THE FIRST ARTICULATED TREMATOSAUR 'AMPHIBIAN' FROM THE LOWER TRIASSIC OF MADAGASCAR: IMPLICATIONS FOR THE PHYLOGENY OF THE GROUP

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ABSTRACT. The temnospondyl *Wantzosaurus elongatus* Lehman, 1961, from the Lower Triassic of Madagascar, is redescribed on the basis of a new specimen, which is the most complete trematosaur ever found. Detailed osteological observations and comparisons provide new data on the anatomy, ontogeny, palaeobiology and palaeoecology of this peculiar marine 'amphibian'. The morphology of this aquatically readapted taxon is compared to that of marine 'reptiles': *Wantzosaurus* might have been able to swim by undulation. A phylogenetic analysis of the trematosauris is performed for the first time and suggests that *Wantzosaurus* is a derived taxon within the clade Trematosauridae. The family is defined on the basis of derived character states and is shown to be monophyletic.

KEY WORDS: Temnospondyl, Madagascar, Triassic, palaeobiology, ontogeny, phylogeny.

THE trematosaurs, a group of Triassic stereospondyl temnospondyls (Fraas 1889, sensu Yates and Warren 2000), resemble gharials in their elongate skull and narrow snout. All were aquatic and piscivorous, and some of them were clearly marine, 'at least for part of their life cycle' (Lindemann 1991, p. 39), since those from Western Australia, Spitsbergen, Pakistan, and Madagascar have indeed been found in deltaic, estuarine (Cosgriff 1984), littoral (Lindemann, 1991), or shallow marine (associated with ceratites; Hammer 1987) deposits. Trematosaurs include about 30 species world-wide, from the Lower (Welles 1993) to the Upper (Hellrung 1987; Milner 1994) Triassic. Despite many attempts at systematic revisions (Säve-Söderbergh 1935; Shishkin 1964; Cosgriff and Garbutt 1972; Warren and Black 1985; Hammer 1987; Hellrung 1987; Welles 1993; Shishkin and Welman 1994), there is still neither consistent definition nor diagnosis of the group. As Warren (2000, p. 1150) argued, '... the family is hard to diagnose except on the basis of skull proportions . . .'. Most of the taxa have been erected on the basis of very poor material, such as parts of the mandible or portions of the skull roof. According to Hammer (1987), more than 50 per cent of these taxa are not valid. However, the recent discovery of an articulated skeleton of a juvenile individual of Wantzosaurus elongatus Lehman, 1961, in the Lower Triassic of Ifasy-Anaborano, northwestern Madagascar, yields new information on both the morphology and the ontogeny of the taxon, which were not entirely available to Lehman (1961). This also allows the first phylogenetic analysis of trematosaurid relationships.

MATERIAL AND METHODS

The new specimen, RHMA01, a cast of which is housed in the Muséum national d'Histoire naturelle (Paris, France), is three-dimensionally preserved in an ironstone nodule. It is the most complete articulated trematosaurian skeleton known to date. The nodule, split open, shows the dorsal and the ventral part of a natural mould. It has been prepared in negative, cast with elastomer and compared to the other trematosaurs of Madagascar and other well-known genera from elsewhere. The exceptional resolution of the elastomer has disclosed new osteological characters and details of *Wantzosaurus elongatus*, especially of the palate, occiput, mandible, and postcranial skeleton.

Institutional abbreviations. BMNH, The Natural History Museum, London, UK; GZG, Göttinger Zentrum für Geowissenschaften, Germany; IGS, Institut de Géologie de Strasbourg, France; MGUH, Geological Museum of Copenhagen University, Denmark; MNB, Museum für Naturkunde der Humboldt-Universität Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; MSNM, Museo di Storia Naturale di Milano, Italy; RHM, Rhinopolis associative Museum, Gannat, France; UMZC, University Museum of Zoology, Cambridge, UK.

Anatomical abbreviations. aa, area asparta; an, angular; arf, articular fossa; ch, choana; cl, clavicle; cle, cleithrum; cp, cultriform process; d, dentary; ect, ectopterygoid; eo, exoccipital; f, frontal; fm, foramen magnum; hsp, hamalus splenialis; icl, interclavicle; j, jugal; m, maxilla; mf, meckelian foramen; n, nasal; na, neural arch; or, orbit; p, parietal; pal, palatine; par, prearticular; pf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; pqf, paraquadrate foramen; ps, postsplenial; pt, pterygoid; psphp, parasphenoid plate; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; r, rib; sa, surangular; scc, scapulocoracoid; slg, sensory-line grooves; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; tpna, transverse process of the neural arch; v, vomer; vf, vomerine fenestra.

SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI Zittel, 1888 STEREOSPONDYLI Fraas, 1889 TREMATOSAURIA Romer, 1947 (*sensu* Yates and Warren, 2000) TREMATOSAURIDAE Watson, 1919

Emended diagnosis (modified according to Yates and Warren 2000). Trematosauria in which the ascending ramus of the pterygoid is not in contact with the squamosal (forming a palatoquadrate fissure); parasphenoid plate extending posteriorly to cover the pedicel of the exoccipital condyles (in ventral view); and cultriform process of the parasphenoid laterally compressed and knife-edged (character 38; unambiguous synapomorphy in present phylogenetic analysis).

Phylogenetic definition (Text-fig. 7). A node-based taxon including *Wantzosaurus* Lehman, 1955 and *Lyrocephaliscus* (Mazin and Janvier, 1983) and all descendants of their most recent common ancestor.

LONCHORHYNCHINAE Säve-Söderbergh, 1935

- 1972 Trematosaurid 'Group 1' Cosgriff and Garbutt, p. 15.
- 1987 Trematosaurid 'Group 3' Hellrung, p. 1.
- 1987 Aphaneramminae Hammer, p. 73
- 1993 Lonchorhynchinae Welles, p. 1.

Emended diagnosis. Trematosauridae with very elongate skull (especially in its anterior part); growth centres between the nostrils and orbits, and anteriorly to the nostrils (character 25; unambiguous synapomorphy in present phylogenetic analysis); very large posterior Meckelian foramen; and vaulted occiput.

Phylogenetic definition (Text-fig. 7). A node-based taxon including *Wantzosaurus* and *Aphaneramma* Smith-Woodward, 1904 and all descendants of their most recent common ancestor.

Genus WANTZOSAURUS Lehman, 1955

Type and only species. Wantzosaurus elongatus Lehman, 1961.

Diagnosis. As for the species.

Remarks. Even though Lehman (1961, p. 114) and Warren and Black (1985, p. 313) have suggested that *Wantzosaurus* may be a juvenile form (consequently a junior synonym) of *Aphaneramma*, the former name has been retained, and its phylogenetic position tested within the trematosaurians (see below). The

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genus *Wantzosaurus* is considered valid by many reviewers (Cosgriff 1984; Hammer 1987; Hellrung 1987; Janvier 1992; Welles 1993; Hewison 1996, Schoch and Milner 2000).

Distribution. Lower Triassic of Madagascar.

Wantzosaurus elongatus Lehman, 1961

Text-figures 1-6

- 1955 Wantzosaurus sp. Lehman, p. 84.
- 1961 Wantzosaurus elongatus Lehman, figs 1–2, pls 1–2; pl. 3, fig. A
- 1963 'stégocéphale néoténique' Lehman, p. 169.
- 1966 Ifasaurus elongatus Lehman, p. 132.
- 1985 trematosaurian *incertae sedis* Warren and Black, p. 313.

Holotype. MNHN MAE3030 (a–f) (Lehman 1961, pls 1–2, pl. 3, fig. A), half of an ironstone nodule containing the mould of the skull roof (a), with parts of its occiput (b–c), of its mandibles (d–e) and of its palate (f).

