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A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus*

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Several authors have drawn attention to the close similarities between the neotheropod dinosaurs *Coelophysis* and *Syntarsus.* Reconstruction and analysis of a skull from a juvenile specimen of *Syntarsus* (collected from the Forest Sandstone Formation of Zimbabwe) show that cranial characters previously used to distinguish these taxa and justify their generic separation (namely the presence of a 'nasal fenestra' in *Syntarsus* and the length of its antorbital fenestra), were based on erroneous reconstructions of disassociated cranial elements. On the basis of this reinterpretation we conclude that *Syntarsus* is a junior synonym of *Coelophysis.* Variations are noted in three cranial characters – the length of the maxillary tooth row, the width of the base of the lachrymal and the shape of the antorbital maxillary fossa – that taken together with the chronological and geographical separation of the two taxa justify separation at species level.

Keywords: Dinosaurs, Neotheropoda, Coelophysoid, taxonomy, Triassic, Jurassic.

INTRODUCTION

Ever since the theropod *Syntarsus rhodesiensis* was first described (Raath 1969), a succession of authors have commented on the close morphological similarity between it and *Coelophysis bauri* (Raath 1969, 1977; Paul 1988, 1993; Colbert 1989; Rowe 1989; Tykoski 1998; Downs 2000). Paul (1988, 1993) went so far as to propose that the two taxa belong in the same genus, and that the differences advanced to justify their generic separation are questionable.

Recent work on a partially disarticulated skull of a juvenile specimen of *Syntarsus,* QG165, has made it possible to clarify details of the relationships between several critical cranial elements that were unclear in previous reconstructions. Reconstruction of the cranium allowed reassessment of the characters used by Raath (1977) to distinguish *Syntarsus* from the closely related *Coelophysis.* These characters included the 'nasal fenestra' (reported by Raath,1977, as present in *Syntarsus* but absent in *Coelophysis*); the nature of the contact between the lachrymal and the jugal bones; and Raath's (1977) observation that the antorbital fenestra in *Syntarsus* represented 43% of total skull length. Analysis of the newly discovered skull has demolished each of these purported characters, leading us to concur with Paul (1988 1993) that i) *Syntarsus* is a junior synonym of *Coelophysis,* and ii) that the recently proposed facetious replacement name for *Syntarsus* (*Megapnosaurus* Ivie, Slipinski & Wegrzynowicz, 2001) should not stand.

TAXONOMIC HISTORY

Coelophysis and *Syntarsus* have, until recently, been classified as ceratosaurian theropod dinosaurs, with *C. bauri* from the Late Triassic of North America and *S. rhodesiensis* from the Early Jurassic of Zimbabwe and South Africa. Following the work of Gauthier (1986), these taxa were suggested to belong to a monophyletic clade known as Ceratosauria. However, more recent works by a number of authors (Sereno 1997, 1999; Holtz 2000; Wilson *et al.* 2003; Rauhut 2003) have re-evaluated theropod interrelationships. For example, Rauhut (2003) proposed that Ceratosauria *sensu* Gauthier (1986) is paraphyletic and that the taxa usually grouped as ceratosaurs instead form two monophyletic clades that represent successive outgroups to the Tetanurae. The most basal clade is the Coelophysoidea from the Upper Triassic of the Chinle Formation in the U.S.A. to the Early Jurassic of 'Stormberg Group' equivalents in southern Africa. The second clade of basal theropods, comprising a more restricted Ceratosauria (*sensu* Rauhut 2003), includes *Ceratosaurus, Elaphrosaurus* and the abelisaurids.

Rauhut (2003) has argued that there are two fundamentally different approaches in the reconstruction of theropod phylogeny. He has pointed out that analyses such as those of Thulborn (1984), Gauthier (1986) and Sereno *et al.* (1996) are based on predetermined lists of synapomorphic characters. The result of this approach has been robust analyses with good resolution and exceptionally high consistency ratios. However, this method does not reflect the high degree of homoplasy that occurs in theropod phylogeny, and only partially represents a test of homology by congruence, the most reliable method of testing for homology (Rauhut 2003). The other method, preferred by Rauhut (2003), is to use as many characters as possible to test for congruence, and to establish synapomorphies in this way. Consistency ratios and cladogram resolution are not nearly as impressive, and the resulting phylogenies demonstrate abundant homoplasy (Rauhut 2003). However, the advantage of this approach is that it avoids preconceptions regarding the distribution of synapomorphic features on any particular

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phylogeny. While character choice will always be contentious, Rauhut (2003) maintains the second method results in a more objective analysis. We have followed Rauhut's approach in this study.

GEOLOGICAL SETTING OF THE QG165 SKULL

All known *Syntarsus*-bearing localities in Zimbabwe are in the fine-grained, pale, buff-coloured Forest Sandstone Formation (Raath 1969, 1977). Based on lithostratigraphic correlation, the Forest Sandstone Formation may be the equivalent of the upper part of the 'Stormberg Group' of the main Karoo Basin in South Africa (Olsen & Galton 1984). The 'Stormberg Group' comprises the Molteno, Elliot and Clarens formations, and the upper 'Stormberg' represents the Upper Elliot and Clarens formations (Olsen & Galton 1984). Olsen and Galton suggested on the basis of comparisons with European faunal assemblages that the lower 'Stormberg' assemblage was Late Triassic (Carnian-Norian) in age. However, on the basis of field evidence, Lucas & Hancox (2001) have assigned the prosauropod-dominated lower Elliot Formation a Norian age. The upper 'Stormberg' assemblage contains more diverse tetrapod assemblages than originally suggested by Kitching & Raath (1984), and Lucas & Hancox (2001) have conservatively assigned it an Early Jurassic age (Hettangian-Pliensbachian). They also considered the overlying Clarens Formation, which contains a limited fauna of taxa common to the underlying upper Elliot assemblages, to be Early Jurassic. The upper 'Stormberg' assemblage broadly correlates with the upper Newark Supergroup (eastern U.S.A.), the Glen Canyon Group (southwestern U.S.A.) and the Lower Lufeng Series (China). The African coelophysoid-bearing deposits are thus separated from the North American bone-beds by a significant period of geological time and a considerable continental distance.

One of the distinctive characteristics of coelophysoid deposits in both geographic locations is that they represent mass burials. One of the three localities in Zimbabwe preserves numerous individuals of *S. rhodesiensis* (Raath 1977, 1980). Two localities in the Kayenta Formation of Arizona, U.S.A., preserved at least three and eleven individuals of *S. kayentakatae*, respectively (Rowe 1989). The Ghost Ranch Quarry is one of the richest Mesozoic dinosaur burials yet discovered, although claims that it has yielded a thousand individuals (Schwartz & Gillette 1994) are difficult to substantiate because there are no data on minimum numbers of individuals recovered (Sullivan 1996). It is, however, accepted that the site has yielded at least hundreds of individuals of *C. bauri* that were buried en masse in the sediments of the Chinle Formation (Rowe *et al.* 1997).

