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ABSTRACT

This work attempts at providing a revised framework for ornithischian phylogeny, based on an exhaustive data compilation of already published analyses, a critical re-evaluation of osteological characters and an in-depth checking of characters scoring to fix mistakes that have accumulated in previous analyses; we have also included recently described basal ornithischians, marginocephalians and ornithopods. 'Heterodontosaurids' are recovered as a paraphyletic group of basal Marginocephalia that progressively lead to the dome-headed 'true' pachycephalosaurs. 'Heterodontosaurids' consequently fall within Pachycephalosauria *sensu* Sereno, 1998. The reconfiguration of basal cerapodan relationships pulls the origins of ornithopods to the earliest stages of the Jurassic. Based on the present analysis, we also discuss ornithopod relationships, with a particular focus on basal Iguanodontia. *Tenontosaurus* is found as the basalmost iguanodontian. The monophyly of Rhabdodontomorpha in a position more derived than *Tenontosaurus* is supported by the present analysis.

Introduction

On the basis of fundamental differences in their pelvic structure, Seeley (1887) divided Dinosauria into two suborders: Saurischia and Ornithischia. The ornithischian pelvis is 'opisthopubic', meaning that the pubis points ventrally and posteriorly parallel with the ischium. Additionally, the ilium has an anteriorly pointing pre-acetabular process, so that the pelvis appears four-pronged in lateral view. Basal ornithischians are poorly documented by scarce fossils; consequently, their origin and phylogenetic relationships with saurischians and silesaurids have long been, and are still discussed (Galton 1970; Bakker and Galton 1974; Gauthier 1986; Langer and Benton 2006; Langer and Ferigolo 2013; Padian 2013; Baron et al. 2017; Baron et al. 2017; Baron and Barrett 2017). Researches dating back from the very first numerical phylogenetic analyses profoundly changed our conception of ornithischian relationships. They notably found that cursorial and sabre-toothed ornithischians – namely the Heterodontosauridae – shared synapomorphies with ornithopods, pachycephalosaurs and ceratopsians (Santa Luca 1980; Cooper 1985; Sereno 1986; Sues and Norman 1990). After Sereno (1986) created the suborder Marginocephalia to group both Ceratopsia and Pachycephalosauria, and Heterodontosauridae was placed within basal Ornithopoda (see also Cooper 1985; Salgado et al. 1997; Calvo et al. 2007). Norman et al. (2004) found heterodontosaurids at an unresolved place at the base of Cerapoda, one of their two Most Parsimonious Trees (MPTs) placed them as either basal ornithopods, whereas the other placed them as the sister group of Marginocephalia. This latter phylogenetic position for heterodontosaurids was also recovered by Xu et al. (2006). Butler et al. (2008) were the first to include an exhaustive set of ornithischians in their data matrix, and notably recovered heterodontosaurids as the basalmost, non-genasaurian ornithischians. Their data matrix was subsequently regarded as the

reference point for most subsequent authors (e.g. Han et al. 2012; Padian 2013; Godefroit et al. 2014; Agnolín and Rozadilla 2017; Baron et al. 2017). Butler et al. (2008, p. 23) claimed that 'resolving the position of heterodontosaurids within Ornithischia is one of the most important tasks facing ornithischian phylogeneticists and future work should aim to combine the data set provided here with that of Xu et al. (2006)'. Although accurate positioning of heterodontosaurids is particularly important for polarising the character acquisition sequence at the base of Ornithischia and therefore for disentangling ornithischian origin (Agnolín and Rozadilla 2017), nobody attempted to combine both data sets so far.

During the last decade, new phylogenies of basal ornithischians have been proposed, mainly at the occasion of new taxonomic descriptions. However, those analyses were often conducted on the basis of reduced taxonomic data sets focusing on the newly described taxa (e.g. Sereno 2012; Brown et al. 2013; Rozadilla et al. 2016), and rarely reached a global consensus whenever using a more exhaustive taxonomic sampling (Godefroit et al. 2014; Boyd 2015; Herne et al. 2019; Cruzado-Caballero et al. 2019; Bell et al. 2019). As a result, the interrelationships between basal forms remain poorly resolved and/or supported. Although Marginocephalia and Ornithopoda were among the most successful and diversified dinosaurs, especially during the Cretaceous, those clades are paradoxically weakly supported, and their origins and early diversifications are consequently poorly understood (Sereno 1986, 2000; Sues and Norman 1990; Weishampel and Heinrich 1992; Xu et al. 2006; Butler et al. 2008; Boyd 2015; Bell et al. 2019). Moreover, the recent discovery of the primitive ornithischian *Laquintasaura venezuelae* (Barrett et al. 2014) and the notable reinterpretation of *Chilesaurus diegosuarezi* as the basalmost ornithischian (Baron and Barrett 2017) continue to raise important questions about the origin of ornithischians (Baron et al. 2017; Langer et al. 2017).

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It is of course very likely that important fossil record lacunae, inadequate revisions of character scoring and homoplasies related to graviportality or quadrupedy (e.g. Dodson 1980; Winkler et al. 1997; Dieudonné et al. 2016) all partly explain difficulties in resolving the ornithischian phylogeny. The long-branch attraction phenomenon is another potential 'usual suspect' perturbating the adequacy of phylogenies. It occurs when longer branches – corresponding to better-scored taxa – are erroneously clustered together because they share more characters in common than with other taxa for which those characters are partly or wholly missing (Felsenstein 1978, 2004). Inaccurate taxon-grouping especially occurs whenever missing characters or missing taxa within the tree are non-randomly distributed (Weishampel and Heinrich 1992; Wiens 2005). For a long time, researches on ornithopods and marginocephalians focused on larger derived taxa, which are usually better preserved and easier to find in the field. The skeletons of smaller ornithischians are usually under-represented in museum collections as they are more easily destroyed during diagenetic processes and therefore more difficult to find. Data sets are consequently biased, as smaller basal taxa tend to be scored for a smaller amount of characters in comparison to larger ones (Weishampel and Heinrich 1992). Fortunately, numerous smaller ornithischian taxa have been described during the past decade (e.g. Pol et al. 2011; Zheng et al. 2012; Ösi et al. 2012; Ruiz-Omeñaca et al. 2012; Godefroit et al. 2014; Dieudonné et al. 2016; Baron and Barrett 2017; Bell et al. 2018; Madzia et al. 2018; Herne et al. 2018, 2019), and their detailed study will certainly allow to partially get rid of the long-branch attraction problem in the future.

The present paper proposes a new phylogeny of ornithischian dinosaurs and set out new hypotheses about early cerapodan and basal iguanodontian origins based on an exhaustive data compilation of already published analyses, a critical re-evaluation of osteological charactersand an in-depth checking of characters scoring to fix mistakes that have accumulated in previous analyses. We include recently described basal ornithischians, marginocephalians and ornithopods.

Institutional abbreviations: CPBA-V: Cátedra de Paleontología de la Facultad de Ciencias Exactas de la Universidad de Buenos Aires, Argentina (Colección de vertebrados); MDS: Museo de Dinosaurios de Salas de los Infantes, Burgos Province, Spain; QM, Queensland Museum of Brisbane, Queensland, Australia.

Material and methods

This work is built on a revised version of the Dieudonné et al. (2016) data set (see character list and excel data matrix in Supplemental material 1 and 2, respectively), which already considered the data matrices from Butler et al. (2008, in its more recent version used by Ösi et al. 2012), Mcdonald et al. (2010), Brown et al. (2013) and Boyd (2015). Character scorings were here thoroughly and exhaustively revised for each taxon based on a strict bibliographic revision and, when possible, on firsthand observations (see Supplemental materials 3.1 and 3.2). For the first time, we also integrated Xu et al.'s (2006) dataset as already proposed by Butler et al. (2008). We also took into consideration improvements, criticisms, modifications and in some instances a few character scoring proposed by Cambiaso (2007), Pol et al. (2011), Gasca et al. (2014), Baron et al. (2016), Rozadilla et al. (2016, 2019), Han et al. (2018), Andrzejewski et al. (2019) and Bell et al. (2019). Thirty-six new characters were created (see Supplemental materials 1 and 2). We reintegrate 12 taxa which were previously coded by Butler et al. (2008) or by the subsequent versions of these datasets but that were excluded in Dieudonné et al.'s

(2016) dataset: *Laquintasaura venezuelae*, Ankylosauria, Stegosauria, *Isaberrysaura mollensis*, *Kulindadromeus zabaikalicus*, *Stenopelix valdensis*, *Chaoyangsaurus youngi*, *Liaoceratops yanzigouensis*, *Archaeoceratops oshimai*, *Wannanosaurus yansiensis*, *Goyocephale lattimorei*, *Homalocephale calathocercos*. We also add twelve taxa for the first time to this data-set: *Camptosaurus aphanoecetes*, *Chilesaurus diegosuarezi*, *Convolosaurus marri*, *Eousdryosaurus nanohallucis*, *Kangnasaurus coetzeei*, *Mahuidacursor lipanglef*, *Morrosaurus antarcticus*, *Pachycephalosaurus wyomingensis*, *Prenocephale prenes*, *Stegoceras validum*, *Thescelosaurus assiniboiensis* and *Valdosaurus canaliculatus*. Psittacosauridae was also recoded and split as *Psittacosaurus major* and *Psittacosaurus mongoliensis*. *Dryosaurus altus* was renamed 'Dryosaurus' because it was actually based on specimens that are now attributed to *D. altus, Dryosaurus* cf. *altus* and *D. elderae* (Carpenter and Lamanna 2015; Carpenter and Galton 2018). Following Baron et al. (2016), we regarded *Stormbergia dangershoeki* as synonymous to *Lesothosaurus diagnosticus* and coded the latter taxon accordingly. *Pisanosaurus mertii* was successively regarded as a non-dinosaurian dinosauriform by Agnolín and Rozadilla (2017) but as a basal ornithischian by Baron et al. (2017) and Langer et al. (2017). It was temporarily omitted from this analysis. *Herrerasaurus ischigualastensis* was used as the outgroup taxon.

Character #110 (Ösi et al. 2012 #78) and #282 (Ösi et al. 2012 #194 and #195) were newly treated as ordered, in addition to the already ordered characters #150 and #203 (from Ösi et al. 2012 #228 and #137, respectively). Characters #190, #202, #270, #273 (from Mcdonald et al. 2010 #87 and #113; Ösi et al. 2012 #135 and #174) were turned to unordered. The phylogenetic analysis was run under equally weighted maximum parsimony using TNT (Tree Analysis using New Technology, Goloboff et al. 2008) in its latest version (Goloboff and Catalano 2016). A heuristic search of 1000 replications of Wagner trees (with random addition sequence) was performed, followed by a Tree Bisection Reconnection branch-swapping algorithm (TBR, holding 10 trees per replicate). 2000 parsimonious trees were hold in memory. We ran a second round of TBR branch-swapping over the latter trees to optimise the total number of MPTs. *Yandusaurus hongheensis* was found to switch inside and outside Ornithopoda. It was pruned *a posteriori* while looking for the strict consensus tree. Indices of branch support (Bootstrap indices ≥50% and Bremer supports) were also obtained through TNT and plotted over the resulting tree (Figures 1, 2). A table was built to show the phylogenetic definitions of each clade recovered in our analysis, and the characters that support them (Supplemental material 5).

We performed three templeton tests in TNT (Templeton 1983) with the TNT script developed by Alexander N. Schmidt-Lebuhn (2016) and tested for three alternative phylogenetic hypotheses with respect to our reference tree (Supplemental material 6, see below). The first hypothesis tests for an arbitrary positioning of Heterodontosauridae as the closest monophyletic sister group of Genasauria, according to the current assumptions about their phylogenetic relationships (Butler et al. 2008; Barrett et al. 2014; Agnolín and Rozadilla 2017). The second hypothesis tests for the positioning of Rhabdodontormopha at the base of Ankylopollexia, and the third one tests for a splitting of Rhabdodontormopha consistent with the hypotheses of Bell et al. (2019) and Madzia et al. (2020), with *Muttaburrasaurus langdoni* and *Fostoria dhimbangunmal* set within a monophyletic sister group of Ankylopollexia, and Rhabdodontidae left in the same positioning as in the strict consensus (see Supplemental Material 6 for details on the results).
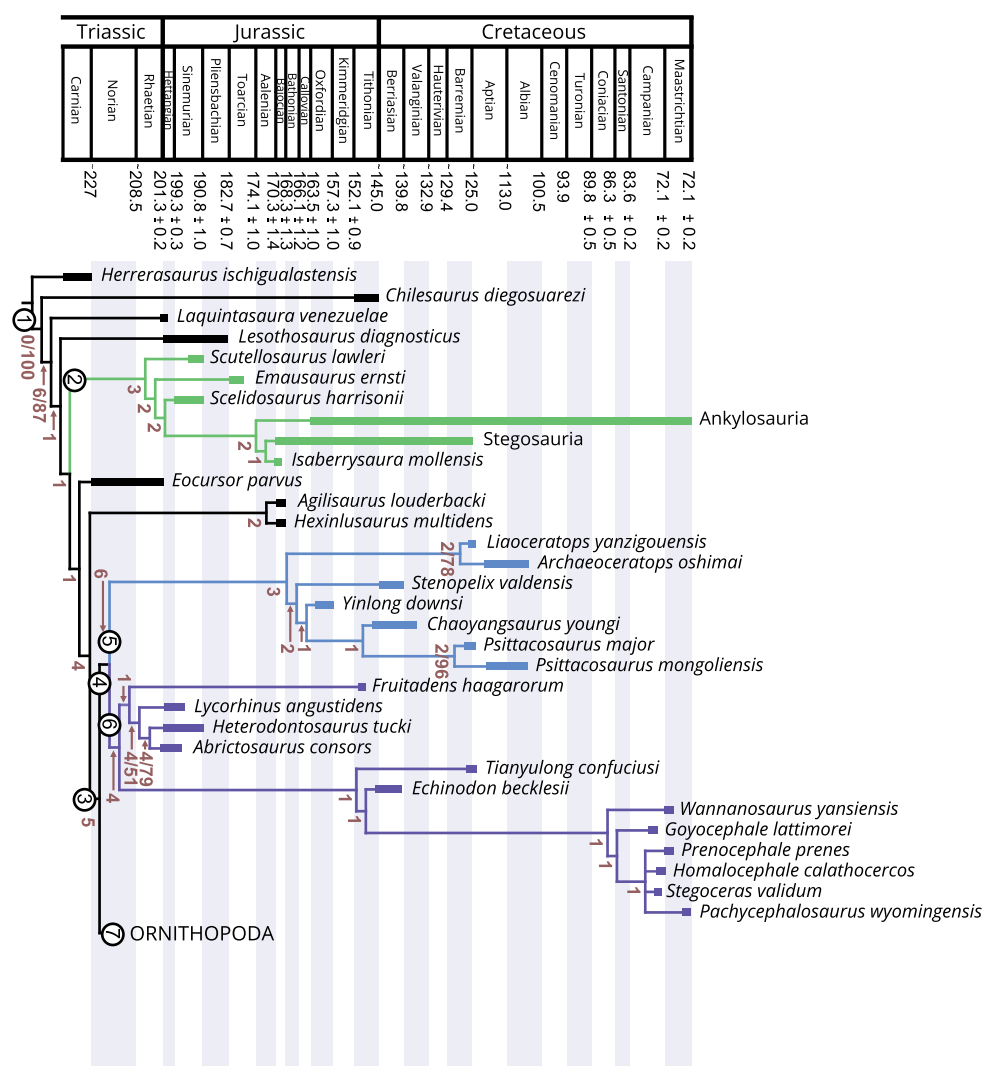
Figure 1. Strict consensus tree calibrated over the chronostratigraphic timescale of Cohen et al. (2013, updated version), showing relationships among non-ornithopodan ornithischians. The analysis was run under equally-weighted parsimony with the *a posteriori* removal of *Yandusaurus hongheensis*. Bremer supports are reported below each node. Bootstrap values are also added to the right of the Bremer indices whenever those are superior to 50%. Specific clades are shown with a circled number, and some of them are highlighted using a specific colour: Ornithischia (1), Tyreophora (2, light-green), Cerapoda (3), Marginocephalia (4), Ceratopsia (5, light-blue), Pachcephalosauria (6, violet), Ornithopoda (7).

