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PALEONTOLOGY

A revision of the pterodactyloid pterosaur *Herbstosaurus pigmaeus* Casamiquela, 1975 from the Late Jurassic of Argentina

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Abstract: *Herbstosaurus pigmaeus* Casamiquela, 1975 is a Late Jurassic pterosaur from northwestern Patagonia. It is based on the natural moulds and a few bony patches of the sacrum, prepubis, ilium, and both femora of a small-sized specimen. The phylogenetic relationships of this species have been a matter of debate, having been originally interpreted as a theropod dinosaur and subsequently as a pterosaur, either as an indeterminate pterodactyloid or a probable dsungaripteroid. However, a detailed and updated reassessment of its anatomy was still lacking. Here, we redescribe and compare the holotype and only known specimen of *Herbstosaurus pigmaeus*. We agree with previous authors in that the specimen is diagnostic to the species level and provide an emended diagnosis, including two autapomorphies. Quantitative phylogenetic analyses consistently find *Herbstosaurus pigmaeus* as deeply nested within the Pterodactyloidea and as a member of the Dsungaripteroidea. The dsungaripteroid affinities of *Herbstosaurus pigmaeus* are weak, based solely on femoral character-states, but is the most parsimonious hypothesis with the evidence at hand. The recognition of *Herbstosaurus pigmaeus* as a deeply nested pterodactyloid expands the taxonomic diversity of the pterosaur record of southwestern Gondwana during the Late Jurassic.

Key words: Dsungaripteroidea, Pterosauria, Tithonian, Upper Jurassic, Vaca Muerta.

INTRODUCTION

Pterosaurs are popularly known as the flying reptiles, and they were the first vertebrates to acquire a powered flight (Wellnhofer 1991, Witton 2013). The oldest pterosaurs known are Late Triassic in age, already appearing in the fossil record with the main features that characterise their body plan (e.g. a hypertrophied fourth manual finger that supported a membranous wing) (Dalla Vecchia 2014). The group witnessed an outstanding evolutionary radiation during the Jurassic and Cretaceous, but then became extinct during the Cretaceous-Palaeogene mass extinction (Wellnhofer 1991, Witton 2013).

Jurassic pterosaur fossils are relatively abundant in Laurasia, mainly during the Middle and Late Jurassic (e.g. Riabinin 1948, Wellnhofer 1975, Harris & Carpenter 1996, Gasparini et al. 2004, Andres et al. 2010, Jagielska et al. 2022, Fernandes et al. 2023, Martill et al. 2023, Martin-Silverstone et al. 2023). By contrast, the Jurassic Gondwanan pterosaur body fossil record is scarcer and composed of more fragmentary specimens (Barrett et al. 2008, Codorniú & Gianechini 2016, Pentland & Poropat 2023), and is limited to: Argentina (Casamiquela 1975, Codorniú et al. 2010, 2013, 2016, Codorniú & Gasparini 2007, 2012), Uruguay (Perea et al. 2018, Soto et al. 2021), Chile (Alarcón-Muñoz et al. 2021), Antarctica (Hammer & Hickerson 1994), Madagascar (Dal

Sasso & Pasini 2003), Tanzania (Reck 1931, Sayão & Kellner 2001), Morocco (Haddoumi et al. 2016), India (Rao & Shah 1963), and probably South Africa (Blackbeard & Yates 2007). In particular, the Vaca Muerta Formation of the Neuquén Basin in the northwest of Argentinian Patagonia has yielded four Late Jurassic pterosaur specimens. The most complete of them is the holotype of the early pterodactyloid *Wenupteryx uzi*, which is represented by most of a postcranial skeleton (Codorniú & Gasparini 2013). The type locality of *Wenupteryx uzi* has also yielded an isolated partial ulna referred to *Wenupteryx uzi* and the natural mould of an indeterminate pterodactyloid tibiotarsus (Codorniú & Gasparini 2013). However, the first pterosaur ever reported from the Vaca Muerta Formation was collected from a different locality, and represents the holotype of *Herbstosaurus pigmaeus*.

The holotype of *Herbstosaurus pigmaeus* (CTES-PZ 1711) comprises mostly natural moulds of a sacrum, partial pelvic girdle, and both femora (Casamiquela 1975, Fig. 1). This species was originally interpreted as a small coelurosaurian

