Longitudinal sliding articulations in pipid frogs

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THE FUSED SACRUM AND UROSTYLE OF THE pipid frog *Xenopus laevis* is a familiar object. It has, for instance, been found at archaeological sites[1] and used to identify the animal in the gut contents or excreta of predators.[2] Yet it exhibits a striking feature which appears to have been mentioned or illustrated very rarely, namely, fluted articulating facets. The fluting, in the longitudinal direction, limits lateral turning and vertical bending between vertebrae. Longitudinal movement also occurs between the ilia and the sacral vertebra, but investigations in the latter half of the twentieth century have not included documentation of earlier work, nor reference to longitudinal fluting of vertebral articulations. In this account, previously unconnected data on the functional anatomy of this familiar animal and its fossil relatives on both sides of the South Atlantic are brought together, and taxonomic implications are indicated.

Mayer,[3] in 1835, published an excellent illustration (Taf. II, fig. 6) of the dorsal view of a skeleton, referred to as *Pipa africana* (*Xenopus laevis*), made available to him by Dr Schlegel of Leyden. It shows greatly expanded diapophyses (transverse processes) of the sacrum, the lateral edges of which appear to be parallel. Peters,[4] in 1882, expanding on his description of *Dactylethra muelleri* Peters, 1844 (now *Xenopus*), provided accurate illustrations of the skeleton of this pipid taxon. A striking feature of the dorsal view was that the posterior tips of the sacral diapophyses are seen in grooves in the parallel ilial shafts. Hilgendorf,[5] in 1884, commented on Peter's illustration when he reported the backwards and forwards movement of the ilia over the sacral diapophyses in the pipid aquatic frogs, *Pipa*, of South America, and *Xenopus* (as *Dactylethra*) of Africa. Hilgendorf's work seems to have been totally overlooked (at least as far as *Xenopus* is concerned).

In a monograph on *Xenopus*, Grobbelaar[6] in 1924 illustrated muscles attached anteriorly and posteriorly to the ilia, namely the M. longissimus dorsi and the M. coccygeo-iliacus, respectively, and referred to the function of the former in relative movement of trunk and head (and by implication antagonism by the latter). As part of his interest in respiratory movements, Willem[7] included *Xenopus* among his subjects. He noticed the iliosacral mobility and first attributed a breathing function to it,[8] and then later[9,10] concluded that it was involved instead in food capture and deglutition. Iliosacral movement affects the length of the post-sacral region of the intact animal; Willem measured the contraction movement as about one and a half centimetres in a specimen of 14 cm snout/vent length, i.e. about 10–11%. Willem's account was well illustrated and his last paper[10] included simultaneous records of movements of the gular region, mid abdomen, flanks, nostrils and pharynx of *Xenopus*; he referred to no previous work on *Xenopus*, and in turn his contribution seems not to have been noticed up to the present time.

Working on a student project in a laboratory where locomotion was a main interest, Palmer independently observed iliosacral movement in *Xenopus.*[11] She found a 20% difference in extended and contracted animals. The stimulus for this work included the discovery in a comparative study on anuran locomotion.[12] Both Palmer and Whiting consider a shock-absorbing function for the iliosacral movement in *Xenopus*, yet both incorrectly state that Grobbelaar[6] considered the iliosacral joints to be more or less immobile, apparently failing to understand that Grobbelaar used *fixiert* to mean to make fast or 'stabilize' (*cf.* Gaupp's classic work,[13] where *fixiert* by bilateral action in *Rana* is contrasted with movement by unilateral action). Whiting[12] also considered respiratory and hydrostatic functions besides increased length of effective stroke in locomotion.

Emerson[14,15] distinguished three types of iliosacral articulation, and the locomotory movement associated with each: where there are more or less cylindrical diapophyses, the ilia rotate dorsoventrally, as in *Rana*, studied by Green[16] and mentioned also by Willem;[17] where the diapophyses are moderately dilated, some lateral rotation in the horizontal plane is possible, one ilium moving forward and the other backward, thus turning the pelvis on the sacrum; where the diapophyses are greatly expanded and have parallel lateral edges, as in the pipids, anterior–posterior movements in a horizontal plane are maximized. Videler and Jorna[18] observed a movement of about 16% of snout/vent length in *Xenopus*. They noted that shortening occurs in response to observed threat, and considered backwards movement a function, in addition to lengthening of effective stroke. Whiting[12] noted from X-ray images, indications of the same type of iliosacral movements in South America *Pipa* as in *Xenopus,* and included another African pipid genus, *Hymenochirus.*