Results

Running the analysis with the *a posteriori* pruning of *Yandusaurus hongheensis* results in 176 MPTs. The strict consensus tree (CI = 0.295, RI = 0.615, 1426 steps) is our reference tree for the discussion.

Chilesaurus diegosuarezi (Novas et al. 2015; Baron and Barrett 2017) is recovered as the basalmost ornithischian. *C. diegosuarezi*, *Laquintasaura venezuelae* (Barrett et al. 2014) and *Lesothosaurus diagnosticus* (Baron et al. 2016) are recovered as successive sister taxa at the base of Genasauria. *Isaberrysaura mollensis* (Salgado et al. 2017) is the sister taxon of Stegosauria. *Eocursor parvus* (Butler et al. 2007; Butler 2010) is found at the base of Neornithischia. Heterodontosaurids are recovered as basal members of Cerapoda, as previously suggested by a few studies (e.g. Cooper 1985; Weishampel and Heinrich 1992; Salgado et al. 1997; Norman et al. 2004; Calvo et al. 2007). They form a paraphyletic grade of taxa stemming 'true' pachycephalosaurs and should, therefore, be regarded as the basalmost members of Pachycephalosauria *sensu* Sereno, 1998, defined as all marginocephalians closer to

Pachycephalosaurus than to *Triceratops*. The arbitrary positioning of a monophyletic 'Heterodontosauridae' at the base of Genasauria was found as significantly different from the optimal tree in the Templeton Test with 38 extra steps (cf. Supplemental Material 6), which supports their newly recovered topology. As in Sereno (2012), we recover the monophyletic subfamily Heterodontosaurinae that groups *Abrictosaurus consors*, *Heterodontosaurus tucki* and *Lycorhinus angustidens*. *Fruitadens haagarorum* is recovered as rooting Heterodontosaurinae, while *Tianyulong confuciusi* and *Echinodon becklesii* are recovered as successive outgroup taxa to dome-headed, 'true' pachycephalosaurs. The clade comprising the derived 'eupachycephalosaurs' *Prenocephale prenes*, *Pachycephalosaurus wyomingensis*, *Homalocephale calathocercos* and *Stegoceras validum* form a polytomy in the strict consensus tree.

The ornithopods *Nanosaurus agilis*, *Changchunsaurus parvus*, *Jeholosaurus shangyuanensis*, *Haya griva*, a clade composed of *Zephyrosaurus schaffi*, *Orodromeus makelai* and *Koreanosaurus boseongensis*, and *Kulindadromeus zabaikalicus* are recovered as successive sister taxa outside Clypeodonta.
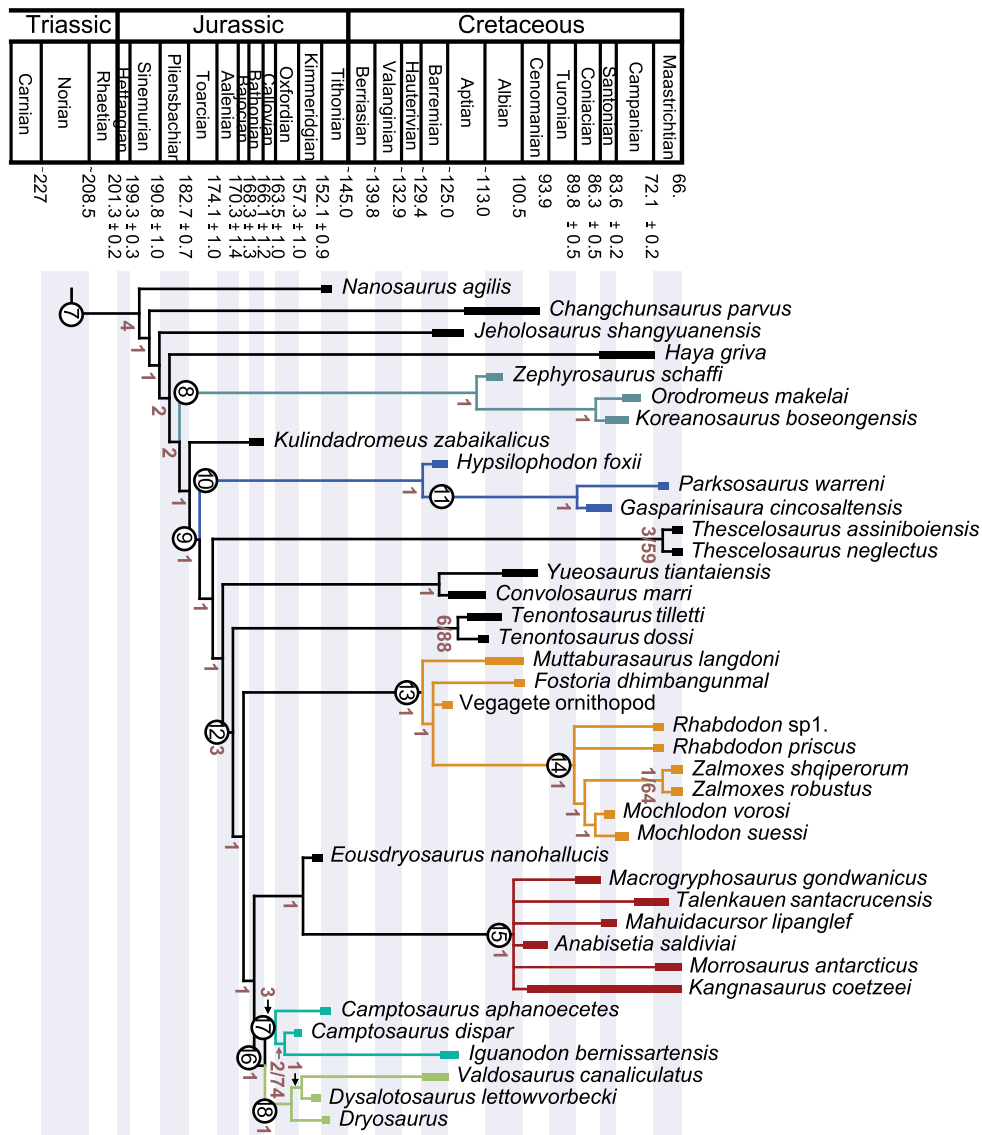
Figure 2. Strict consensus tree calibrated over the chronostratigraphic timescale of Cohen et al. (2013, updated version), showing relationships within Ornithopoda. The analysis was run under equally-weighted parsimony with the *a posteriori* removal of *Yandusaurus hongheensis*. Bremer supports are reported below each node. Bootstrap values are also added to the right of the Bremer indices whenever those are superior to 50%. Specific clades are shown with a circled number, and some of them highlighted using a specific colour: Ornithopoda (7), Orodrominae (8), Clypeodonta (9), Hypsilophodontidae (10, blue) and Parksosauridae (11, included within the latter, dubious Hypsilophodontidae), Iguanodontia (12), Rhabdodontomorpha (13), Rhabdodontidae (14), Elasmaria (15), Dryomorpha (16), Ankylopollexia (17, turquoise) and Dryosauridae (18, light-green).

Hypsilophodon foxii is recovered in monophyly with another sub-clade formed by *Parksosaurus warreni* and *Gasparinisaura cincosal-tensis*. This whole group is dubious and falls within a weakly supported Hypsilophodontidae *sensu* Boyd (2015). Concerning iguanodontian ornithopods, our phylogenetic result is similar to that found earlier by Calvo et al. (2007) and Barrett et al. (2011). Elasmaria is formally defined as *Talenkauen santacrucensis, Macrogryphosaurus gondwani-cus*, their common ancestor and all of their descendants (Calvo et al. 2007). Consistently with earlier analyses (Cruzado-Caballero et al. 2019; Rozadilla et al. 2019), elasmarians are recovered as an intrinsi-cally unresolved but separate lineage of gondwanan iguanodontians. As already suggested by Escaso et al. (2014), we find them as probably stemming from an early shoot of Late Jurassic dryosauroid-like ornithopods, with *E. nanohallucis* as their closest outgroup.

Herne et al. (2019); Bell et al. (2019) and Madzia et al. (2020) suggested more exclusive affinities between *Muttaburrasaurus lang-doni, Fostoria dhimbangunmal* and basal dryomorphs. Despite earlier

criticisms (Herne et al. 2019; Bell et al. 2019), the clade Rhabdodontomorpha finds renewed support as a monophyletic group in our analysis (Figure 2). The arbitrary positioning of Rhabdodontomorpha as the closest sister-taxon of Ankylopollexia implies 13 extra-steps with respect to the strict consensus. This is more than what would be expected from sampling error: this alter-native topology is therefore not supported by our data matrix (0.01 < p < 0.025, Supplemental Material 6). By contrast, the artificial splitting of Rhabdodontomorpha with *M. langdoni* and *F. dhimbangunmal* set as a monophyletic sister group of Ankylopollexia and rhabdodontids left as basal iguanodontians is an alternative solution that is plausible with respect to the strict consensus (11 extra steps, p > 0.05, Supplemental material 6). However, we remark that the sum of negative ranks – which favours the alternative hypothesis (Templeton 1983) – stands only very close to the upper limit corresponding to a p-value of 0.05 (Supplemental material 3), so this alternative result has no strong support.

Discussion

Heterodontosauridae: a controversial origin as basal ornithischians

According to Butler et al. (2008) and Galton (2014), the skeleton of heterodontosaurids is characterised by a series of plesiomorphic characters that are also present in the basal saurischian *Herrerasaurus ischigualastensis*, thus justifying their basal rooting within Ornithischia. Among these, we find the presence of unexpanded premaxillary crowns (#113 in Butler et al. 2008), a v-shaped dentary symphysis (#97 in Butler et al. 2008), and the presence of epipophyses on the anterior cervicals (#133 in Butler et al. 2008). The manus of heterodontosaurids and *H. ischigualastensis* also shares synapomorphies that are all likely related with enhanced grasping capabilities: a manus length that is more than 40% the combined length of the humerus and radius (#156 in Butler et al. 2008), elongate penultimate phalanges of the second and third manual digits (#159 in Butler et al. 2008), the presence of extensor pits on the distal metacarpals and manual phalanges (#162 in Butler et al. 2008) and strongly recurved manual unguals with prominent flexor tubercles (#163 in Butler et al. 2008). However, we consider the coding of some of those characters controversial. For example, the dentary symphysis of *H. ischigualastensis* is straight, unexpanded and restricted to its very distal tip (Sereno and Novas 1993, Figure 1(f)), which is in marked contrast with the massively buttressed and v-shaped symphysis of *Heterodontosaurus tucki* (Norman et al. 2011, appendix 6.D). The humerus of *H. ischigualastensis* is incompletely preserved, so the relative proportion of its manus with respect to its humerus and radius cannot be adequately assessed (Sereno 1993, figs. 3–4). Finally and in contrast to heterodontosaurids, the penultimate phalanges of fingers II and III are not longer than those from the first row in *H. ischigualastensis* (Sereno 1993, fig. 13 and 15).

Some incongruences were subsequently raised, e.g. by Barrett and Maidment (2011) and Porro et al. (2015) about the basal positioning of heterodontosaurids as hypothesised by Butler et al. (2008). Early Jurassic heterodontosaurids are characterised by closely packed and chisel-shaped maxillary and dentary teeth, as well as by a higher coronoid process (Sereno 2012) all of which are highly atypical for basal ornithischians (Porro et al. 2015, p. 2). Barrett and Maidment (2011) also pointed out that the basal rooting of heterodontosaurids enforced important homoplasies concerning the evolution of the ornithischian pelvis. A prominent and laterally projecting supra-acetabular crest encloses the femoral head into a cup-shaped structure in all advanced archosaurs and basal ornithischians having achieved an upright limb-posture (Charig 1972). This supra-acetabular crest was subsequently lost in neornithischians more derived than *Agilisaurus louderbacki* (e.g. Peng 1992, Figure 5) as an improvement of their bipedal stance. The insertion of their adductor limb musculature probably shifted from their well-developed preacetabular process of ilium towards a secondarily developed prepubic process (Charig 1972). As Barrett and Maidment (2011) pointed out, heterodontosaurids are unusual basal ornithischians in that they already lost their supraacetabular crest of the ilium and developed a stub-like prepubic process.

Several authors already noticed that heterodontosaurids shared synapomorphies with marginocephalians. Among these are the presence of three premaxillary teeth (Norman et al. 2011; Han et al. 2015) or the loss of the ischial obturator process (Galton 2014). More recently, Becerra and Pol (2020) identified interesting correspondences in the enamel microstructure of the heterodontosaurid *Manidens condorensis* and pachycephalosaurids, both featuring the presence of incipient divergent crystallite units devoid of clear mutual limits, followed by an outer layer of parallel/divergent crystallites. Similar enamel types were also found in more basally branching tyreophorans and sauropodomorphs (Becerra and Pol 2020).