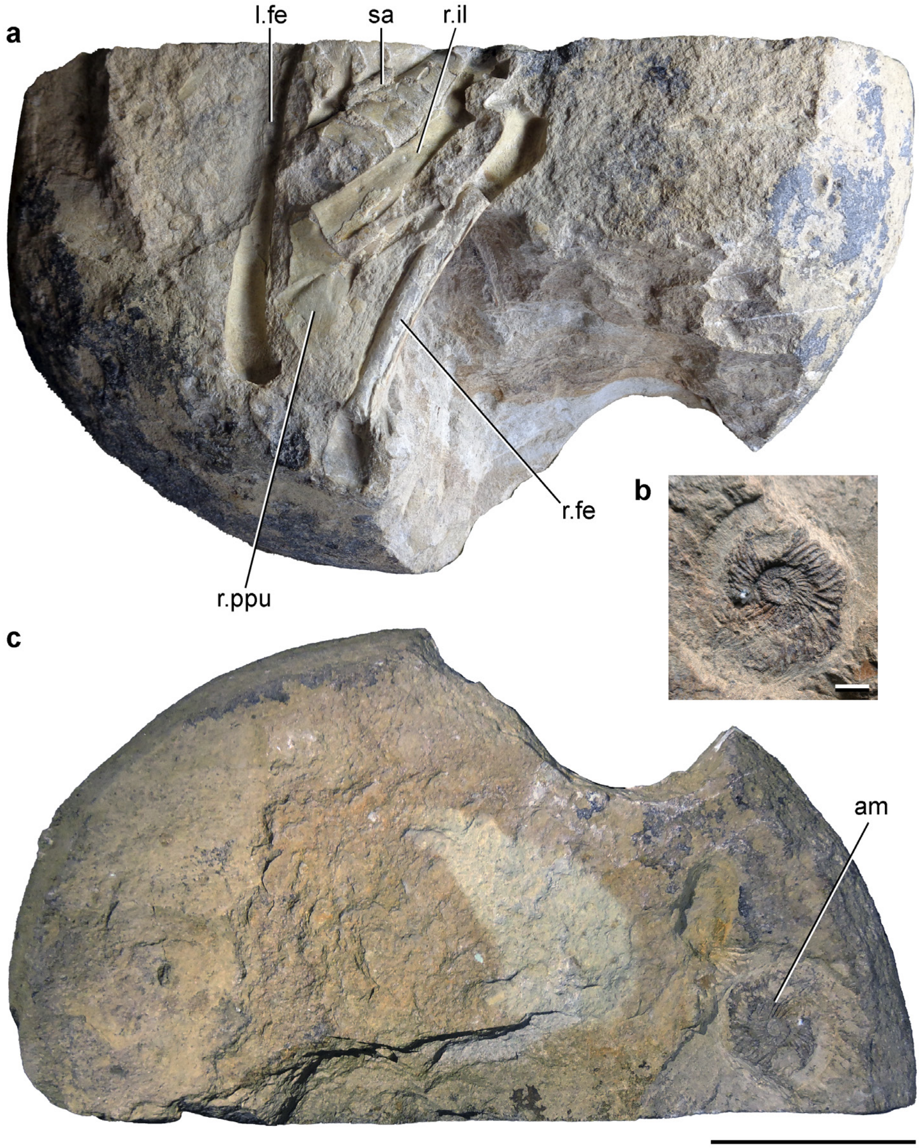

Figure 1. **Photographs of the nodule (CTES-PZ 1711) that preserves the holotype of the pterosaur *Herbstosaurus pigmaeus* with a specimen referrable to the ammonite *Lytohoplites alternans*. a) Side of the nodule that preserves the pterosaur bones and molds, b) close up of the ammonite, and c) side of the nodule that preserves the ammonite specimen. Abbreviations: am, ammonite; l.fe, left femur; r.fe, right femur; r.il, right ilium; r.ppu, right prepubis; sa, sacrum. Scale bars equal 5 cm in a, c, and 5 mm in b.**

theropod closely related to *Compsognathus longipes* from the Late Jurassic of Germany (Casamiquela 1975), but it was subsequently reinterpreted as a pterosaur (Ostrom 1978, Bonaparte 1978). Bonaparte (1978) concluded that *Herbstosaurus pigmaeus* could be a pterodactyloid, but Wellnhofer (1991) noted more similarities with non-pterodactyloid pterosaurs. Unwin (1996) claimed probable dsungaripteroid affinities (among the pterodactyloids) based on the femoral morphology of this species, which was a hypothesis subsequently followed in other papers (Unwin &Heinrich 1999, Unwin 2003). More recently, Codorniú & Gasparini (2007) agreed with the placement of *Herbstosaurus pigmaeus* within Pterodactyloidea but claimed that the purported dsungaripteroid affinities needed revision and discussed some features that were ambiguous or differed from the condition present in dsungaripteroids. The most detailed anatomical description of the holotype of *Herbstosaurus pigmaeus* has been that originally provided by Casamiquela (1975), almost 50 years ago, when the species was interpreted as a theropod dinosaur. Similarly, this specimen has been only illustrated with old photographs (Casamiquela 1975) and line drawings of the whole specimen (Codorniú & Gasparini 2007, 2013). A first-hand revision of the holotype of *Herbstosaurus pigmaeus* by the authors of this study showed the necessity of an anatomical reassessment. The well-preserved natural moulds of this specimen, coupled with physical (latex) and digital positive casts allow for assessing its features in greater detail and in different views (not only in the view that it has always been illustrated the specimen). We also provide several photographs showing close-ups of key features based on the positive digital cast. This new information allows us to revise the taxonomy and phylogenetic relationships of *Herbstosaurus pigmaeus*.

Institutional abbreviations

CTES-PZ, Colección de Paleozoología, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; MACN-Pv, Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina.

MATERIALS AND METHODS

Study of the specimen. The holotype of *Herbstosaurus pigmaeus* (CTES-PZ 1711) was studied first-hand using natural moulds (Fig. 1), as well as positive casts that allowed for an ameliorated interpretation and visualisation of anatomical features (Fig. 2). A positive latex cast of the bones is housed in the Colección Nacional de Paleovertebrados of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” under the number MACN-Pv 20120. We do not have information about when and by whom this mould was made. An additional positive digital cast of the specimen was built using photogrammetry. A textured 3D model was generated with the software Agisoft PhotoScan Professional v. 1.3.3 (Agisoft LLC, https://www.agisoft.com/, 2017), using 35 photographs taken with a digital camera Sony DSC-W830 of 20.1-megapixels using a focal length of 4.5 and an ISO of 80. The 3D model of the side of the nodule (where the bones are preserved) has 5 million faces. Subsequently, this model was cropped to focus only on the region that preserves the bone moulds, retaining 2.4 million faces, and its inner side was lightened to generate a positive relief of the bones. This final model, without texture, has been used here to illustrate the positive casts of CTES-PZ 1711 (Additional Data).

Phylogenetic analysis. The phylogenetic relationships of *Herbstosaurus pigmaeus* were tested using the data matrix of Martin-Silverstone

