1956: footnote to p. 393), mentioned the possibility, in some extant reptiles, of fusion of the astragalus with additional ("adjacent") tarsal elements with no bearing on "the question of primary formation of the bone". Without commenting any further on the homology of the amniote astragalus with the amphibian tibiale, intermedium and proximal centrale, the "adjacent" tarsal element which contributes to the formation of the astragalus in some extant reptiles is most likely to represent an epiphyseal calcification, as here described for *Varanus*.

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