A review of Marginocephalia

Marginocephalia: an historically weakly supported clade

The first diagnoses of Marignocephalia were proposed by Sereno (1984, 1986, 2000) and Maryanska and Osmolska (1985). The
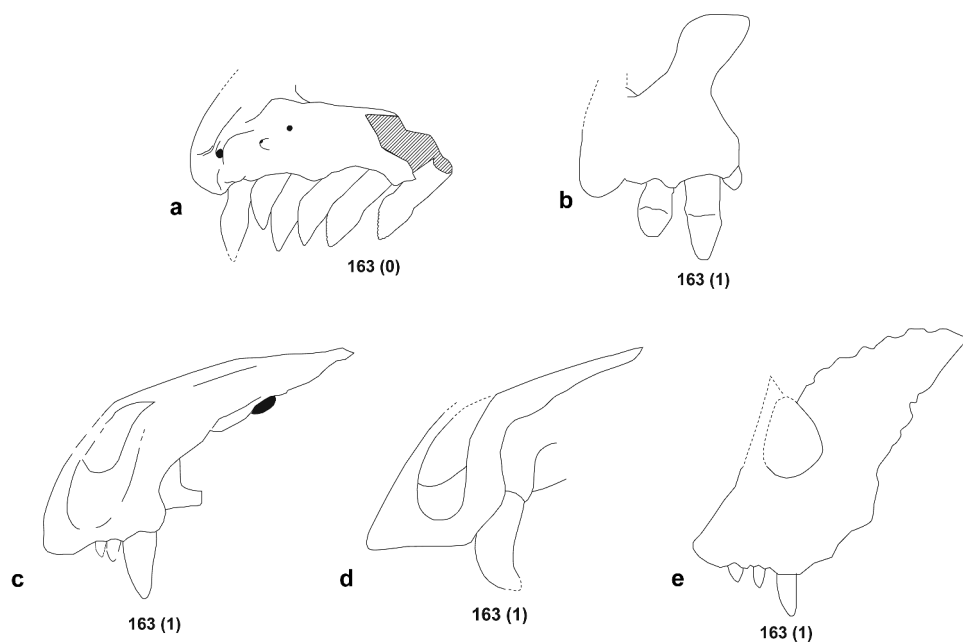

Figure 3. Marginocephalian premaxillary teeth compared to those of *Lesothosaurus diagnosticus* in labial view, with: (a) *L. diagnosticus* (after Sereno, 1991); (b) *Yinlong downsi* (after Han et al. 2015); (c) *Heterodontosaurus tucki* (after Norman et al. 2011); (d) *Tianyulong confuciusi* (after Zheng et al. 2009); (e) *Prenocephale prenes* (Maryanska and Osmolska 1974). Not to scale.
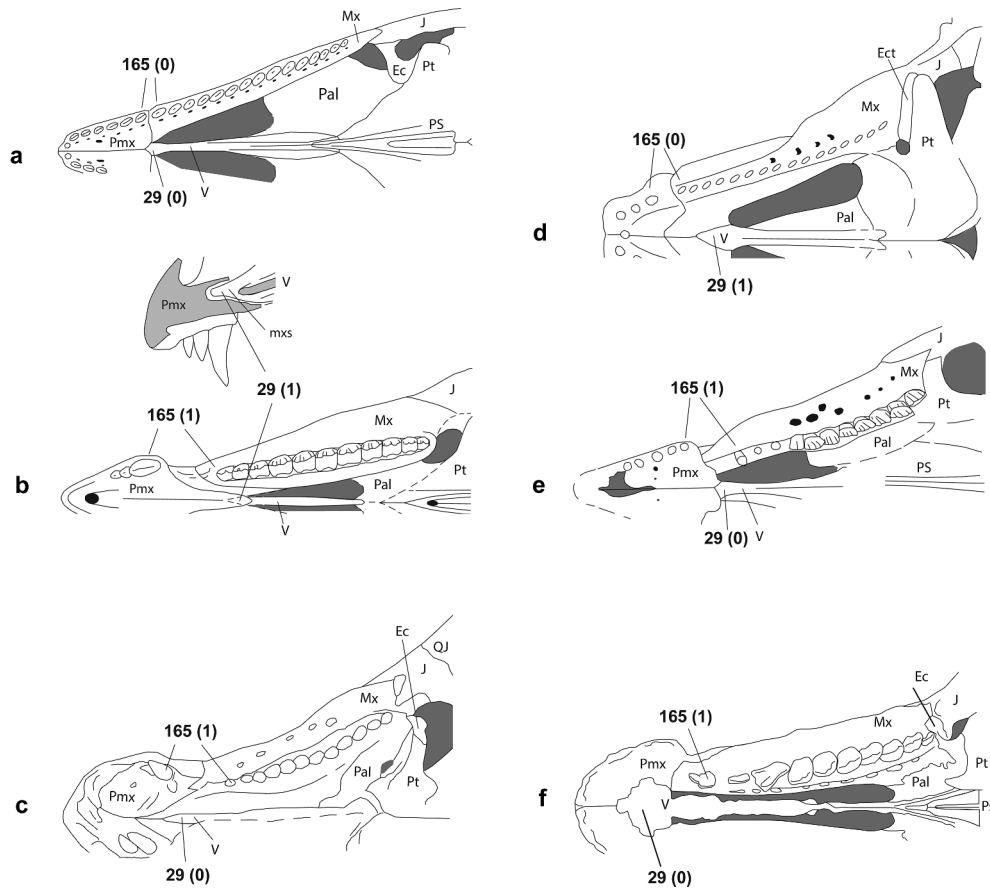
Figure 4. Marginocephalians snouts compared to those of other ornithischians in ventral view, with: (a) *Lesothosaurus diagnosticus* (after Sereno, 1991), (b) *Heterodontosaurus tucki* (after Norman et al. 2011); (c) *Liaoceratops yanzigouensis* (after Xu et al. 2002); (d) *Stegoceras validum* (after Sues and Galton 1987); (e) *Hypsilophodon foxii* (after Galton 1974a); (f) *Tenontosaurus tilletti* (after Thomas 2015). Abbreviations: Ec, Ectopterygoid; J, jugal; Mx, maxilla, mxs, intermaxillary suture; Pal, palatine; Pmx, premaxilla; PS, parasphenoid; Pt, pterygoid; QJ, quadratojugal; V, vomer. Not to scale.

number of synapomorphies for the clade went progressively reduced throughout the years from nine (Sereno 1984) to three (Sereno 2000). These three characters are: (1) the posterior extension of a parietosquamosal shelf obscures the occiput from a dorsal view, (2) a median contact between the maxillae excludes the premaxillae from participation to the anterior margin of internal nares, (3) the postpubic process is short and lacks a distal pubic symphysis. However, in the light of new descriptions and discoveries, we consider that solely one of these characters is valid.

We agree with Sues and Galton (1987) that the parietosquamosal shelf of ceratopsians shows no close resemblance with that of pachycephalosaurs. As already noticed by Sereno (2000), the relative contribution of the parietal and squamosal to the parietosquamosal shelf is different in both clades. In pachycephalosaurs, the parietal shelf is anteroposteriorly thick, and the parietal contribution to the parietosquamosal shelf is narrow (e.g. *Stegoceras validum*, Gilmore 1924, pl., 4). In ceratopsians, the parietal shelf consists in a dorsoventrally wide and anteroposteriorly thin strap of bone (e.g. *Archaeoceratops oshimai* and *Yinlong downsi*, You and Dodson 2003; Han et al. 2015). Moreover, the occiput is still visible from a dorsal view in basal ceratopsians (e.g. *Yinlong downsi*, Han et al. 2015, Figure 4(b)). The second character deals with the anterior contact of the internal nare – that is enclosed by the paired vomers – with the mutually contacting maxillae. As will be discussed below this character remains a marginocephalian synapomorphy even considering our new tree topology, as it is also present in heterodontosaurids (Norman et al. 2011, Figure 11). Yet, our formulation of this character slightly differs

from that of Sereno's (2000) as we consider the vomeral head instead of the internal nare (#29) for the anterior contact with the paired maxillae. We concur with Sereno (2000) in that a postpubic reduction is shared by ceratopsians (You and Dodson 2004) and *Homalocephale calathocercos*, the only 'true' pachycephalosaur in which a broken but likely very short postpubis is known (Maryanska and Osmolska 1974, Figure 5(b)). However, the placement of Heterodontosauridae within Pachycephalosauria as suggested in the present analysis leads us to reconsider the postpubic reduction as independently acquired in both the pachycephalosaurian and the ceratopsian lineages. *Tianyulong confuciusi* (Zheng et al. 2009) is the only non-heterodontosaurine pachycephalosaur that preserves a complete postpubis and that clearly shows a post-pubic reduction. The postpubic process is as long as the ischium in *Heterodontosaurus tucki* (Galton 2014) and *Manidens condorensis* (Pol et al. 2011). The post-pubic reduction occurred several times independently within Ornithischia: in addition to pachycephalosaurs and ceratopsians, it also occurred in ankylosaurs (Vickaryous et al. 2004), iguanodontoids (Norman 2004) and hadrosaurids (Horner et al. 2004).

Synapomorphies of Marginocephalia

The main result of the phylogenetic analysis proposed in the present paper is the placement of heterodontosaurids as a paraphyletic group of basal marginocephalians closer to 'true' pachycephalosaurs than to Ceratopsia. This hypothesis significantly increases the number of synapomorphies shared by Marginocephalia. Sereno (1998) defines pachycephalosaurs as all marginocephalians
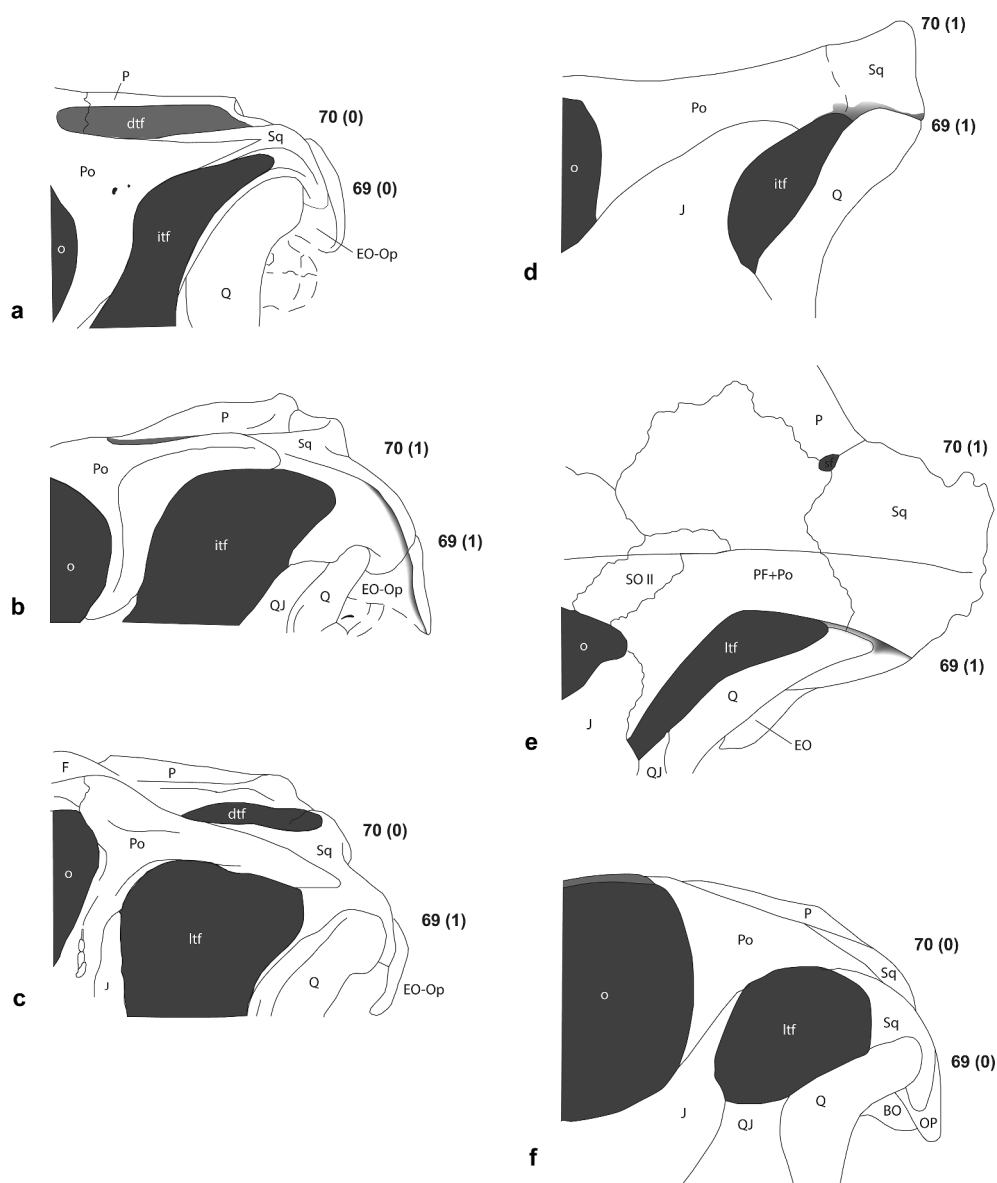
Figure 5. Marginocephalians squamosals compared to those of other ornithischians in lateral view, with: (a) *Lesothosaurus diagnosticus* (after Sereno, 1991); (b) *Heterodontosaurus tucki* (Norman et al. 2011); (c) *Psittacosaurus major* (after You et al. 2008, fig. 1B1); (d) *Archaeoceratops oshimai* (after You and Dodson 2003); (e) *Stegoceras validum* (Sues and Galton 1987); (f) *Hypsilophodon foxii* (Galton 1974a). Abbreviations: BO, basioccipital; Eo-Op, exoccipital-opisthotic; sf, supratemporal fenestra; if, infratemporal fenestra; J, jugal; o, orbit; OP, opisthotic; P, parietal; Po, postorbital; SOII, supraorbital ll; Q, quadrate; QJ, quadratojugal; Sq, squamosal. Not to scale.

closer to *Pachycephalosaurus* than to *Triceratops*. According to this definition and to their phylogenetic position in the present analysis, 'heterodontosaurids' should, therefore, be regarded as basal members of Pachycephalosauria. 'Heterodontosaurids' lack the typically thickened squamosals and frontoparietal of formerly referred 'true' pachycephalosaurs (e.g. Sereno 2000). We will therefore informally refer to those marginocephalians fitted with a thickened dorsal skull roof as 'eupachycephalosaurs'. The paraphyletic 'sabre-toothed' pachycephalosaurs devoid of a thickened dorsal skull roof will be referred to here as 'heterodontosaurids' between quote marks because this group is paraphyletic according to this analysis. The newly recovered synapomorphies for Marginocephalia are listed and discussed below.

(1) The presence of three premaxillary teeth (#159, Figure 3) is shared by *Heterodontosaurus tucki* (Figure 3(c), Norman et al. 2011, fig. 20), *Abrictosaurus consors* (Sereno 2012, fig. 31), *Echinodon becklesii* (Sereno 2012, Figure 13(c–d), 19),

Fruitadens haagarorum (Butler et al. 2012, Figure 1), *Archaeoceratops oshimai* (You and Dodson 2003, p. 264), *Liaoceratops yanzigouensis* (Xu et al. 2002), *Yinlong downsi* (Han et al. 2015) and eupachycephalosaurs (Figure 3(e), Maryanska and Osmolska 1974, fig. 1A1, C1; Perle et al. 1982, p. 118). Those three premaxillary teeth were later lost progressively and possibly also several times within Marginocephalia: *Chaoyangsaurus youngi* has two premaxillary teeth (Zhao et al. 1999), psittacosaurids (e.g. Sereno 2010) and *Protoceratops andrewsi* (Brown and Schlaikjer 1940) have none and *Tianyulong confuciusi* has two premaxillary teeth (Sereno 2012).

