

The phylogenetic nomenclature of ornithischian dinosaurs (#60693)

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The phylogenetic nomenclature of ornithischian dinosaurs

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Ornithischians were a large clade of globally distributed Mesozoic dinosaurs, and one of their three major radiations. Throughout their evolutionary history, exceeding 134 millions of years, ornithischians evolved considerable morphological disparity, expressed especially through the cranial and osteodermal features of their most distinguishable representatives. The nearly two-century-long research history of ornithischians has resulted in recognition of numerous diverse lineages, many of which have been named. Following the formative publications establishing the theoretical foundation of the phylogenetic nomenclature throughout the 1980s and in the 1990s, many of the proposed names of ornithischian clades were provided phylogenetic definitions. Some of these definitions have proven useful and have not been changed, beyond the way they were formulated, since their introduction. Some names, however, have been provided multiple definitions, making their application ambiguous. Recent implementation of the *International Code of Phylogenetic Nomenclature (ICPN, or PhyloCode)* offers the opportunity to explore the utility of previously proposed definitions of established taxon names. Since the Articles of the *ICPN* are not to be applied retroactively, all phylogenetic definitions published prior to its implementation remain formally ineffective. Here, we revise the nomenclature of ornithischian dinosaur clades; we revisit 68 preexisting ornithischian clade names, review their recent and historical use, and formally establish their phylogenetic definitions. Additionally, we introduce three new clade names; one for a robustly supported clade of later-diverging ceratopsians and two for clades of advanced nodosaurids. Our study marks the first step towards the formal phylogenetic nomenclature of ornithischian dinosaurs.

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Abstract. Ornithischians were a large clade of globally distributed Mesozoic dinosaurs, and one of their three major radiations. Throughout their evolutionary history, exceeding 134 millions of years, ornithischians evolved considerable morphological disparity, expressed especially through the cranial and osteodermal features of their most distinguishable representatives. The nearly two-century-long research history of ornithischians has resulted in recognition of numerous diverse lineages, many of which have been named. Following the formative publications establishing the theoretical foundation of the phylogenetic nomenclature throughout the 1980s and in the 1990s, many of the proposed names of ornithischian clades were provided phylogenetic definitions. Some of these definitions have proven useful and have not been changed, beyond the way they were formulated, since their introduction. Some names, however, have been provided multiple definitions, making their application ambiguous. Recent implementation of the *International Code of Phylogenetic Nomenclature (ICPN, or PhyloCode)* offers the opportunity to explore the utility of previously proposed definitions of established taxon names. Since the Articles of the *ICPN* are not to be applied retroactively, all phylogenetic definitions published prior to its implementation remain formally ineffective. Here, we revise the nomenclature of ornithischian dinosaur clades; we revisit 68 preexisting ornithischian clade names, review their recent and historical use, and formally establish their phylogenetic definitions. Additionally, we introduce three new clade names; one for a robustly supported clade of later-diverging ceratopsians and two for clades of advanced nodosaurids. Our study marks the first step towards the formal phylogenetic nomenclature of ornithischian dinosaurs.



Keywords: Phylogenetic nomenclature, phylogenetic definition, *PhyloCode*, *International Code of Phylogenetic Nomenclature*, *Ornithischia*, *Dinosauria*.

Introduction


The ornithischian, or ‘bird-hipped’, dinosaurs were a species-rich clade of Mesozoic archosaurs that first appeared in the Trias (e.g., Langer and Ferigolo, 2013; Cabreira et al., 2016; Pacheco et al., 2019; Desojo et al., 2020; Müller & Garcia, 2020) or the earliest Jurassic (Agnolín & Rozadilla, 2018; Baron, 2019) and died out during the Cretaceous/Paleogene extinction event (e.g., Brusatte et al., 2015). Throughout their >134 million-year-long evolutionary history, ornithischians achieved global distribution (Boyd, 2015), evolved considerable taxic diversity (Tennant et al., 2018), and an apparent morphological disparity, expressed through their markedly different body sizes (Benson et al., 2018) and especially the ‘exaggerated’ structures of the crania and osteodermal armor of some of their most distinctive members (Brown, 2017; Stubbs et al., 2019).

