The phylogenetic position of the ornithischian dinosaur *Stenopelix valdensis* from the Lower Cretaceous of Germany and the early fossil record of Pachycephalosauria

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The holotype of *Stenopelix valdensis* is the most completely known dinosaur specimen from the "Wealden" (Lower Cretaceous) of northwestern Germany, but its phylogenetic position has remained highly controversial. Most recent authors have suggested affinities with the ornithischian clade Marginocephalia, and most commonly to the marginocephalian subclade Pachycephalosauria. A pachycephalosaurian identity would make *Stenopelix* the only confirmed pre-Late Cretaceous member of this clade, breaking up an extensive ghost lineage which extends to the inferred origin of Pachycephalosauria in the Middle–Late Jurassic. Based upon re-examination of the holotype we here review the characters that have previously been used to assign *Stenopelix* to either Pachycephalosauria or Ceratopsia. All of these characters are problematic, being based upon inaccurate anatomical interpretations, or having more widespread distributions within Ornithischia than previously realised. We conclude that although the overall anatomy of *Stenopelix* is consistent with marginocephalian affinities, there is insufficient evidence to support referral to either Pachycephalosauria or Ceratopsia; we consider *Stenopelix* ?Marginocephalia. A brief review indicates that there is no compelling fossil evidence for pachycephalosaurs prior to the Late Cretaceous.

Key words: Dinosauria, Ornithischia, Pachycephalosauria, Marginocephalia, *Stenopelix,* Cretaceous, Germany.

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Introduction

The enigmatic ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, is the most completely known dinosaur specimen from the "Wealden" (Lower Cretaceous) of Germany, and the phylogenetic position of this taxon has been the subject of considerable debate. The holotype and only known specimen (GZG 741/2) was collected from the Obernkirchen Sandstone (Berriasian) near Bückeburg, Lower Saxony (NW Germany), in 1855. Since its discovery *Stenopelix* has been assigned to a variety of clades within Ornithischia; most recent speculation has focused on the suggestion that *Stenopelix* might be referable to the clade Marginocephalia (e.g., Sereno 1987, 1999, 2000; Dodson 1990; Maryańska et al. 2004; Sullivan 2006). *Stenopelix* has been assigned to both of the constituent clades of Marginocephalia, Ceratopsia (e.g., Ostrom 1970; Sues and Galton 1982) and Pachycephalosauria (e.g., Maryańska and Osmólska 1974; Coombs 1982; Sereno 1987, 2000; Maryańska et al. 2004), and has additionally been considered as the sister taxon to Marginocephalia (Dodson 1990). The few published numerical phylogenetic analyses to include *Stenopelix* as a terminal taxon have identified it as the most basal known pachycephalosaur (Sereno 1999, 2000; Butler et al. 2008), although this phylogenetic position is generally weakly supported and the taxon acts as a "wildcard" in suboptimal trees (Butler et al. 2008). An identification as a basal pachycephalosaur would make *Stenopelix* an extremely important taxon for understanding the evolution of the clade; such an identification would break up the extensive ghost lineage between the inferred origin of Pachycephalosauria in the Middle–Late Jurassic (based upon the Oxfordian age of the ceratopsian *Yinlong downsi*, Xu et al. 2006) and the abundant Late Cretaceous pachycephalosaur material known from North America and Asia (e.g., Maryańska and Osmólska 1974; Sereno 2000; Sullivan 2003, 2006; Maryańska et al. 2004; all other proposed pre-Late Cretaceous pachycephalosaur records are questionable, see below). However, in a recent review of pachycephalosaurian taxonomy, Sullivan (2006) dismissed the evidence in favour of a pachycephalosaurian identity for *Stenopelix*. Furthermore, Sullivan (2006) and Bakker et al. (2006) have argued that the evidence in

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support of marginocephalian monophyly is weak, although work published contemporaneously by Xu et al. (2006), and later by Butler et al. (2008), provided additional evidence for the monophyly of this clade. Given its putative basal position, *Stenopelix* is a potentially important taxon in elucidating pachycephalosaurian evolution and testing marginocephalian monophyly. For those reasons we here provide a review of the validity of the characters that have been suggested in support of pachycephalosaurian and ceratopsian affinities for *Stenopelix*; we additionally note several potentially phylogenetically informative characters not previously discussed. We do not attempt to provide a comprehensive redescription of *Stenopelix* (other than to document relevant inaccuracies in previous descriptions): descriptions and figures of *Stenopelix* are provided by Meyer (1859), Koken (1887), Schmidt (1969), Sues and Galton (1982), and Sereno (1987).

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Bejing, People's Republic of China; JLUM, Jilin University Museum, Changchun, People's Republic of China; GZG, Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany; SAM-PK, South African Museum (Iziko Museums of Cape Town), Cape Town, South Africa; ZDM, Zigong Dinosaur Museum, Dashanpu, People's Republic of China.

Material and methods

The holotype of *Stenopelix valdensis* was examined firsthand in the collections of the GZG on two separate occasions in the spring of 2005 and 2007 by RJB and independently by RMS on a separate occasion, also in the spring of 2007. Comparative material of basal ceratopsians, pachycephalosaurs and other ornithischians has been examined in numerous other institutions; see Sullivan (2003) for a summary of pachycephalosaur material examined by RMS, and Butler (2005) and Butler et al. (2008) for details of ornithischian material examined by RJB. Furthermore, the holotypes of the recently described basal ceratopsian *Yinlong downsi* (IVPP 14530; Xu et al. 2006) and the basal ornithopod *Changchunsaurus parvus* (JLUM L0203-j-Zn2; Zan et al. 2005) were examined by RJB as part of this study.

Interpretation of the holotype of *S. valdensis* is difficult due to its mode of preservation; the partial skeleton is preserved as impressions on two sandstone slabs (Fig. 1A, C) that only partly overlap, making detailed examination of the material difficult. Furthermore, the skeleton is dorsoventrally compressed and many of the bones have been subjected to crushing. Latex casts of the holotype, prepared by Sues and Galton (1982), are currently held at Göttingen, and form the primary basis for this discussion (Figs. 1B, D, 2–6), although details were checked against the original sandstone slabs. The larger of these latex casts (Fig. 1B) shows the left partial forelimb and scapula, dorsal vertebrae, sacral and pelvic region, hindlimbs and proximal caudal vertebrae in dorsal view; the smaller latex cast (Fig. 1D) exposes the sacral and caudal vertebrae and parts of the pelvis and hindlimb in ventral view. The difficulty of interpreting the preserved material should be kept in mind and provides one major problem in assessing the phylogenetic position of this taxon; the other major problem is the absence of cranial material (Sues and Galton 1982). This is particularly unfortunate as most pachycephalosaur synapomorphies (and most ceratopsian and ornithopod synapomorphies) are cranial character states (e.g., Sereno 1999, 2000; Butler et al. 2008).