(2) The presence of a posterior caniniform premaxillary tooth (#163, Figure 3) and an anterior caniniform dentary tooth (#184) are outstanding features commonly found in nearly all 'heterodontosaurids', except in *Abrictosaurus consors* (Sereno 2012, fig. 34, 35). Caniniform premaxillary and dentary teeth are also found in the primitive eupachycephalosaur

Goyocephale lattimorei (Perle et al. 1982, pl. 42.5, 42.9). Hou (1977, p. 3) cited an anterior caniniform dentary tooth in *Wannanosaurus yansiensis* that is now unfortunately lost (Butler and Zhao 2009). Its apex was not completely freed from the matrix at the time of its description, and the whole tooth did not appear significantly enlarged apicobasally (Hou 1977, Figure 1). A posterior increase in the size of premaxillary tooth crowns is also observed in *Prenocephale prenes* (Figure 3(e), Maryanska and Osmolska 1974, pl. 23.1C) and in the primitive ceratopsian *Yinlong downsi* (Figure 3(b), Han et al. 2015, fig. 21A).

(3) The presence of a premaxilla-lacrimal contact (#17) is shared by *Heterodontosaurus tucki* (Norman et al. 2011, Figure 8), *Tianyulong confuciusi* (Sereno 2012, p. 55), psittacosaurids (Sereno 2010, fig. 2.3, 2.7) and *Yinlong downsi* (Xu et al. 2006 #34; Han et al. 2015, Figure 8(b)).

(4) Another potentially important synapomorphy of Marginocephalia is an anterior midline contact between both maxillae that prevents the vomer from contacting the premaxillae (#29, Figure 4). As discussed above, a slightly different version of this character was already identified as a synapomorphy for Marginocephalia by Sereno (2000). It is actually observed in nearly all marginocephalians – with the possible exception to the basal ceratopsian *Yinlong downsi* in which this midline contact is dubious and possibly absent. A midline exclusion of the anterior vomeral head from the paired premaxillae is apparent in the pachycephalosaurs *Goyocephale lattimorei* (Perle et al. 1982, pl. 41.3B), *Prenocephale prenes* and *Stegoceras validum* (Figure 4(d), Maryanska and Osmolska 1974, fig. 1A3, C3), but also in the ceratopsians *Liaoceratops yanzigouensis* (Figure 4(c), Xu et al. 2002, Figure 1(d)). In *Heterodontosaurus tucki*, the vomer would intercede in the complex interlocking joint prior to an intermaxillary contact, at a level dorsal to the ventral premaxillary branches, so a premaxillary-vomeral contact would be absent (Figure 4(b), see also Norman et al. 2011, p. 204, fig. 10, 11). In *Psittacosaurus major*, 'the vomer attaches to the dorsal surface of the maxillary symphysis' so we infer that there is a maxillary symphysis that prevents the vomer from contacting the premaxillae (You et al. 2008, p. 190). In *Y. downsi*, Han et al. (2015, p. 11) observes that 'the diamond-shaped rostral part of the vomers underlies and intercedes a short distance between the premaxillae at the rear of the premaxillary palate'. They further mention that 'the medial aspect of the articular peg [of maxilla] extends medial to the body of the maxilla; its surface is striated for articulation with either the vomer or contralateral maxilla' (Han et al. 2015, p. 12). They add that the intermaxillary contact is not visible in ventral view but could have occurred 'deep to the vomer' (Han et al. 2015, p. 12). This description recalls the complex interlocking contact of the vomeral head posteriorly with the short intermaxillary suture in *H. tucki*, which is only visible from a sagittal section but not from a mere ventral view (Figure 4(b)). There remains a possibility that the vomeral contact of *Y. downsi* resembles that of *H. tucki*, although this cannot be ruled out from the available descriptions.

(5) *Heterodontosaurus tucki* (Norman et al. 2011, appendix 3A, 4A-B), *Manidens condorensis* (Pol et al. 2011, Figure 2(a–b)), *Yinlong downsi* (Han et al. 2015, fig. 3(a), 5(a), 8(a)), *Psittacosaurus major* (You et al. 2008, Figure 1(b)), *Wannanosaurus yansiensis, Prenocephale prenes,*

Stegoceras validum, Homalocephale calathocercos (Maryanska and Osmolska 1974, fig. 1A4, C4, D4), *Goyocephale lattimorei* (Perle et al. 1982, pl. 42.1), *Pachycephalosaurus wyomingensis* (Brown and Schlaikjer 1943, pl. 39), all have squamosals with a varyingly developed dorsolateral overhang (#69, Figure 5(b,c,e)). Such a lateral overhang seems to have been reduced convergently and might have expanded down to the quadrate cotylus in basal neoceratopsians *Archaeoceratops oshimai* (Dong and Azuma 1997, Figure 2(a); You and Dodson 2003, Figure 1(e)) and *Liaoceratops yanzigouensis* (Xu et al. 2002, Figure 1(a,c)).

(6) The squamosal is high and its posterodorsal margin is set away from the quadrate cotylus (#70, Figure 5) in *Heterodontosaurus tucki* (Norman et al. 2011, Appendix 3A, 4A-B), *Manidens condorensis* (Pol et al. 2011, Figure 2(a–b)), *Yinlong downsi* (Han et al. 2015, fig. 3(a), 8(a)), *Archaeoceratops oshimai* (Figure 5(d), You and Dodson 2003, Figure 1(a,c)), *Liaoceratops yanzigouensis* (Xu et al. 2002, Figure 1(a,b)), *Wannanosaurus yansiensis* (Butler and Zhao 2009, Figure 5(c)), *Prenocephale prenes, Homalocephale calathocercos, Stegoceras validum* (Figure 5(e), Maryanska and Osmolska 1974, fig. 1A4, C4, D4), *Pachycephalosaurus wyomigensis* (Brown and Schlaikjer 1943, pl. 39). Note that the squamosal-quadrate articulation is set close to the posterodorsal border of the squamosal in psittacosaurids (Figure 5(c), You et al. 2008; Sereno 2010, fig. 2.7).

(7) The angular reaches the dorsal margin of the mandibular ramus (#157, Figure 6) in the ceratopsians *Archaeoceratops oshimai* (You and Dodson 2003, Figure 1(a–c); Tanoue et al. 2010, fig. 16.3), *Liaoceratops yanzigouensis* (Xu et al. 2002, Figure 1(a–b)), *Chaoyangsaurus youngi* (Zhao et al. 1999, Figure 2(a)), and the pachycephalosaurs *Heterodontosaurus. tucki* (Figure 6(d), Norman et al. 2011, Fig. 19A), *Manidens condorensis* (Pol et al. 2011, Figure 2(c)), *Tianyulong confuciusi* (Zheng et al. 2009, Figure 1(d)), *Stegoceras validum* (Figure 6(c), Gilmore 1924, pl. 1). In *Yinlong downsi*, the angular reaches the upper mandibular margin in the left side of IVPP V14530 and both sides of IVPP V18636 and IVPP V18686 (Han et al. 2015, fig. 3, 8(a), 11(a) respectively), but not in the right side of IVPP V14530 (Han et al. 2015, Figure 2). In any case, *Y. downsi* is also characterised by a dorsoventrally tall angular as in the aforementioned taxa. The angular is more than half the height of the mandibular ramus but does not reach its upper level in derived psittacosaurids (You et al. 2008, Figure 4; Sereno 2010, fig. 2.7).

(8) Marginocephalians uniquely share the presence of 12 to 13 dorsal vertebrae (#203). This condition was actually reported in the ceratopsians *Archaeoceratops oshimai* (Dong and Azuma 1997, p. 78), *Yinlong downsi* (Han et al. 2018, Figure 2(a)), *Psittacosaurus mongoliensis* (Hailu and Dodson 2004, p. 487), but also in the basal pachycephalosaur *Heterodontosaurus tucki* (Galton 2014, Figure 6(b)).

(9) The marginocephalians *Yinlong downsi* (Han et al. 2018, Figure 5), *Heterodontosaurus tucki* (Galton 2014, Figure 3(a)) and *Stegoceras validum* (Gilmore 1924, pl. 9.1) have elongated and strap-like scapulae, i.e. that is more than nine times as long as its minimum width at the level of the scapular neck (#224, Figure 7(b,d,e)). We shall remark that the scapula is not strap-like in *Psittacosaurus*
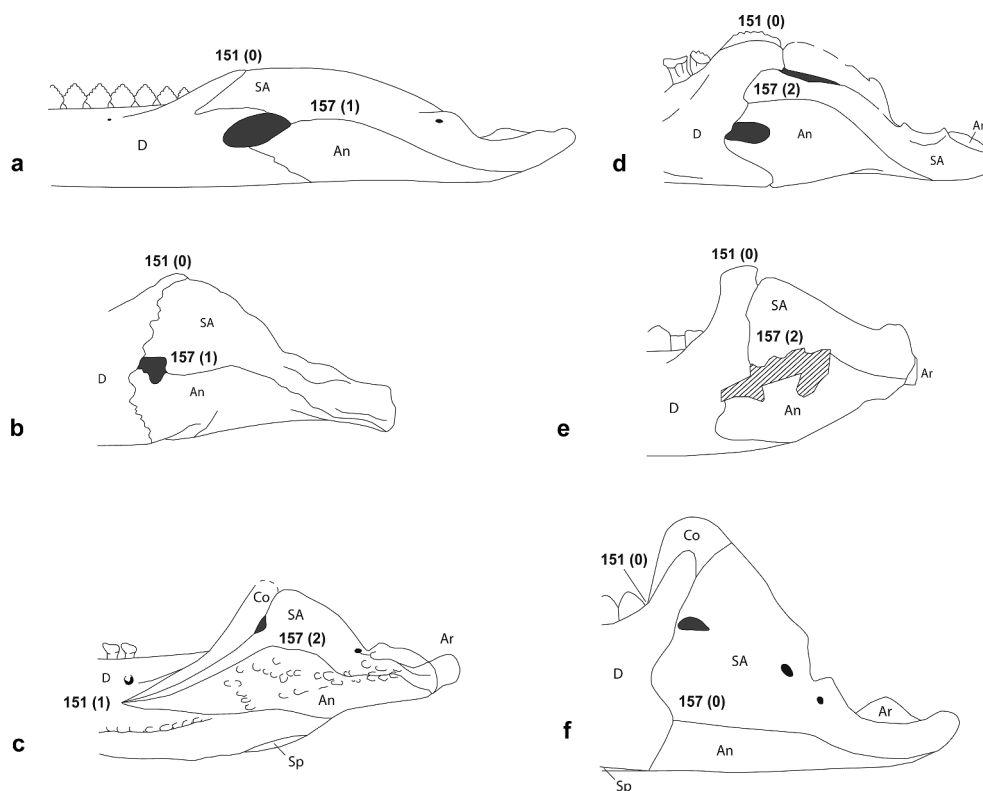
Figure 6. Marginocephalians lower jaws compared to those of other ornithischians in lateral view, with: (a) *Lesothosaurus diagnosticus* (after Sereno, 1991); (b) *Psittacosaurus mongoliensis* (after Sereno 2010); (c) *Stegoceras validum* (after Sues and Galton 1987); (d) *Heterodontosaurus tucki* (after Norman et al. 2011); (e) *Archaeoceratops oshimai* (after Tanoue et al. 2010); (f) *Hypsilophodon foxii* (after Galton 1974a). Abbreviations: An, angular; Ar, articular; Co, coronoid; D, dentary; SA, surangular; Sp, splenial. Not to scale.
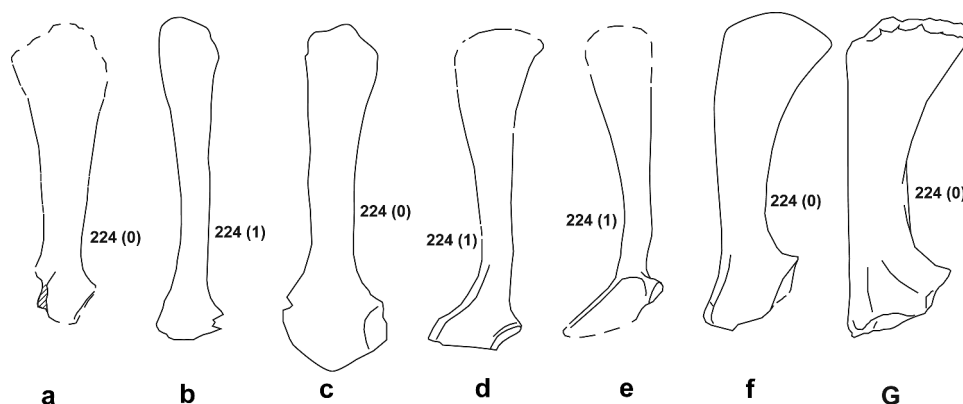

Figure 7. Marginocephalian scapulae (b–e) compared to those of other ornithischians (a, f, g) in lateral view, with: (a) *Lesothosaurus diagnosticus* (after Baron et al. 2016); (b) *Yinlong downsi* (after Han et al. 2018); (c) *Psittacosaurus mongoliensis* (after Slowiak et al. 2019); (d) *Heterodontosaurus tucki* (after Galton 2014); (e) *Stegoceras validum* (after Sues and Galton 1987; reversed)); (f) *Hypsilophodon foxii* (after Galton 1974a); (g) *Tenontosaurus tilletti* (after Forster 1990). Not to scale.

mongoliensis (Senter 2007, Figure 3(j); Slowiak et al. 2019, Figure 4(i)).

(10) The postpubic shaft and prepubic process are widely open and their axes are nearly parallel to each other in all marginocephalians in which this character can be observed (#283, Figure 8). This is notably the case in the ceratopsians *Psittacosaurus mongoliensis* (Figure 8(c), Osborn 1924, Figure 8) and *Yinlong downsi* (Han et al. 2015, Figure 11 (e)), and in the basal pachycephalosaur *Heterodontosaurus tucki* (Figure 8(d), Galton 2014, Figure 12(f–g)). This feature cannot be observed in any other more derived pachycephalosaur. In *Homalocephale calathocercos*, the

postpubic shaft is broken a few millimetres past the articulation with the ischium, but its proximal portion appears extremely reduced (Maryanska and Osmolska 1974, fig. 5A5-8).