Here, we provide a nomenclatural revision of ornithischian dinosaur clades. Following the pivotal, early formative publications establishing the theoretical foundation of the phylogenetic nomenclature in the 1980s and early 1990s (e.g., Ghiselin, 1984; Gauthier, 1986; Rowe, 1987; de Queiroz, 1988; Estes et al., 1988; Gauthier et al., 1988; de Queiroz and Gauthier, 1990, 1992, 1994), many names of the ornithischian clades were provided phylogenetic definitions (e.g., Padian & May, 1993; Currie & Padian, 1997; Sereno, 1998; Sereno, 1999), some of which have proven useful and have not been changed, beyond the way they were formulated, since their introduction.

The implementation of the *International Code of Phylogenetic Nomenclature*, or the *PhyloCode* (de Queiroz & Cantino, 2020), an evolution-based system for naming organisms, hereafter abbreviated and referred to as *ICPN* (accessible at <http://phylonames.org/code/>), and parallel publication of *Phylonoms: A Companion to the PhyloCode* (de Queiroz et al., 2020), offers the opportunity to consider the utility of previously proposed phylogenetic definitions of established taxon names and, in appropriate cases, formalize their use, as specified by the Articles of the *ICPN*.

Recent studies have thoroughly assessed the use of clade names applied to some ornithischian lineages, mostly early-diverging neornithischians and ornithopods (Boyd, 2015; Madzia et al.,

2018; Herne et al., 2019; Madzia et al., 2020). However, the Articles of the *ICPN* are not to be applied retroactively (*ICPN*: Preamble 6, see also Art. 7.1). As such, all these efforts remain formally ineffective in the light of the Code.

We formalize some of the nomenclatural acts of previous studies and introduce phylogenetic definitions for 71 names of ornithischian dinosaur clades. Specifically, we provide formal phylogenetic definitions for the following 68 preexisting taxon names: *Ankylopollexia*,  *Ankylosauria*, *Ankylosauridae*, *Ankylosaurinae*, *Ankylosaurini*, *Aralosaurini*, *Brachylophosaurini*, *Camptosauridae*, *Centrosaurinae*, *Cerapoda*, *Ceratopsia*, *Ceratopsidae*, *Ceratopsoidea*, *Chaoyangsauridae*, *Chasmosaurinae*, *Clypeodonta*, *Coronosauria*, *Dryomorpha*, *Dryosauridae*, *Edmontosaurini*, *Elasmaria*, *Euhadrosauria*, *Euiguanodontia*, *Euornithopoda*, *Eurypoda*, *Genasauria*, *Hadrosauridae*, *Hadrosauriformes*, *Hadrosaurinae*, *Hadrosauroidea*, *Hadrosauroomorpha*, *Heterodontosauridae*, *Huayangosauridae*, *Hypsilophodontia*, *Hypsilophodontidae*, *Iguanodontia*, *Iguanodontidae*, *Jeholosauridae*, *Kritosaurini*, *Lambeosaurinae*, *Lambeosaurini*, *Leptoceratopsidae*, *Marginocephalia*, *Neoceratopsia*, *Neoiguanodontia*, *Neornithischia*, *Nodosauridae*, *Nodosaurinae*, *Ornithischia*, *Ornithopoda*, *Orodrominae*, *Pachycephalosauria*, *Pachycephalosauridae*, *Parasaurolophini*, *Polacanthinae*, *Protoceratopsidae*, *Rhabdodontidae*, *Rhabdodontomorpha*, *Saurolophinae*, *Saurolophini*, *Shamosaurinae*, *Stegosauria*, *Stegosauridae*, *Styracosterna*, *Thescelosauridae*, *Thescelosaurinae*, *Thyreophora*, and *Tsintaosaurini*. These names cover all major ornithischian clades and the vast majority of their subclades for which taxon names were used and defined in the past. Additionally, we introduce three new clade names: *Euceratopsia*, for the well-supported node uniting leptoceratopsid and coronosaur ceratopsians, and *Panoplosaurini* and *Struthiosaurini* for clades of derived nodosaurids.