Type locality and horizon. Madiromiary, Ambilobe region, north-western Madagascar; Middle Sakamena Formation, Induan, Lower Triassic (Scythian A1, after Cosgriff 1984).

Referred specimens. All are natural moulds of ironstone nodules from the Middle Sakamena Formation of the Ambilobe region, north-western Madagascar: RHMA01, a nearly complete skeleton (described below) from the Ifasy-Anaborano district, together with a cast deposited in the MNHN; and MNHN 3034, a skull fragment (holotype of *'Ifasaurus' elongatus* Lehman, 1966) from Anjavimilai (see below).

Emended diagnosis (according to Lehman 1955, 1961, 1966, and Hammer 1987). A Lonchorhynchinae with large orbits; slightly concave posterior border of the skull roof; large pineal foramen; frontal not extending behind orbits; tabular not extended, with a slightly rounded posterior extremity; shallow and posteriorly open otic notches; comparatively large postorbital region with quadrate condyle posterior to the occipital one; vomerine fenestrae in the mid-line of the premaxillo-vomerine suture; posteriorly widened interpterygoid vacuity; comparatively small and well-separated occipital condyles; posterior end of the mandible at the same level as that of the quadrate condyle (in lateral view); and numerous teeth on the posterior coronoid (Lehman 1961, p. 121).

Remarks. A pair of dental foramina anterior to the nostrils, in dorsal view of adult individuals, and the choana overlapping the nostril (characters 23 and 30 respectively in present phylogenetic analysis) are not only typical of *Wantzosaurus* but also convergences with *Cosgriffius* Welles, 1993 and *Benthosuchus* Efremov, 1937, respectively (see Appendix).

Description of the new specimen

Skull roof. The skull shows a typical gharial-like morphology, with a narrow, elongate snout and large, oval, relatively laterally orientated orbits (Text-figs 1, 3–4). It is comparatively shorter (109 mm of midline length) and lower (21 mm from the ventral extremity of the quadratojugal to the dorsal extremity of the postparietal, in lateral view) than that of the holotype (175 mm long and 33 mm high). No lacrimal has been observed on the skull roofs of these specimens (both RHMA01 and MNHN MAE3030), as is the case in *Erythrobatrachus* Cosgriff and Garbutt, 1972 and *Cosgriffius*, but not in *Aphaneramma*. Both the holotype and new specimen show the same diagnostic characters (see diagnosis above), and the same main sensory-line grooves, but they display different degrees of ossification and proportions of the skull roof. The numbered arrows in Text-figure 4 show the anatomical differences between the two skull roofs. Compared to the holotype, the new specimen indeed shows a shorter snout (i.e. more anteriorly situated orbits), with a wider posterior part (arrow no. 1), a more pointed (rather than rounded) anterior extremity (2), which however lacks anterodorsal dentary foramina (3); shorter and more anteriorly situated nostril (4), the long axis of which is not parallel to the lateral outline of the skull; comparatively (and relative to the size of the skull) larger pineal foramen, situated medially (i.e. not posteriorly) to the interparietal suture (5); less laterally facing orbits (6); wider and shorter



TEXT-FIG. 1. *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar, juvenile individual; RHMA01. A, cast in dorsal view. B, interpretive drawing. Scale bar represents 10 mm.

posterior region of the skull (7); and more finely striated (rather than pitted or anastomosed) ornamentation on dermal bones (such as on the parietal: 8). Characters 5–8 are differences between the juvenile and adult specimens of *Aphaneramma* (Säve-Söderbergh 1935), and the other characters also relate to ontogeny (Bystrow 1935, Schoch 1992; Steyer 1996, 2000). The new specimen RHMA01 is consequently interpreted as a juvenile individual of *Wantzosaurus elongatus*.



TEXT-FIG. 2. *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar, juvenile individual; RHMA01. A, cast in ventral view. B, palatal side of the nodule showing the cultriform process and position of the orbits. c, interpretive composite drawing. Scale bar represents 10 mm.

Lateral line system. In both juvenile (RHMA01) and adult (MNHN MA3030) individuals, the sensory-line grooves are well developed (Text-figs 1, 3–4), as is the case in numerous aquatic stereospondyls (Warren 2000). Their depth remained constant (*c.* 1mm) during the development of *Wantzosaurus elongatus*. Four canals have been observed on each half of the dermal skull roof and lateral surface of the mandible.



TEXT-FIG. 3. *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar, juvenile individual; RHMA01. Cast in lateral (A–B), and occipital (D) views. C, composite interpretive drawing of A and B. E, interpretive drawing of D. Scale bar represents 10 mm.

1. The supra-orbital groove extends along the midline of the skull, from the rear of the orbit to the tip of the snout, and passes across the postfrontal, frontal, prefrontal, maxilla, nasal, and premaxilla. It is also visible in *Aphaneranma* and to some extent *Luzocephalus* Shishkin, 1980 (where grooves are comparatively wider), *Lyrocephaliscus*, and *Tertrema* Wiman, 1915, but extends further posteriorly in *Cosgriffius*. It is curved just anterior to the orbit and just posterior to the nostril. The latter (anterior) curve is more marked in the juvenile than in the adult individual (Text-fig. 4). The reconstruction by Lehman (1961, p. 115, fig. 1), showing a commissure between the paired grooves at the level of the tip of the snout, is speculative (the surface of the rostral dermal bones is poorly preserved).

2. The infra-orbital groove extends ventrolaterally on the skull roof, and passes across the nasal, maxilla, and jugal, bifurcating posteriorly to the orbit in three branches: across the postorbital and supratemporal, the postfrontal, and the squamosal. This pattern is also known in *Lyrocephaliscus* and *Aphaneramma*, but with a posteriorly oriented groove behind the orbit. This pattern is apparently lacking in *Cosgriffius* (but this could be an artefact of preservation; Warren, pers. comm. 2001) and not fully determinable in *Luzocephalus* where only some segments are visible across its maxilla, lacrimal, and squamosal.

3. The short posterior groove, extending along the posterior margin of the skull table and passing across the postparietal and tabular, is only visible in the holotype (Text-fig. 4B). It is clearly visible in *Aphaneramma*, but restricted to the tabular in *Lyrocephaliscus*, and is totally lacking in *Luzocephalus*. Comparison with *Cosgriffius* is not possible because of the absence of the preserved posterior part of its skull.

4. The mandibular groove, following the upper margin of the mandible, passes across the surangular and the dentary of both the holotype (Lehman 1961, pl. 2, fig. E) and the new specimen (Text-fig. 3c). In *Aphaneranma*, it reaches the angular ventrally, and partly follows the lower margin of the mandible.

The patterns of the sensory-line grooves clearly differ between genera, and even between species (pers. obs.). The pattern of these subaquatic sensory receptors (Warren 2000) has been optimized here in the phylogenetic analysis.