(11) As previously suggested by Gilmore (1924), the total absence of an ischial obturator process is an apomorphy of Marginocephalia (#292, Figure 9). The ischium of *Yinlong downsi* has a 'plate-like' distal expansion (Figure 9(b), Han et al. 2018, Figure 11(e,g)), but no real obturator process. *Archaeoceratops oshimai* (Figure 9(c), Dong and Azuma 1997, Figure 7), *Psittacosaurus mongoliensis* (Figure 9(d), Osborn 1924, Figure 8), *Stenopelix valdensis* (Butler
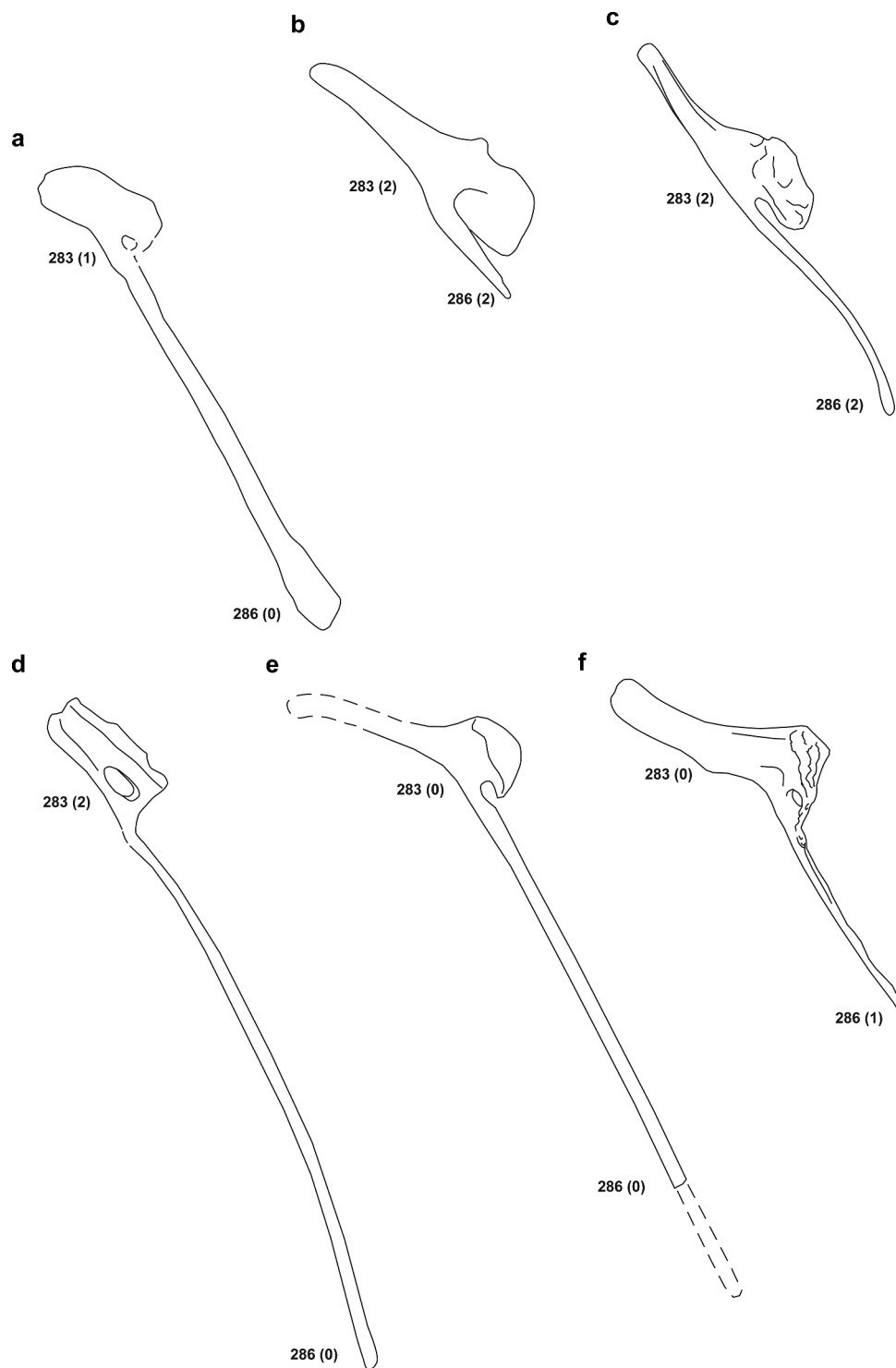
Figure 8. Marginocephalian pubes (b–d) compared to those of other ornithischians (a, e, f) in lateral view, with: (a) *Lesothosaurus diagnosticus* (after Baron et al. 2016); (b) *Archaeoceratops oshimai* (after Dong and Azuma 1997); (c) *Psittacosaurus mongoliensis* (after Osborn 1924); *Heterodontosaurus tucki* (after Galton 2014); *Hypsilophodon foxii* (after Galton 1974a); *Tenontosaurus tilletti* (Forster 1990). Abbreviations: pop, postpubic process; prp, prepubic process; of, obturator foramen; Not to scale.

and Sullivan 2009, Figure 3), *Prenocephale prenes* (Maryanska and Osmolska 1974, pl. 25.3B), *Stegoceras validum* (Figure 9(f), Gilmore 1924, p. 35, pl. 10.3), and also the 'heterodontosaurids' *Heterodontosaurus tucki* (Figure 9(e), Galton 2014, Figure 9(j)) and *Tianyulong confuciusi* (Zheng et al. 2009, supp. info. p. 5) all lack a tab-shaped obturator process.

(12) The main axis of the proximal ischial shaft is parallel to the main axis of the pubic peduncle (#289, Figure 8). This character is reported in *Heterodontosaurus tucki* (Galton 2014, Figure 12(f,g)), *Manidens condorensis* (Pol et al. 2011, Figure 1(a–b)), *Stegoceras validum* (Figure 8(f), Gilmore 1924, Figure 3(a)), *Prenocephale prenes* and *Homalocephale calathocercos* (Maryanska and Osmolska 1974, pl. 25.3B
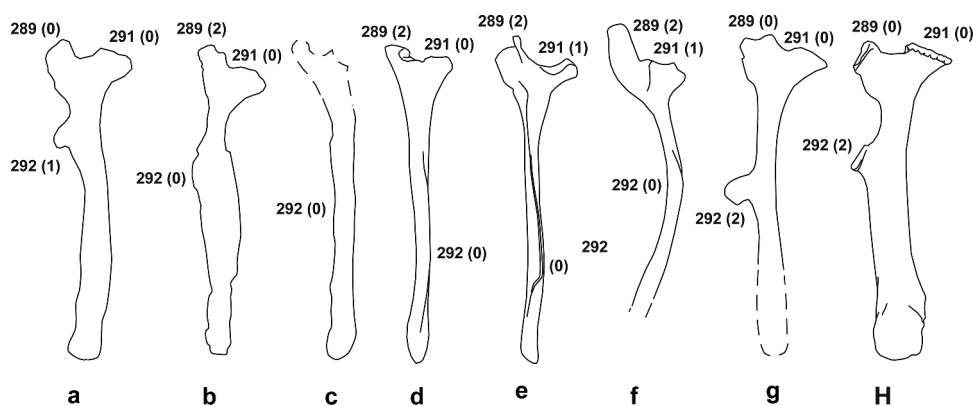
Figure 9. Marginocephalian ischia (b–f) compared to those of other ornithischians (a, g, h) in lateral view, with: (a) *Lesothosaurus diagnosticus* (after Baron et al. 2016); (b) *Yinlong downsi* (after Han et al. 2018); (c) *Archaeoceratops oshimai* (after Dong and Azuma 1997; reversed); (d) *Psittacosaurus mongoliensis* (after Osborn 1924; reversed); (e) *Heterodontosaurus tucki* (after Galton 2014); (f) *Stegoceras validum* (after Gilmore 1924); (g) *Hypsilophodon foxii* (after Galton 1974a); *Tenontosaurus tilletti* (after Forster 1990). Not to scale.

and pl. 29 respectively), *Yinlong downsi* (Figure 9(b), Han et al. 2018, Figure 11(e,g)), *Psittacosaurus mongoliensis* (Figure 9(d), Osborn 1924, Figure 8), and *Stenopelix valdensis* (Butler and Sullivan 2009, Figure 3).

Heterodontosauridae and the origins of Pachycephalosauria

Pachycephalosaurs ('Heterodontosauridae' and Eupachycephalosauria) are grouped together based on the following synapomorphies.

(1) Braincases are rarely observable, unless a sagittal section or a Ct-Scan digital reconstruction is available. In *Heterodontosaurus tucki* (Figure 10(a), Norman et al. 2011, Figure 2(b)) and *Stegoceras validum* (Figure 10(c), Snively and Theodor 2011, Figure 5(b); Bourke et al. 2014, Figure 1 (f)) the ventral margin of the braincase – which follows the inclination of the ventral margin of the laterosphenoid anteriorly – forms an angle of less than 35° with respect to the basioccipital and basisphenoid (#122, Figure 10(a,c)). This angle is steeper in *Psittacosaurus major* (You et al. 2008, Figure 2), *Psittacosaurus lujiatunensis* (Bullar et al. 2019, fig. 20A) and most other non-marginocephalian taxa (Figure 10 (b,d)).

(2) The cervical centra of *Heterodontosaurus tucki* (Galton 2014, Figure 4(a)) decrease in length passing throughout the neck. The same occurs between the isolated anterior and posterior cervical centra of *Fruitadens haagarorum* (Carpenter and Galton 2018, Figure 5(j,l)), and between the cervical centra four and nine of *Pachycephalosaurus wyomingensis* (Bakker et al. 2006, fig. 10(b), 11(b)). Such a posterior decrease is likely synapomorphic to Pachycephalosauria, but given the absence of complete and articulated necks in derived eupachycephalosaurs we coded these taxa as those keeping the same length of cervical centra throughout the neck (#201).

(3) The olecranon fossa is shallow to totally absent (#242, Figure 11) in the humeri of the basal pachycephalosaurs *Fruitadens haagarorum* and *Heterodontosaurus tucki* (Figure 11(c,e), Santa Luca 1980; Galton 2014, Figure 9(s,j)), and in the eupachycephalosaurs *Stegoceras validum* (Figure 11(f), Gilmore 1924, pl. 9.2, p. 34) and *Goyocephale lattimorei* (Perle et al. 1982, pl. 43.4A). In *Wannanosaurus yansiensis*,

both the olecranon and coronoid fossae are only slightly depressed (Butler and Zhao 2009, Figure 8(d)).

(4) The distal end of the radius is mediolaterally more expanded than the ulna, and distally expands without crossing over the distal end of ulna (#245) in *Heterodontosaurus tucki* (Galton 2014, Figure 11(a)), *Tianyulong confuciusi* (Sereno 2012, fig. 27), *Stegoceras validum* (Gilmore 1924, Figure 11(c,d)).

(5) The posterior margins of the iliac peduncle of ischium and proximal main axis of the ischial shaft make an angle equal or inferior to 120° (#291) in *Heterodontosaurus tucki* (Figure 8(e), Galton 2014, Figure 12(g)), *Prenocephale prenes* and *Homalocephale calathocercos* (Figure 8(f), Maryanska and Osmolska 1974, pl. 25.3B, 29.1).

The first phylogenetic definition of Heterodontosaurinae was proposed by Sereno (2012). This subfamily is defined as the most inclusive group containing *Heterodontosaurus tucki* but not *Tianyulong confuciusi*, *Fruitadens haagarorum* and *Echinodon becklesii*, and was also recovered as a valid monophyletic clade in this analysis. Heterodontosaurinae share dental synapomorphies: the tooth crowns of the heterodontosaurines *H. tucki* (Figure 10 (g), Sereno 2012, fig. 55) and *Abrictosaurus consors* (Sereno 2012, fig. 32, 33) are high, parallel-sided (#179, #181) and asymmetrically enamelled (#171). Note that those characters are also present in ceratopsians (Figure 10(f–h), *Yinlong downsi*, Han et al. 2015, fig. 21E; *Chaoyangsaurus youngi*; Zhao et al. 1999, Figure 3(a); Sereno 2010, fig. 1.6A). A posterior maxillary fragment from the Norian of Argentina was referred to cf. *Heterodontosaurus* sp. (CPBA-V-14091a, Báez and Marsicano 2001). The maxillary crowns of this specimen show clear heterodontosaurine and basal ceratopsian affinities, with the presence of parallel-walled mesiodistal crown edges and the absence of a cinculum. This specimen is possibly associated with a caniniform tooth, which would make it more akin to some kind of basal pachycephalosaur. CPBA-V-14091a is tentatively referred to as Heterodontosaurinae indet.

The non-heterodontosaurine 'heterodontosaurids' *Fruitadens haagarorum* (Butler et al. 2012), *Tianyulong confuciusi* (Zheng et al. 2009) and *Echinodon becklesii* (Owen 1858) share with eupachycephalosaurs the following cranial and postcranial synapomorphies:
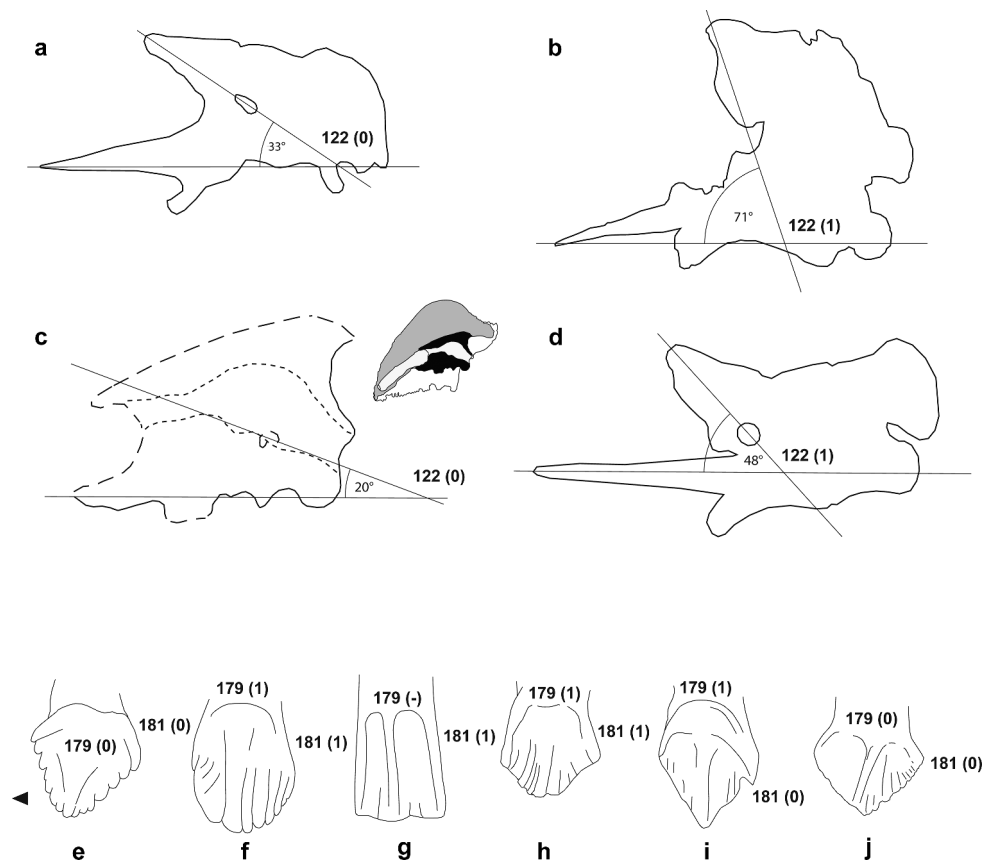
Figure 10. Pachycephalosaurian braincases in lateral view (a–d) and maxillary teeth in labial view (e–j) compared to those of other ornithischians, with: (a) *Heterodontosaurus tucki* (after Norman et al. 2011); (b) *Psittacosaurus major* and *P. lujiatunensis* (after You et al. 2008; Bullar et al. 2019); *Stegoceras validum* (after Bourke et al. 2014); (e) *Hypsilophodon foxii* (after Galton 1974a); (e) *Lesothosaurus diagnosticus* (after Sereno, 1991); (f) *Psittacosaurus major* (after Sereno 2010); (g) *Heterodontosaurus tucki* (after Norman et al. 2011); (h) *Yinlong downsi* (complete reconstruction after Han et al. 2015); (i) *Tianyulong confuciusi* (after Sereno 2012); (j) *Stegoceras validum* (after Sues and Galton 1987). Not to scale.