For the purposes of this study we assume that Marginocephalia is a monophyletic clade, as supported by recent numerical phylogenetic analyses (Sereno 1999, 2000; Butler 2005; Xu et al. 2006; Butler et al. 2007, 2008), although one of us (RMS) retains doubts as to the accuracy of this result (e.g., Bakker et al. 2006; Sullivan 2006). Marginocephalia and Ornithopoda are sister-taxa within the node-based clade Cerapoda, which is itself a subclade of the stem-based clade Neornithischia (see Barrett et al. 2005 and Butler et al. 2008 for discussion of the definitions of Neornithischia and Cerapoda) which also includes some probable non-cerapodan taxa such as the Middle Jurassic *Agilisaurus* and *Hexinlusaurus* (e.g., Butler 2005; Barrett et al. 2005) and the Early Jurassic ornithischian *Stormbergia* (Butler 2005). Neornithischia is the sister-taxon to Thyreophora, together forming Genasauria. Non-genasaurian taxa include *Eocursor parvus* (Butler et al. 2007), and possibly *Lesothosaurus diagnosticus* (Sereno 1986, 1999) although the phylogenetic position of this latter taxon is highly unstable (e.g., Butler 2005; Butler et al. 2007, 2008). The phylogenetic position of Heterodontosauridae within Ornithischia is poorly resolved: the clade has been identified as basal members of Ornithopoda (Sereno 1986, 1999), the sister-clade to Marginocephalia (Xu et al. 2006) or as non-genasaurian basal ornithischians (Butler et al. 2007, 2008). Based upon the senior author's phylogenetic analyses, we favour a non-genasaurian phylogenetic position, although this interpretation does not significantly affect our discussion of the position of *Stenopelix*.

Systematic palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

?Marginocephalia Sereno, 1986

Genus *Stenopelix* Meyer, 1859

Type species: *Stenopelix valdensis* Meyer, 1859.

Diagnosis.—As for type and only known species.

Stenopelix valdensis Meyer, 1859

Figs. 1–6.

Holotype: GZG 741/2 (formerly GPI Gö 741-2), impressions in sandstone of a partial articulated skeleton in dorsal and ventral views, includ-

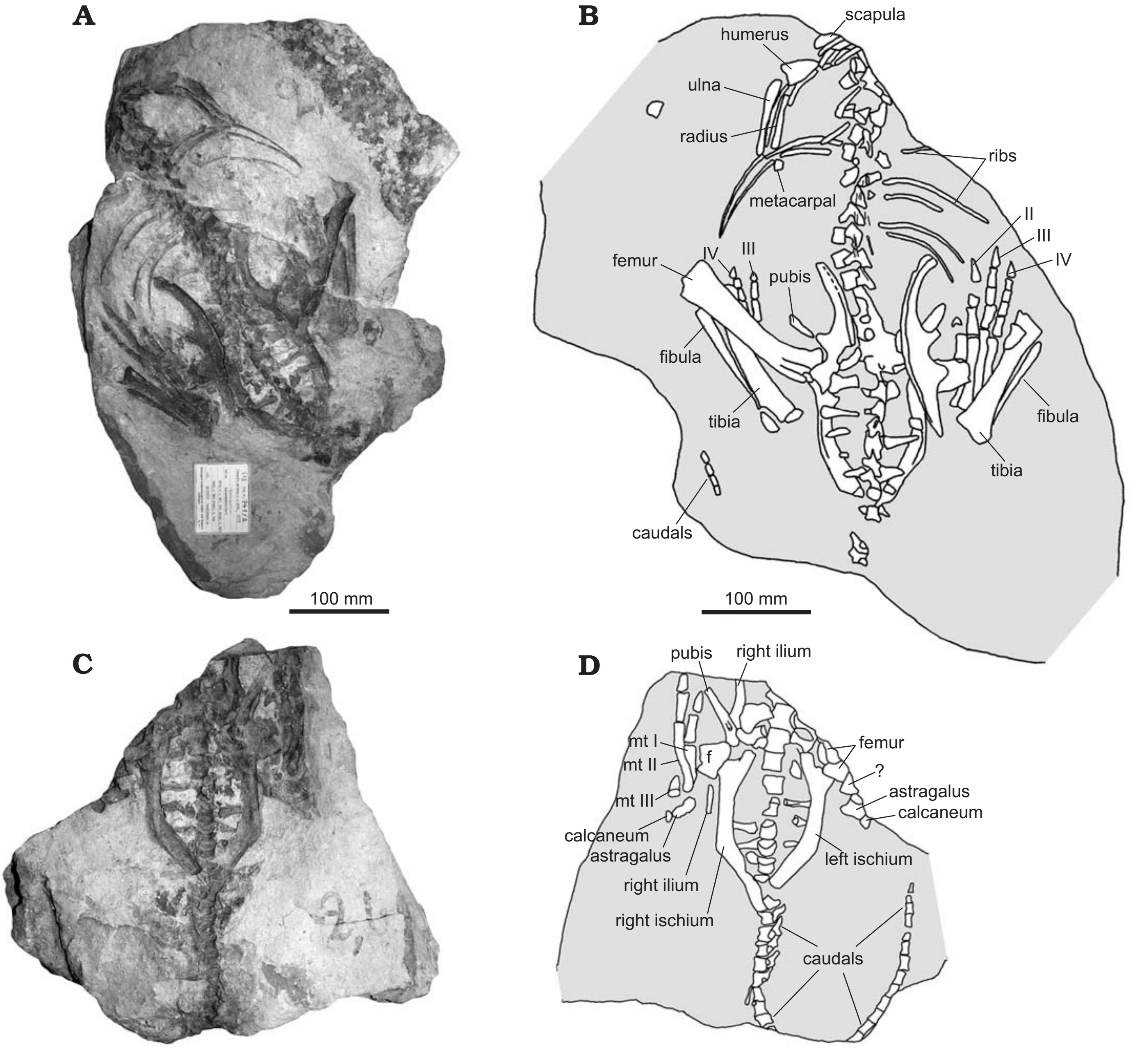

Fig. 1. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. **A**. Large sandstone slab. **B**. Interpretative outline drawing of large latex cast (prepared from large sandstone slab), showing majority of postcranial skeleton in dorsal view. **C**. Small sandstone slab. **D**. Interpretative outline drawing of small latex cast (prepared from small sandstone slab), showing sacrum and caudals, pelvic region and partial hindlimbs in ventral view. For clarity elements in and around the sacral region have not been labelled—these areas are shown in greater detail in Fig. 3. Roman numerals II–IV correspond to respective digits. Abbreviations: mt, metatarsals; f, femur; ?, unidentified element.

ing at least 13 dorsal vertebrae, five or six sacral vertebrae, more than 30 caudal vertebrae, ribs, ossified tendons, distal left scapula, distal left humerus, left radius, left ulna, left metacarpal 1, left and right ilia, pubes, and ischia, left femur, proximal right femur, left and right tibiae, fibulae and proximal tarsals, complete right pes and partial left pes. The holotype represents a small individual (less than one metre in length); subadult status is suggested by the absence of fusion between neural arches and centra, adjacent sacral centra, and sacral/caudal ribs and neural arches.

Type horizon and locality: Obernkirchen Sandstone (Early Cretaceous: Berriasian; Schmidt 1969), near Bückeburg, Lower Saxony, NW Germany.