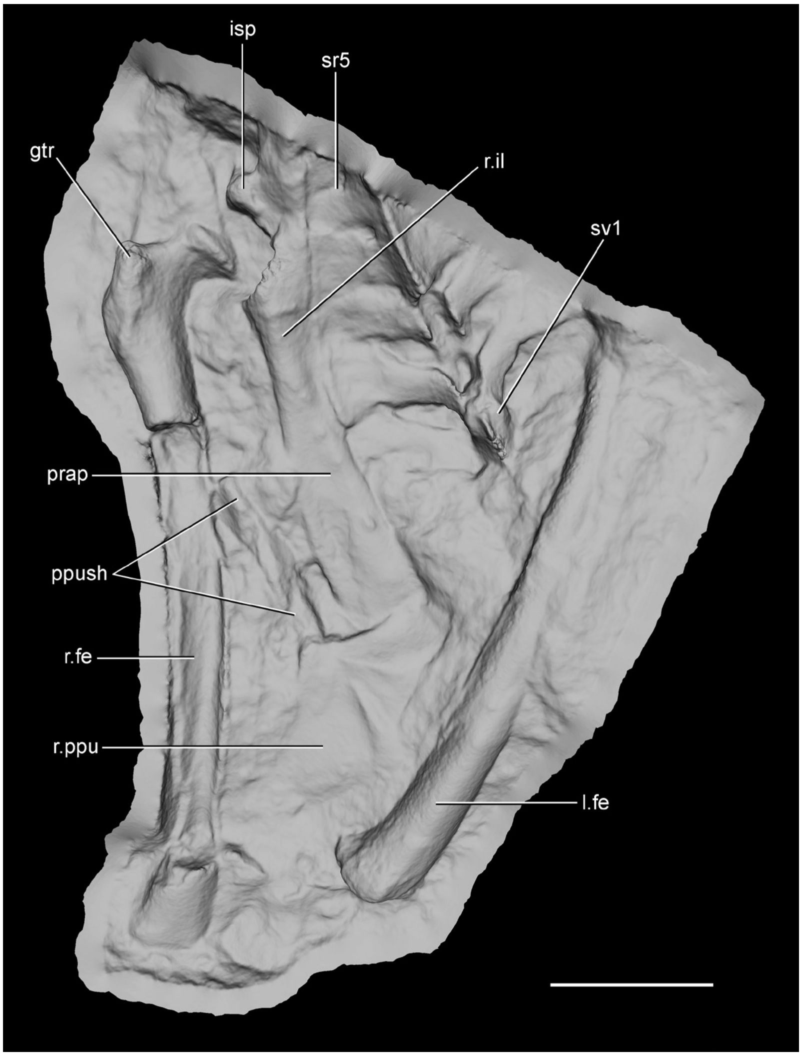

Figure 2. Positive digital cast of the holotype of the pterosaur *Herbstosaurus pigmaeus* (CTES-PZ 1711). Abbreviations: gtr, greater trochanter; isp, ischial peduncle; l.fe, left femur; ppush, prepubic shaft; prap, preacetabular process; r.fe, right femur; r.il, right ilium; r.ppu, right prepubis; sr5, sacral rib 5; sv1, sacral vertebra 1. Scale bar equals 2 cm.

et al. (2023), after adding the Jurassic species from Patagonia. The modified version of the data matrix is composed of 136 characters scored across 70 active terminals (Additional Data). The data set was analysed under implied weighting maximum parsimony in the program TNT version 1.6 (Goloboff & Morales 2023). This decision of weighting against homoplasy follows the results of the analyses of Goloboff et al. (2018) (based on simulations) and Ezcurra (2024) (based on empirical data), in which implied weighting outperformed equal weighting in topological accuracy and stability, respectively. A series of analyses were conducted with a range of concavity constant values (k) between 3 and 9 following the suggestion of Ezcurra (2024) for a matrix with the number of terminals used here. The following 21 characters were considered as ordered based on the nexus data matrix published by Martin-Silverstone et al. (2023): 5–7, 24, 27, 39, 41, 74, 86, 95, 103, 106, 112, 113, 115–119, 131 and 135. The tree searches involved 1,000 replications of Wagner trees (with random addition sequence) followed by TBR branch swapping (holding 10 trees per replicate). The shortest trees obtained were then subjected to a final round of TBR branch swapping. Zero-length branches among any of the recovered most parsimonious trees (MPTs) were collapsed [rule 3 of Swofford & Begle (1993), and Coddington &

Scharff (1994), and all the trees were rooted with *Euparkeria*. Homoplasy indices for each analysis under the different k values were calculated with ‘STATSb.run’ (Spiekman et al. 2021). Group supports were quantified using no-zero weight symmetric resampling analyses, using 1,000 pseudo-replications (each with 10 replications of Wagner trees + TBR) and reporting both absolute and GC (group present/contradicted) frequencies. Finally, a global strict consensus tree (GSCT) was generated from all the most parsimonious trees (MPTs) found in all the analyses using the different k values. Similarly, absolute and GC resampling frequencies were calculated from all the resampling trees recovered using the different k values and plotted on the branches of the GSCT (taxa that were pruned a posteriori to recover the GSCT were pruned from the resampling trees before frequency calculations). These analyses were implemented in one custom script written here for TNT and named ‘treeSearches_protocol.run’ (Additional Data). This script, ‘STATSb.run’, the data matrix files, and a subfolder called ‘output’ (it has to be created manually in Windows) should all be in the same working directory. The script needs the following four arguments that allow the user to customise the analysis: 1) the name of the matrix file without the “.tnt” extension, 2) the lower limit of the *k* values range, 3) the upper limit of the *k* values range, and 4) the number of pseudo-replications of the resampling analyses. Hence, to reproduce the analyses conducted here, the script should be run as follows in TNT (GUI users should deactivate the ‘Preview trees’ option before running the script): ‘run treeSearches_protocol_Herbstosaurus.run Ezcurra_et_al_data_matrix 3 9 1000;’.

RESULTS

Systematic Palaeontology

Pterosauria Kaup, 1834 sensu Padian (2004)
Monofenestrata Lü, Unwin, Jin, Liu and Ji, 2010
Pterodactyloidea Plieninger, 1901 sensu Padian (2004)
Dsungaripteroidea Young, 1964 sensu Kellner (2003)
Herbstosaurus pigmaeus Casamiquela, 1975
Figures 1–4

Holotype. CTES-PZ 1711 (misquoted as CTES-PZ 1709 in Codorniú & Gasparini 2007): partial postcranium mostly preserved as natural moulds with a few bony portions, that include sacral vertebrae and ribs exposed in dorsal view, most of the preacetabular process and acetabular region of the right ilium and right prepubis exposed in lateral views, right femur exposed in anterior view, and left femur without proximal end exposed in anterior and medial views (Additional Data). A possible metapodial and phalanx originally reported by Casamiquela (1975) could not be clearly identified. A latex cast generated from the natural moulds (i.e. showing the bones as positive reliefs) is housed in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-Pv 20120).

Geographic occurrence. Southern sector of the Arroyo Picún Leufú anticlinal, where it meets the National Route 40, central Neuquén Province, Argentina.

Chronostratigraphic occurrence. The holotype of *Herbstosaurus pigmaeus* was originally interpreted as coming from the Middle Jurassic levels of the Lotena Formation (Casamiquela 1975). However, Codorniú & Gasparini (2007) reported that the ammonite preserved on the other side of the same nodule that preserves *Herbstosaurus pigmaeus* (Fig. 1b, c) was identified as *Berriasiella* sp., the occurrence of which indicated that the nodule came from the late Tithonian (latest Late Jurassic)