These mass burials occur in a variety of depositional environments (Rowe & Gauthier 1990). The Ghost Ranch Quarry fossils are found in 1-metre-thick mudstone of fluvial origin (Rowe & Gauthier 1990). The *S. kayentakatae* burials are preserved in overbank deposits, and the mass burial of *S. rhodesiensis* was found in a thin fluvial lens within aeolian deposits (Raath 1977; Rowe & Gauthier 1990), but all localities suggest water-borne deposition of the vertebrate remains. By virtue of the numbers of individuals found at the Ghost Ranch and the Chitaki River sites, it can be concluded that these were catastrophic mass death events. Another exceptional feature of coelophysoid bone-beds is their monospecificity, supporting the conclusion that coelophysoids were gregarious (Raath 1977; Colbert 1989).

MATERIALS AND METHODS

In this account the following institutional abbreviations are used: AMNH, American Museum of Natural History, New York, U.S.A.; CM, Carnegie Museum, Pittsburgh, U.S.A.; GR, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, U.S.A.; MCZ, Museum of Comparative Zoology, Cambridge, U.S.A.; MNA, Museum of Northern Arizona, Flagstaff, U.S.A.; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe

Specimen QG165 was found in a detached block of Forest Sandstone from the Chitaki River bone-bed (approx. 16°07′S, 29°30′E), which was collected by one of the authors (M.A.R.) in 1972, and is now housed in the collections of the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe. It consists of a partially disarticulated almost complete skull of a juvenile specimen, lacking only the snout, and is associated with a number of poorly preserved postcranial elements. This study focused on the skull.

The cranial elements of QG165 are closely associated, which is unusual for material from the Chitaki River site, where the bulk of the collection consists of isolated skeletal elements that have been randomly mixed together. In spite of this, the preservation of the often delicate and fragile bones is excellent and there is no clear evidence of abrasion or predation. Although partially disarticulated as a result of postmortem collapse and drifting by gentle currents, many of the individual elements are still close to their original life positions, providing new insights as to their articular relationships.

Other *Syntarsus* material (also collected by M.A.R.) was compared with QG165, including QG193, 194, 195, 196, 197, 202, 235, 241, 265, 278 and 307. All this material is also stored in the Zimbabwe Natural History Museum. Data on *Coelophysis* material used for comparison in this study was taken from Colbert (1989), in which he used AMNH 7223, 7224, 7227, 7228, 7230, 7239, 7240, 7241, 7242; MCZ4326, 4327, 4333; MNAV3315; YPM41196 and CM-C481. Other material referred to herein includes specimens of *C. bauri* (CM31374, a disarticulated juvenile with CM field number C-3-82-31, GR141, GR142 and GR1442: Downs 2000); and *S. kayentakatae* (MNA V2623: Rowe 1989; Tykoski 1998).

After initial mechanical preparation of QG165 to expose the extent of the skull, it was scanned at the Sunninghill Hospital, Sandton, Johannesburg, in a series of fine slices using a Philips Multidetector MX 8000 spiral CT scanner with effective slice thickness of 0.6 mm. The resulting images were manipulated on a Philips MxView workstation using maximal intensity projection imaging techniques and saved on CD in DICOM format. The formatted images were converted at the School of Mechanical,

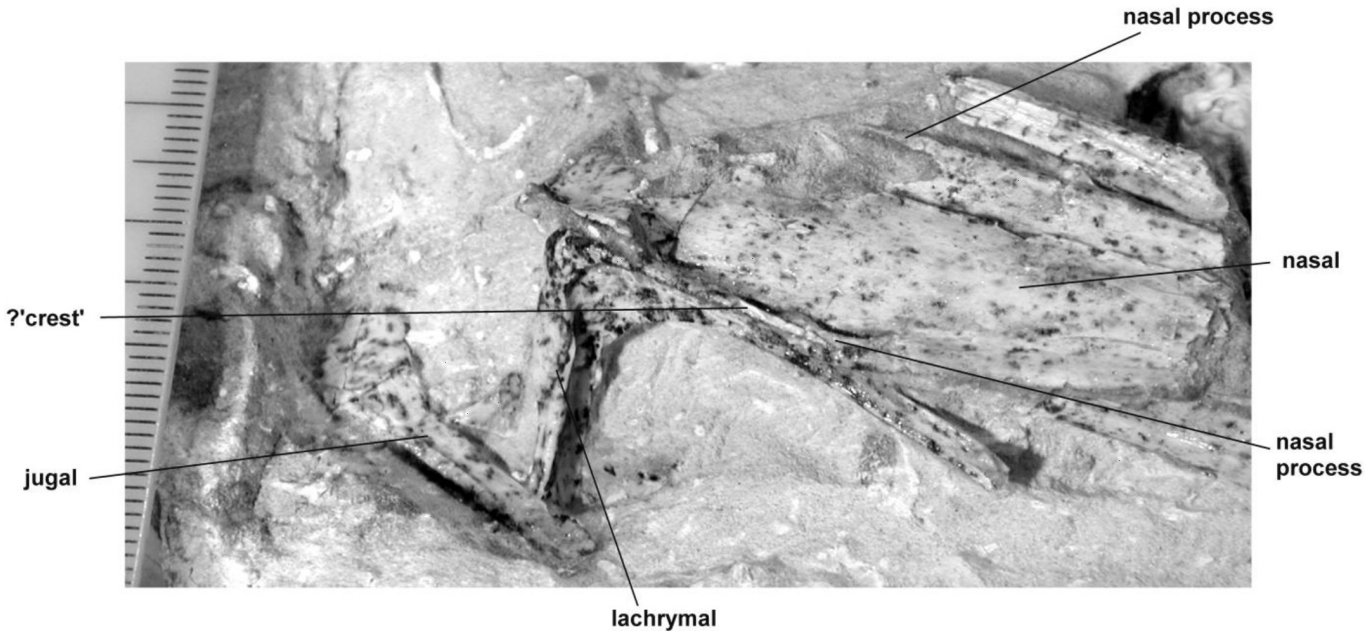


Figure 1. The right lachrymal of QG165 shown in partial articulation with the nasal and nasal process (or 'nasal fenestra' as described by Raath 1977) (scale divisions = mm).