Emended diagnosis.—Small ornithischian dinosaur with the following autapomorphies: postacetabular process of ilium tapers uniformly to a rounded point; ischial blade with distinct bend at mid shaft; ischial blade is broadest at mid shaft, tapers proximally and distally; prominent proximodistally extending ridge present on the medial surface of the proximal

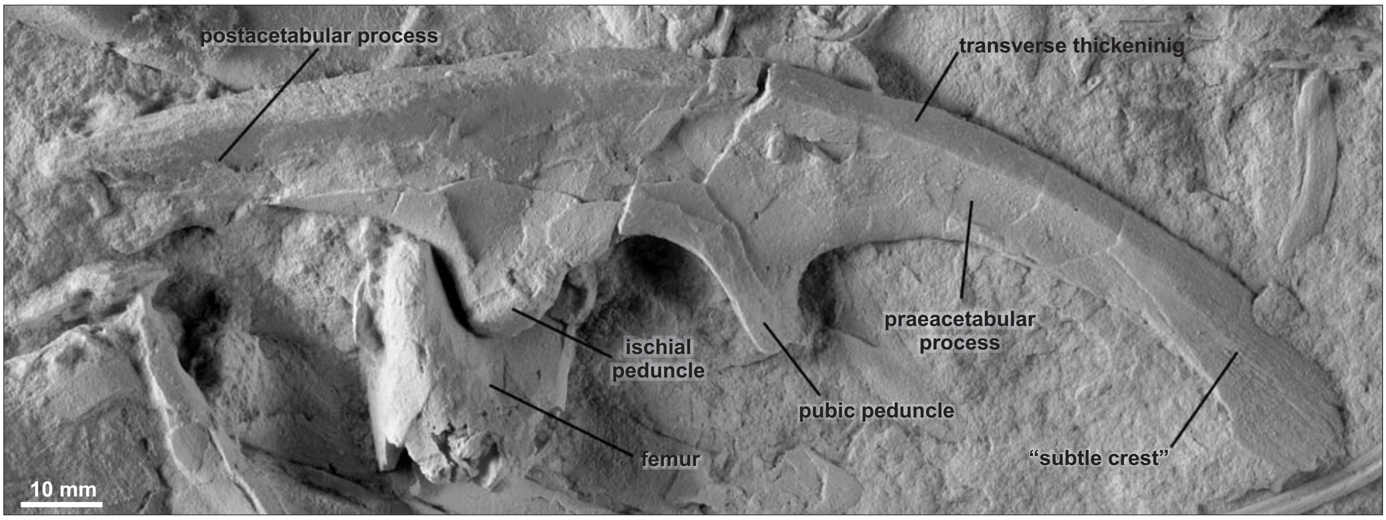

Fig. 2. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. Latex cast of right ilium (large slab) in lateral view.

50% of the shaft of the ischium; distal end of ischial blade is arched dorsoventrally, with a convex lateral surface and a concave medial surface (modified from Sereno 1987).

Comments.—Sereno (1987) provided the first formal diagnosis for *Stenopelix*, based upon five autapomorphies, although these autapomorphies were neither described nor discussed. The first of the autapomorphies proposed by Sereno (1987) refers to the morphology and length of the postacetabular process of the ilium (Fig. 2). The relatively short postacetabular process probably represents an ornithischian plesiomorphy (see below), but the uniformly tapering form of the process does appear to be unique.

Three of the autapomorphies proposed by Sereno (1987) refer to the morphology of the ischia (Figs. 3, 4), and a fourth ischial autapomorphy is added here. The ischia of *Stenopelix* are highly unusual and are marked by a distinct and prominent bend at mid shaft (Fig. 4). At this point the ischial blade is at its broadest, and it tapers both proximally and distally from this point. As noted by Sues and Galton (1982), but not by Sereno (1987), there is a prominent ridge present on the medial surface of the proximal half of the ischial shaft (Fig. 3). Distally, the ischial blade is transversely compressed, and is arched dorsoventrally, with the lateral surface convex and the medial surface gently concave.

The last of the possible autapomorphies listed by Sereno (1987) refers to the dorsoventrally compressed prepubic process. As discussed by Sereno (1987), the prepubic process of *Stenopelix* (Figs. 1D, 3B) is considerably longer than reconstructed by Galton and Sues (1982), appears to be strongly dorsoventrally compressed, and tapers slightly anteriorly. The strong dorsoventral compression of the process is not considered here to be autapomorphic for *Stenopelix*: a similar strongly dorsoventrally compressed prepubic process is also known in *Yinlong* (Xu et al. 2006: fig. S2F), *Archaeoceratops* (IVPP V11114) and *Psittacosaurus* (Sereno 1987; Averianov et al. 2006).

Results

General features

The ornithischian identity of *Stenopelix* is confirmed by a large number of features identified as ornithischian synapomorphies by previous phylogenetic analyses (e.g., Sereno 1986, 1999; Norman et al. 2004a; Butler 2005; Butler et al. 2007, 2008), including: the presence of ossified epaxial tendons in the dorsal region; the increased number of sacral vertebrae (at least five are present, see below); the elongated, strap-like preacetabular process of the ilium (Fig. 2); the presence of an opisthopubic pelvis and a prepubic process (Figs. 1D, 3B); the well-developed anterior trochanter of the femur; the strong transverse expansion of the distal end of the tibia (Fig. 6). Within Ornithischia, a number of features link *Stenopelix* to Neornithischia—several of these features were listed by Sereno (1987: 364–365). The features linking *Stenopelix* to Neornithischia include: the absence of a supraacetabular flange on the ilium (Fig. 2; retained in basal ornithischians and thyreophorans, *Agilisaurus* and *Stormbergia*; absent in all other neornithischians; Butler et al. 2008); the absence of a ventral flange partially backing the acetabulum (Fig. 2; retained in basal ornithischians and thyreophorans, *Agilisaurus* and *Stormbergia*; absent in all other neornithischians; Butler et al. 2008); the absence of a vertically oriented brevis shelf (Fig. 2; a nearly vertical brevis shelf is retained in basal ornithischians and thyreophorans, *Agilisaurus* and *Stormbergia*; the brevis shelf is either horizontal or absent in all other neornithischians; Butler et al. 2008); reduction of the pubic peduncle of the ilium relative to the ischiadic peduncle (Fig. 2; the pubic peduncle remains large in basal ornithischians, thyreophorans and *Stormbergia*; Butler et al. 2008); an elongate prepubic process (Figs. 1D, 3B; the prepubic process remains short in basal ornithischians, basal thyreophorans and *Stormbergia*;