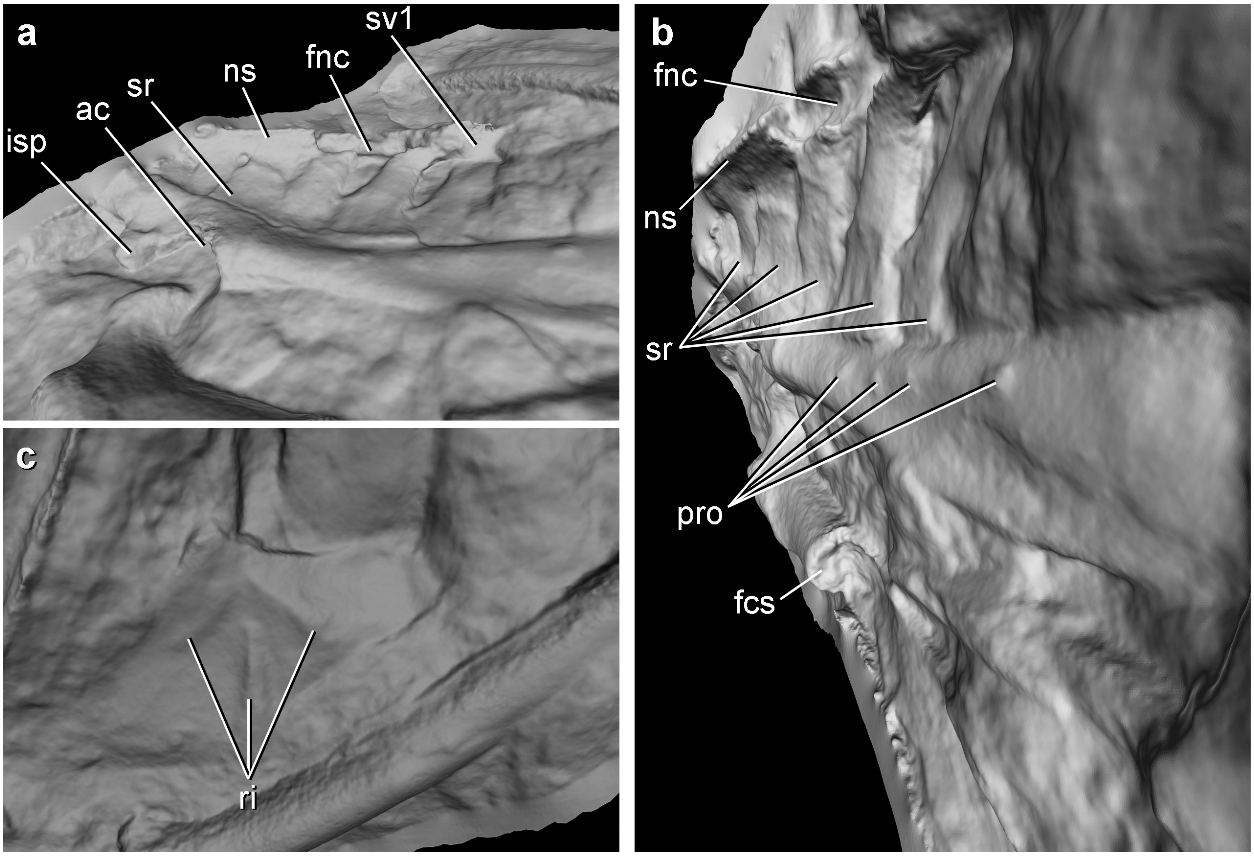

Figure 3. Close-ups of the positive digital cast of the holotype of the pterosaur *Herbstosaurus pigmaeus* (CTES-PZ 1711). a) Sacrum in right lateral and slightly dorsal view and acetabular region and most of the preacetabular process of the right ilium in lateroventral and slightly anterior view. b) Sacrum in anterodorsal view, preacetabular process of the right ilium in anterolateralview, and right femur in mediodistal view. c) Right prepubis in ventrolateral view. Abbreviations: ac, acetabulum; fcs, femoral cross-section; fnc, floor of the neural canal; isp, ischial peduncle; ns, neural spines; pro, prominences; ri, ridges; sr, sacral ribs; sv1, sacral vertebra 1. Photographs not to scale.

of the Vaca Muerta Formation. Our colleague V. Vennari reidentified this ammonite as *Lytohoplites alternans*, which is recorded in the basalmost levels of the *Substeuroceras koeneni* zone that is likely late Tithonian in age, and belongs to the Vaca Muerta Formation (Vennari pers. comm. 2024). Thus, this re-identification of the ammonite is still in agreement with previous claims of a latest Jurassic age for *Herbstosaurus pigmaeus*.

Emended diagnosis. The original diagnosis of *Herbstosaurus pigmaeus* was based on the assumption that it represented a theropod dinosaur (Casamiquela 1975), and hence, it is not currently useful to diagnose the species among pterosaurs. Here, we re-diagnose *Herbstosaurus pigmaeus* as a pterodactyloid pterosaur that can be distinguished from other species of the clade because of the presence of the following combination of character states (potential autapomorphies indicated with an asterisk): a row of four, anteroposteriorly aligned, knob-like prominences on the lateral surface of the preacetabular process of the ilium*; prepubic plate transversely broader than anteroposteriorly long; dorsal surface of the prepubic plate with three ridges radiating from a point medially displaced from the transition between the shaft