Palate. The palate is partly preserved in the holotype (Lehman 1961, pl. 3, fig. A), but the new specimen provides new data (Text-fig. 2). Its well-ossified palate reveals elongate choanae. Shagreened and granulous surfaces (the area asparta sensu Bystrow and Efremov 1940) are visible on the ventral side of the parasphenoid plate and of the anterior branch of the pterygoid. The parasphenoid plate does not show any marked arterial canal. The contact between the pterygoid and parasphenoid is very long, as in many trematosaurians; however no 'pockets' are visible on the pterygoid, as is the case in Stoschiosaurus Säve-Söderbergh, 1935. The posterior branch of the pterygoid is comparatively shorter than that of other trematosaurians (except for *Platystega* Wiman, 1915), but seems to lengthen during development: it is longer in the adult individual (Lehman 1961, pl. 2, fig. B) than in the juvenile. The interpterygoid vacuities of Wantzosaurus are very wide and long, and separated from each other by the slender, narrow cultriform process of the parasphenoid (Text-fig. 2B; see also Lehman 1961, pl. 3, fig. A). In the trematosaurians, the elongation of these vacuities does not seem to be directly related to longirostry: for example, Aphaneranma and Erythrobatrachus both have very elongate skulls that do not show proportionately long interpretygoid vacuities. Those of Wantzosaurus are wider than the vacuities of Aphaneramma, Cosgriffius, and Erythrobatrachus, yet narrower than those of Luzocephalus, Lyrocephaliscus, and Platystega. The anterior vomerine fenestrae of Wantzosaurus are smaller and more rounded than those of Lyrocephaliscus, Platystega, Tertrema, and Trematosaurus. In Luzocephalus, the anterior fenestrae are fused into a large median, heart-shaped cavity, whereas they appear to be lacking in *Cosgriffius*. No comparison of these elements is possible with Aphaneramma, Erythrobatrachus, and Stoschiosaurus, because the anterior part of their snouts are not preserved. In both the holotype (Lehman 1961, pl. 3, fig. A) and new specimen (Text-fig. 2c) of Wantzosaurus, the palatine does not seem to contribute to the anterior margin of the interpretygoid vacuities, as is also the case in Cosgriffius. Two insertion areas for tusks are visible on the ventral surface of the palatine and one on that of the vomer. Two vomerine fenestrae are clearly visible on the palatal side of the holotype (Lehman 1961, pl. 3, fig. A). The quadrate is narrower than that of Aphaneranma and Stoschiosaurus, and its suture with the posterior branch of the pterygoid is longer in these two taxa.

Occiput. The occiput of the holotype was partly described by Lehman (1961, pl. 2, fig. A). That of the new specimen is better preserved (Text-fig. 3D–E), although both stapes are lacking. The fact that the basioccipital is not preserved, in both the new specimen and the holotype, suggests that it was not ossified (Lehman 1961, p. 119), at least at the juvenile stage. In occipital view, the skull of the new specimen is very narrow, deep and vaulted, with ventrally directed tabulars, as is the case in *Aphaneramma* and *Tertrema*. The posttemporal fenestrae are deep and dorsolaterally extended, although they are more rounded in the holotype (Lehman 1961, pl. 2, fig. A). The foramen magnum, clearly visible on the new specimen, is keyhole-shaped and limited dorsally by the vaulted postparietal. No nerve canal has been observed on the roughened surface of the partly preserved exoccipital. However, the wide and smooth occipital face of the quadratojugal shows a tiny paraquadrate foramen, just above the quadrate boss; an apomorphic condition of the Limnarchia (Yates and Warren 2000). On the right side, the mandible lies in articulation with the quadrate.

Mandible. Few data on trematosaurid mandibles are available. A few specimens of Trematosaurus Burmeister, 1849 and Inflectosaurus Shishkin, 1960, are preserved with their mandibles. Damiani et al. (2000) recently mentioned partial mandibles of an indeterminate trematosaurine specimen from South Africa. In Wantzosaurus, Lehman (1961, pl. 2, figs E-F) noted only radiating ornamentation on the labial surface of mandible of the holotype. The mandibles of the new specimen (Text-figs 2, 3A-C) are almost complete, very long and low, with a posterior part that does not clearly project beyond the quadrate condyle. As in the adult individual, the angular of the juvenile (Text-fig. 3c) is already radially ornamented on its labial surface. The dentary covers half the depth of the anterior part of the mandible. The surangular is comparatively flattened. On the lingual side, the Meckelian foramen is very elongated in shape (a typical condition of the long-snouted trematosaurs; Jupp and Warren 1986), but is comparatively shorter than that of Inflectosaurus. The adductor fossa of both the juvenile and adult individuals of Wantzosaurus is deep and elongated. The dorsal view of the juvenile mandible reveals a very long symphysial suture, also typical for the long-snouted trematosaurs (Jupp and Warren 1986), with a flattened symphysial region (the hamalus splenialis sensu Bystrow and Efremov 1940; here Text-fig. 2c), yet without any visible symphysial teeth. The postglenoid area (PGA) of the holotype is visible in dorsal view, just behind the adductor fossa. That of the new specimen, in posterior view, also seems to be comparatively short and of type I (sensu Jupp and Warren 1986), i.e. with a comparatively deep and high articular fossa, bounded by the angular, surangular and prearticular (Text-fig. 3E). This type of PGA is considered primitive with regard to that of the Mastodonsauridae (sensu Damiani 1998). Putative presence of lips, based on the



TEXT-FIG. 4. Cranial ontogeny of *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar. Skull roof comparison between A, the juvenile individual (RHMA01), and B, the adult, redrawn from the holotype MNHN MAE3030. Scale bar represents 20 mm. Numbered arrows point out the differences related to growth (see text).

mandibular sensory-line groove and the smooth and vascularized region on the lateral side of the dentary (Janvier 1992), cannot be corroborated here.

Teeth. The marginal teeth of the new specimen are 2–4 mm high (Text-figs 2C, 3C). Those on the palatine could reach about 8 mm, estimating from their preserved broad bases. These conical, labyrinthodont elements lie alternately between the lower and upper jaw, with a slight overlap when the mouth was closed. Anterior mandibular and premaxillary teeth are slightly tilted posteriorly in *Wantzosaurus*, whereas they are slightly tilted anteriorly in the mastodonsaur *Watsonisuchus* Ochev, 1966 (Damiani 1998; pers. obs.).

Axial skeleton. Very few data are available on the postcranial remains of trematosaurians. Some isolated vertebrae were referred to *Aphaneramma* with doubt by Wiman (1914, pl. 6, figs 1–4), yet with more certainty by Nilsson (1943). The postcranial skeletons of *Trematosaurus* and *Lyrocephaliscus* are better known thanks to well-preserved material from Germany (Burmeister 1849) and Spitsbergen (Mazin and Janvier 1983), respectively. Warren and Snell (1991) made an interesting comparison of the postcranial elements in the major stereospondyl families. In the RHMA01 specimen, 13 neural arches and their 26 associated ribs are in articulation (Text-figs 1–2). The preserved portion of the vertebral column is composed of five 'thoracic' (lying on the internal surface of the interclavicle) and eight 'dorsal' (lying posterior to the interclavicle) neural arches. These neural arches and ribs are tiny and short, respectively. The vertebrae of the new specimen are smaller and probably more numerous (its neural arch/interclavicle length ratio is lower) than those of *Aphaneramma*, which surprisingly shows large intercentra. The neural arches of the



TEXT-FIG. 5. *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar, juvenile individual; RHMA01. Stereoscopic photograph of the ventral side of the left putative scapulocoracoid. Scale bar represents 5 mm.

new specimen resemble those of the mastodonsauroid *Benthosuchus* (Bystrow and Efremov 1940). They are higher and anteroposteriorly shorter (Text-fig. 1B) than those of the rhytidosteid *Rewana* (Warren and Snell 1991), and the 'dorsal' neural arches especially show better-developed pre- and post-zygapophyses than those of *Lyrocephaliscus* (Mazin and Janvier 1983). Their transverse processes (Text-fig. 2c) are, however, shorter than those of *Benthosuchus*. In the new specimen, the intercentra were probably not ossified. No transverse apophysis is visible on the dorsal extremity of the neural arches, as is the case in numerous adult temnospondyls (Bystrow and Efremov 1940; Werneburg and Steyer 1999, in press). The 'thoracic' ribs are more elongate, and more sigmoid in shape than the 'dorsal' ones, and their length obviously decreases posteriorly along the vertebral column. They show no uncinate processes, neither in their proximal nor in their distal parts, which is typical of an adult condition (Bystrow and Efremov 1940, fig. 40E; Werneburg and Steyer 1999, in press; Schoch and Milner 2000, fig. 11). The 'dorsal' ribs are comparatively straight, with flatter and wider extremities.