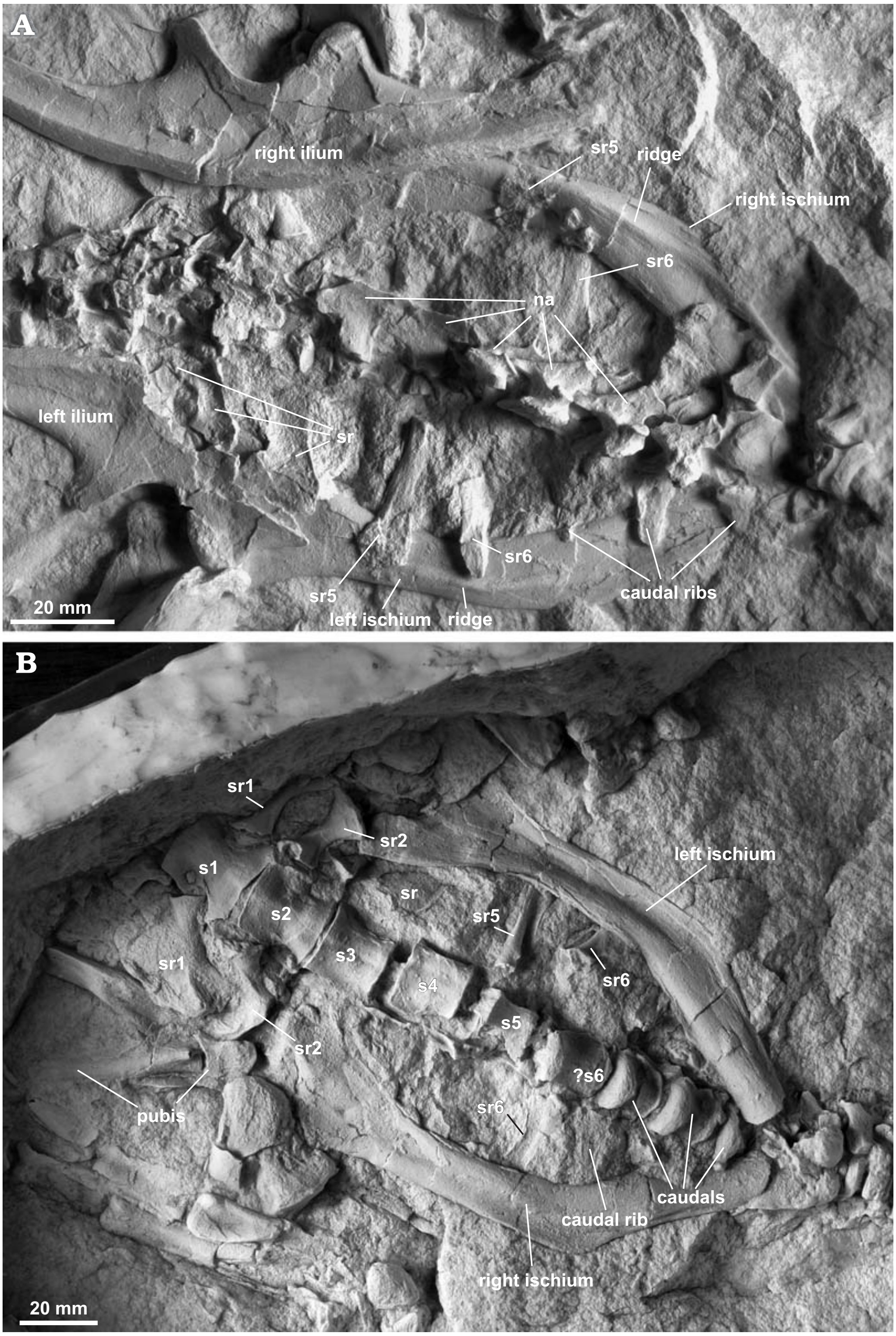

Fig. 3. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. Latex casts of sacral region. **A**. Large slab, dorsal view. **B**. Small slab, ventral view. Abbreviations: na, neural arches and spines; s1, s2, s3, s4, s5, sacral centra; ?s6, possible 6th sacral centrum (may instead represent first caudal centrum); sr, sr1, sr2, sr5, sacral ribs; sr6, possible 6th sacral rib (may instead represent first caudal rib).

Butler et al. 2008); fossa trochanteris of femur is modified into distinct constriction separating head and greater trochanter (there is no constriction between the head and greater trochanter in basal ornithischians, basal thyreophorans, *Agilisaurus* and *Stormbergia*; a constriction is present in all other neornithischians; Butler et al. 2008).

Fig. 4. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. Latex cast of ischia (small slab, both ischia are exposed in lateral view, anterior is to the right). Note the pronounced bend along the dorsal edge of the bone (arrows). Sacral and caudal centra between the ischia are exposed in ventral view.

Although a number of features support referral to Neornithischia, two characters that are generally present in basal cerapodans are absent in *Stenopelix*, and a further character (number of sacral vertebrae) is ambiguous:

Length of the postacetabular process of the ilium.—In basal ornithischians and basal neornithischians (*Agilisaurus louderbacki*, 32%, ZDM T6011; *Heterodontosaurus tucki*, 27%, SAM-PK-K1332; *Stormbergia dangershoeki*, 30%, BMNH R11000) and *Stenopelix* (31%) the postacetabular process accounts for about 27–32% of the length of the ilium (Fig. 2). By contrast, in basal cerapodans including ornithopods (*Hypsilophodon foxii,* 38%, Galton 1974; *Orodromeus makelai*, 42%, Scheetz 1999: fig. 24), pachycephalosaurs (e.g., *Homalocephale*, 39%, Maryańska and Osmólska 1974: fig. 5), and ceratopsians (e.g., *Psittacosaurus sibericus*, 38%, Averianov et al. 2006; *Archaeoceratops oshimai*, 37%, IVPP V11115) the postacetabular process of the ilium is elongated and forms nearly 40% of the total length of the ilium. Butler et al. (2008) included the length of the preacetabular process as a character in their analysis (their character 174), and found elongation of the postacetabular process to be an unambiguous synapomorphy of cerapodans, subsequently reversed in *Stenopelix*.

Ischial peduncle of the ilium broadly swollen and projects ventrolaterally.—In basal ornithischians (e.g., *Stormbergia dangershoeki*, BMNH R11000) and in *Stenopelix* (Sereno 1987) the ischial peduncle of the ilium (Fig. 2) projects ventrally and is not broadly swollen. By contrast, in most basal cerapodans including ornithopods (e.g., *Hypsilophodon foxii*, Galton 1974: figs. 48A, 50A), pachycephalosaurs (e.g., *Homalocephale calathocercos*, Maryańska and Osmólska 1974: fig. 5A1), and ceratopsians (e.g., *Archaeoceratops oshimai*, IVPP V11114) the ischial peduncle is broadly swollen and projects ventrolaterally. Sereno (1987: 355) noted the absence of this feature in *Stenopelix*, and suggested that it might be a result of post-mortem compression. However, a strongly laterally projecting ischial peduncle is also absent in the basal ceratopsian *Psittacosaurus sibiricus* (Averianov et al. 2006), so it may be that the distribution of this character is more complex than previously realised. Butler et al. (2008) included this character in their analysis (their character 177) and found that the derived state represented an unambiguous synapomorphy

Fig. 5. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. Latex cast of distal left scapula and associated elements of the forelimb (large slab).

of the clade consisting of Cerapoda and *Othnielia rex*, with subsequent reversal in *Stenopelix*.

Six sacral vertebrae.—Four or five sacral vertebrae are present in basal ornithischians and basal neornithischians (*Agilisaurus louderbacki*, Peng 1992; *Hexinlusaurus multidens*, He and Cai 1984; *Scutellosaurus lawleri*, Colbert 1981; *Stormbergia dangershoeki*, Butler 2005). By contrast, six or more sacral vertebrae are present in basal cerapodans, including ornithopods (e.g., *Parksosaurus warreni,* Parks 1926; *Gasparinisaura cincosaltensis,* Coria and Salgado 1996; *Orodromeus makelai*, Scheetz 1999), ceratopsians (You and Dodson 2004), and pachycephalosaurs (Maryańska et al. 2004).

The number of sacral vertebrae/ribs in *Stenopelix valdensis* has been controversial and is difficult to interpret. Koken (1887) and Schmidt (1969) believed that at most three sacrals were present, whereas Sues and Galton (1982) argued that there were at least six (possibly seven) sacrals. Sereno (1987) argued that there was evidence for at least five and probably six sacrals, but that there is no evidence for a seventh sacral.