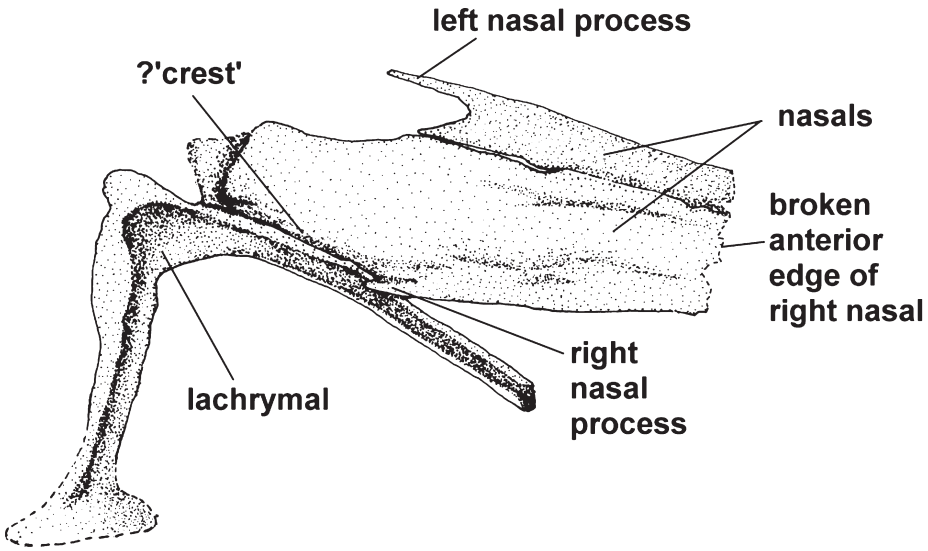


Figure 2. Interpretive drawing of right lachrymal of QG165 shown in contact with the nasal process and the body of the nasal, forming a small incipient crest.

Industrial and Aeronautical Engineering at the University of the Witwatersrand using the Mimics package Version 7.3, into a digital volume, which was exported to STL (stereolithographic) file format. The STL file was sent to a commercial prototyping company where a three-dimensional was replica was produced. This replica was used to supplement examination of those areas of QG165 which would have been endangered by further physical preparation.

DESCRIPTION

Raath (1977) identified a posterolateral nasal process – bordering what he termed the 'nasal fenestra' – as a defining character of *Syntarsus.* In QG165, the left nasal process is disassociated from the left nasal, but the distinctive V-shaped embayment is preserved (Fig. 1). However, the right nasal and the right nasal process are still essentially in articulation with the right lachrymal (Figs 1, 2). The nasal process is similar in every respect, other than size, to that seen in a juvenile *Coelophysis* specimen (C38231: Downs 2000, Fig. 3). The dorsal ramus of the right lachrymal and the lateral edge of the right nasal articulate to form what could be interpreted as a slightly raised incipient parasagittal crest, similar to the longitudinal crest described by Rowe (1989) in *S. kayentakatae,* but on a much smaller scale (Figs 1, 2). This 'crest' is slight, measuring no more than 3 mm in height and approximately 2 mm wide at the base. The right nasal process articulates with the anterior edge of this crest. Since there is no evidence of a similar crest on the left nasal, although the nasal process itself is preserved (Fig. 1), it seems likely that the small 'crest' on the right side is an artefact of slight displacement and distortion of the very thin and plastic lachrymal and nasal bones.

Compared with the flat, featureless appearance of most of the skull bones, the lachrymals are curved and sinuous. The right lachrymal articulates with the lateral margin of the right nasal and the nasal process. It is a slender L-shaped bone with an anteriorly projecting upper ramus and a ventrally projecting vertical process that expands into a footplate (Raath 1977). The base of the footplate is noticeably narrower anteroposteriorly than in *Coelophysis*, measuring less than 30 per cent of the height of the vertical arm of the lachrymal, compared to more than 30 per cent in a number of specimens of *Coelophysis*, most notably in the well-preserved complete skull CM31374 (Fig. 4). The medial and lateral margins of the vertical process of the right lachrymal border an anterior sulcus that tapers into a grooved lip along the lateral border as it reaches the ventral footplate. The footplate of the right lachrymal flares into a posterolateral process and an anterior process. The anterior process is cupped and expands outward around a noticeable sulcus. The footplate of the left lachrymal is not preserved. When restored, the footplate of the right lachrymal would have articulated with the dorsomedial margins of the jugal and maxilla.

The jugal is a long, flat, thin bone, reinforced by longitudinal ridges along the lateral surface (Figs 5, 6). It forms both the lateroventral border and part of the posterior border of the orbit. The bone divides into two rami posteriorly – a dorsal ramus that articulates with the ventral process of the postorbital, and a posterior ramus that overlaps the anterior ramus of the quadratojugal (Figs 5, 6). The anterior end of the jugal tapers to a finely pointed tip, and articulates with the posterior end of the maxilla and the ventral footplate of the lachrymal. It is excluded from the antorbital fenestra. The posterior end of the jugal is forked to receive the corresponding anterior process of the quadratojugal.

This reconstruction of the palatine presented herein takes into account research on palatine recesses by Witmer (1997) and by Harris (1998). The right palatine in QG165 is reconstructed as a tetraradiate element comprised of four conjoined processes (Figs 7, 8). There is a deeply excavated fossa (Fig. 7) on the dorsal surface of the palatine and the pterygoid that Witmer (1997) terms the muscular fossa. The muscular fossa is bordered by a pronounced ridge that reaches anteromedially from the maxillary contact in front of the suborbital fenestra to the

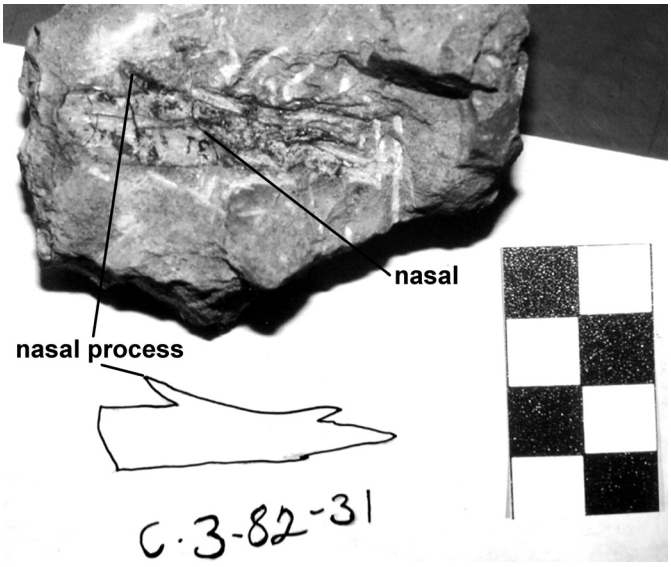


Figure 3. Isolated juvenile nasal of *C. bauri* C38231; anterior is towards the right of the figure (photograph: A. Downs) (scale divisions = cm).

vomeropterygoid contact. The vomeropterygoid process is expanded and extends both anteriorly and medially, creating a surface for the origin of the M. pterygoideus, pars dorsalis (Witmer 1997). A slender tapering maxillary process extends anteriorly, ventral to the vomeropterygoid process. The maxillary process and the vomeropterygoid process form the posterior borders of the choana. The fourth element of the palatine is what Harris (1998) terms the medial process, which like the maxillary process is long, tapering and laterally compressed. The medial process forms the ventral border of the palatine fenestra.