Pectoral girdle. The clavicle and interclavicle show ornamentation of both anastomosed and radial types (in the centre and lateral zones of their ventral surface, respectively) (Text-figs 1-2). This suggests a juvenile condition (Werneburg and Stever 1999, in press; Stever 2000). The flattened interclavicle is very elongate and lozengeshaped, with concave lateral margins. This is also the case in Aphaneranma. The interclavicle of the Permian stereospondylomorph Archegosaurus Goldfuss, 1847 is also lozenge-shaped (a convergent character in the elongate and aquatically readapted non-amniotic tetrapods). Juvenile individuals of this taxon have an interclavicle, the anterior part of which is more elongate than the posterior (pers. obs.). In the juvenile individual of Wantzosaurus, the anterior and posterior parts have the same length and are symmetrical. The interclavicle of Lyrocephaliscus, with enlarged posterior laminae and a medial constriction (Mazin and Janvier 1983, fig. 12), has a markedly different shape from that of the juvenile individual of Wantzosaurus, but it bears the same ornamentation. The clavicle is also very elongate in shape, with an ornamented and typically spoon-shaped ventral plate, partly covering the interclavicle. Its lateral lamina is slightly curved, and its dorsal process is more elongated, straighter and narrower than that of Lyrocephaliscus, Aphaneramma, and that known in metoposaurs, plagiosaurs, and capitosauroids (Warren and Snell 1991; Bystrow and Efremov 1940). Wantzosaurus shares with the Brachyopoidea an elongate dorsal process of the clavicle (Warren and Marsicano 2000, fig. 6), which is, however, posteriorly oriented, unlike brachyopids.



TEXT-FIG. 6. Reconstruction of a juvenile individual of *Wantzosaurus elongatus* Lehman, 1961 from the Lower Triassic of Madagascar. A, the preserved part (in black) of the articulated skeleton. B, the animal with hypothetical limbs and tail. Scale bars represent 40 mm.

Scapulocoracoid? A pair of bones lie posteroventrally to the pectoral girdle (Text-figs 2, 5). These short elements are medially constricted and show wide and roughened extremities, which are dorsoventrally connected by a medial crest. The proximal end is mediolaterally oriented, whereas the distal one is dorsoventrally oriented. These symmetrical and robust elements could be the poorly ossified centre-sections of bones of unknown final shape (Milner, pers. comm. 2001), and their identification, therefore, remains difficult. They look like either scapulocoracoids or humeri of *Aphaneranma*, the central parts of these elements showing unfortunately the same global shape in that genus (Nilsson 1943, figs 6–7, pls 1–2). No large supraglenoid process is visible, as is the case in the incompletely ossified scapulocoracoids of *Aphaneranma* (Nilsson 1943, pl. 2) and *Benthosuchus* (Bystrow and Efremov 1940, figs 47–49, 76), but a tiny foramen is visible at mid-height of the external side of each bone (Text-fig. 5 for the left one). Assuming that any humerus of a temnospondyl 'higher' than *Dendrerpeton* and *Balanerpeton* bears a foramen (Milner, pers. comm. 2001), these elements are much more likely to be scapulocoracoids than humeri. They are more cylindrical and more massive than the scapulocoracoids of *Benthosuchus* (Bystrow and Efremov 1940). They do not resemble scapulocoracoids of *Watsonisuchus*, which show bifurcate and flat extremities (pers. obs.), but they look like those of *Trimerorhachis* (Berman and Reisz 1980, fig. 2).

STEYER: TRIASSIC TREMATOSAURIAN

DISCUSSION

Locomotion and mode of life of Wantzosaurus

The neural arches of *Wantzosaurus* are smaller and probably more numerous than those of *Aphaneramma* (see above). This could suggest that *Wantzosaurus* had a long, shallow trunk and was more aquatic (or pelagic) than the latter. These neural arches are also higher than wide, in proportion. This could have limited vertical movement during locomotion. *Wantzosaurus*, with its relatively deep skull and probable long trunk, might have swum by lateral undulation. Its teeth, alternated and posteriorly tilted (see above), are probably the most specialized within the non-amniotic tetrapods readapted to aquatic life. They appear to be similar in some ways to that of some marine 'reptiles', such as the mosasaurs, which show an elongate snout bearing posteriorly directed and alternate teeth (DeBragga and Carroll 1993). This dentition is probably linked with rapid prey capture. Both dentition and probable lateral undulation suggest that *Wantzosaurus* might, therefore, be a fast marine hunter.

The evolution of the trematosaurid 'concept'

The first trematosaur, Trematosaurus brauni, was described by Burmeister (1849) from the Lower Triassic of Germany, Hellrung (1987, p. 15) argued for the priority of Trematosaurus von Braun, 1842, a nomen nudum according to Schoch and Milner (2000). Since Watson (1919, p. 67) erected the family Trematosauridae for Trematosaurus and other genera, many taxa have been included and/or removed from this family. Säve-Söderbergh (1935, p. 90) used the superfamily Trematosauroidea to unite the Trematosauridae and Archegosauridae. This superfamily has since been used for the trematosaurids, rhytidosteids, and some problematical taxa (Warren and Black 1985). However, a recent phylogenetic analysis of the 'higher' stereospondyls (Yates and Warren 2000) closely linked the rhytidosteids with the brachyopoids, and led to a new definition of the Trematosauria of Romer (1947) as a stem-based taxon including all stereospondyls that share a more recent common ancestor with *Trematosaurus* than with Parotosuchus Ochev and Shishkin, 1968. Yates and Warren (2000) addressed the definition of the suborder Trematosauroidei of Säve-Söderbergh (1935) and of the 'trematosaurian group' of Warren and Black (1985). Since Säve-Söderbergh (1935), there has been no general agreement on what a trematosaurian is. For example, Lehman (1979) proposed a diagnosis based on a few characters such as an elongated snout, a pineal foramen situated far from the orbits, and sometimes the absence of a lacrimal. The aim here is not to revise all known trematosaur species (which is a project in progress with R. J. Damiani and D. P. Sengupta), but to revise the genus Wantzosaurus on the basis of a new articulated specimen. At least eight attempts at revisions (Säve-Söderbergh 1935; Cosgriff and Garbutt 1972; Warren and Black 1985; Hammer 1987; Hellrung 1987; Welles 1993; Bierring 1999; Schoch and Milner 2000) have led to four different definitions of the family Trematosauridae. They are presented here in order to introduce the valid taxa, which are used in the phylogenetic analysis below.

Säve-Söderbergh (1935) and Cosgriff and Garbutt (1972) divided the family Trematosauridae into three subfamilies (not two, *contra* Welles 1993) on the basis of the elongation of the skull: (1) the Lonchorhynchinae (Säve-Söderbergh 1935; Schoch and Milner 2000) or 'group 1' (Cosgriff and Garbutt 1972) for '*Lonchorhynchus*' (= *Aphaneramma*) and other forms with very a elongate skull; (2) the Trematosaurinae (Säve-Söderbergh 1935) or 'group 2' (Cosgriff and Garbutt 1972) for moderately elongate skulls; and (3) the Lyrocephalinae (Säve-Söderbergh 1935) or 'group 3' (Cosgriff and Garbutt 1972) for comparatively short skulls, such as *Lyrocephaliscus euri* (Wiman, 1914) and *Platystega* (which however belongs to the 'group 2' according to Cosgriff and Garbutt 1972). Regarding these subdivisions, Säve-Söderbergh (1935, p. 86) argued that '... the classification must remain provisional as far as so little is known about the endocranium of the discussed forms ...'.