(1) The anterior maxillary tooth row is not medially deflected anteriorly and is aligned with the posterior premaxillary teeth (#165, Figure 4) in *Fruitadens haagarorum* (Butler et al. 2012, Figure 7(c,d)), *Echinodon becklesii* (Sereno 2012, fig. 12, 13), *Stegoceras validum, Prenocephale prenes* (Figure 4(d), Maryanska and Osmolska 1974, fig. 1A3, C3) and *Goyocephale lattimorei* (Perle et al. 1982, pl. 41.3).

(2) *Echinodon becklesii* (Galton 1978, Figure 1(d)) and *Tianyulong confuciusi* (Zheng et al. 2009) share with the eupachycephalosaurs *Wannanosaurus yansiensis* (Butler and Zhao 2009, Figure 7(a)) and *Stegoceras validum* (Figure 6(c), Gilmore 1924, pl. 1; Sues and Galton 1987, Figure 1(a)) the presence of a ventrolaterally extending branch of the coronoid bone that reaches a level ventral to the last dentary teeth (#151). This feature is absent in *Heterodontosaurus tucki* (Figure 6(d), Norman et al. 2011, fig. 16).

(3) The teeth of non-heterodontosaurine 'heterodontosaurids' are triangular, 'palmate' (#179, #181, Figure 10(i,j)) and uniformly enamelled on both sides (#171) (Galton 1978, p. 143; Sereno 2012; Butler et al. 2012), as in eupachycephalosaurs (e.g. Butler and Zhao 2009, Figure 1(b,e), 7(c)).

(4) A continuous tooth wear is not developed in non-heterodontosaurine pachycephalosaurs (#168, e.g. Butler et al. 2012, p. 11), so their food processing was probably limited to simple puncture crushing of ingesta (Button and Zanno 2020, p. 4).

(5) Sereno (2000, p. 482) had already listed the extremely short forearm – i.e. with a humerus forming less than half the length of the femur – as a pachycephalosaurian characteristic (#233, Figure 11(f)). However, extreme shortening of the forelimb was also found in *Tianyulong confuciusi* (Zheng et al. 2009), so this character might, in fact, characterise non-heterodontosaurine pachycephalosaurs.

(6) The postpubis of *Tianyulong confuciusi* is extremely reduced (#286, Zheng et al. 2009, supp. info. p. 5). The only pubis known in a eupachycephalosaur so far is that of *Homalocephale calathocercos*. Although it is unfortunately broken, its preserved portion indicates that its postpubis might have been strongly reduced and splint-like (Maryanska and Osmolska 1974, Figure 5(a), pl. 29.2).

(7) The distal fibular end of *Tianyulong confuciusi* (Zheng et al. 2009, p. 6) and *Stegoceras validum* (the only pachycephalosaur preserving a fibula, cf. Gilmore 1924, pl. 11.2) is splint-like (#317).

Ornithopod relationships

An early ornithopod radiation consistent with the fossil record

The dryomorph *Callovosaurus leedsi*, from the Callovian of England (Ruiz-Omeñaca et al. 2007), has long been regarded as the oldest ornithopod. Other dryosaurids are represented in the Late Jurassic Morrison Formation of United States (e.g. Carpenter
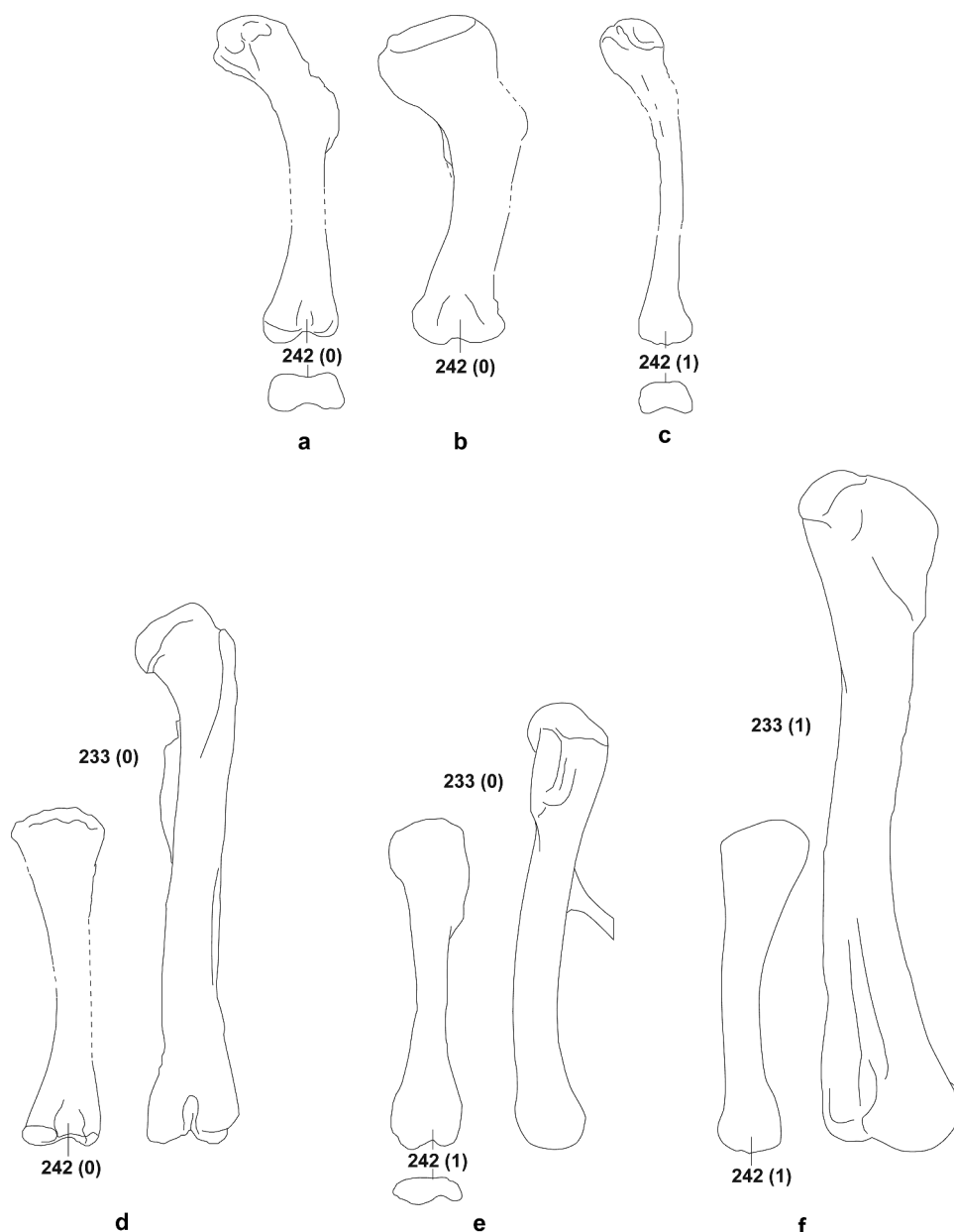
Figure 11. Pachycephalosaurian humeri (c, e–f) compared to those of other ornithischians (a, b, d). Humeri are shown in posterior, and posterior and distal views (a, c, e) with their associated femora when available (d–f), with: (a) *Yinlong downsi* (after Han et al. 2018); (b) *Psittacosaurus mongoliensis* (after Senter 2007; reversed); (c) *Fruitadens haagarorum* (after Butler et al. 2012); (d) *Lesothosaurus diagnosticus* (after Baron et al. 2016; reversed); (e) *Heterodontosaurus tucki* (after Galton 2014; reversed); (f) *Stegoceras validum* (after Gilmore 1924; reversed). Humeri and femora set proportionally to each other by specimen, all humeri without scale and set to the same length.

and Galton 2018), Tendaguru Formation of Tanzania (Janensch 1955; Galton 1981) and Lourinhã Formation of Portugal (Rotatori et al. 2020). The Late Jurassic Morrison Formation has also yielded the basal ornithopod *Nanosaurus agilis* and the Iguanodontia *Camptosaurus* spp. More primitive ornithopods are mostly recovered later during the Cretaceous. Our setting of 'heterodontosaurids' as basal members of Marginocephalia throws the ornithopod origins back to the earliest stages of the Jurassic (Figure 1). Although increasing the ghost lineage of every non-iguanodontian ornithopods, this result is coherent with the previous contention that the ornithopod radiation was more ancient than the Late Jurassic 'burst' of dryomorph forms (e.g. Weishampel and Heinrich 1992; Mcdonald et al. 2010; Boyd 2015). *Kulindadromeus zabaikalicus*, from the Bathonian of Siberia (Cincotta et al. 2019) is regarded as a non-clypeodont basal

ornithopod (Figure 2). The early age of this taxon is coherent with our new tree topology, and conforts the polarity of ornithopod characters found in earlier works (Butler et al. 2008; Mcdonald et al. 2010; Dieudonné et al. 2016; Rozadilla et al. 2019). The basal position of *Kulindadromeus zabaikalicus* is partly supported by its retention of a very slender and ventrally directed ischial peduncle of ilium (#275, Godefroit et al. 2014, fig. S7A). This character is plesiomorphic for neornithischians (e.g. *Hexinlusaurus multidens*, He and Cai 1984, fig. 17), but is absent in most ornithopods (e.g. *N. agilis*, Carpenter and Galton, 1018, Fig. 15A; *Hypsilophodon foxii*, Galton 1974a, fig. 50A).

Problematic basal ornithopod relationships

Orodrominae was defined by Brown et al. (2013) as 'all thescelosaurids [or ornithopods, cf. Supplemental material 5] more closely
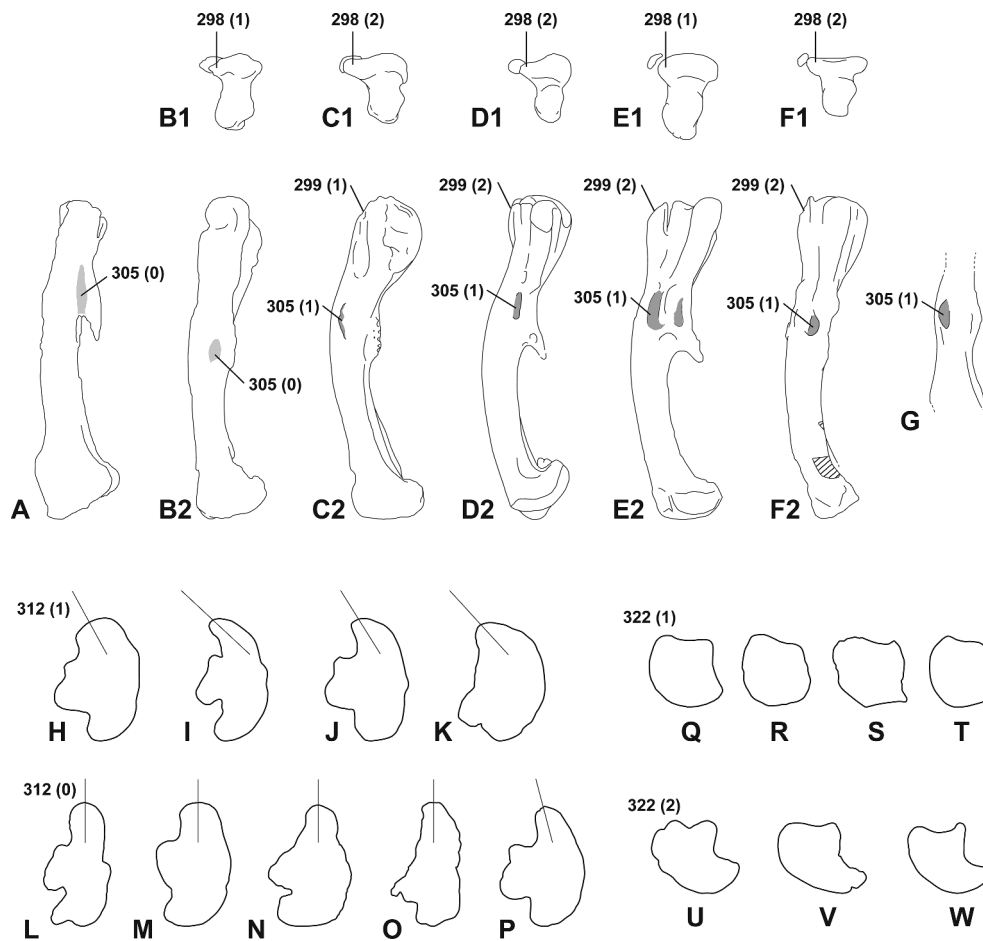
Figure 12. Polarisation of some ornithopodan and basal iguanodontian features on their femora, tibiae and calcanei. Femora in proximal (top) and medial (down) views, with: (a) *Convolosaurus marri* (after Andrzejewski et al. 2019); (b) *Thescelosaurus assiniboiensis* (after Brown and Druckenmiller 2011); (c) *Kangnasaurus coetzeei* (after Cooper 1985); (d) *Anabisetia saldiviai* (after Coria and Calvo 2002; Cambiaso); (e) *Dryosaurus altus* (after Carpenter and Galton 2018); (f) *Eousdryosaurus nanoallucis* (after Escaso et al. 2014); (g) *Elrhazosaurus nigeriensis* (after Galton, 2009). Tibiae in proximal view with: (h) *Hyosilophodon foxii* (after Galton 1974a); (i) *Camptosaurus aphanoecetes* (after Carpenter and Wilson 2008); (j) *Dysalotosaurus lettowvorbecki* (after Janensch 1955); (k) *Draconyx loureiroi* (after Mateus and Antunes 2001); (l) *T. assiniboiensis* (after Brown and Druckenmiller 2011); (m) *C. marri* (after Andrzejewski et al. 2019); (n) *Tenontosaurus tilletti* (after Forster 1990); (o) *Talenkauen santacrucensis* (after Rozadilla et al. 2019); (p) *A. saldiviai* (after Cambiaso 2007). Calcanei in lateral view, with: (q) *H. foxii* (after Galton 1974a); (r) *C. marri* (after Andrzejewski et al. 2019); (s) *T. tilletti* (after Tennant 2013); (t) *T. assiniboiensis* (after Brown and Druckenmiller 2011); (u) *E. nanohallucis* (after Escaso et al. 2014); (v) *T. santacrucensis* (after Rozadilla et al. 2019); (w) *D. lettowvorbecki* (after Janensch 1955). Not to scale. N.B.: each bone was subjected to mirror effect whenever necessary so that only right femora, left tibiae and left calcanei are observed for ease of observation.

related to *Orodromeus makelai* Horner and Weishampel, 1988 than to *Thescelosaurus neglectus* Gilmore, 1913′. This subfamily was here recovered at the base of Clypeodonta and comprises *O. makelai, Zephyrosaurus schaffi* and *Koreanosaurus boseongensis*. Orodrominae is unambiguously supported by the presence of an anterolateral boss on the maxilla (#31, Scheetz 1999, Figure 5; Sues 1980, Figure 3(a)), and the presence of subparallel dorsoventral margins of the jugal maxillary process (#86, Scheetz 1999, Figure 4; Sues, 1980, Figure 8). *Koreanosaurus boseongensis* might bear a closer relationship with *O. makelai* on account of its ventrally keeled cervical vertebrae (#199, Scheetz, fig. 11–12, Huh et al. 2010, p. 6), but this character is also widespread and found in an array of more derived ornithopod forms, including elasmarians (e.g. Cambiaso 2007, fig. 99). Evidence supporting the orodromine affinity of *K. boseongensis* is rather poor.