It is clear from this reinterpretation that Raath (1977: fig. 4h,i) inverted the disarticulated right palatine in his reconstruction. If an image of the isolated palatine QG241 is rotated through 180 degrees (Fig. 9), the bone closely resembles the palatine in both QG165 (Fig. 7), and Witmer's (1997) reconstructions of *Coelophysis* (Fig. 10). In addition, the palatine in QG165 was found in close association with the pterygoid and the maxilla, suggesting that it was in, or close to, its natural position, adding further support to the reconstruction proposed herein. Witmer (1997) has used the palatine of *Coelophysis*, CM31374, to demonstrate the presence of a muscular fossa on the palatine and the sharply delineated ridge (Fig. 7). Witmer's

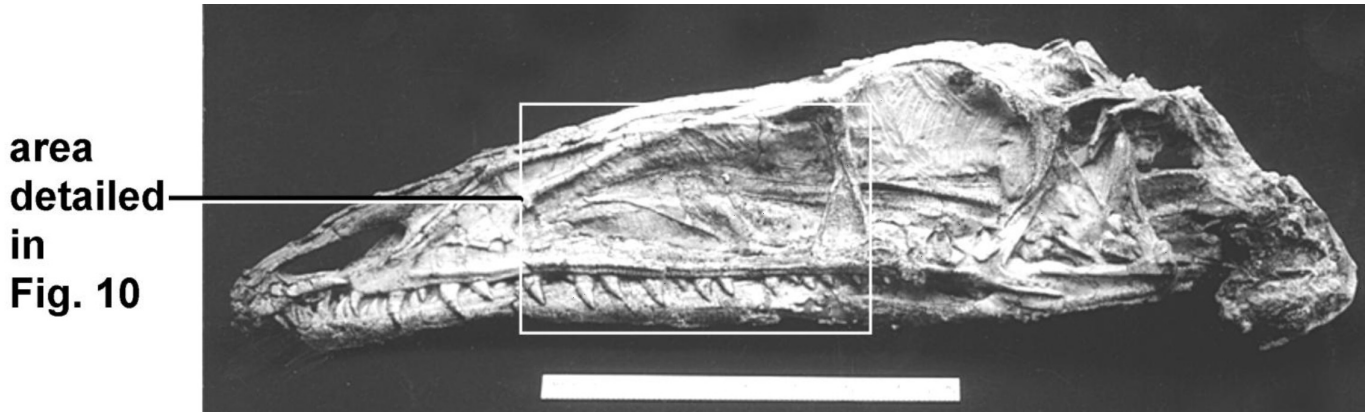


Figure 4. Subadult *Coelophysis* skull, CM31374, on which Witmer (1997) based his drawings in Fig. 10 (photograph: A. Downs) (scale bar = 8 cm).

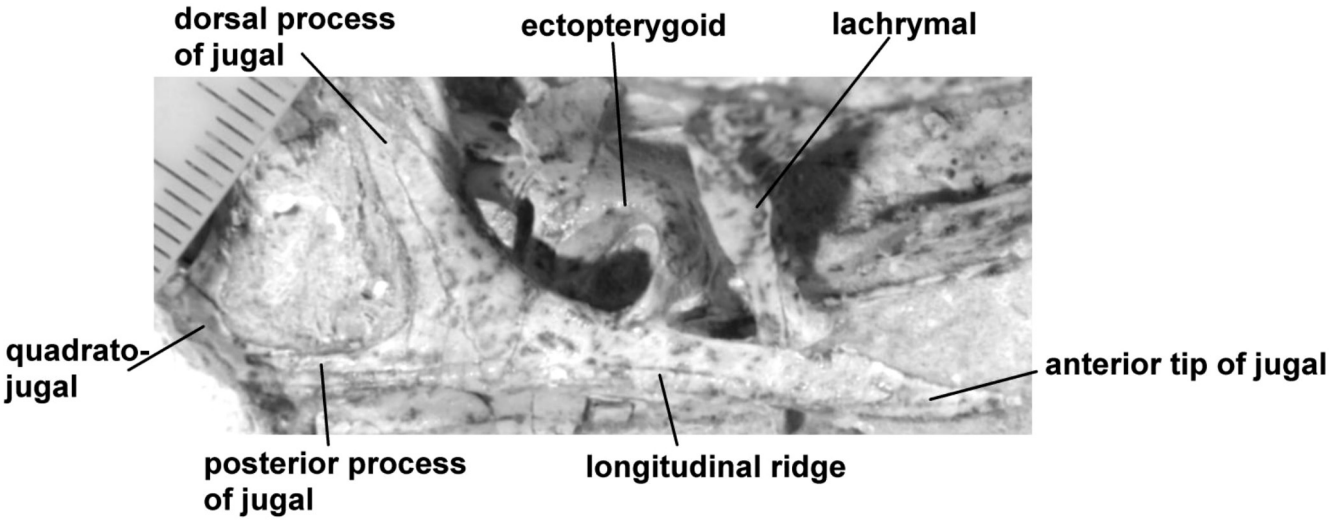


Figure 5. Right jugal of QG165, still in articulation with the quadratojugal. The right ectopterygoid articulates with the medial surface (scale divisions = mm).

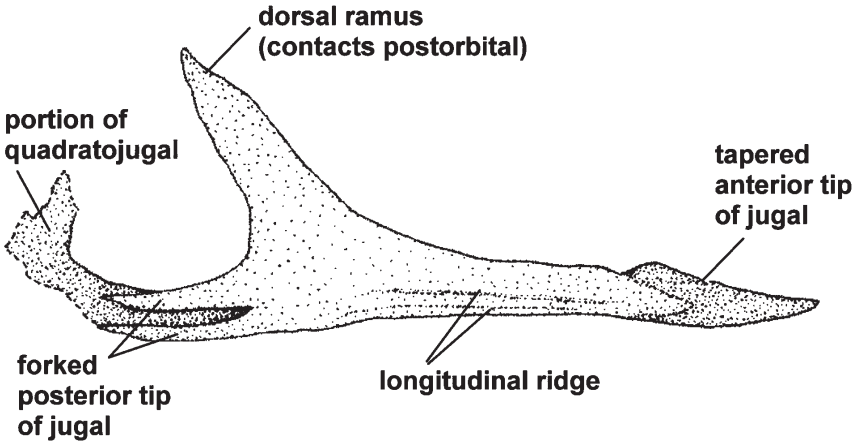


Figure 6. Interpretive drawing of the right jugal of QG165, with longitudinal ridges, a delicate anterior tip and forked posteriorly.

(1997) drawings are indistinguishable from the palatine of QG165 (Fig. 10). The vomer in QG165 was not preserved but the posterior ends of these long, slender elements would have contacted the elongate, anterior processes of the pterygoid.