Institutional abbreviations

CPC, Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo, Mexico; **PASAC**, Paleontological Association of Sabinas, Coahuila, Mexico; **ROM**, Royal Ontario Museum, Department of Natural History, Toronto, Canada; **UTEP**, Centennial Museum and Chihuahuan Desert Gardens, University of Texas at El Paso, Texas, USA; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Methods

Protocol

In order to be formally established under the *ICPN*, clade names must comply especially with the provisions of Articles 7 and 9–11 of the Code (*ICPN*: Art. 7.2d). These Articles are fully followed here. The entries, provided in ‘Phylogenetic nomenclature of ornithischian clades’ below, partly follow the scheme used in *Phylonyms* (de Queiroz et al. 2020); they include the following sub-sections: ‘Definition’, ‘Reference phylogeny’, ‘Composition’, ‘Synonyms’, and ‘Comments’. The sub-sections ‘Diagnostic apomorphies’ and ‘Etymology’, as used in *Phylonyms*, have been omitted. Note that detailed discussion of apomorphies is not strictly required by the Code, and inclusion of a reference phylogeny alone is sufficient (*ICPN*: Art. 9.13). Recent assessments of the phylogenetic relationships of numerous taxa, particularly those nested near the basal neornithischian-ornithopod transition, but also within some major clades, such as ornithopods, currently provide conflicting results (e.g., Norman, 2015; Han et al., 2018; Madzia et al., 2018; Herne et al., 2019; Dieudonné et al., 2020; Barta & Norell, 2021). It is extremely difficult, and perhaps impossible at the moment, to list unambiguous diagnostic apomorphies for many clades that have long been associated with widely-used names, and detailed discussion would be far beyond the scope of the paper. Instead, emphasis was placed on using definitions that are reflective of all currently inferred phylogenies. In turn, ‘Etymology’ was omitted because all but three of the clade names that are established in the present study are preexisting (Art. 6.2 of the *ICPN*). The only reason for discussing the etymological origin of taxon names would be to provide arguments for the inclusion of certain internal specifiers (e.g., within the context of Art. 11.10 of the *ICPN* which specifies that “[...] when a clade name is converted from a preexisting name that is typified under a rank-based code or is a new or converted name derived from the stem of a typified name, the definition of the clade name must use the type species of that preexisting typified name or of the genus name from which it is derived (or the type specimen of that species) as an internal specifier.”). With that respect, relevant comments are provided in the ‘Comments’ sub-section of the name entries. The three new clade names introduced in the present study are provided with their etymologies. Additionally, owing to the fact that the phylogenetic relationships of ornithischian dinosaurs are intensively researched, each clade name entry could be supplemented with numerous reference phylogenies. Rather than list all of the relevant phylogeny reconstructions available, we decided

to refer to a subset of the more recent tree topologies that justify the ‘conversion’ of the taxon name in accordance with the *ICPN*. Similarly, with respect to the clade ‘Composition’, we list only those subtaxa that are included in the primary reference phylogeny. We also realize that the list of taxon names provided in ‘Synonyms’ is not exhaustive and does not list all historically used approximate synonyms. When discussing names that may be considered synonymous with those whose application is preferred here, we have focused especially on those names that have been used for the same or very similar contents in recent years, or those that have been used interchangeably with those that we define (e.g., *Iguanodontidae* and *Iguanodontoidea*, *Thescelosauridae* and *Parksosauridae*). Therefore, long-disused names have been mostly omitted. Further, Article 8.1 of the *ICPN* states that, “[i]n order for a name to be established under [the *ICPN*], the name and other required information must be submitted to the registration database for phylogenetically defined names (see Art. 22.2). A name may be submitted to the database prior to acceptance for publication, but it is given only a temporary registration number at that time. The registration number will become permanent after the author notifies the database that the paper or book in which the name will appear has been published, provides a full reference to the publication, and confirms that the definition in the database is identical to that in the publication”. We have therefore registered all names, whose phylogenetic definitions are established in the present study, to the database of phylogenetically defined names, the *RegNum* (*ICPN*: Art. 22; Appendix A), and obtained registration numbers that are included in the clade name entries. Finally, we follow the *ICPN* in that all scientific names are italicized (*ICPN*: Recommendation 6.1A.) and that names are attributed to the earliest author(s) to spell the name rather than according to the Principle of Coordination (*ICPN*: Note 9.15A.3).