Bystrow and Efremov (1940), Shishkin (1964), and Shishkin and Welman (1994) have simply suggested that the trematosaurs may be diphyletic and consequently questioned the validity of the family Trematosauridae.

Hellrung (1987) divided the family Trematosauridae into five (not four, *contra* Warren 2000, p. 1130) groups based on the structure of the palate; the '*Aphaneramma*-like' (= the Lonchorhynchinae, see above),

'*Trematosaurus*-like', '*Tertrema*-like', '*Platystega*-like', and '*Lyrocephaliscus*-like' forms. This classification is similar to those of Hammer (1987), Welles (1993), and Schoch and Milner (2000), except for the latter two or three sub-groups, which include either doubtful (Hammer 1987; Welles 1993) or non-trematosaurid (Schoch and Milner 2000) taxa.

Finally, Hammer (1987) and Welles (1993) divided the Trematosauridae into two subfamilies on the basis of the elongation of the snout, the dentary symphysis and the interclavicle, as well as on the position of the nostrils and choanae. These two sub-families are:

1. The Lonchorhynchinae *sensu* Welles 1993 (or the Aphaneramminae *sensu* Hammer 1987; or 'the *Aphaneramma*-like forms' *sensu* Hellrung 1987), with narrow and very elongate rostra (Welles 1993; Warren 2000), includes *Aphaneramma ocella* (Meyer) Huene, 1920, *Aphaneramma* (= 'Halobatrachus' Hammer, 1987) *rostratum* (= 'Lonchorhynchus obergi' Wiman, 1910 = 'Trematosaurus kannemeyeri' Broom, 1909), Cosgriffius campi, Erythrobatrachus noonkanbahensis (according to Welles 1993, but *E. hoonkanbahensis* in Hellrung 1987), and Wantzosaurus elongatus.

2. The Trematosaurinae (*sensu* Welles 1993), with triangular-shaped skulls and a short prenarial region, includes *Inflectosaurus amplus*, *Lyrocephaliscus euri*, *Platystega depressa*, *Tertrema acuta*, *Trematosaurus brauni* (= '*Trematosaurus fuchsi*' Seidlitz, 1920), *T. madagascariensis* Lehman, 1966, *Trematosuchus sobeyi*, *T.* (= *Thoosuchus*) *yakovlevi* Riabinin, 1927, and possibly *Angusaurus tsylmensis* Novikov, 1990 from the Lower Triassic of Timan, depending whether or not this taxon is a junior synonym of *Trematosaurus*.

Some taxa, such as *Stoschiosaurus nielseni* from the Lower Triassic of East Greenland, remain problematical and difficult to place in either of these two subfamilies. *Latiscopus disjunctus* Wilson, 1948, from the Upper Triassic of Texas, first considered as either a Rhytidosteidae (Cosgriff 1965) or a Trematosauridae (Warren and Black 1985), has recently been turned into a *nomen dubium* by Bolt and Chatterjee (2000). *Luzocephalus blomi* from the Lower Triassic of Russia was originally described as the type genus of the then monotypic Luzocephaluae (Shishkin 1980). Other species were later included in this family, such as *Luzocephalus* (= '*Lyrocephalus*' Säve-Söderbergh, 1935) *kochi* from the Lower Triassic of Greenland (a capitosauroid according to Bjerring 1999), or *Chomatobatrachus hali* Cosgriff, 1974 from the Lower Triassic of Tasmania (Milner 1990). These taxa, which show a mix of capitosaurian and trematosaurian characters, were also assigned to the family Lydekkerinidae (Cosgriff 1984; Warren and Black 1985; Milner 1991; Schoch and Milner 2000).

In all of these revisions, the following taxa have often been considered as either invalid or nontrematosaurids, because of their poorly preserved holotypes and/or synonymy: *Gonioglyptus* (='Indolyrocephalus' Tripathi, 1969) huxleyi Lydekker, 1882, G. kokeni Huene, 1920, Gonioglyptus (='Panchetosaurus' Tripathi, 1969) longirostris Huxley, 1865, Hyperokynodon keuperinus (Plieninger, 1852) (H. keuperinum in Hammer 1987, and Warren and Black 1985), Icanosaurus rectifrons Rusconi, 1951, Ifasaurus elongatus Lehman, 1966 (see below), Indolyrocephalus panchetensis, Luzocephalus johannsoni (Säve-Söderbergh, 1935), L. kochi (Säve-Söderbergh, 1935), Lyrosaurus australis Lehman, 1967 (see below), Microposaurus casei Haughton, 1925, Tertremoides ambilobensis Lehman, 1979 (see below), Trematosaurus kannemeyeri, and Trematotegmen otschevi Getmanov, 1982. Consequently, they have not been taken into account in the phylogenetic analysis of the group.

Comparison of Wantzosaurus with the other trematosaurians from Madagascar

The temnospondyls from Madagascar, first reported by Piveteau (1926) and mainly described by Lehman (1955, 1961, 1963, 1966, 1967, 1979), have been partly revised: they comprise the lydekkerinid *Deltacephalus whitei* Swinton, 1956 (Hewison, 1996), one (possibly two; see below) rhytidosteid(s), *Mahavisaurus dentatus* Lehman, 1966 (Steyer, redescription in progress), the mastodonsaurians (= 'capitosaurians') '*Benthosuchus' madagascariensis* Lehman, 1961 and '*Wetlugasaurus milloti*' Lehman, 1961 (Steyer in press), three trematosaurids (see below) and possibly one metoposaur (Dutuit 1978) and one rhinesuchid ['*Uranocentrodon madagascariensis*' (Piveteau, 1926) Ochev, 1966]. A complete redescription of the lydekkerinid(s) and trematosaurids is in progress (Steyer unpublished). It is, however, possible to give here a preliminary list of synonyms, because Lehman (1955–1979)

had clearly overestimated the diversity of the stereospondyl fauna from Madagascar. Lindemann (1991) and Hewison (1996) have already noted the striking resemblance of this assemblage to that from the Lower Triassic of Spitsbergen. As for trematosaurians other than *Wantzosaurus elongatus*, Lehman reported:

1. Trematosaurus madagascariensis Lehman, 1966 (not madagascarensis, contra Hewison 1996): MNHN MAE 3039, 3045–46. The holotype (MNHN MAE3039), half of an ironstone nodule containing the skull roof, with its partly preserved mandibles, comes from Mahatsara, north-eastern Madagascar. It was first erected by Lehman (1966) on the basis of its more rounded and spaced nostrils, different supraand infra-orbital grooves, and larger orbits than in *T. brauni* Burmeister, 1849 from Germany, Spitsbergen and south-eastern Russia. In the holotype of *T. madagascariensis*, fusion of the frontal bones might be the result of individual variation. Based on a large skull from Ambodipo (MNHN MAE3045), Janvier (1992) showed that this taxon has circular, concentrically striated dorsal body scales, a lacrimal flexure of the supra-orbital sensory-line groove (a plesiomorphic character), and a premaxilla bearing tiny teeth that become increasingly widely spaced during growth. The latter character, also present in the Malagasy 'capitosaur' *Watsonisuchus* (pers. obs.), may have been linked to prey capture strategy (Janvier 1992), several other morphological characters suggest that *T. madagascariensis* might be a juvenile individual of ubiquitous *T. brauni*. Pending a detailed revision of this taxon, it is, however, preferable to retain *T. madagascariensis* as a distinct species.