Adjacent sacral vertebrae are unfused, and sacral ribs are not fused to sacral centra. The first two sacrals are clearly identifiable in ventral view (Fig. 3B), and their centra are transversely expanded and anteroposteriorly elongate. The first sacral rib is borne on the lateral surface of the first sacral centrum; the right first sacral rib is disarticulated and angles posteroventrally, distally overlapping the second right sacral rib, whereas the left first sacral rib projects nearly straight laterally. At its distal end the left first sacral rib is expanded anteroposteriorly and forms a small but distinct contact with the distal end of the left second sacral rib (Sues and Galton 1982; contra Sereno 1987). The articular surface for the second sacral rib is positioned at the anterior end of sacral centrum two and extends a short distance onto the posterior end of sacral centrum one; the right second sacral rib is disarticulated and angles posteroventrally whereas the left second sacral rib projects laterally and only slightly posteriorly. In dorsal view the left second sacral rib contacts the ilium medial to the acetabulum.

More posteriorly, additional sacral ribs are visible in dorsal and ventral views, although matching ribs with neural arches is problematic because the centra have been tilted anteroventrally, resulting in their unfused neural arches being displaced anteriorly in dorsal view (Fig. 3A). As discussed by Sereno (1987), the left fifth sacral rib is clearly identifiable in ventral view by counting posteriorly from the first and second sacral centra and ribs; it is also exposed in dorsal view (Figs. 3A, B), is offset laterally from its articulation, is expanded anteroposteriorly at its distal end, and would have contacted the medial surface of the postacetabular process of the ilium. The next (sixth) pair of ribs is visible in both dorsal and ventral views, although the left of the pair is displaced laterally and slightly anteriorly. As noted by Sereno (1987), the distal end of the right sixth rib extends nearly as far laterally as the right fifth sacral rib, but is not expanded anteroposteriorly and tapers to a narrow pointed tip. There is no obvious surface for contact with the postacetabular process of the ilium, and it is appears unlikely that this rib formed a substantial contact with the iliac blade. The neural arch of the vertebra that bore this rib resembles the neural arches of the succeeding proximal caudal vertebrae in having an anteroposteriorly narrow neural spine, and postzygapophyses positioned at a high angle (about 80°) to the horizontal. It is unclear whether this vertebra and ribs represent the sixth sacral or the first caudal. Therefore, there is unambiguous evidence for at least five sacral vertebrae in *Stenopelix* and no evidence to support the suggestion that there might be a seventh sacral (Sues and Galton 1982); however, the evidence for a sixth sacral is ambiguous.

Ceratopsian characters

Characters that have been suggested to link *Stenopelix valdensis* with ceratopsians are:

Ischium with downward curvature (Ostrom 1970).—Ostrom (1970: 134) commented on the phylogenetic relationships of *Stenopelix valdensis*, suggesting it was of "psittacosaurian, if not ceratopsian, affinity". Ostrom (1970) did not explicitly outline the reasons for this referral, but he did note that *Stenopelix* shared with ceratopsians a strong downward curvature of the ischium (Figs. 3, 4). However, Sereno (1987) noted that the ischium is curved, to varying degrees, in ankylosaurs, advanced ornithopods, pachycephalosaurs and ceratopsians, and that curvature of the ischium is absent in psittacosaurs (Sereno 1987; although more recent data indicates that a curved ischium is present in *Psittacosaurus sibiricus*, Averianov et al. 2006). Moreover, as noted by Sereno (1987) and discussed above (see diagnosis), the ischia of *Stenopelix valdensis* have a pronounced bend midway along the bone (Fig. 4), a unique morphology that does not resemble the gentle bow or arc that characterizes most ceratopsians and pachycephalosaurs. We agree with Sereno (1987) in concluding that this character provides little evidence for uniting *Stenopelix valdensis* with ceratopsians.

"The structure of the pelvic girdle, especially the form of the ilium and the reduced pubis" (Galton and Sues 1982: 188).—As discussed by Sereno (1987, 2000), there do not appear to be any characters of the pelvic girdle that are shared uniquely by ceratopsians and *Stenopelix*, nor to date have pelvic synapomorphies been identified for Ceratopsia. The prepubic process of *Stenopelix* is well-developed and not obviously "reduced". Although the preserved base of the postpubis is slender and may not have supported a substantial process, it is impossible to accurately assess the postpubis length on the basis of the available material (Sereno 1987). Furthermore, reduction of the postpubis also characterises pachycephalosaurs (e.g., Maryańska and Osmólska 1974).

Pachycephalosaurian characters

The characters that supposedly link *Stenopelix valdensis* with pachycephalosaurs are:

Anterior caudal ribs long (Maryańska and Osmólska 1974).—As discussed by Sues and Galton (1982) and Sereno (1987), the anterior caudal ribs of *Stenopelix* (see Fig. 3A) are not elongate like those of pachycephalosaurs: Maryańska and Osmólska (1974) misidentified the elongate posterior sacral ribs (sacral rib 5, and the rib belonging to the following vertebra—see discussion above) present in *Stenopelix* as anterior caudal ribs. The only possible caudal with elongate ribs is the vertebra that as discussed above may represent either the last (sixth) sacral or the first caudal. More posterior caudals have short caudal ribs. This character does not, therefore, provide support for pachycephalosaurian affinities.

Pubis excluded from the acetabulum (Maryańska and Osmólska 1974; Coombs 1982; Maryańska et al. 2004).—As previously noted by Schmidt (1969), Sues and Galton (1982) and Sereno (1987), a reconstruction of the pelvic girdle of *Stenopelix valdensis* requires a substantial contribution of the pubis to the acetabulum, and there is no substantial evidence that the pubis was excluded from the acetabulum. This character does not, therefore, provide support for pachycephalosaurian affinities.

Postpubic process absent (Coombs 1982).—Coombs (1982: 99) suggested that a postpubic process was absent in *Stenopelix valdensis*; however, as noted by Schmidt (1969: fig. 1), Sues and Galton (1982), and Sereno (1987), the base of a postpubic process is clearly preserved on the right pubis, although, as discussed above, the length of the postpubic process is known.

Tibia shorter than femur (Maryańska and Osmólska, 1974).—As discussed by Maryańska and Osmólska (1974), Sues and Galton (1982) and Sereno (1987), the tibia is distinctly shorter than the femur in *Stenopelix* with a tibia:femur ratio of approximately 0.93. The equivalent ratio in *Stegoceras validum* is 0.98 (Sues and Galton 1987) and the tibia is also shorter than the femur in *Wannanosaurus yansiensis*, although the exact ratio cannot be determined due to poor preservation (RJB and Zhao Qi, unpublished data). Tibiofemoral ratios greater than 1.0 occur primitively for Ornithischia (e.g., Thulborn 1972; Galton 1974; Santa Luca 1980), but tibiofemoral ratios less than 1.0 also occur independently among at least four independent clades within Ornithischia (in pachycephalosaurs, in some derived "hypsilophodontids" and Iguanodontia, in Ceratopsidae, and in nearly all thyreophorans). Furthermore, as discussed by Sereno (1987), the tibiofemoral ratio of *Stegoceras* is actually closer to that in *Psittacosaurus sinensis* (1.01; Sereno 1987) than to that of *Stenopelix*. We therefore agree with Sereno (1987) that this character provides only weak support for pachycephalosaurian affinities.