Gasparinisaura cincosaltensis was originally defined as a member of Elasmaria (Coria and Salgado 1996; Rozadilla et al. 2016, 2019). *G. cincosaltensis* actually shares some derived characters with basal iguanodontians and elasmarians, including:

(1) The presence of low and poorly developed cervical neural spines up to their posteriormost cervical vertebrae (#195; Coria and Salgado 1996; Cambiaso 2007, fig. 56A), as also observed in *Dryosaurus altus* (Carpenter and Galton 2018, fig. 29B), *Camptosaurus dispar* (Carpenter and Galton 2018, fig. 14), *Orodromeus makelai* (Scheetz 1999, Figure 12(a)), and the elasmarians *Mahuidacursor lipanglef* (Cruzado-Caballero et al. 2019), *Talenkauen santacrucensis* (Rozadilla et al. 2019, Figure 13(c,d)), *Macrogryphosaurus gondwanicus* (Calvo et al. 2007, Figure 3) and *Anabisetia saldiviai* (Cambiaso 2007, p. 215, fig. 99). Cervical neural spines are taller and more prominent in the posterior part of the neck in *Tenontosaurus tilletti* (Forster 1990, Figure 1), *Hypsilophodon foxii* (Galton 1974a, fig. 19), *Thescelosaurus neglectus* (Galton 1974b, pl. 3.3), *Convolosaurus marri* (Andrzejewski et al. 2019, Figure 13 (b)), and *Zalmoxes robustus* (Weishampel et al. 2003).

(2) The presence of three manual phalanges on its third finger (#256; Cambiaso 2007, fig. 65), as in *Tenontosaurus tilletti*
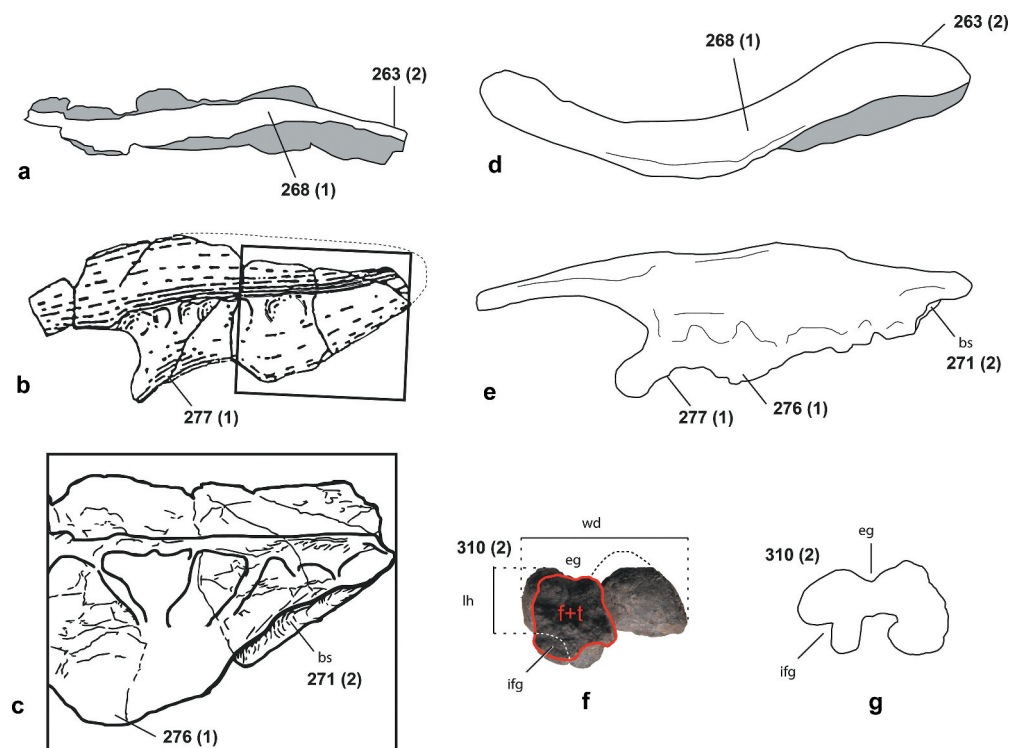
Figure 13. Rhabdodontomorphans features and synapomorphies. (a–c): right ilium of *Muttaburrasaurus langdoni* (QM F6140) in dorsal view (a) and medial views ((b), original sketch from Bartholomai and Molnar 1981; (c) close-up of postacetabular process); (d–e): left and right ilium of *Zalmoxes shqiperorum* (after Godefroit et al. 2009) in dorsal (d) and medial ((e), reversed) views; (f) right femur of the Vegagete ornithopod (MDS-VG, 135) in distal view, with fibula and tibia stuck to the distal lateral condyle; (g) right femur of *Fostoria dhimbangunmal* in distal view (after Bell et al. 2019). N.B.: Line drawing in (a) and (c) were made-up from original photographs of *Muttaburrasaurus'* ilium (QM F6140). Abbreviations: bs, brevis shelf; eg, extensor groove; f + t, fibula and tibia stuck to the distal extremity of femur; ifg, *iliofibularis* groove; lh, lateral height without distolateral condylid; wd, distal width. Not to scale.

(Forster 1990, fig. 14B), *Camptosaurus dispar* (Carpenter and Galton 2018, fig. 23B) and *Iguanodon bernissartensis* (Norman 1980, fig. 60). More basal ornithopods have usually four phalanges (e.g. *Convolosaurus marri*, Andrzejewski et al. 2019, fig. 20). Note that the phalangeal series of the third finger is incompletely known in dryosaurids, elasmarians or rhabdodontids.

(3) The presence of an extremely elongated greater trochanter of femur (#298, Salgado et al. 1997, fig. 4.3) is shared with *Orodromeus makelai* (Scheetz 1999, fig. 28B) but also with *Eousdryosaurus nanohallucis* (Escaso et al. 2014, Figure 4(e)) and elasmarians (Rozadilla et al. 2016, Figure 3). This character is regarded as an unambiguous synapomorphy of the clade formed by *E. nanohallucis* and Elasmarians (see below).

Gasparinisaura cincosaltensis is here recovered as a basal, non-iguanodontian ornithopod probably because of its retention of an array of basal features such as the lack of extensor groove on its distal femur (Coria and Salgado 1996). Our strict consensus tree recovers *G. cincosaltensis* and *Parksosaurus warreni* within a monophyletic 'Hypsilophodontidae' (Figure 2), a clade that was for a long time deemed invalid (Galton 1981; Butler et al. 2008). The taxa included within this family form a fragile and dubious grouping, and share the following synapomorphies:

(1) The dorsoventral margins of the dentary converge anteriorly (#145, *Hypsilophodon foxii*, Galton 1974a, Figure 10(a); *Parksosaurus warreni*, 1973, Figure 1; *Gasparinisaura cincosaltensis*, Coria and Salgado 1996, Figure 2). Note that this apomorphy must be carefully regarded because it was found to be under ontogenetic control in more derived

iguanodonts (see Ösi et al. 2012). Note also that although converging anteriorly, the ventral margin of the dentary is straighter in *G. cincosaltensis* and *P. warreni*.

(2) The proximolateral margin of the humerus is straight and aligned with the distolateral margin of the humeral shaft (#239) in *Hypsilophodon foxii* (Galton 1974a, fig. 38D, 39D) and *Gasparinisaura cincosaltensis* (Coria and Salgado 1996, Figure 6(a)). This character is also found in *Orodromeus makelai* (Scheetz 1999, fig. 21A) and dryosaurids (e.g. Galton 1981, fig. 6(b), 7(c)).

(3) The pre-acetabular process of the ilium is smoothly curved anteriorly without any break in slope (#262, *Hypsilophodon foxii*, Galton 1974a, fig. 46–48; *Gasparinisaura cincosaltensis*, Coria and Salgado 1996, Figure 7; *Parksosaurus warreni*; Parks 1926, Figure 9). This character is plesiomorphic for Ornithopoda and is also found in *Nanosaurus agilis* (Carpenter and Galton 2018, fig. 15E), *Jeholosaurus shangyuanensis* (Barrett and Han 2009, Figure 4(c)) and *Haya griva* (Makovicky et al. 2011, Figure 3).

(4) The second metatarsal is proximally slender with respect to the third metatarsal (#328) in *Hypsilophodon foxii* (Galton 1974a, fig. 57H) and *Gasparinisaura cincosaltensis* (Salgado et al. 1997, fig. 5.5–6). This character is also a synapomorphy of the clade comprising Elasmaria and *Eousdryosaurus nanohallucis* (cf. below). Although the second metatarsal of *H. foxii* is mediolaterally narrow, it is wider than that of *G. cincosaltensis* and elasmarians with respect to their third metatarsal (e.g. Rozadilla et al. 2016, Figure 5(a)).

The Argentinian ornithopod *Gasparinisura cincosaltensis* and the Canadian ornithopod *Parksosaurus warreni* fall within the

family Parksosauridae *sensu* Boyd (2015). Among other characters, they share the following outstanding synapomorphies:

(1) The lower margin of their infratemporal fenestra ends at a level lower than the ventral margin of the orbit (#4, Galton 1973, Figure 1; Coria and Salgado 1996, Figure 2).

(2) The ventral extent of the jugal wing (consisting in both the posterior process of the jugal and the quadratojugal) contacts the quadrate well above the distal quadrate condyles/quadratomandibular joint (#81, Galton 1973, Figure 1; Coria and Salgado 1996, Figure 2).

(3) The quadratojugal is like a 'T' rotated clockwise to 90°, with a pronounced angle between its anterior and dorsal branches (#97, Galton 1973, Figure 1; Coria and Salgado 1996, Figure 2).

(4) Their mid-caudal chevrons are strongly asymmetrically expanded distally (#218, Parks 1926, pl. 11; Coria and Salgado 1996, fig. 15). Note that this feature is also typically found in Elasmaria (e.g. Cruzado-Caballero et al. 2019) and *Convolosaurus marri* (Andrzejewski et al. 2019, fig. 17B).

The North American iguanodontian Tenontosaurus and its relatives

In spite of its larger size, *Tenontosaurus* has long been interpreted as more similar to a large *Hypsilophodon* in functional terms than to a small *Iguanodon* (Dodson 1980; Winkler et al. 1997, p. 346). Calvo et al. (2007) placed *Thescelosaurus* and *Tenontosaurus* as a close paraphyletic grouping near the base of Iguanodontia. *Tenontosaurus* was subsequently placed closer to Dryomorpha (Han et al. 2012; Dieudonné et al. 2016; Bell et al. 2019). *Convolosaurus marri* is a new ornithopod from the Aptian of the Twin-Mountain Formation in North America (Andrzejewski et al. 2019) and was at first interpreted as very close to *Hypsilophodon* (Winkler et al. 1988). The present phylogenetic analysis recovers *Thescelosaurus, Convolosaurus* and *Tenontosaurus* as successive sister taxa stemming from a long ghost lineage close to the base of Iguanodontia (Figure 2).

The positioning of *Tenontosaurus* at the base of Iguanodontia (in the sense of Madzia et al. 2018) is supported by its retention of plesiomorphic characters that were lost in other iguanodonts. These characters are as follows:

(1) The posterolateral premaxillary branch of *Tenontosaurus tilletti* does not contact the prefrontal (#30, Thomas 2015, Figure 2) as in *Hypsilophodon foxii* (Galton 1974a, Figure 3). By contrast, this branch contacts the prefrontal in *Dryosaurus* (Galton 1983, Figure 2(a)), *Dysalotosaurus lettowvorbecki* (Janensch 1955, Figure 1(a)), *Camptosaurus dispar* (Gilmore 1909, Figure 2), *Iguanodon bernissartensis* (Norman 1980, Figure 2) and *Muttaburrasaurus langdoni* (Bartholomai and Molnar 1981, Figure 1(a)).

(2) The ventral extent of the jugal wing ends only very slightly above the distal quadrate condyles in *Tenontosaurus tilletti* (#81, Thomas 2015, Figure 2) and *Tenontosaurus dossi* (Winkler et al. 1997, Figure 12(b)) as in *Hypsilophodon foxii* (Galton 1974a, Figure 3). In iguanodonts more derived than *Tenontosaurus*, the ventral extent of the jugal wing ends well above those distal quadrate condyles (e.g. *Muttaburrasaurus langdoni*, Bartholomai and Molnar 1981, Figure 1(a); *Dysalotosaurus lettowvorbecki*; Janensch 1955, Figure 1(a); *Iguanodon bernissartensis*, Norman 1980, Figure 2; *Camptosaurus dispar*, Gilmore 1909, Figure 2).

(3) The quadratojugal foramen pierces the central part of the quadratojugal in *Tenontosaurus tilletti* (#100, Thomas 2015,

Figure 2) instead of the anterior quadrate margin as in dryosaurids, *Camptosaurus dispar* (e.g. Carpenter and Lamanna 2015, Figure 13) and *Iguanodon bernissartensis* (Norman 1980, Figure 2). The quadratojugal of *Zalmoxes robustus* is devoid of a foramen (Weishampel et al. 2003, Figure 6(c)).

(4) The main body of the quadrate is leant posteriorly (#102) in *Tenontosaurus tilletti* (Thomas 2015, Figure 2) and also in more primitive ornithopods such as *Hypsilophodon foxii* (Galton 1974a, Figure 3). By contrast, it is vertical in other iguanodonts (*Zalmoxes robustus*, Weishampel et al. 2003, fig. 2(a), 7; dryosaurids and *Camptosaurus dispar*, Carpenter and Lamanna 2015, Figure 13; *Iguanodon bernissartensis*, Norman 1980, Figure 2). It is even anteriorly inclined in *Muttaburrasaurus langdoni* (Bartholomai and Molnar 1981, Figure 1(a)).