2. Tertremoides ambilobensis Lehman, 1979. The holotype (MNHN MAE3040a-c) comes from Ambilobe, north-western Madagascar. It is represented by a complete ironstone nodule containing the skull in dorsal, palatal and occipital views, and articulated mandibles visible in lateral and lingual views. The diagnosis proposed by Lehman (1979, p. 43) is questionable: except for the splayed posterior plate of the parasphenoid, the other characters, such as a concave occipital margin of the skull, non-confluent infra and supra-occipital sensory-line grooves, comparatively large orbits, and an ornamentation lacking tubercles, could be related to ontogeny (Bystrow 1935; Steyer 1996, 2000). Consequently, following Janvier (1992) and Hammer (1987), and contra Cosgriff (1984), this taxon could be a junior synonym of Trematosaurus madagascariensis. According to Schoch and Milner (2000), Trematosaurus madagascariensis and Tertremoides ambilobensis must be combined in Tertremoides madagascariensis. However, the holotype of Tertremoides ambilobensis is similar to that of *Trematosaurus madagascariensis*, with a more elongated snout and shallower sensory grooves. Tertremoides ambilobensis could, therefore, be either a late juvenile form of Trematosaurus madagascariensis, or an early juvenile individual of T. brauni (if T. madagascariensis actually is a juvenile form of T. brauni), although according to Warren and Black (1985), Tertremoides could be a synonym of Tertrema. In all cases this taxon is invalid.

3. '*Ifasaurus*' *elongatus* Lehman, 1966. The holotype (MNHN MAE3034) is a poorly preserved skull (Lehman 1966, pl. 5, fig. B) from Anjavimilai, north-western Madagascar. The taxon was diagnosed by Lehman (1966, p. 20) on the basis of its orbits, which are larger than those of *Tertrema*, and its confluent supra- and infra-orbital grooves. This 'néoténique' temnospondyl, as first (yet simply) noted by Lehman (1963), corresponds to an indeterminate genus according to Cosgriff (1984), Cosgriff and Garbutt (1972), Janvier (1992), and Welles (1993). It is indistinguishable from *Wantzosaurus elongatus* according to Hammer (1987), and Schoch and Milner (2000).

4. *Lyrosaurus australis* Lehman, 1967, from the Sakamena beds. This was considered invalid by Hammer (1987). There is, however, general agreement that this species, referred to the Rhytidosteidae and not the Trematosauridae (Howie 1972; Shishkin 1980), in fact belongs to the genus *Mahavisaurus*, along with *M. dentatus* from the same locality (Cosgriff and Garbutt 1972; Cosgriff and Zawiskie 1979; Warren and Black 1985; Milner 1990, 1991; Hewison 1996; Schoch and Milner 2000).

5. Aphaneramma sp. This could also be present in Madagascar according to Lehman (1966), but the poorly preserved material, an isolated parietal table from Antsaba, north-western Madagascar, is insufficient to prove this. The specimen could also belong to *Wantzosaurus elongatus* according to Cosgriff and Garbutt (1972), and Schoch and Milner (2000), or to an indeterminate trematosaur according to Cosgriff (1984), Janvier (1992), and Welles (1993). Interestingly, Lehman (1961), on comparing this

specimen with more complete remains of *Aphaneramma rostratum* (Nilsson 1943), showed that this taxon possibly underwent tooth replacement from the back to the front of the dentary during its growth.

6. *Tertrema* sp. This may also be present in Madagascar according to Lehman (1979), on the basis of the recovery of a large anterior extremity of a snout. This specimen has subsequently been regarded as indeterminate by Cosgriff (1984), Janvier (1992), and Welles (1993).

7. An isolated parasphenoid posterior plate (with parts of pterygoids) (Lehman 1961, pl. 3, fig. E). This may indicate the presence of an indeterminate trematosaurid or brachyopoid in Madagascar.

Phylogenetic position of Wantzosaurus elongatus

In order to test the phylogenetic position of *Wantzosaurus* within the trematosaurids, a cladistic analysis of the group has been performed for the first time (Hammer's 1987 analysis was phenetic). Eighteen taxa, including six non-trematosaurid temnospondyls, have been used to test the monophyly of the trematosaurs. These non-trematosaurid temnospondyls are the two mastodonsauroids (sensu Damiani 1998) Watsonisuchus (Lower Triassic of Australia, South Africa, and Madagascar; Damiani 1998; Stever in press) and Benthosuchus (Lower Triassic of Russia), the two metoposauroids (sensu Yates and Warren 2000) Almasaurus Dutuit, 1972 and Dutuitosaurus (Dutuit, 1976) Hunt, 1993 (both from the Upper Triassic of Morocco), the stereospondylomorph (sensu Yates and Warren 2000) Archegosaurus (Lower Permian of the Czech Republic and Germany), and the eryopid Onchiodon Geinitz, 1861 (Lower Permian of France and Germany: Werneburg and Stever 1999) as the outgroup. Sixty-nine homologous osteological characters (28 in the skull roof, 17 in the palate, 11 in the occiput, 11 in the mandible, and two in the postcranial skeleton; see Appendix) have been polarized in the 18 terminal taxa (see Appendix) according to the outgroup criterion. All the characters have been given the same weight. Hennig86 version 1.5 (Farris 1988), using an exhaustive search (branch bounding) of the most parsimonious trees, has been used to optimize characters. The analysis generated two most parsimonious trees (length, L, 216 steps; consistency index, CI, 0.37; retention index, RI, 0.42) the strict consensus of which (L, 218 steps; CI, 0.36; RI, 0.41) is illustrated in Text-figure 7.

The result is that the trematosaurids form a monophyletic group, with mastodonsauroids as stem-group. This clade, supported by the presence of a knife-edged cultriform process of the parasphenoid (character 38; unambiguous synapomorphy) and additional synapomorphies (see systematic section above), is more closely related to the mastodonsauroids (*Watsonisuchus* and *Benthosuchus*) than to the metoposauroids (*Almasaurus* and *Dutuitosaurus*) or to the archegosaurids (*Archegosaurus*). This result is congruent neither with that of Yates and Warren (2000) nor with that of Schoch and Milner (2000), both of whom argued for the sequence of archegosaurids/capitosauroids (*sensu* Schoch 2000 or mastodonsauroids *sensu* Damiani 1998)/trematosaurids/metoposauroids.

The distribution of taxa within the trematosaurid clade is congruent with the classification of Hammer (1987) and Welles (1993), both of whom defined the subfamilies Trematosaurinae and Lonchorhynchinae. These subfamilies correspond here to the sister-clades (((*Lyrocephaliscus, Platystega*), *Tertrema*), (*Luzocephalus, (Trematosaurus, Trematosuchus*))) and (*Aphaneramma, (Erythrobatrachus, Cosgriffius, (Stoschiosaurus, Wantzosaurus)*)), respectively (Text-fig. 7). The lonchorhynchinine clade, defined by the presence of a prenarial growth zone (character 25; unambiguous synapomorphy) and additional synapomorphies (see systematic section above) is also congruent with the classification of Schoch and Milner (2000), who considered, however, the trematosaurines to be either stem-taxa (not sister-taxa) of the lonchorynchinines or non-trematosaurids.