Posterior sacral ribs elongate (Sereno 1987, 2000).—Sereno (1987: 365) noted that, "In *Stenopelix* and pachycephalosaurs the fourth through sixth sacral ribs are noticeably longer than the second and third [sacral ribs]." The result of this elongation, according to Sereno (1987), is that the posterior end of the sacrum is at least 30% broader than the anterior end. This statement was supported for *Stenopelix valdensis* by comparing measurements of the right second sacral rib (21 mm according to Sereno 1987) with the left fifth and sixth sacral ribs (32 mm according to Sereno 1987).

The second sacral ribs are moderately shorter than the more posterior sacral ribs (see Table 1). However, the maximum length of the right first sacral rib (29.3 mm), measured in ventral view, is nearly 90% of the length of the most elongate posterior sacral rib. Furthermore the right second sacral rib has a maximum length (25 mm) that exceeds that given by Sereno (1987) and exceeds the maximum measurable length of the second left sacral rib. The discrepancy in measurements between right and left anterior sacral ribs is explained by the fact that the left sacral ribs are incompletely exposed.

Sereno (1987, 2000) appears to have underestimated the length of the anterior sacral ribs of *S. valdensis*, and the first sacral rib certainly had a length nearly comparable to that of the posterior sacral ribs. Even if the posterior sacral ribs were slightly more elongate than the anterior sacral ribs, this does not necessarily imply that the posterior end of the sacrum was broadened as occurs in pachycephalosaurs: the bases of the anterior sacral ribs would have been positioned further from the midline than the bases of the posterior sacral ribs, as a result of the transverse expansion of the anterior sacral centra. Furthermore, there is no evidence that the postacetabular process of the ilium was deflected laterally to accommodate a posterior transverse expansion of the sacral comparable to that seen in pachycephalosaurs (in fact, as noted by Sereno [1987:354], the postacetabular process appears to be deflected weakly medially rather than laterally; see below). Slight broadening of the posterior part of the sacrum also occurred in some basal ceratopsians, as demonstrated by the holotype specimen of *Archaeoceratops* (IVPP V11114) in which the last sacral rib is notably more elongate than sacral ribs 1–3 (You and Dodson 2003: fig. 2C). In light of these observations, we do not believe that this character provides substantial evidence to support a pachycephalosaurian identification for *Stenopelix*.

Table 1. Measurements of the maximum length of the sacral ribs of the holotype specimen of *Stenopelix* (GZG 741/2).

	Left side	Right side
Sacral rib 1	+25	29.3
Sacral rib 2	+20.1	25.0
Sacral rib 5	33.6	–
Sacral rib 6/caudal rib 1	–	28.1

Preacetabular process of the ilium distally expanding (Sereno 1987, 2000).—The dorsal margin of the ilium of *Stenopelix valdensis* is thickened into a narrow horizontal plane along much of its length and slightly overhangs the lateral margin of the ilium (Figs. 2, 3A). This thickening is weak and narrow at the distal end of the postacetabular process, but expands transversely immediately posterior to the ischiadic peduncle to a width of around 7 mm. It remains at a similar (although variable) thickness along most of the length of the blade anterior to the ischiadic peduncle. Anteriorly, the preacetabular process curves gently laterally and undergoes weak torsion along its length so that its lateral surface faces dorsolaterally rather than strictly laterally. This torsion, and possibly post-mortem compression, has reduced the distinction between the dorsal and lateral surfaces of the preacetabular process of the ilium such that they resemble a single surface; however, these surfaces can still be distinguished from one another by a weak anteroposteriorly extending ridge, referred to by Sereno (1987: 354) as a "subtle crest". Thus, strictly speaking the dorsal margin of the preacetabular process of the ilium does not expand significantly toward its distal end; the apparent expansion is a result of the torsion of the preacetabular blade. A comparable morphology occurs in the basal ceratopsian *Yinlong* (RJB personal observations of IVPP 14530; Xu et al. 2006: fig. S2a–d): the dorsal margin of the ilium is thickened along most of the length of the blade, while the lateral surface of the preacetabular process undergoes torsion such that it faces dorsolaterally towards its anterior end. Combined, this results in the anterior end of the preacetabular process being compressed dorsolaterally/ventromedially; moreover, in dorsal or ventral view the preacetabular process appears to expand slightly in the transverse plane at its distal tip (Xu et al. 2006: fig. S2c, d). A similar morphology is also present in a previously undescribed fragment of the preacetabular process of the left ilium of the paratype specimen of the primitive pachycephalosaur *Wannanosaurus yansiensis* (Butler and Zhao 2009).

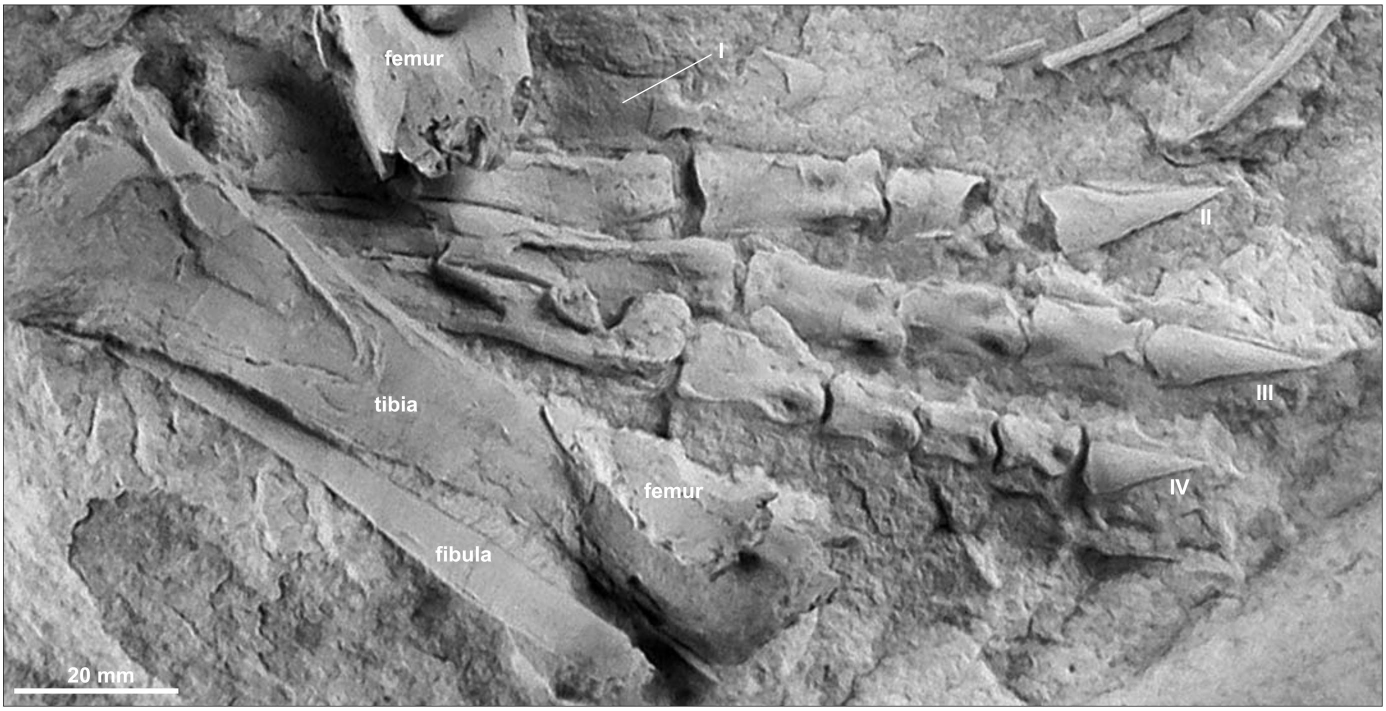

Fig. 6. Ornithischian dinosaur *Stenopelix valdensis* Meyer, 1857, holotype (GZG 741/2, formerly GPI Gö 741-2), from the Obernkirchen Sandstone (Early Cretaceous: Berriasian), near Bückeburg, Niedersachsen, Germany. Latex cast of right tibia and fibula, partial right femur, and right pes (large slab). Tibia and fibula are exposed in posterior view; pes is exposed in anterior view. Note first phalanx of digit I. Roman numerals I–IV correspond to respective digits.