A pair of hyoids that match those described in *C. bauri* (Colbert 1989) and in *S. kayentakatae* (Rowe, 1989) is preserved in QG165; they were not initially visible but were revealed in the rapid-prototyped replica. The hyoids in QG165 are long slender rods that are slightly bowed or angled toward the centre. They taper anteriorly, and expand and flatten posteriorly. One hyoid lies in close association with the ventral edge of the left dentary and the other in association with the right dentary. Because of damage to the left dentary, it is not possible to estimate the length of the hyoids as Rowe (1989) did in *S. kayentakatae,* but clearly these are long slender rods that could easily have reached one third of the length of the dentary. The hyoids of QG165 differ substantially from the elements identified by Raath (1977) as hyoids, lending support to the suggestion by Tykoski *et al.* (1993) that the latter elements are in fact furculae.

TAXONOMIC ANALYSIS

This analysis aims to test the validity of the historical distinctions between *Syntarsus* and *Coelophysis* to determine whether or not the former is a junior synonym of the latter. The technique of taxonomic analysis (comparison of the different character states of the two taxa) was preferred over cladistic analysis because a cladistic analysis would only reveal that *Syntarsus* and *Coelophysis* are sister taxa. However, the analysis is based on the list of theropod characters developed by Rauhut (2003) for his comprehensive cladistic analysis. He used 224 characters, 87 of which are cranial. Four additional characters have been added to his list of characters: (88) the presence or absence of a posterolateral nasal process (what Raath 1977, termed the 'nasal fenestra'); (89) size of the antorbital fenestra more than 40 per cent of total skull length, or less than 40 per cent; (90) width of the base of the vertical ramus of the lachrymal expressed as a percentage of its height; and (91) the presence or absence of interdental plates.

Overall, this analysis reiterates the remarkable similarity between *Syntarsus* and *Coelophysis.* Of the 91 cranial characters used, only 13 points of doubt or difference between the two taxa emerged, most of the uncertainty caused by preservational artefacts or missing data. The remaining 78 cranial characters were identical in the two taxa. For those 13 characters where differences were noted between the genera, ten characters were scored as uncertain in *Coelophysis* because they were either obscured or distorted, or

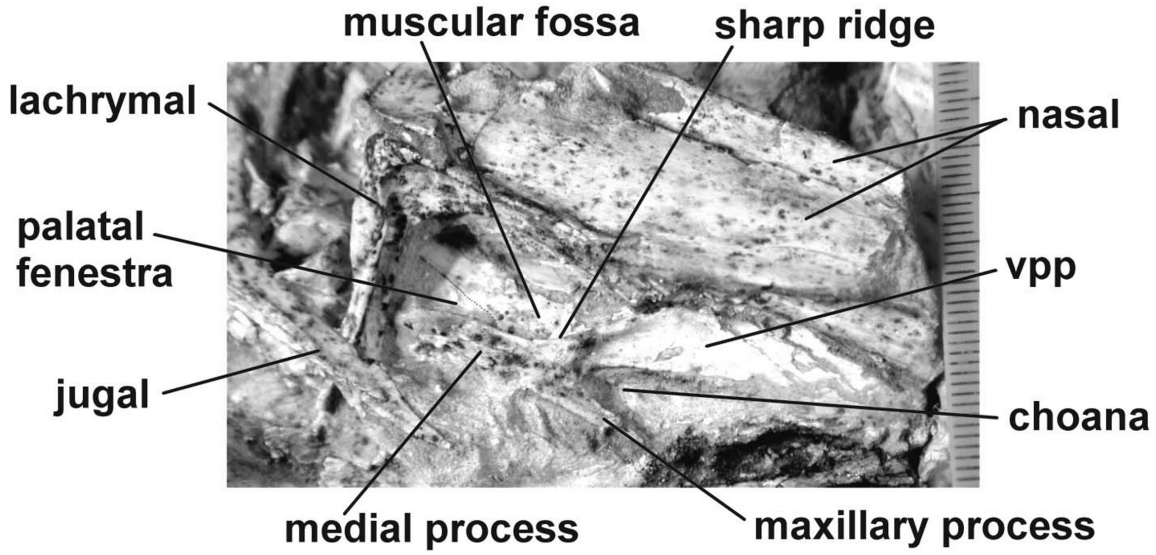


Figure 7. Tetraradiate right palatine bone of QG165 showing the deep muscular fossa and sharply delineated ridge as described by Witmer (1997). 'vpp' = vomeropterygoid process (scale divisions = mm).

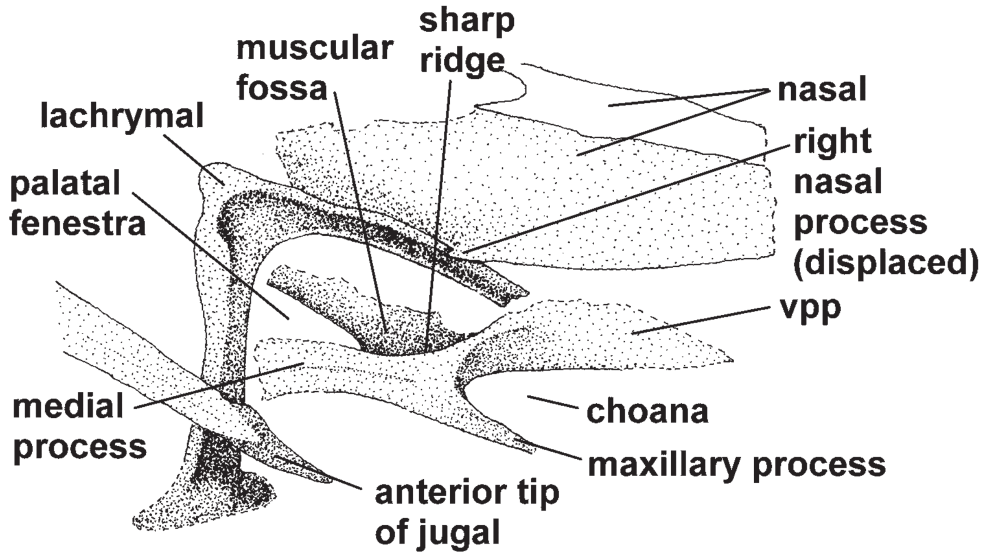


Figure 8. Interpretative drawing of palatine of QG165 in relation to surrounding elements (see also Figs 6 and 8).

there was insufficient information to score the character with confidence. Most *Coelophysis* skulls have been so bilaterally compressed that they provide information only in lateral view, and for this reason it is difficult to establish the nature of endocranial characters. Characters dealing with the pneumatization were difficult to score for the same reason, and because Colbert (1989) provided little detail on this aspect of the morphology. Characters of the dentary teeth in *Coelophysis* were problematic because the jaws of most specimens are clamped shut and the upper jaw tends to obscure dentary teeth. The ten uncertain characters in *Coelophysis* are: (37), (41), (49), (53), (60), (61), (63), (72), (74) and (83) (see Appendix 1). The three characters where points of distinction were confirmed are (13), (70) and (90). Character 13 relates to the shape of the maxillary antorbital fossa: in *Coelophysis* it is pointed, whereas in *Syntarsus* it is squared. Character 70 relates to the length of the maxillary tooth row and the posterior point at which it ends: the maxillary tooth row is longer in *Coelophysis* than in *Syntarsus.* Character 90 relates to the width of the ventral base of the vertical ramus of the lachrymal in relation to its height: in *Syntarsus* the width of the base of the lachrymal is less than 30 per cent of the height of the vertical ramus, whereas in *Coelophysis* it is more than 30 per cent.