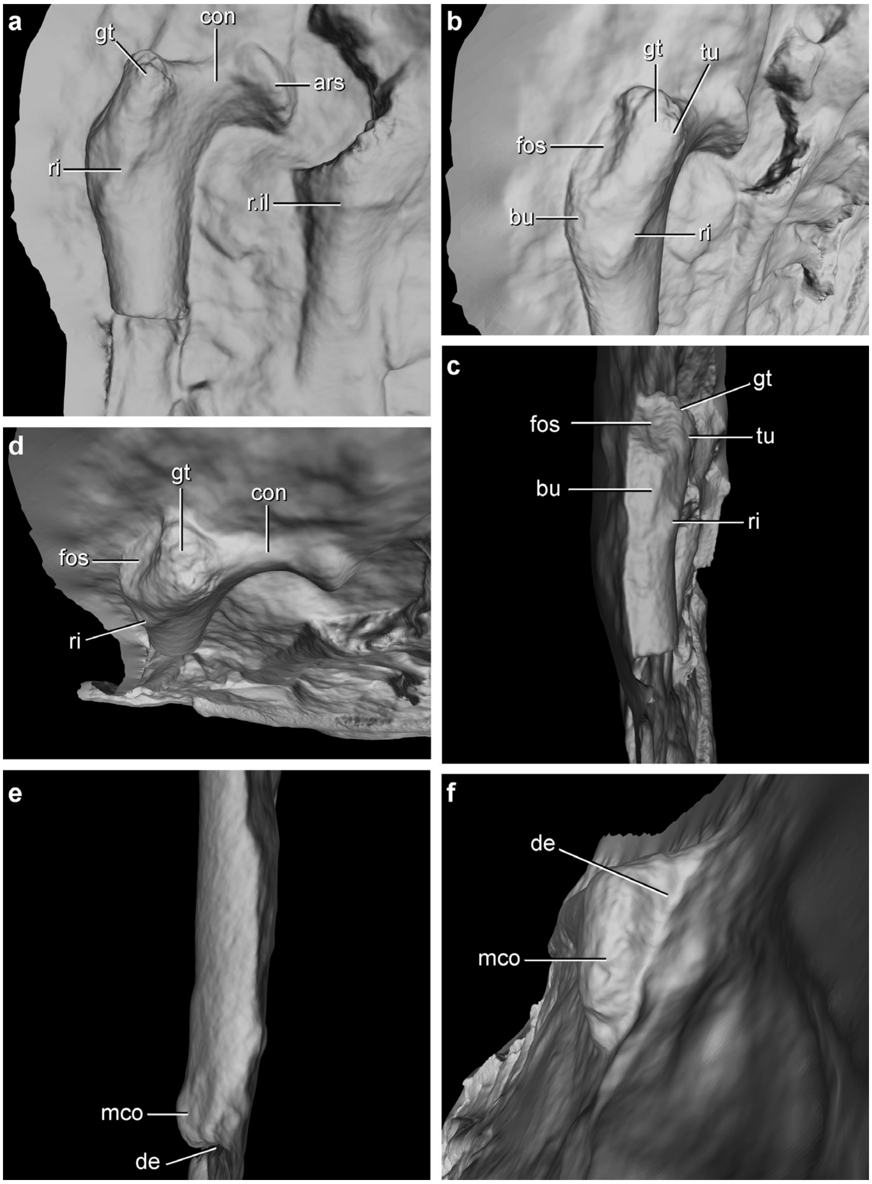

Figure 4. Close-ups of the positive digital cast of the right femur of the holotype of the pterosaur *Herbstosaurus pigmaeus* (CTES-PZ 1711). Proximal portion in a) anterior, b) proximoanterolateral, c) proximal, and d) lateral views. Distal portion in e) anterior and f) distal views. Abbreviations: ars, articular surface; bu, bulge; con, constriction; de, depression; fos, fossa; gt, greater trochanter; mco, medial condyle; r.il, right ilium; ri, ridge; tu, tubercle. Photographs not to scale.

and the plate; femoral neck distinctly medially projected in an angle of ca. 102° with respect to the proximal portion of the femoral shaft in anterior view*; and proximomedially-to-distolaterally oriented ridge distal to the greater trochanter on the anterolateral surface of the proximal region of the femur.

Description

Sacrum. The sacrum comprises at least five vertebrae and ribs preserved as natural moulds of their dorsal surface (Casamiquela 1975; Codorniú & Gasparini 2007; Figs. 1: sa, 2: sr5, sv1). The sacral vertebral count of *Herbstosaurus pigmaeus* is higher than in *Eudimorphodon ranzii* (Dalla Vecchia 2014), *Dimorphodon macronyx* (Sangster 2021), *Rhamphorhynchus muensteri* (Wellnhofer 1975), *Campylognathoides liasicus* (Wellnhofer 1974), and *Pterodactylus antiquus* (Naish et al. 2013: character 21), but resembles the presence of five or more sacral vertebrae in *Dsungaripterus weii*, *Nyctosaurus gracilis*, *Anhanguera* sp., *Pteranodon longiceps*, and *Anurognathus ammoni* (Naish et al. 2013: character 21). The width of the vertebrae and their respective sacral ribs decreases posteriorly (Casamiquela 1975; Fig. 2), as occurs in other pterosaurs (e.g. *Dimorphodon macronyx*: Sangster 2021; *Rhamphorhynchus muensteri*: Wellnhofer 1975; *Anhanguera spielbergi*: Veldmeijer 2003; *Nyctosaurus gracilis*: Williston, 1903). The width of the sacrum at the level of the mid-length of the acetabula is lower than the length of the iliac body (i.e. without the pre- and postacetabular processes), as in *Pterodactylus antiquus*, *Anurognathus ammoni* and *Dsungaripterus weii*. By contrast, the opposite condition occurs in *Rhamphorhynchus muensteri*, *Pteranodon longiceps* and *Nyctosaurus gracilis* (Naish et al. 2013: character 20). The transverse processes are posterolaterally oriented, decreasing their posterior slanting towards the caudal series (Casamiquela 1975). The sacral ribs expand gradually anteroposteriorly towards their distal end. The distal ends of the sacral ribs can be easily individualised from each other, indicating that they were not fused to each other into a sacral shield (Fig. 3a, b: sr), contrasting with most pterosaurs (Naish et al. 2013: character 22). However, the lack of fusion between sacral ribs could result from a non-skeletally mature ontogenetic stage (Naish et al. 2013). The distal end of the second sacral rib overlaps the first and third sacral ribs, and the fourth rib overlaps the fifth rib. The zygapophyses and neural spines cannot be individualised because of the fusion of the sacral elements. The postzygapophysis of the first sacral vertebra is posteriorly oriented and extends posteriorly beyond the level of the base of the first sacral rib. Although fused, it can be determined that the neural spines are short and lack a distal transverse expansion, thus forming a continuous ridge-like longitudinal structure along the median line of the sacrum (Fig. 3a: ns). This fusion between the sacral neural spines results in the presence of a supraneural plate in *Herbstosaurus pigmaeus*, as also occurs in adult specimens of *Dsungaripterus weii*, *Anhanguera spielbergi*, and *Pteranodon longiceps*, but not in *Rhamphorhynchus muensteri*, *Pterodactylus antiquus*, *Germanodactylus rhamphastinus*, and *Nyctosaurus gracilis* (Naish et al. 2013: character 23; Hyder et al. 2014).

Ilium. Most of the preacetabular process and the acetabular region of the right ilium are preserved as a natural mould of its lateral surface; only a minor region of the preacetabular process preserves a bony patch (Fig. 1a, 2: r.il). The preacetabular process is strongly elongated and gradually increases in dorsoventral height towards its anterior end, as in *Germanodactylus rhamphastinus*, *Pterodactylus antiquus* (Naish et al. 2013: fig. 8), *Gallodactylus suevicus* (Fabre 1976), and *Ceoptera evansae* (Martin-Silverstone et al. 2023). In addition, the preacetabular process of *Herbstosaurus pigmaeus* curves dorsally, resembling the condition in *Pterodactylus antiquus* (Naish et al. 2013: character 11), *Gallodactylus suevicus* (Fabre 1976), and *Rhamphorhynchus muensteri* (Wellnhofer 1975). By contrast, the preacetabular process is straight or ventrally curved in *Germanodactylus rhampastinus* (Naish et al. 2013) and *Wenupteryx uzi* (Codorniú et al. 2006). The base of the preacetabular process is dorsoventrally convex, and the degree of convexity decreases anteriorly. The lateral surface of the preacetabular process possesses a series of four anteroposteriorly aligned knob-like prominences, which are positioned slightly dorsal to the level of mid-height of the process (Fig. 3b: pro). Each of these prominences is not aligned with a sacral rib; thus, they do not seem to be an epirelief generated from crushing against the ribs that would be extending beneath the preacetabular process, nor of small fractures because the surface is very well preserved. This is a rare condition among pterosaurs, and we have not seen it in other species that we are aware of. Only the base of the pubic peduncle is preserved. The ischial peduncle is short, vertically oriented and with a slightly convex articular surface (Fig. 3a: isp). The dorsal edge of the acetabulum is semicircular in lateral view and there is no supraacetabular crest framing it. Only the base of the postacetabular process is preserved and it is not informative.