Luzocephalus is here a trematosaurid, more precisely a trematosaurine, and consequently should no longer be considered as an uncertain trematosauroid; as mentioned by Warren and Black (1985). Inflectosaurus is not a trematosaurid here, and should be considered a stem-taxon of the metoposauroids, as suggested by Schoch and Milner (2000). Wantzosaurus is one of the most derived trematosaurids. The only unresolved node of this cladogram (except for the basal polytomy) corresponds to either Cosgriffius or Erythrobatrachus, or both, as a sister group of the clade (Stoschiosaurus, Wantzosaurus). This node is unresolved in the strict consensus of the two most parsimonious trees obtained in this analysis. The best supported node corresponds to the ingroup (i.e. the stereospondyls used in this analysis) and is based on a



TEXT-FIG. 7. Phylogenetic position of *Wantzosaurus* Lehman, 1961 within trematosaurians and other temnospondyls, based on a preliminary analysis of 18 taxa and 69 characters. Strict consensus of two most parsimonious trees obtained by exhaustive search (branch bounding) using Hennig86 version 1.5. (length L = 218 steps; CI = 0.36; RI = 0.41). Skulls are not to scale. The incomplete state of *Inflectosaurus* and *Stoschiosaurus* reflects the poor preservation of their type and only known specimens; note the crownward position of *Wantzosaurus* among the Lonchorhynchinae.

very short or absent pterygoid/palatine suture, an elongate pterygoid/parasphenoid suture, a ventrally constricted foramen magnum, deep posttemporal fenestrae (characters 39–40, 51 and 54, respectively; unambiguous synapomorphies); and on the posterior end of the mandible situated behind the quadrate condyle, and an extended dentary symphysis (characters 57 and 60, respectively; ambiguous synapomorphies). Finally, *Archegosaurus* and *Onchiodon* are the outgroup of the clade ((metoposauroids, *Inflectosaurus*), (mastodonsauroids + trematosaurids)). This corroborates the hypothesis of the convergent longirostry ('narrow and elongate snout') between the aquatic and piscivorous archegosaurs and trematosaurs (Steyer 1996). This longirostry is different according to the group; the elongation of the preorbital part of the skull chiefly involves the nasal and the frontal in the archegosaurs, whereas it mainly involves the premaxilla in the lonchorhynchine trematosaurs.

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APPENDIX

Terminal taxa	Specimens	Literature				
Almasaurus	MNHN ALM42, 46, 57, 60, 64 MNHN ALM66, 69–70, 73	Dutuit 1972; Hunt 1993				
Aphaneramma		Säve-Söderbergh 1936, 1937; Welles 1993				
Archegosaurus	GZG no number MNB Am114–119, 121–131, 137 MNHN1868-1–4, 1870-479–480, MNHN1884-10, 21–25: IGS UUL2, 5	Gubin 1997; Jaeckel 1896; Meyer 1857				
Benthosuchus Cosgriffius	UMZC T1223, T68–74	Bystrow and Efremov 1940 Welles 1993				
Dutuitosaurus	MNHN AZA258, 269, 271, 273, 276 MNHN AZA279, 330–332, 334, 355	Dutuit 1976; Hunt 1993				
Erythrobatrachus Inflectosaurus Luzocephalus Lyrocephaliscus		Cosgriff and Garbutt 1972 Jaeckel 1922; Shishkin 1960 Shishkin 1980 Säve-Söderbergh 1935, 1936, 1937;				
Onchiodon Platystega	MNHN 1908-20-26	Mazin and Janvier 1983 Werneburg and Steyer 1999 Säve-Söderbergh 1936; Wiman 1914				
Stoschiosaurus Tertrema	MGUH At.6, 12, 23, 43, 45, 46 (p)	Säve-Söderbergh 1935 Säve-Söderbergh 1936; Wiman 1915				
Trematosaurus	BMNH 30270, 36354–75, 40042 GZG 7 MNB Am943 1/3 MNHN MAE3039–40, 3045–46 MNHN AC9573	Burmeister 1849; Drevermann 1920; Lehman 1966, 1979; Werneburg 1993				
Trematosuchus		Haughton 1915; Shishkin and Welman 1994				
Watsonisuchus	MNHN MAE3000-3009; UMZC T173; MSNM V2992(c)	Damiani 1998; Lehmnan 1961; Warren 1980				
Wantzosaurus	MNHN MAE3030, 3034; RHMA01	Lehman 1961				

Terminal taxa used in the phylogenetic analysis

(c) or (p) following a specimen number indicates that either a cast or a photograph of the specimen was examined, respectively.

Character-taxa matrix

Character number	00000	00001	11111	11112	22222	22223	33333	33334	44444
	12345	67890	12345	67890	12345	67890	12345	67890	12345
Taxon									
Almasaurus	11101	$1\ 0\ 1\ 1\ 0$	$1\ 0\ 1\ 1\ 1$	$0\ 0\ 0\ 1\ 1$	01000	02110	22112	11111	01011
Aphaneramma	10211	$1\ 0\ 1\ 0\ 0$	00101	00111	21?11	01110	??212	$1\ 0\ 2\ 1\ 1$	11110
Archegosaurus	10210	11200	$1\ 0\ 0\ 1\ 0$	00010	$1\ 0\ 0\ 2\ 0$	01110	10012	00000	01110
Benthosuchus	10200	10100	00100	00011	01020	00111	10211	00011	01110
Cosgriffius	10?11	1?210	??101	$0\ 0\ ?\ ?\ ?$??121	?2110	0 - 2 ? ?	??21?	???0?
Dutuitosaurus	11000	10100	00111	00011	01010	02000	20111	11011	01011
Erythrobatrachus	10211	1?201	??????	00?0?	????1	?2110	?11?1	0?2?1	1???0
Inflectosaurus	10110	0?000	??????	? ? ? ? ? ?	????0	?110?	0 - 2 1 1	00?11	10000
Luzocephalus	10010	10110	00100	00012	00020	01100	$1\ 0\ 0\ 1\ 0$	00211	10011
Lyrocephaliscus	00001	10000	01101	00002	$1\ 0\ 0\ 0\ 0$	02100	22110	10211	01101
Onchiodon	00000	00000	00000	00000	00000	00000	$0 - 0 \ 00$	00000	00000
Platystega	10111	1?001	11??0	0?00?	???20	01100	21110	10211	1??10
Stoschiosaurus	????1	1???0	00?00	$0\ 0\ 0\ ?\ 1$?1??1	0????	???11	01211	001?0
Tertrema	10011	10210	??101	???1?	???20	?1110	22110	?1?11	10000
Trematosaurus	10011	10100	10101	00012	01010	02110	20211	00211	10001
Trematosuchus	$1\ 0\ 0\ 1\ 1$	00000	10011	01002	00020	02110	0 - 2.00	00211	10?01
Wantzosaurus	10201	11210	10100	00012	00121	01111	2?0?2	0?2?1	00??0
Watsonisuchus	10200	11100	00100	$1 \ 0 \ 1 \ 1 \ 1$	$2\ 1\ 0\ 1\ 0$	$1 \ 0 \ 1 \ 0 \ 0$	$1 \ 0 \ 1 \ 1 \ 1$	00011	11000