DISCUSSION

There are no generally accepted criteria for distinguishing taxonomically significant differences from mere individual variation, and Molnar (1990) cautions against the assumption that taxonomically significant differences are always expressed in the skeleton, as there is a tendency to underestimate taxonomic diversity in fossils. However, an advantage when comparing *Coelophysis* and *Syntarsus* is that the taxa are based on samples of material that are quantitatively more than adequate and qualitatively excellent, especially where *Syntarsus* is concerned (Raath 1990).

The first step in assessing whether *Syntarsus* is a synonym of *Coelophysis* is to review Raath's (1977) list of thirteen characters that he considered diagnostic of the taxon. Five of these relate to differences in the length of a

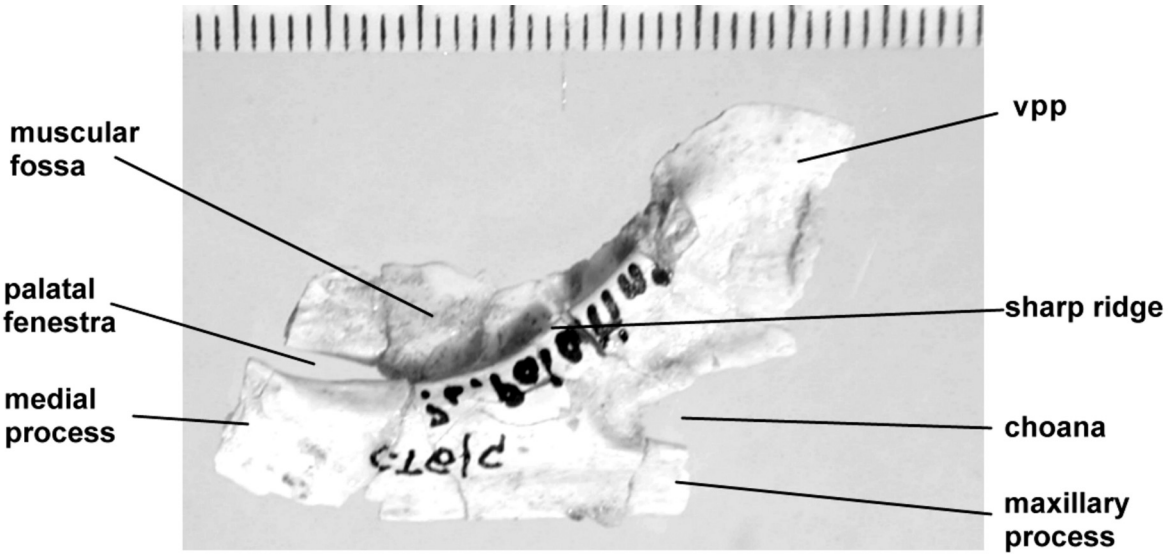


Figure 9. The right palatine of QG241, reversed left-to-right for comparison with QG165 in Fig. 7 (photograph: M.A. Raath) (scale divisions = mm).

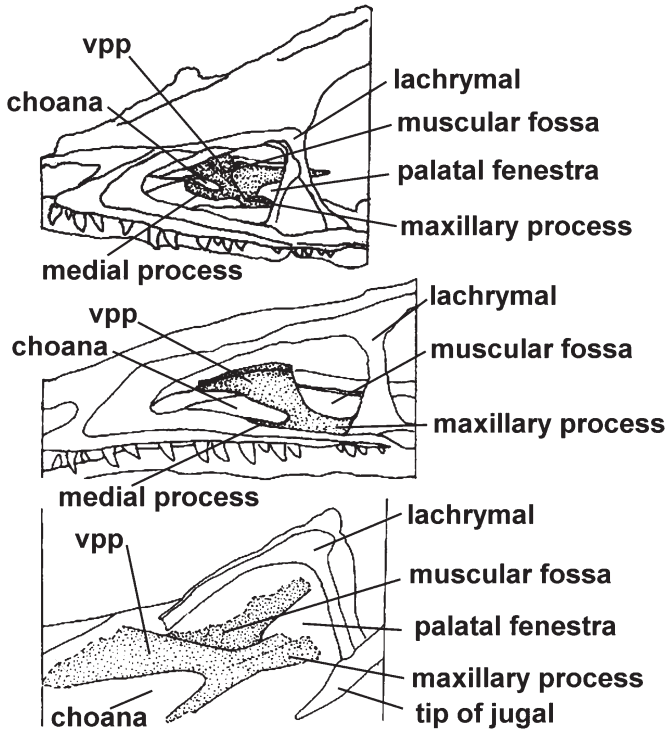


Figure 10. Comparison of tetraradiate coelophysoid palates illustrating the muscular fossa described by Witmer (1997). A. *C. bauri* (CM31375) redrawn from Witmer (1997); B. *C bauri* (CM31374), redrawn from Witmer (1997); C. *C. rhodesiensis* QG165. 'vpp' = vomeropterygoid process.

number of elements of the skull, expressed as percentages. Estimates given by Raath (1977) all indicate that *Syntarsus* is generally smaller than *Coelophysis*, except for the proportional length of the antorbital fenestra. Raath (1977) estimated the length of the antorbital fenestra at 43 per cent of total skull length in *Syntarsus.* Owing to the partial disarticulation of QG165 it is not possible to estimate the length of the antorbital fenestra, but Rowe (1989) estimated that the antorbital fenestra of S. *kayentakatae* was approximately 26 per cent of total skull length, which is similar to the figure obtained for *Coelophysis* (27 per cent: Colbert 1989). It is difficult to assess dental characters in QG165 because its jaws are incompletely preserved. However, Colbert (1989) noted that the upper tooth row in *Coelophysis* extends to a point beneath the middle of the orbit while in *Syntarsus* the upper tooth row extends to the posterior border of the antorbital fenestra. Also, it has not been possible to estimate ratios of skull height to length, or skull length to presacral length in QG165 because of its incompleteness: Raath's (1977) estimates have not been accepted because the new reconstruction of the nasal and lachrymal contact proposed here would affect his ratios, making the antorbital fenestra in *Syntarsus* proportionally significantly smaller than he estimated. As far as the palatine is concerned, it is noted that Raath's (1977) reconstruction was based on a disarticulated right palatine bone that was inverted in the reconstruction. The reconstruction proposed herein follows the pattern found in most non-avian theropods as described by Witmer (1997) and Harris (1998) – it is a tetraradiate bone consisting of four conjoined processes.