Prepubis. The right prepubis is exposed in dorsal view and the mediodistal edge of the prepubic plate is not preserved (Figs. 1a, 2: r.ppu, 3c). The prepubic shaft is straight and very long, developed as a rod-like structure (Fig. 2: ppush), resembling the condition in *Dimorphodon macronyx*, *Rhamphorhynchus muensteri*, *Pterodactylus antiquus*, and *Wenupteryx uzi* (Codorniú & Gasparini 2012, Naish et al. 2013: character 3, Sangster 2021). The facet for articulation with the pubis is flat and relatively small. The prepubic plate is strongly transversely expanded, distinctly transversely broader than anteroposteriorly long (Fig. 1a). By contrast, the prepubic plate is only slightly broader than long in *Wenupteryx uzi* (Codorniú & Gasparini 2012). The prepubic plate of *Herbstosaurus pigmaeus* is better developed medially than laterally. The medial expansion is projected, forming an almost right angle with the shaft, whereas the lateral expansion forms a much higher angle. The dorsal surface of the prepubic plate has three ridges that radiate from a point close to the transition with the shaft, but medially displaced from it (Fig. 3c: ri). Very similar ridges are also present in *Pterodactylus antiquus* (Wellnhofer 1970), and at least one similar ridge occurs in *Wenupteryx uzi* (Codorniú & Gasparini 2012). The central ridge is the most distinct of the three and is aligned to the main axis of the prepubic shaft, positioned at the base of the medial expansion. This ridge becomes transversely broader towards the distal margin of the plate. The lateral and medial oblique ridges are more subtle. In particular, the medial ridge defines a change in slope of the dorsal surface resulting from the ventral curvature of this portion of the plate. The rest of the pubic plate is flat. The symphysis is not preserved. Although the anterior margin is not completely preserved, it is clear that the plate is paddle-shaped, as in *Eudimorphodon ranzii*, *Dimorphodon macronyx*, *Pterodactylus antiquus*, *Wenupteryx uzi*, *Gallodactylus suevicus*, *Germanodactylus rhampastinus*, and *Dorygnathus bantehnsis*, whereas it contrasts with the branching plate of *Rhamphorhynchus muensteri*, *Pteranodon longiceps* and *Nyctosaurus gracilis* (Kuhn 1967: fig. 14; Wellnhofer 1970, Fabre 1976, Codorniú & Gasparini 2012, Naish et al. 2013: character 2; Dalla Vecchia 2014, Sangster 2021).

Femur. The right femur is complete and exposed in anterior view (Figs. 1a, 2: r.fe, 4). The proximal region of the bone and its distal end are preserved as natural moulds, whereas the vast majority of the shaft is preserved as bone that has lost most of its cortical portion. As a result of this damage, it can be determined that the bone wall is extremely thin, measuring 0.8 mm of a complete bone transverse diameter of 6.1 mm. The left femur lacks its proximal end and is preserved mostly as a natural mould exposing its medial (proximal half) and anterior and medial (distal half) surfaces (Figs. 1a, 2: l.fe).

The femur has a total length of 8.8 cm and a maximum distal width of 1.0 cm. The femur is distinctly sigmoid in anterior view (Fig. 2: r.fe), as occurs in some Triassic species (e.g. *Raeticodactylus filisurensis*: Ezcurra et al. 2020; *Austriadraco dallavecchiai*: Dalla Vecchia 2021) and some monofenestratan pterosaurs (e.g. *Dsungaripterus weii*: Khun 1967; *Germanodactylus rhampastinus*: Martin-Silverstone et al. 2023: character 128; *Pterodaustro guinazui*: Bonaparte 1970; *Nyctosaurus gracilis*: Williston 1903). The femur is also distinctly posteriorly bowed in medial view (Fig. 2: l.fe), as in dsungaripteroids (sensu Kellner 2003) (Unwin 2003). The femoral head is medially oriented, in which the main axis of the femoral neck forms an angle of ca. 102° with the proximal portion of the femoral shaft (Fig. 4a), resembling the morphology of *Wukongopterus lii* (Song et al. 2023). This condition differs from that of the vast majority of post-Early Jurassic pterosaurs (e.g. *Pterodactylus antiquus*: Wellnhofer 1970; *Gallodactylus suevicus*: Plieninger 1907; *Dorygnathus bantehnsis*: Theodori 1852; *Campylognathoides zitteli*: Plieninger 1894; *Rhamphorhynchus muensteri*: Wellnhofer 1975; *Dsungaripterus weii*: Young 1964; *Pteranodon longiceps*: Eaton 1910; *Nyctosaurus gracilis*: Williston 1903), in which the femoral head is more proximally oriented, usually with an angle greater than 120° with respect to the femoral shaft (e.g. Lü et al. 2018, Song et al. 2023). The femoral neck is constricted between the articular surface and the rest of the proximal end of the bone in anterior and proximal views (Fig. 4a, d: con). The articular surface is strongly convex and expands as a mushroom-like structure, as occurs in other breviquartossan pterosaurs (Martin-Silverstone et al. 2023: character 126). The greater trochanter (= external trochanter) is proximally well developed, being positioned slightly below the proximalmost level of the femoral head (Fig. 4a-d: gt). The greater trochanter has a prominent, anteriorly directed tubercle close to its proximal apex (Fig. 4b, c: tu), a condition also reported in the anurognathid *Vesperopterylus lamadongensis* (Lü et al. 2018) and several pterodactyloids (e.g. *Germanodactylus rhampastinus*, *Dsungaripterus weii*, *Azhdarcho lancicollis*; Martin-Silverstone et al. 2023: character 129). The lateral surface of the greater trochanter possesses a large, distinct, but shallow fossa that is proximodistally longer than transversely broad (Fig. 4b-d: fos), which is also present in at least some pterodactyloids, such as *Dsungaripterus weii* (Fastnacht 2005), an indeterminate dsungaripteroid from the Late Jurassic of the USA (McLain & Bakker 2018), an indeterminate dsungaripteroid from the Late Jurassic of Portugal (Bertozzo et al. 2021), and an indeterminate azhdarchoid from the Early Cretaceous of China (Song et al. 2023). Distally to this fossa there is a distinct, laterally projected bulge (Fig. 4b, c: bu). The lateral surface of the greater trochanter has a rounded accessory prominence with a rough surface. Immediately distal to the greater trochanter, there is a proximomedially-to-distolaterally oriented, short, and thick ridge restricted to the lateral half of the anterior surface of the bone (Fig. 4a-d: ri). This ridge is not connected to the lateral bulge described above and closely resembles the condition present in the indeterminate dsungaripteroid from the Late Jurassic of the USA (McLain & Bakker 2018: fig. 1c) and the somewhat more vertical ridge of *Azhdarcho lancicollis* (Averianov 2010). This ridge was probably involved in the insertion of the *M. iliofemoralis* (Averianov 2010, Song et al. 2023). It is impossible to determine the absence or presence of a pneumatic foramen on the posterior surface of the base of the femoral neck because this area is not preserved.