By contrast, in other pachycephalosaurs the dorsal margin of the ilium is everted into a much broader shelf along most of its length and this shelf expands anteriorly as a flat horizontal surface (e.g., Maryańska and Osmólska 1974: pl. 29: 1). It is probable that the thickened dorsal margin of the ilium and the torsion of the preacetabular process seen in *Stenopelix* and *Wannanosaurus* represent the initial stage in the development of the morphology seen in other pachycephalosaurs. However, given that a similar condition is present in the most basal known ceratopsian, *Yinlong*, it is plausible that this character represents a marginocephalian plesiomorphy. Furthermore, expansion of the dorsal margin of the ilium is seen in a range of other ornithischians, including all thyreophorans (RJB and Susannah Maidment, unpublished data), the ornithopod *Zalmoxes* (Weishampel et al. 2003), and ceratopsids (Hatcher et al. 1907), demonstrating that this character is highly homoplastic within Ornithischia. As a result, this character provides little support for pachycephalosaurian affinities.

Scapula blade narrow and strap-like (Sereno 1987, 2000). —Only the distal-most portion of the left scapula (Fig. 5) is preserved in *Stenopelix valdensis*, and was first identified by Sereno (1987). It is narrow and only slightly expanded at its distal end, and was compared (Sereno 1987, 2000) with the scapula of the pachycephalosaur *Stegoceras validum* (Sues and Galton 1987: fig. 10). However, as noted by Sereno (1987, 2000), a narrow and strap-like scapula is also known in *Heterodontosaurus* (Santa Luca 1980: fig. 10), and in many basal ceratopsians including *Protoceratops andrewsi* (Brown and Schlaikjer 1940: fig. 26), *Graciliceratops mongoliensis* (Maryańska and Osmólska 1975: fig. 2) and *Psittacosaurus sinensis* (Young 1958: fig. 53). As a result, this character probably has a widespread distribution at the base of Marginocephalia. Furthermore, the true proportions of the scapula are difficult to confirm for *Stenopelix* (due to its incomplete exposure in the holotype specimen). For these reasons, this character provides little support for pachycephalosaurian referral.

Iliac blade with gentle sigmoid curve (Sereno 1987).—Sereno suggested that the postacetabular process of *Stenopelix valdensis* underwent a subtle medial deflection at its base, and that this might be homologous with the stronger medial deflection of the distal portion of the pachycephalosaurian postacetabular process. The right ilium has a well-preserved postacetabular process that does appear to undergo a weak medial deflection at its base. However, as noted by Sereno (1987) the medial flexure in *Stenopelix* is extremely subtle (and could possibly be explained by post-mortem compression), and occurs at the base of the postacetabular process, rather than at mid length along the process as occurs in pachycephalosaurs (e.g., Maryańska and Osmólska 1974). We therefore agree that “the subtle flexure of the postacetabular process in *Stenopelix* does not constitute convincing evidence for pachycephalosaur affinity” (Sereno 1987: 370).

In summary, the preceding eight characters provide only weak and ambiguous support for pachycephalosaur affinities. As noted by Sereno (1987), a number of pachycephalosaurian synapomorphies are definitively absent in *Stenopelix* *valdensis*. These include: sixth sacral rib more elongate than fifth sacral rib; anterior caudal vertebrae with elongate caudal ribs; caudal "basket" of ossified tendons; reduction in relative length of forelimb; medially directed tab-shaped process on the dorsal margin of the ilium; pubic peduncle of the ischium strongly dorsoventrally compressed; body of pubis very small and nearly excluded from the acetabulum. Although Sereno (1987) suggested that interlocking grooves and ridges were absent from the dorsal pre- and postzygapophyses, this can only be assessed for two vertebrae located at the anterior end of the preserved dorsal series.

Other characters

Several previously undiscussed features of the postcranial skeleton of *Stenopelix* are potentially phylogenetically informative. We discuss these in greater detail here:

First phalanx of digit I is the longest non-ungual phalanx of the pes.—In basal neornithischians and basal ornithopods the first phalanx of digit I is shorter than that of digits II or III. This character-state occurs in *Agilisaurus louderbacki* (Peng 1992), *Othnieliosaurus* (Galton and Jensen 1973), *Hexinlusaurus multidens* (He and Cai 1984), *Heterodontosaurus tucki* (Santa Luca 1980), *Orodromeus makelai* (Scheetz 1999) and *Camptosaurus* (Gilmore 1909). However, in *Stenopelix valdensis* phalanx I-1 is 110% of the length of phalanx II-1 and 120% of the length of phalanx III-1 (Fig. 6). This is also seen in ceratopsians including: *Psittacosaurus mongoliensis* (126% of III-1, Sereno 1987), *Archaeoceratops oshimai* (127% of III-1, IVPP V11115), *Protoceratops andrewsi* (131% of III-1, Brown and Schlaikjer 1940), *Graciliceratops mongoliensis* (129% of III-1, Maryańska and Osmólska 1975), *Avaceratops lammersi* (169% of III-1, Penkalski and Dodson 1999) and other ceratopsids (Dodson et al. 2004), and there appears to be a general trend in ceratopsian evolution towards relative elongation of phalanx I-1. Caution should be utilised in interpreting this character, as the first phalanx of digit one is also moderately elongate in some basal ornithopods, including *Parksosaurus warreni* (104% of III-1, Parks 1926), *Hypsilophodon foxii* (104% of III-1, Galton 1974) and *Thescelosaurus neglectus* (110% of III-1, Gilmore 1915) although never as elongated as in ceratopsians. Moreover, elongation of the first phalanx of digit one is present in the iguanodontian *Tenontosaurus tilletti* (133% of III-1, Forster 1990). As the pedal proportions remain virtually unknown in pachycephalosaurs, this character can only, at present, provide weak evidence supporting a marginocephalian position.

Absence of obturator process on ischium.—As noted by Sues and Galton (1982), an obturator process is absent from the ischium in *Stenopelix* (Figs. 3, 4). An obturator process is absent in the basal ornithischians *Eocursor parvus* (Butler et al. 2007) and *Lesothosaurus diagnosticus* (Sereno 1991; Butler 2005; contra Thulborn 1972), thyreophorans (e.g., Norman et al. 2004b; Galton and Upchurch 2004), *Heterodontosaurus tucki* (Santa Luca 1980), rhabdodontid ornithopods (Weishampel et al. 2003), pachycephalosaurs (*Stegoceras validum*, Sues and Galton 1987; undescribed Triebold specimen, RMS personal observations), and all ceratopsians (Sereno 1987; You and Dodson 2004; Dodson et al. 2004). A tab-shaped obturator process on the ischium was apparently absent primitively for Ornithischia, and its presence has generally been considered diagnostic of Ornithopoda (e.g., Sereno 1986). However, Butler (2005) documented an obturator process on the ischium of the primitive Early Jurassic neornithischian *Stormbergia dangershoeki*, and subsequent phylogenetic analyses (Butler et al. 2007, 2008) have suggested that the presence of an obturator process may be primitive for Neornithischia. If this hypothesis is correct, it suggests that marginocephalians have secondarily lost the obturator process, and this reversal may be a synapomorphy supporting Marginocephalia (Butler et al. 2008). The absence of an obturator process in *Stenopelix*, combined with other character information, might therefore support a marginocephalian identity for this taxon.