Secondly, the *Syntarsus* characters listed as definitive by Rowe (1989), (23) antorbital fenestra more than 40 per cent of total skull length, and (24) lachrymal overlaps the jugal laterally and reaches the alveolar border, must be re-examined. Both characters were based on Raath's reconstruction of disarticulated cranial elements. Rowe (1989) believed that if these characters were not sustained by articulated material, the diagnosis of *S. rhodesiensis* might need to be reconsidered.

Thirdly, it was found that *Syntarsus* and *Coelophysis* differed in only three of 91 phylogenetically informative cranial characters (see above). All these characters 13, 70 and 90 (see Appendix 1), relate to and affect the shape of the antorbital fenestra, subtly reducing its size in *Syntarsus.*

Previously contested characters were then re-evaluated using new evidence gleaned from the reconstruction of QG165. Because the right nasal and the right lachrymal of QG165 are still esentially in articulation, it is possible to propose a different reconstruction from that given by Raath (1977). The dorsal ramus of the right lachrymal and

the lateral edge of the right nasal articulate in the region of the feature described above as an incipient parasagittal crest (although more likely an artefact of distortion) in a position comparable to the longitudinal crest described by Rowe (1989) in *S. kayentakatae.* The posterolateral nasal process (which Raath, 1977, suggested defined what he termed the 'nasal fenestra') articulates with the anterior edge of this slightly raised feature, which extends from the posterior end of the lachrymal to a point about midway along its dorsal ramus. The nasal process could be interpreted as a derived feature of neotheropods including the coelophysoids. The character is not found in basal theropods such as the Herrerasauridae, although this is not surprising since there are significant morphological disparities between the coelophysoids and the herrerasaurids (Sereno & Novas 1993; Rauhut 2003). A homologous structure is found in various other derived neotheropods such as the much younger *Tyrannosaurus rex* (Brochu, 2003). There is, however, an analogous structure in basal sauropodomorphs such as *Plateosaurus* (Galton 1984).

The footplate of the lachrymal is noticeably narrower in *Syntarsus* than in *Coelophysis,* measuring less than 30 per cent of the height of the vertical arm of the lachrymal, compared with more than 30 per cent in a number of specimens of *Coelophysis,* most notably CM31374 (see Fig. 4), but the extent of individual variation in this character remains unknown. In the reconstruction of QG165 proposed here, the lachrymal would articulate partially with the medial surface of the jugal and maxilla. In Raath's (1977) reconstruction the lachrymal overlaps the jugal and maxilla laterally, reaching the alveolar border, and shortening the height of the skull. In the light of the new evidence from QG165, this interpretation is patently incorrect.

There are different interpretations of the jugal in coelophysoids: according to Rowe (1989) the anterior process of the jugal of *S. kayentakatae* is forked; photographs of *Coelophysis* specimen CM 31374 show the jugal tapering to a fine point; the anterior end of the jugal in *Syntarsus* QG278 appears blunt, but the end is clearly broken; in Raath's (1977) reconstruction, the lachrymal overlaps and therefore obscures the anterior end of the jugal; and Colbert (1989) makes no mention of this character at all in his monograph on *Coelophysis.* In view of the excellent state of preservation of the right jugal and the anterior tip of the left jugal in QG165, this character was coded as 'tapering' in the taxonomic analysis.

This articulation between the jugal and the antorbital fenestra has also been variously interpreted but in QG165 the jugal is unambiguously excluded from the antorbital fenestra by the posterior end of the maxilla and the ventral footplate of the lachrymal. In *S. rhodesiensis,* Raath (1977) contended that the jugal was excluded from the antorbital fenestra by the lachrymal footplate, which overlapped the jugal. Rowe (1989) reported that the anterior end of the jugal in *S. kayentakatae* was excluded from the antorbital fenestra by the posterior end of the maxilla. In Colbert's (1989) reconstruction, the anterior tip of the jugal of *C. bauri* reaches the rim of the antorbital fenestra, whereas in photographs of CM31374 and other *Coelophysis* specimens, the tapered tip of the jugal is excluded from the fenestra and this is held to be correct.

The shape of the maxillary antorbital fossa (13): the snout of *Syntarsus* (BP/1/5278) is squared at the anterior margin, forming an angle of approximately 70 degrees to the horizontal dentigerous ramus, whereas the corresponding region of a cast of *Coelophysis* (CM31374) is pointed, forming an angle of approximately 50 degrees.

The next question to consider is whether the shape of a cranial cavity such as the antorbital fenestra represents a significant functional character in coelophysoids, important enough to justify generic separation between the two taxa. Witmer (1997) advances three hypotheses for the function of the antorbital cavity: it could be to house (1) a gland, (2) a muscle, or (3) a paranasal air sac. Having tested all three hypotheses, he concludes that only a paranasal air sac would involve all the bone structure associated with the antorbital fenestra, and that the function of the air sac is simply to pneumatize bone in an opportunistic way. According to Witmer (1997), factors such as weight reduction and optimizing design are secondary effects of air sacs. On this basis characters 13, 70 and 90 do not appear sufficiently significant to justify a generic separation of the taxa, although they might well be significant at species level.

There are other reasons for supporting a distinction at species level, such as the geographic and chronological separation between the two taxa. Geographic separation would not of necessity imply generic differentiation, although it might promote specific divergence. In the Late Triassic, coelophysoids represented the first successful worldwide radiation of theropods (Farlow 1993; Rauhut 2003). Coelophysoids are found in both the Late Triassic and the Early Jurassic, covering a span of around 15–20 million years, from the Carnian-Norian in North America (about 220 Ma) to the Hettangian in southern Africa (about 205.7 Ma to 201.9 Ma; Harland *et al.* 1990). Rauhut (2003) has identified four major theropod radiations in all, with coelophysoids being replaced by ceratosaurs (*sensu* Rauhut 2003) and tetanurans in the Middle Jurassic. Early Mesozoic theropod faunas lived in a world where the movement from one landmass to another was possible because of continental configuration and, as a result, faunas were globally rather uniform. The differences between theropod faunas became more marked with the subsequent fragmentation of Pangaea. The distinctions in faunas between Laurasia and Gondwana increased from the Triassic to the Cretaceous (Farlow 1993; Rauhut 2003), reflecting both early endemism, and the geographic separation of the continents. As an Early Mesozoic fauna, coelophysoids match the pattern of uniformity described by Fowler (1993) and Rauhut (2003), supporting the notion of an early Mesozoic supercontinental fauna (Paul 1993).

The chronological separation of *Coelophysis* (Late Triassic) and *Syntarsus* (Early Jurassic), might be responsible for some of the minor morphological differences that do exist. Niche adaptations to local (desert) conditions in the southern African portion of Gondwana undoubtedly also

account for some part of this variation over time.