The distal end of the femur is poorly transversely expanded with respect to the shaft mid-length (Fig. 4e). The anterior surface of the distal end is slightly transversely convex without an extensor fossa (Fig. 4f). The medial condyle is posteriorly well developed with respect to the shaft, and the anteromedial corner of the bone forms an obtuse angle in distal view. A median depression separates the medial condyle from the lateral portion of the distal end of the femur (Fig. 4e, f: de).

Results of the phylogenetic analysis

The global strict consensus tree (GSCT) of all the most parsimonious trees (MPTs) found in the analyses using the seven different concavity constant values (k = 3–9) is poorly resolved, with a massive polytomy that includes multiple breviquartossan species (see homoplasy indices and fit values in Table I). The major clades recovered within this polytomy are Pteranodontoidea/Lanceodontia (sensu Kellner 2003 and Andres et al. 2014, respectively) and Azhdarchoidea. All the clades resolved within Breviquartossa have high absolute resampling frequencies (≥ 70%). The iterPCR protocol found that *Eosipterus*, *Cycnorhamphus*, *Cuspicephalus*, *Ceoptera* and *Cacibupteryx* are topologically unstable taxa among the MPTs recovered with k = 3–9. The global reduced strict consensus tree (GRSCT) is considerably more resolved with only two massive polytomies within Dsungaripteroidea (sensu Kellner 2003) and Azhdarchoidea (Fig. 5). The topology of the GRSCT is generally very congruent, including all the higher-level interrelationships, with the reduced strict consensus tree (RSCT) recovered after the analysis under equal weights reported by Martin-Silverstone et al. (2023). The main differences in our results are the unambiguous position of anurognathids at the base of Pterosauria, better resolved Rhamphorhynchidae and Darwinoptera, and more poorly resolved Pterodaustrini, Dsungaripteroidea, and Azhdarchoidea.

Herbstosaurus pigmaeus is recovered as a member of Dsungaripteroidea (sensu Kellner 2003) in all the MPTs found under the different analysed k values (Fig. 5) because of the presence of a strongly bowed femur (character 128: 0→1; Fig. 2: r.fe). The Patagonian form acquires all possible positions within Dsungaripteroidea among the MPTs, but they are not supported by apomorphies. In addition, *Herbstosaurus pigmaeus* shares with other members of the clade composed of Dsungaripteroidea + Azhdarchoidea the presence of a femur with a prominent anteriorly directed tubercle on the dorsal apex of the greater trochanter (character 129: 0→1; Fig. 4b, c: tu). Among the clades closer to the root of the tree, *Herbstosaurus pigmaeus* is positioned within Novialoidea because of the presence of a transversely expanded prepubis (character 124: 0→1; Fig. 3c) and within Breviquartossa because of the presence of a constricted femoral neck (character 126: 0→1; Fig. 4a, d: con). The resampling frequencies for Dsungaripteroidea are very high (absolute = 98% and GC = 97%) in the GRSCT, and similarly high

Table I. Number of most parsimonious trees (MPTs) found and homoplasy indices of the seven analyses under implied weighting with the different concavity constant values.

Concavity constant value (k)	Number of MPTs	Consistency index	Retention index	Fit (adjusted homoplasy)
3	345	0.34974	0.76990	53.58074
4	>10,000	0.35409	0.77425	46.24252
5	>10,000	0.35536	0.77550	40.69893
6	>10,000	0.35791	0.77799	36.37428
7	>10,000	0.35856	0.77861	32.88905
8	>10,000	0.35856	0.77861	30.02524
9	>10,000	0.35856	0.77861	27.63097

values are also calculated for all the internal nodes leading to Monofenestrata (absolute ≥ 89% and GC ≥75%) (Fig. 5).

DISCUSSION

Herbstosaurus pigmaeus is among the first pterosaur species named for South America (e.g. *Pterodaustro guinazui*: Bonaparte 1970; *Araripesaurus castilhoi*: Price 1971; *Puntanipterus globosus*: Bonaparte & Sánchez 1975; *Araripedactylus dehmi*: Wellnhofer 1977). Throughout its relatively long history, spanning 49 years, assessments of this species were limited to comments about its phylogenetic relationships, or references to it were made in the context of some more general reviews of Patagonian or Argentinian pterosaurs (Ostrom 1978, Bonaparte 1978, Wellnhofer 1991, Unwin 1996, Unwin & Heinrich 1999, Unwin 2003, Codorniú & Gasparini 2007, 2013, Codorniú & Gianchini 2016). The incompleteness and kind