Character number	44445	55555	55556	66666	6666
Character number	67890	12345	67890	12345	6789
Taxon					
Almasaurus	$1 \ 0 \ 0 \ 0$	$1\ 1\ 0\ 0\ 1$	00110	1?111	1000?
Aphaneramma	1111	11011	11110	????1	???11
Archegosaurus	1001	10?00	??010	00100	00011
Benthosuchus	1010	01011	01100	11100	01000
Cosgriffius	????	? ? ? ? ? ?	? ? ? ? ? ?	? ? ? ? ? ?	?????
Dutuitosaurus	$1 \ 0 \ 0 \ 0$	11000	10110	11101	10100
Erythrobatrachus	????	? ? ? ? ? ?	? ? ? ? ? ?	? ? ? ? ? ?	?????
Inflectosaurus	1 0 ? 1	$1\ 1\ ?\ ?\ 1$	00?01	11101	11???
Luzocephalus	1010	11011	20???	? ? ? ? ? ?	?????
Lyrocephaliscus	1011	01111	$2\ 1\ ?\ ?\ ?$? ? ? ? ? ?	???10
Onchiodon	0000	00000	0?000	00000	00000
Platystega	????	? ? ? ? ? ?	? ? ? ? ? ?	? ? ? ? ? ?	?????
Stoschiosaurus	????	? ? ? ? ? ?	? ? ? ? ? ?	? ? ? ? ? ?	?????
Tertrema	?101	011?1	1????	?????	?????
Trematosaurus	$1 \ 0 \ 0 \ 0$	01011	1?100	????0	?????
Trematosuchus	1???	?????	?????	?????	?????
Wantzosaurus	1110	01011	1?110	1???0	0??11
Watsonisuchus	1010	11011	01101	10110	00101

(0 is the plesiomorphic state)

List of the characters

(a) = multistate character treated as additive on the basis of the ontogeny. The characters have been observed on adult specimens.

Characters of the skull roof

1. Skull roof elongate (midline length > maximum width; 1) or not (0).

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- 2. Position of the centre of the orbit along the dorsal midline of the skull: orbit posteriorly (0) or anteriorly (1) situated.
- 3. Short (0), constricted (1), or elongated (2) snout (preorbital part of the skull twice longer than the postorbital one; 2).
- 4. Large (0) or small orbit (maximum size < 14 per cent of the dorsal midline length; 1).
- 5. Orbit facing laterally (1) or dorsally (0).
- 6. Rounded (0) or oval (1) orbit.
- 7. Slightly concave (0) or semicircular (1) posterior margin of the skull roof.
- 8(a). Nostril rounded (0), ovoid (1), or elongate (2).
- 9. Nostril in lateral position (1) or not (0).
- 10. Skull roof bulged (1) or not (0) at the level of the orbits.
- 11. Pineal foramen small (0) or large (1) relative to the size of the skull roof.
- 12. Pineal foramen rounded (0) or not (1).
- 13. Presence (1) or absence (0) of sensory-line grooves in front of the orbits.
- 14. Presence (0) or absence (1) of sensory-line grooves behind orbits.
- 15. Frontal extended behind orbit (1) or not (0).
- 16. Frontal in contact with orbit (1) or not (0).
- 17. Presence (1) or absence (0) of the interfrontal.
- 18. Presence (1) or absence (0) of the centroparietal.
- 19. Septomaxilla visible (0) or not (1) on the dorsal side of the skull.
- 20. Otic notch deep and narrow (0), or deep and open (1), or shallow and open (2).
- 21(a). Tabular rounded (0), pointed (1), or hook-shaped (2).
- 22. Quadrate condyle posterior (0) or anterior (1) to the occipital condyle.
- 23. Presence (1) or absence (0) of an anterodorsal dentary foramen.
- 24(a). Premaxilla/nasal suture posteriorly directed (the premaxilla is partly extended posterior to the nostril; 0), straight (1), or anterior directed (2).
- 25. Presence (1) or absence (0) of a prenarial growth zone.
- 26. Presence (1) or absence (0) of a 'temporal fossa' (*sensu* Damiani 1998; a slight depressed region of the skull roof anteriorly to the otic notches).
- 27(a). Ventral opening of the orbit at the level of the posterior half (0), in the mid part (1), or in the anterior half (2) of the interpterygoid vacuity.

Characters of the palate

- 28. Vomer in contact (1) or not (0) with the maxilla.
- 29. Choana rounded (0) or elongate (1).
- 30. Choana overlapping the nostril (1) or not (0).
- 31(a). Absence (0) or presence of a single (1) or of a paired (2) anteropalatal vacuity.
- 32(a). Anteropalatal vacuity(ies) posterior (0), between (1), or anterior (2) to the premaxilla/vomerine suture.
- 33. Interpterygoid vacuity posteriorly (0) or anteriorly (1) widened, or not widened at all (2).
- 34. Presence (1) or absence (0) of a crista obliqua on the ventral surface of the pterygoid.
- 35. Anterior branch of the pterygoid laterally extended (0), entirely wide (1), or narrow (2).
- 36. Posterior branch ('quadrate ramus') of the pterygoid narrow and elongate (0), or short and wide (1).
- 37. Presence (0) or absence (1) of an area asparta of the pterygoid.
- 38. Wide (0), narrow (1) or knife-edged (2) cultriform process of the parasphenoid.
- 39. Elongate (0) or very short (or absent) (1) suture between the palatine and the pterygoid.
- 40. Very short (0) or elongate (1) suture between the pterygoid and parasphenoid.
- 41. Wide (width>length; 0) or narrow (length > width; 1) parasphenoid plate.
- 42. Presence (1) or absence (0) of the crista muscularis of the parasphenoid.
- 43. Carotid canal visible (1) or not (0) on the ventral surface of the parasphenoid.
- 44. Presence (0) or absence (1) of ectopterygoidal tusks.
- 45. Suture between the exoccipital and the pterygoid visible (1) or not (0) in ventral view.

Characters of the occiput

- 46. Presence (1) or absence (0) of the paraquadrate foramen (foramen for the chorda tympani).
- 47. Flattened (0) or deep (1) occiput, in occipital view.

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- 48. Dorsally (0) or ventrally (1) directed tabular, in occipital view.
- 49. Small (0) or large (1) occipital condyle.
- 50. Occipital condyles widely separated (0) or not (1) from each other.
- 51. Foramen magnum ventrally constricted (1) or not (0).
- 52. Curved (0) or straight (1) dorsal margin of the foramen magnum.
- 53. Presence (1) or absence (0) of the crista falciformis of the squamosal, in occipital view.
- 54. Shallow (0) or deep (1) posttemporal fenestra.
- 55. Elongate (0), triangular (1) or rounded (2) posttemporal fenestra.
- 56. Wide (0) or narrow (1) proximal part of the stapes.

Characters of the mandible

- 57(a). Posterior end of the mandible situated at the same level (0) or behind (1) the quadrate condyle.
- 58. Mandible deep (0) or shallow (1) in lateral view.
- 59. Presence (1) or absence (0) of an anterior constriction of the ventral outline of the mandible, in lateral view.
- 60. Reduced (0) or extended (1) dentary symphysis.
- 61. Presence (1) or absence (0) of a parasymphysial tusk.
- 62. Presence (0) or absence (1) of a parasymphysial tooth row.
- 63. Presence (1) or absence (0) of denticles on coronoids 2 and 3.
- 64. Presence (1) or absence (0) of sensory-line grooves on the mandible.
- 65. Meckelian foramen short (0) or elongate (1).
- 66. Poorly developed or absent (0), or well-developed (1) crista medialis (*sensu* Damiani 1998); a vertical blade on the midline of the postglenoid area (PGA *sensu* Jupp and Warren 1986).
- 67. Presence (1) or absence (0) of the crista articularis (*sensu* Damiani 1998); a vertical blade on the postero-lingual border of the PGA.

Characters of the postcranial skeleton

- 68. Interclavicle narrow (1) or not (0).
- 69. Interclavicle with (0) or without (1) dorsal crest(s) (trabeculae *sensu* Bystrow and Efremov 1940; i.e. relatively wide and flat walls posteriorly and antero-laterally directed on the dorsal surface of the interclavicle).