Prepubic process is dorsoventrally flattened along its entire length.—Primitively for Ornithischia, the short prepubic process is transversely compressed and dorsoventrally deep (*Eocursor parvus*, Butler et al. 2007; *Heterodontosaurus tucki*, Santa Luca 1980). In some basal neornithischians and all basal ornithopods the process is either rod-like with a cross-section that is subcircular or slightly wider than deep (e.g., *Hexinlusaurus multidens*, He and Cai 1984; *Hypsilophodon foxii*, Galton 1974; *Othnielosaurus*, Galton and Jensen 1973; *Parksosaurus warreni*, Parks 1926), or "sword-like", being dorsoventrally shallow but transversely compressed (e.g., *Orodromeus makelai*, Scheetz 1999). In pachycephalosaurs the pubis is only known for *Homalocephale calathocercos*; it differs from the pubis of ornithopods in being dorsoventrally compressed at its base, but transversely compressed at its anterior end (Maryańska and Osmólska 1974). By contrast to all of these conditions, the prepubic process of *Stenopelix* appears to be dorsoventrally compressed along its entire length; Sereno (1987) considered this an autapomorphic feature, but as discussed above, this feature is also seen in a number of basal ceratopsians. This character might provide some support for a ceratopsian identity for *Stenopelix*; however, more work on the range of pubic variation within Ornithischia is required—the range of variation within Pachycephalosauria, for example, is completely unknown.

Discussion

Taxonomic position of *Stenopelix*

The holotype of *Stenopelix valdensis* is difficult to interpret and, without the discovery of additional material, this taxon may never be phylogenetically positioned with certainty. Most features of the skeleton suggest affinities with Cerapoda, but assignment of *Stenopelix* to any one of the constituent clades of Cerapoda (Ornithopoda, Pachycephalosauria, Ceratopsia) is difficult. No characters have been proposed to support referral to Ornithopoda, and we feel that such a referral is unlikely, largely in light of the absence of an obturator process on the ischium and the presence of a number of features that suggest affinities with Marginocephalia. These features include: the strap-like scapula blade; the transverse expansion of the dorsal margin of the ilium and the transverse expansion of the distal end of the preacetabular process in dorsal view; dorsoventral compression of the proximal part of the prepubic process; the absence of an obturator process; and the elongate pedal phalanx I-1. Within Marginocephalia evidence in favour of either a ceratopsian or a pachycephalosaurian identity is weak, and we cannot support referral to either clade on the basis of the available evidence. Dodson (1990) suggested that *Stenopelix* might be a sister taxon to Marginocephalia; this is plausible, but we are unaware of any features that are shared by pachycephalosaurs and ceratopsians but absent in *Stenopelix*. As discussed above, recent phylogenetic analyses place *Stenopelix* within Marginocephalia, but find it to be a highly unstable wildcard taxon (Butler et al. 2008). In light of these uncertainties we recommend that *Stenopelix* is best considered as ?Marginocephalia.

The early fossil record of pachycephalosaurs

In the absence of compelling evidence of a pachycephalosaurian identity for *Stenopelix valdensis*, are there any definite pachycephalosaurs prior to the Late Cretaceous? There have been unpublished reports of possible pachycephalosaurian material from the Upper Triassic of India (Chatterjee, cited in Naish and Martill 2001); however, these specimens lack pachycephalosaurian synapomorphies and cannot be assigned to any known dinosaurian clade (RMS personal observations). Averianov et al. (2005) described and named *Ferganocephale adenticulatum* from the Middle Jurassic (Callovian) of Kyrgyzstan, based upon eight isolated, abraded, cheek teeth. *F. adenticulatum* was referred to Pachycephalosauria on the basis of a number of dental characters; however, no dental synapomorphies have previously been identified for Pachycephalosauria, and all of the features identified by Averianov et al. are plesiomorphic for Cerapoda. In addition, recent discoveries (e.g., Parker et al. 2005; Irmis et al. 2007) have demonstrated the problems inherent in determining the phylogenetic position of isolated, ornithischian-like teeth. As also recognised by Sullivan (2006), there is no substantial evidence to support referral of *F. adenticulatum* to Pachycephalosauria; *F. adenticulatum* is here considered Ornithischia *incertae sedis*, and may represent a *nomen dubium*.

Galton (1971) described a new taxon of pachycephalosaur, *Yaverlandia bitholus*, on the basis of an isolated skull fragment from the Wessex Formation (Early Cretaceous: Barremian) of England. Although highly fragmentary, this taxon has survived many recent pachycephalosaurian taxonomic reviews (e.g., Maryańska 1990; Sereno 2000; Maryańska et al. 2004). However, a number of authors have noted that the phylogenetic position of this taxon is problematic. Sullivan (2000, 2003, 2006) argued that *Y. bitholus* lacks synapomorphies of Pachycephalosauria, and removed this taxon from the clade. Darren Naish (personal communication 2005, 2007; cited in Sullivan 2006) indicates that *Y. bitholus* possesses synapomorphies of theropods (see list of supporting synapomorphies in Sullivan 2006). The putative pachycephalosaur taxon *Majungatholus atopus* (Sues and Taquet 1979), from the Late Cretaceous of Madagascar, was revealed on the basis of more complete material to represent an abelisaurid theropod (Sampson et al. 1998). It is not therefore implausible that *Y. bitholus* could also represent a non-ornithischian taxon.

This brief review demonstrates that there are no definite pachycephalosaurs known prior to the Late Cretaceous, with all well-verified pachycephalosaurian taxa known from the Santonian–Maastrichtian of North America and Asia (Sullivan 2006). Assuming that recent work supporting marginocephalian monophyly (e.g., Xu et al. 2006; Butler et al. 2008) is correct, this implies a ghost lineage of around 75 million years extending from the Oxfordian (based upon the occurrence of the basal ceratopsian *Yinlong downsi*) to the base of the Santonian. Even if discovery of additional material eventually demonstrates that *Stenopelix* does represent an early pachycephalosaur, this would still only represent a point occurrence that would break-up rather than reduce the overall ghost lineage duration, which is the longest known for any dinosaurian clade. The absence of definite pre-Cretaceous pachycephalosaurs creates problems for understanding the early evolution of the clade; this is compounded by recent work which hypotheses that "flat-headed" pachycephalosaurs such as *Goyocephale* and *Homalocephale*, generally thought to represent plesiomorphic morphological intermediates between domed pachycephalosaurids and other ornithischians (e.g., Sereno 1999, 2000), may in fact represent early ontogenetic growth stages of domed pachycephalosaurs such as *Prenocephale* (Horner et al. 2007; Sullivan 2007). If such hypotheses are proved correct, then it will mean that we have virtually no insight into the sequence and tempo of construction of the pachycephalosaur body plan. Discoveries of pre-Late Cretaceous pachycephalosaurs will be critical for a deeper understanding of the group's evolution.

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