(5) The calcaneum of *Tenontosaurus tilletti* lacks a posterodistal 'lip-like' process (#322, Figure 12(s), Tennant 2013, fig. 30D) as in the more basal ornithopods *Hypsilophodon foxii* (Figure 12(q), Galton 1974a, fig. 56A), *Convolosaurus marri* (Figure 12(r), Andrzejewski et al. 2019, fig. 25B), *Thescelosaurus assiniboiensis* (Figure 12(t), Brown and Druckenmiller 2011, fig. 21D). The more derived iguanodonians *Eousdryosaurus nanohallucis* (Figure 12(t), Escaso et al. 2014 Figure 5(m)), *Talenkauen santacrucensis* (12U, Rozadilla et al. 2019, fig. 27C), *Dysalotosaurus lettowvorbecki* (Figure 12(v), Janensch 1955, pl. 14.7A) are characterised by a better-developed posterodistal lip-like process. *Yueosaurus tiantaiensis* is only represented by scarce remains (Zheng et al. 2012). It is recovered as the sister-taxon of *Convolosaurus marrii*, as both share anteroposteriorly expanded chevrons on their mid caudals (#218, Andrzejewski et al. 2019, fig. 17A, B). However, this character is relatively widespread and found in *Gasparinisaura cincosaltensis* (Coria and Salgado 1996), *Tenontosaurus tilletti* (Forster 1990, Figure 5(a–c)), *Macrogryphosaurus gondwanicus* (Rozadilla et al. 2020, Figure 9) and *Camptosaurus dispar* (Gilmore 1909, fig. 19, 20, p. 245).

The basal iguanodontian affinities of Elasmaria

Rozadilla et al. (2016) already listed synapomorphies that characterise elasmarians, including a globular lateral surface of the greater trochanter (#301). Moreover, the sternals of *Mahuidacursor lipanglef* (Cruzado-Caballero et al. 2019) and *Macrogryphosaurus gondwanicus* (Calvo et al. 2007, Figure 6) markedly differ from those of all other ornithopods. These sternals are right-angled triangles closely appressed to each other along their medial edge and along their paired, anteriorly thinning anterior branches. Their posterolateral process is short and does not expand in a separate rod as in *Iguanodon bernissartensis* (#232). In *I. bernissartensis* the sternals are hatched-shaped with a posterolaterally extending process but with a wider semilunar anteromedial margin (Norman 1980, fig. 56). The sternals of *Dryosaurus altus, Camptosaurus dispar, Camptosaurus aphanoecetes, Tenontosaurus tilletti* and *Tenontosaurus dossi* are semi-lunar (Galton 1981, Figure 6(m); Winkler et al. 1997; Dodson and Madsen 1981; Carpenter and Wilson 2008, fig. 18; Carpenter and Galton 2018, fig. 23 N). Sternals are unfortunately not known in other iguanodontians, including rhabdodontids.

Iguanodontia Baur (1891) was recently redefined by Madzia et al. (2018) as *Iguanodon bernissartensis, Dryosaurus altus, Rhabdodon priscus, Tenontosaurus tilletti*, their common ancestors and all of their descendants. According to the present phylogeny and as already proposed by Calvo et al. (2007), Elasmaria are

therefore members of Iguanodontia, based on the following synapomorphies:

(1) *Talenkauen santacrucensis, Tenontosaurus* and dryomorphans share a lack of space between adjacent functional teeth and their alveolar border (#175, Rozadilla et al. 2019, Figure 9; Thomas 2015, fig. 51, 52; Carpenter and Wilson 2008, Figure 5(a,b); Norman 1980, Figure 9).

(2) As in *Tenontosaurus tilletti* (Thomas 2015, Figure 2), *Camptosaurus dispar* (Gilmore 1909, Figure 2), *Dryosaurus* (Galton 1981, pl. 1) and *Iguanodon bernissartensis* (Norman 1980), the external nares of *Talenkauen santacrucensis* are enlarged posteriorly so they would have overlapped the maxilla posteriorly (#22, Rozadilla et al. 2019, Figure 2(c,d)).

(3) A gradual posterior elongation of cervical vertebrae throughout the neck (#201) is found in *Dryosaurus altus* (Carpenter and Galton 2018), *Camptosaurus dispar* (Carpenter and Galton 2018) and elasmarians (Cruzado-Caballero et al. 2019). Posterior cervical centra are not specially lengthened in *Dysalotosaurus lettowvorbecki* (Janensch 1955, pl. 12.10), *Iguanodon bernissartensis* (Norman 1980, fig. 22) and *Tenontosaurus tilletti* (Forster 1990, Figure 1) although the latter is characterised by having increased its number of cervicals from 9 to 12.

Phylogenetic position of Eousdryosaurus

Escaso et al. (2014) placed *Eousdryosaurus nanohallucis* - from the Late Jurassic Lourinhã Formation of Portugal - within the dryosaurid clade, as it shares with the dryosaurids *Elrhazosaurus nigeriensis* (Figure 12(g), Galton and Taquet 1982), *Dryosaurus altus* and *Dysalotosaurus lettowvorbecki* (Fig. 1E2, Galton 1981) the presence of a *caudifemoralis longus* muscle scar that is anteriorly displaced with respect to the fourth trochanter medially (#305, Fig. 12F2). However, this character is also present in the elasmarians *Kangnasaurus coetzeei* (Fig. 12C2, Cooper 1985), *Anabisetia saldiviai* (Fig. 12D2, Coria and Calvo 2002, p. 506, Figure 7(c)) and in the basal camptosaurid *Draconyx loureiroi* (Mateus and Antunes 2001). This character is clearly absent in more massively built ankylopollexians, such as *Camptosaurus aphanoecetes* (Carpenter and Wilson 2008, fig. 30 C, N) or *Iguanodon bernissartensis* (Norman 1980, fig. 68B). The lesser trochanter of *E. nanohallucis* is high and reaches the upper level of the fourth trochanter (#299, Fig. 12F2, Escaso et al. 2014, Figure 4), as also observed in dryosaurids (Fig. 1E2, Galton 1981, Figure 13(c), 14 C, I), *A. saldiviai* (Coria and Calvo 2002, Figure 7), and *Valdosaurus canaliculatus* (Barrett et al. 2011, pl. 1.4), but not in *K. coetzeei* (Fig. 12C2, Cooper 1985, Figure 12(a)), *Morrosaurus antarcticus* (Rozadilla et al. 2016, Figure 2(a)) and *E. nigeriensis* (Galton and Taquet 1982). *Camptosaurus aphanoecetes* is polymorphic for this character (Carpenter and Wilson 2008, fig. 30). In dorsal view, the cnemial crest of the tibia of *E. nanohallucis* projects straight anteriorly (#312, Escaso et al. 2014, Figure 4(m)), as in *A. saldiviai, M. antarcticus* (Figure 12(p), Cambiaso 2007, fig. 49D, 117E), *T. santacrucensis* (Figure 12(o), Rozadilla et al. 2019, fig. 24E), but also other iguanodontians such as *V. canaliculatus* (Barrett et al. 2011, Figure 7(b,h)), *Convolosaurus marri* (Figure 12(m), Andrzejewski et al. 2019, fig. 24I) and *Tenontosaurus tilletti* (Figure 12(n), Forster 1990, fig. 20B). By contrast, the cnemial crest is laterally deflected in *D. altus* (Galton 1981, fig. 16E), *D. lettowvorbecki* (Figure 12(j), Janensch 1955, pl. 14.3C), *D. loureiroi* (Figure 12(k), Mateus and Antunes 2001, Figure 8), and ankylopollexians such as *C. aphanoecetes* (Figure 12(i), Carpenter and Wilson 2008, fig. 31E). We suspect that such a lateral deflection of the cnemial crest is plesiomorphic within

Ornithopoda, as it is also present in *Hypsilophodon foxii* (Figure 12(h), Galton 1974a, fig. 56E), and *Nanosaurus agilis* (Galton and Jensen 1973, Figure 5(b–c)). *E. nanohallucis* retains the plesiomorphic presence of a proximal articular surface on its first metatarsal (#335, Escaso pers. comm.), a feature that is shared with *T. santacrucensis* (Rozadilla et al. 2019, fig. S7E), *A. saldiviai* (Cambiaso 2007, fig. 120B), *Gasparinisaura cincosaltensis* (Cambiaso 2007, fig. 76C), but that had been lost in rhabdodontids (Dieudonné et al. 2016) and ankylopollexians (e.g. *C. dispar*, Carpenter and Galton 2018, fig. 26GG).

In the present phylogeny, *Eousdryosaurus nanohallucis* is the sister-taxon of Elasmaria based on the following synapomorphies:

(1) The greater trochanter of the femur is anteriorly elongated (#298). This character is found in *Eousdryosaurus nanohallucis* (Fig. 12F1, Escaso et al. 2014, Figure 4(e)), *Morrosaurus antarcticus, Anabisetia saldiviai* and *Kangnasaurus coetzeei* (Fig. 12C2, D2, Rozadilla et al. 2016, Figure 3(a–b,g)).

(2) The lateral surface of its second metatarsal is flat to broadly concave for resting against the third metatarsal (#327, Escaso et al. 2014, Figure 6), a primitive condition resulting from a secondary reversion in Elasmaria (e.g. *Kangnasaurus coetzeei*, Cooper 1985, fig. 19; *Morrosaurus antarcticus*, Cambiaso 2007, fig. 52A). A proximal lateral 'step' is observed in the second metatarsal of dryomorphs (e.g. Herne et al. 2018, fig. 32H-I) but also in that of the more basal iguanodontian *Tenontosaurus tilletti* (Forster 1990, fig. 22A). However, the position of *Eousdryosaurus nanohallucis* as rooting Elasmaria remains weakly supported and would certainly be reassessed with the discovery of more complete material.

A re-appraisal of Rhabdodontomorpha

Bartholomai and Molnar (1981) proposed a close relationship of *Muttaburrasaurus langdoni* with ankylopollexians based on the presence of a 'cushion-shaped' ulnare in the latter (#247). Dieudonné et al. (2016) included *M. langdoni* and rhabdodontids within a node-based Rhabdodontomorpha. Recently, Herne et al. (2019) and Bell et al. (2019) again suggested a closer affinity of *M. langdoni* with basal ankylopollexians than with rhabdodontids, thus querying the validity of Rhabdodontomorpha. This clade was redefined by Madzia et al. (2020) as the least inclusive group comprising *Rhabdodon priscus* but not *Iguanodon bernissartensis*, and find *M. langdoni* within Ankylopollexia.

Indeed, However, the present phylogenetic analysis supports the monophyly of Rhabdodontomorpha, which we regard as a node-based clade following its original definition (Dieudonné et al. 2016). Rhabdodontomorpha is supported by the following synapomorphies:

(1) The outline of the dorsal iliac margin is sigmoidal in dorsal view, with the postacetabular process deflected medialward and the pre-acetabular process deflected laterally (#263, Figure 13(a,d), Weishampel et al. 2003, fig. 22C; Godefroit et al. 2009, Figure 13(a–b), 18C).

(2) As previously mentioned (Dieudonné et al. 2016), the dorsal iliac margin of *Muttaburrasaurus langdoni* is mediolaterally broader and swollen from above the ischiac peduncle anteriorly (#268, Figure 13(a)) and that of *Zalmoxes robustus* and *Zalmoxes shqiperorum* is mediolaterally swollen from above the postacetabular process all along (Figure 13(d), Weishampel et al. 2003, fig. 22C; Godefroit et al. 2009, Figure 13(a,b)). Such a broadening over the dorsal iliac margin is quite unique among ornithopods.

(3) The brevis shelf was never described in any rhabdodonto-morph. Yet, *Muttaburrasaurus langdoni* (Figure 13(c)) and *Zalmoxes shqiperorum* (Figure 13(e), Godefroit et al. 2009, fig. 18B) share the presence of a weak, dorsally convex ridge on the ventromedial side of their postacetabular process. We refer this ridge to a vestigial brevis shelf. Such a weak ridge might characterise the brevis shelf of every rhabdodonto-morphs (#271).

(4) The ischiac peduncle of the ilium is lenticular and uniquely anteroposteriorly long (#276) in *Muttaburrasaurus langdoni* (Figure 13(c)) and rhabdodontids (Figure 13(e); Weishampel et al. 2003, fig. 22A; Godefroit et al. 2009, fig. 18A-D).

(5) The acetabulum is noticeably low (#277) in *Muttaburrasaurus langdoni* (Figure 13(b), Bartholomai and Molnar 1981, Figure 8(a)), *Zalmoxes shqiperorum* (Figure 13 (e)), Godefroit et al. 2009, fig. 18A-B), *Zalmoxes robustus* (Weishampel et al. 2003, fig. 22A).

The Rhabdodontidae as defined by Sereno (2005) is more inclu-sive than Rhabdodontomorpha as defined by Dieudonné et al. (2016). We stick to the original node-based definition of Rhabdodontidae (Weishampel et al. 2003). The Vegagete ornitho-pod becomes the closest outgroup of this family. The polytomy between *Fostoria dhimbangunmal*, the Vegagete ornithopod and rhabdodontids in the strict consensus (Figure 2) is likely an artefact related to the skeletal incompleteness of these taxa. Indeed, most features characterising the Vegagete ornithopod and rhabdodontids remain unknown in *F. dhimbangunmal*. *F. dhimbangunmal* only shares the following synapomorphies with the Vegagete ornithopod and the rhabdodontid lineage:

(1) A nearly vertical suture between its supraoccipital and opisthotics (#112, Bell et al. 2019, p. 6; Weishampel et al. 2003, Figure 10(b); Godefroit et al. 2009, Figure 4(c,d)); this character is not clearly defined in *Muttaburrasaurus langdoni*.

(2) The length of the distolateral condyle on the distal extremity of femur (not accounting for its posterolateral condylid) is less than 40% the total distal width of the femur (#310) in *Fostoria dhimbangunmal* (Figure 13(g), Bell et al. 2019, Figure 8(e)), the Vegagete ornithopod (Figure 13(f), Dieudonné et al. 2016, fig. 8D2, E2)and all rhabdodontids (Dieudonné et al. 2016, fig. 16). In *Muttaburrasaurus lang-doni* (Bartholomai and Molnar 1981, Figure 9(g)), *Tenontosaurus tilletti* (Forster 1990, fig. 19) and *Camptosaurus aphanoecetes* (Carpenter and Wilson 2008, fig. 30E) the distal femora are mediolaterally broad although their length-to-breadth proportions slightly exceeds 40%.

The templeton test (Supplemental material 6) suggests that *Muttaburrasaurus langdoni* bears some affinities with basal anky-lopollexians, as was previously argued by Herne et al. (2019) and Bell et al. (2019). However, the monophyly of Rhabdodontomorpha is supported by the present analysis. An alternative positioning of the whole clade closer to the base of Ankylopollexia would require the discovery of more common, overlapping skeletal elements between European rhabdodontomorphs and ankylopollexians.

Conclusion

The present phylogenetic analysis recovers 'heterodontosaurids' as basal members of Marginocephalia, forming a paraphyletic lineage at the base of Pachycephalosauria. This hypothesis significantly reduces the ghost lineage for Pachycephalosauria and pulls the ornithopod origins back to the earliest stages of the Jurassic. Basal ornithopod relationships remain poorly resolved. *Tenontosaurus* is found as the basalmost iguanodontian. *Eousdryosaurus nanohallu-cis*, previously included within the dryosaurid clade, is here regarded as the sister-taxon of Elasmaria. The monophyly of Rhabdodontomorpha, in a position more derived than *Tenontosaurus*, is supported by the present analysis.

Disclosure statement

No potential conflict of interest was reported by the authors.

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