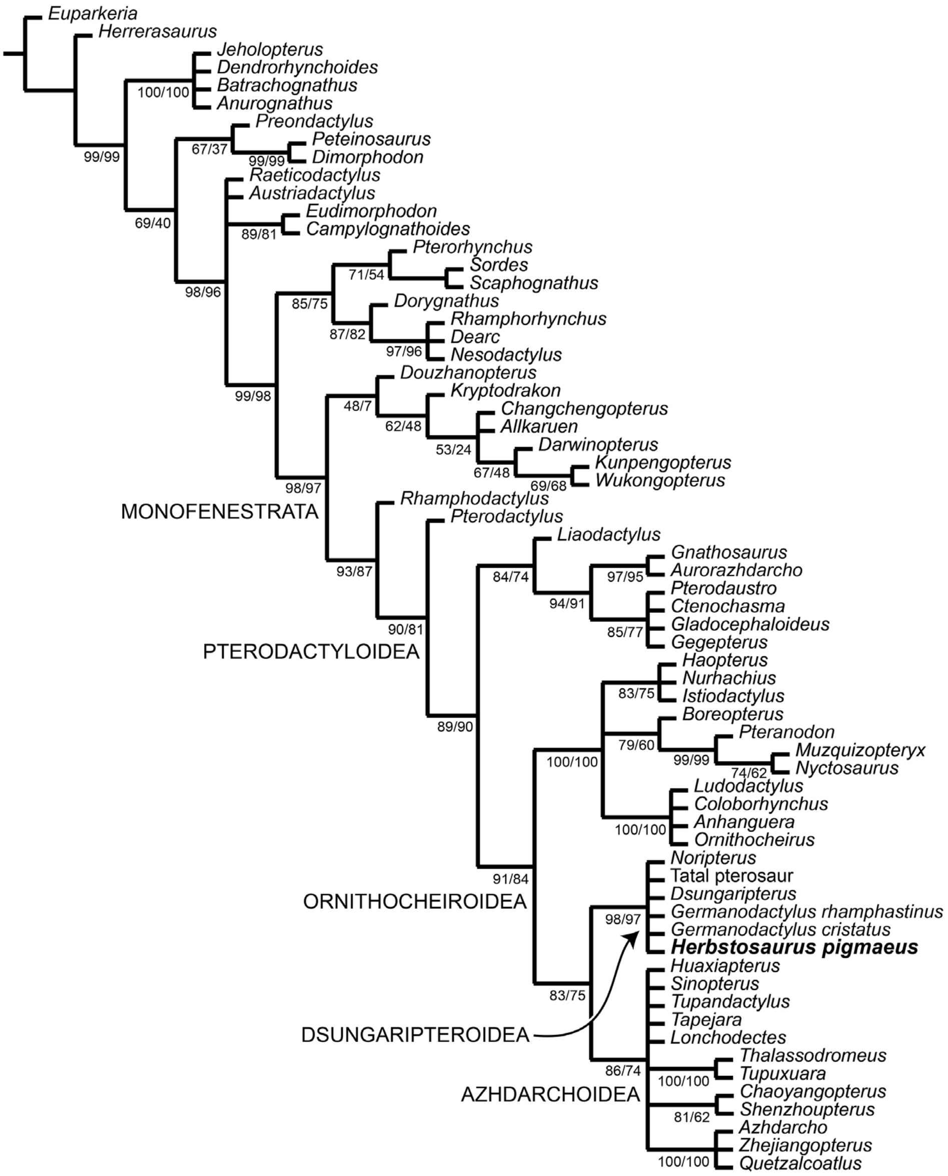

Figure 5. Global reduced strict consensus tree of all the most parsimonious trees recovered in all analyses under implied weighting (k values = 3–9). No-zero weight symmetric resampling absolute (left) and GC (right) frequencies are indicated below each branch.

of preservation (mostly as negative moulds) of the holotype of *Herbstosaurus pigmaeus* were probably the main factors that hampered a more detailed restudy of its anatomy since the original description by Casamiquela (1975).

Although the taxonomic validity of *Herbstosaurus pigmaeus* has not been questioned, the species was lacking an updated diagnosis focused on comparisons with other pterosaurs. Our first-hand restudy of the specimen allowed us to describe and illustrate novel information about the anatomy of *Herbstosaurus pigmaeus*, compare it with other pterosaurs, and include it in quantitative phylogenetic analyses focused on early pterodactyloid pterosaurs. Here we agree with the diagnostic nature of the holotype of *Herbstosaurus pigmaeus* to a species level and propose a unique combination of character-states (see Systematic Palaeontology) that distinguishes this species from other pterosaurs. Furthermore, the recognition of two autapomorphies (a row of knob-like prominences on the lateral surface of the preacetabular process of the ilium; a femoral neck that is medially projected at an angle of ca. 102° with respect to the proximal portion of the femoral shaft in anterior view) bolsters the taxonomic validity of *Herbstosaurus pigmaeus*. Casamiquela (1975) highlighted the small size of the holotype of *Herbstosaurus pigmaeus* when it was thought to be a theropod dinosaur, as evidenced by the etymology of its specific epithet. Evidence to determine the ontogenetic stage of the holotype of *Herbstosaurus pigmaeus* is ambiguous; the lack of fusion between the sacral ribs likely indicates skeletal immaturity (Naish et al. 2013, contra Codorniú & Gasparini 2007), but the fusion of the sacral neural spines into a supraneural plate denotes some degree of skeletal maturity (Hyder et al. 2014). Thus, it seems that the holotype of *Herbstosaurus pigmaeus* was not, at least, an early juvenile. Hence, size comparisons with other pterosaurs based on a skeletally immature specimen are not very informative.

Our anatomical comparisons and results of the phylogenetic analyses bolster previous claims of pterodactyloid affinities for *Herbstosaurus pigmaeus* (Bonaparte 1978, Unwin 1996, Codorniú & Gasparini 2007). The femoral morphology of *Herbstosaurus pigmaeus* resembles that of early azhdarchoids and dsungaripteroids (e.g. prominent anteriorly directed tubercle on the dorsal apex of external trochanter), and it more strongly resembles dsungaripteroids in its overall gracility and strong sigmoid profile in anterior and posterior views. Codorniú & Gasparini (2007) claimed that the purported dsungaripteroid affinities of *Herbstosaurus pigmaeus* need revision because most of the apomorphies of the clade were concentrated in the skull and the Patagonian species lacks this region of the skeleton. Regarding the postcranium, Codorniú & Gasparini (2007) reported that two dsungaripteroid apomorphies could be potentially evaluated in *Herbstosaurus pigmaeus*: the presence of thick walls of the long bones and a femur bowed in both anteroposterior and mediolateral planes. These authors claimed that the walls of the femur of *Herbstosaurus pigmaeus* were thick, contrasting with those of dsungaripteroids. We agree with this observation, in which the bony wall is 0.13 thinner than the transverse diameter of the femoral shaft. Codorniú & Gasparini (2007) concluded that the second postcranial apomorphy of the dsungaripteroids could not be determined in *Herbstosaurus pigmaeus* because the specimen is two-dimensionally preserved. However, we do not agree with this observation because both femora are distinctly bowed in both anteroposterior and mediolateral planes (Fig. 2), closely resembling the condition in dsungaripteroids

(Unwin 2003; e.g. *Dsungaripterus weii*: Young 1964). Indeed, this is the only synapomorphy shared between *Herbstosaurus pigmaeus* and other dsungaripteroids in our quantitative phylogenetic analyses.

CONCLUSIONS

We acknowledge that the dsungaripteroid (sensu Kellner 2003) affinities of *Herbstosaurus pigmaeus* are weak, but it seems to be the most parsimonious hypothesis with the evidence at hand (Fig. 5). In addition, the presence of a prominent anteriorly directed tubercle on the dorsal apex of the external trochanter of the femur reinforces the idea that *Herbstosaurus pigmaeus* is not an early pterodactyloid, but an ornithocheiroid. Therefore, the recognition of *Herbstosaurus pigmaeus* as a deeply nested pterodactyloid expands the taxonomic diversity of the pterosaur record of southwestern Gondwana during the Late Jurassic.

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Additional data

Input and output files of the phylogenetic analyses, and 3D models of the holotype of the pterosaur *Herbstosaurus pigmaeus* (CTES-PZ 1711) can be downloaded from: https://doi.org/10.5281/zenodo.13864613.

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MDE and MBvB designed the study. MDE wrote the first draft of the manuscript. MDE, MR, and MBvB built the 3D model. MDE analysed the data and did the figures. MDE and AEF interpreted the results. All authors contributed to the writing and reviewing of the manuscript.