We therefore conclude that *Syntarsus* is indeed a junior synonym of *Coelophysis,* as first articulated by Paul (1988), but that the current species distinctions between the Laurasian form (*C. bauri*) and the Gondwanan form (*C. rhodesiensis*) remain valid. We acknowledge, however, that being limited to study of cranial elements only, and relying largely on a single incomplete skull, the foundation on which these conclusions are based is not as solid as we would have preferred. But we are confident that discovery of further articulated cranial material of the Gondwanan coelophysoid material will settle the matter and show that these conclusions are correct.

SYSTEMATIC PALAEONTOLOGY

Class Dinosauria Owen, 1842
Order Saurischia Seeley, 1887
Suborder Theropoda Marsh, 1881
Superfamily Coelophysoidea Welles, 1984 (*sensu* Holtz, 1994)
Family Coelophysidae Paul, 1988

Genus *Coelophysis* Cope, 1889

Type species

Coelophysis bauri Cope 1889 (by designation: Colbert, Charig, Dodson, Gillette, Ostrom & Weishampel 1992). A holotype was not designated by Cope in 1887 and was subsequently selected by Hay in 1930. Specimen AMNH 2722, four sacral vertebrae and an associated pubic process of an ilium, was selected as the lectotype (Colbert 1989).

Synonyms

Tanystropheus von Meyer 1855; (partim; non *T. conspicuus* von Meyer 1855; *T. longobardicus* (Bassani, 1886); *T. antiquus* von Huene, 1905; *T. meridensis* Wild, 1980).
Coelurus Cope 1887
Podokesaurus Talbot 1911
Syntarsus Raath 1969 (non *Syntarsus* Fairmaire 1869)
Longosaurus Welles 1984
Rioarribasaurus Hunt & Lucas 1991
Megapnosaurus Ivie, Slipinski & Wegrzynowicz 2001

Diagnosis (Rauhut 2003)

The diagnosis of the genus *Coelophysis* is founded on a hypodigm consisting of the specimens discovered by Cope and attributed to *C. bauri* and the species regarded as synonyms, *C. longicollis* and *C. willistoni,* as well as complete skeletons of *C. bauri* excavated at Ghost Ranch, New Mexico, by Colbert. *Coelophysis* differs from *Eoraptor, Herrerasaurus* and *Staurikosaurus* in the presence of pleurocoels in the dorsal vertebrae, the more elongated dorsal vertebrae, five fused sacral vertebrae, dolichoiliac ilium, presence of a small lateral projection on the distal end of the tibia and the functionally tridactyl foot with metatarsal I that is attached to metatarsal II and does not reach the ankle joint (Rauhut 2003). It differs from *Gojirasaurus* in the relatively lower dorsal neural spines and the significantly smaller size, from *Liliensternus* in the absence of the broad ridge that extends from the posterior end of the diapophyses to the posterior end of the vertebral centra in cervical vertebrae and the smaller size, from *Procompsognathus* in the considerably larger overall size, and from *Shuvosaurus* in the lack of any derived cranial features of the latter taxon (Rauhut 2003). The posterolateral nasal process is the same in *C.bauri* as in *C. rhodesiensis* and *C. kayentakatae.*

Referred species

C. rhodesiensis (Raath 1969)
?*C. kayentakatae* (Rowe, 1989)

Distribution

U.S.A.: Chinle Formation, Arizona, New Mexico, Petrified Forest National Park, Arizona, Kayenta Formation, Rock Head, Willow Springs, Arizona

Africa: Zimbabwe (Nyamandhlovu, Chitaki River, Maura River); South Africa (northeastern Free State Province)

Europe: ?Wales (D. Warrener, pers. comm. to M. Raath 1984)

Stratigraphic range

Late Triassic: Carnian/Norian (227.4Ma 220.7Ma) – Chinle Formation

Early Jurassic: Hettangian (205.7Ma 201.9Ma) – Forest Sandstone Formation, Elliot/Clarens Formation

Coelophysis rhodesiensis (Raath 1969)

Synonyms

Syntarsus rhodesiensis Raath, 1969
Megapnosaurus rhodesiensis Ivie, Slipinski & Wegrzynowicz, 2001

Holotype QG1 housed in the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe.

Locality and horizon of the holotype

From exposures in the Kwengula stream on Southcote Farm at 19°58′S; 28°24′ 35″E, about 38km northwest of Bulawayo, Zimbabwe (Raath 1969). The Forest Sandstone of Zimbabwe correlates with the upper 'Stormberg Group' in South Africa, and is thus Early Jurassic in age.

Revised diagnosis

C. rhodesiensis is a small bipedal coelophysoid dinosaur (*sensu* Rauhut 2003) that can be distinguished from *C. bauri* by the following cranial characters: the anterior margin of the maxillary antorbital fossa in *C. rhodesiensis* is blunt and squared; the width of the base of the vertical ramus of the lachrymal is less than 30 per cent of its height; and the maxillary tooth row ends at the anterior rim of the lachrymal with the lower tooth row corresponding. These three characters define the margins of the antorbital fenestra, which would be proportionally smaller than the fenestra in *C. bauri.*

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APPENDIX I

Data matrix of cranial characters based on Rauhut (2003). [(Numbers in brackets are the values scored by Rauhut (2003)]

Character	*Coelophysis*	*Syntarsus*
1	0	0
2	1	1
3	0	0 (1)
4	1	1
5	1	1
6	2	2
7	0	0
8	1 (?)	1
9	1	1
10	0	0
11	0	0
12	1	1
13	0 (1)	1
14	0	0
15	1	1
16	0	0
17	0	0
18	0	0
19	0	0
20	0	0
21	0	0
22	1	1
23	0 (?)	0 (1)
24	1 (?)	1 (0/1)
25	0	0
26	0	0
27	1 (0)	1 (0)
28	1	1
29	1	1
30	0	0
31	0	0
32	0	0
33	0	0
34	0	0
35	0	0
36	0 (?)	0 (1)
37	?	0
38	0	0
39	0	0
40	0	0
41	? (?)	0
42	0	0
43	0	0
44	0	0
45	0	0
46	1 (?)	1
47	0	0
48	0 (?)	0
49	?	1 (?)
50	0 (?)	0
51	0	0
52	1 (?)	1
53	?	0
54	0	0
55	0 (?)	0
56	1	1
57	1	1
58	0	0
59	0 (?)	0 (1)
60	?	0
61	?	0
62	0	0
63	?	0
64	0 (?)	0
65	1 (?)	1
66	1 (0)	1 (0)
67	1 (?)	1
68	1	1 (?)
69	1 (0)	1 (0)
70	(0)	2 (0)
71	0	0
72	? (0)	1 (0)
73	(0)	(0)
74	? (0)	? (0)
75	0	0
76	0	0
77	0	0
78	?	?
79	0 (?)	0 (?)
80	?	0
81	0	0
82	0	0
83	?	0 (1)
84	1	1
85	0	0
86	0	0
87	0	0
88	0	0
89	1	1
90	0	1
91	1	1