Vergnaud-Grazzini[19] described the sacra of Moroccan xenopodine fossils from the Miocene, but these did not have intact transverse processes. The ilia all lacked much of the shaft, but were very like that of *Xenopus*, including *X. tropicalis* to which she considered the fossils closest. She noted that the vertebral zygapophyses were simple, unlike those of *X. laevis, X. muelleri, X. fraseri* and *X. tropicalis*, which had longitudinal furrows (*sillons*). Similar furrows had been reported by Bolkay[20] and illustrated by Zaplata,[21] and described in developing *Xenopus laevis* by Bernasconi.[22] Estes[23,24] referred to Vergnaud in describing *Xenopus romeri* from the South American Palaeocene, which he also considered closest to *Xenopus tropicalis.* He illustrated ventral views of fused first and second vertebrae of *X. romeri* and *X. tropicalis*, showing the zygapophyses. There is no indication of fluting of the postzygapophyses in the former, while shading indicates its presence, although not mentioned, in the latter.[24] A lateral view of a fragmentary ilium gives no indication of the heightening anteriorly, which would indicate an internal shelf, as in *Silurana* (*X. tropicalis* + *epitropicalis*) and presumably all extant *Xenopus* species. Báez and Trueb,[25] in redescribing the Palaeogene South American pipid *Shelania*, collated information on a number of pipids and produced consensus trees based on 51 features. They found that *Xenopus*, *Silurana* and *X. romeri* shared a common node (node F) characterized by one shared derived feature — the scapula is reduced in size. *Xenopus* and *Silurana* had several features in common, including prezygapophyses with 'sulci and ridges'. They illustrated a vertebra of *Xenopus muelleri*. Whether the outer edges of the sacral diapophyses, or the anterior ends of the ilia, are near parallel, is not one of the characteristics included in the analysis. Henrici and Báez[26] reported as follows on an Upper Oligocene *Xenopus*: 'Although they are not clearly visible because the vertebrae are preserved in articulation in all the specimens, sulci and ridges are present on the pre- and postzygapophyses.' (p. 876). The ilia are parallel and the sacrum expanded as in other *Xenopus*.

In 1997 I examined Pliocene anuran fossils from Langebaanweg, west coast of the Western Cape, South Africa.[27] The zygapopophyses of all the xenopodine post-atlas vertebrae, including the sacrum,

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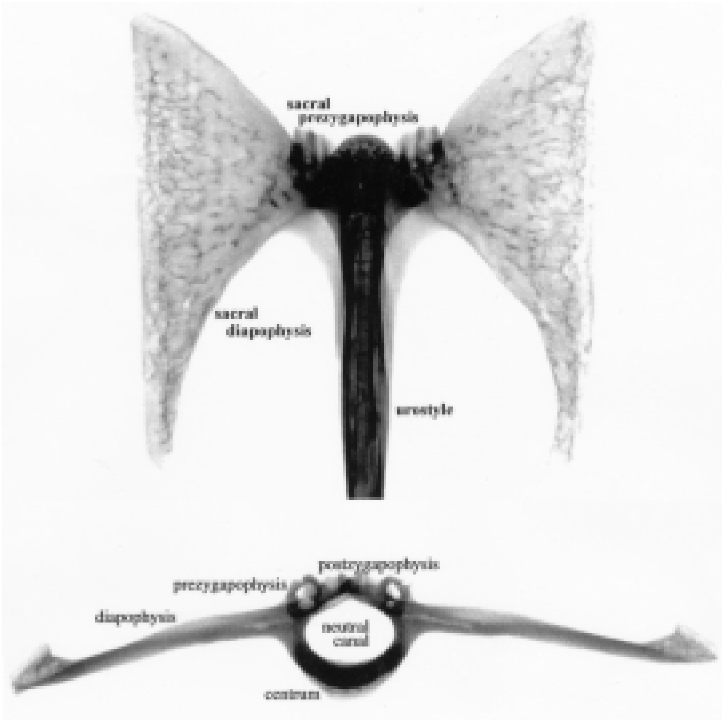

Fig. 1. X-ray images of the sacrum and third vertebra of a *Xenopus laevis*. **Top**: dorsal view of the sacrum. **Bottom**: posterior/anterior view of the third vertebra. Note the tilt of the planes of both anterior and posterior zygapophyses to near vertical and thus close to parallel to the sagittal plane; the prezygapophyses are closer and facing outwards, the postzygapophyses are further apart and facing inwards.

were found to be longitudinally fluted, as in *Xenopus*, but the plane of the zygapophyses was less tilted than in *Xenopus* (Fig. 1). No sacrum has yet been found with sufficient of a diapophysis preserved to establish whether its lateral edge was parallel to the sagittal plane. The similarity of the inner aspects of specimens of ilia found to those of extant *Xenopus* suggests that the sacro-iliac articulations are similar. This would mean that sacral shape and fluted zygapophyses occur together in a Pliocene xenopodine, in common with *Xenopus* and *Silurana*.

Longitudinal displacement of the ilia relative to the sacrum, possibly due to post-mortem contracture, is evident, sometimes in only some specimens, in a number of fossil pipids.[28–32] The ilia slide over the sacrum independently of fluting of the zygapophyses. It is noteworthy that fluted zygapophyses are reported from the Late Oligocene of Yemen,[26] are specifically stated to be absent in Miocene fossils of Morocco,[19] and are clearly present in the Pliocene. The high angle of the zygapophyses evident in Fig. 1 (bottom) is not confined to *Xenopus*. It is not uncommon in isolated Pliocene vertebrae at Langebaanweg, and have been observed, especially in the more anterior vertebrae, in preparations of the various genera of southern African genera used as diagnostic aids.

There appears to be little literature on the functional morphology of intervertebral articulations in Anura in general. The articulations may limit the amount of energy used to maintain particular postures. A case in point is the maintenance of trim in aquatic species, since the stomach lies obliquely across the roll axis.

An emetic function in *Xenopus* has recently been suggested,[33] and facilitation of oviposition and micturition in anurans by similar action is mentioned. Small, rapid movements are required for the attachment of single eggs to submerged objects during the acrobatic mating manoeuvres performed by pipid frogs; even small movements between vertebrae may be adequate. The study of diving and respiration in *Xenopus* by de Jongh[34] does not refer to longitudinal contraction of the body or to the work of Willem, and has an illustration, drawn from an X-ray image, which does not show that the ilia are parallel.

I thank Pippa Haarhoff and others who made it possible for me to study the Langebaanweg (and *Eoxenopoides*) material in the South African Museum, Anna Henderson for her valuable advice, and anonymous referees for useful comments.

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