Phylogenetic definitions

The names of ornithischian clades are defined using the following two types of definitions: (a) minimum-clade definition, known previously as ‘node-based’ definition (*ICPN*: Art. 9.5) and (b) maximum-clade definition, known previously as ‘branch-based’ or ‘stem-based’ definition (*ICPN*: Art. 9.6). We refer to the appropriate Articles of the *ICPN* for details.

Adopted conventions for abbreviated definitions. We abbreviate the definitions using the following conventions (as per Notes 9.4.1 and 11.12.1 of the *ICPN*): max = the largest; min = the smallest; ∇ = clade; () = containing; & = and; v = or; ~ = but not (in trivial maximum-clade definitions) or it does not (while using a qualifying clause); | = on the condition that. See also Note 9.6.2 of the *ICPN* for explanation of differences between the use of ‘&’ and ‘v’ in the definitions. Additionally, we apply the set theory symbols \in , that means “belongs to”, and \notin , meaning “not element of”, to indicate that a name is applied *within* or *outside* another clade, respectively (see, e.g., *Euornithopoda*, *Jeholosauridae*, *Orodrominae*, and *Polacanthinae* for some examples).

Selection of specifiers. Specifiers are selected following Art. 11 of the *ICPN*. Numerous names pertaining to ornithischian clades have been informally defined in the past and these definitions can still be considered applicable. We have attempted to formalize most of these definitions, providing only the changes that were necessary to reflect all currently inferred phylogenies and to comply with the Articles of the *ICPN*. However, in some cases we have decided to replace certain specifiers with taxa that we consider to be more appropriate candidates. For example, we have replaced *Parasaurolophus walkeri* Parks, 1922 in some definitions with *Iguanodon bernissartensis* Boulenger in Beneden, 1881 (designated as the type species of *Iguanodon* Mantell, 1825 by the *International Commission on Zoological Nomenclature* [ICZN 2000]), provided that this taxon has always been considered part of the clade (when selected as an internal specifier) or outside the clade (when selected as an external specifier) whose name is being defined. *I. bernissartensis* is known based on multiple complete or near-complete individuals of different ontogenetic stages and is being extensively researched (e.g., Norman, 1980; Verdú et al., 2017). It has also been frequently used as the specifier in previous, informal phylogenetic definitions, and was recently included as the internal specifier of *Dinosauria* (Langer et al., 2020).

Phylogenetic nomenclature of ornithischian clades

For the sake of clarity, all clade names are provided in alphabetical order. The definitions are summarized in **Table 1**. The extent of all clade names is further depicted on **Fig. 1**, that shows

the relationships of the taxa included in the present study as specifiers (both, internal as well as external).

[Table 1 here]

Ankylopollexia Sereno, 1986 [converted clade name]

Registration number: 585

Definition. The smallest clade containing *Camptosaurus dispar* (Marsh, 1879) and *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Camptosaurus dispar* [Marsh, 1879] & *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Madzia et al. (2018), Figure 20 of Verdú et al. (2018), Figure 11 of McDonald et al. (2021), and Figure 9 of Verdú et al. (2021).

Composition. The clade *Ankylopollexia* comprises *Camptosaurus dispar* and members of the clade *Styracosterna*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ankylopollexia* was introduced by Sereno (1986) for a group of ornithopods comprising *Camptosaurus dispar* and taxa more derived than *C. dispar*. Sereno (1998: 62) later (informally) defined the name using the minimum-clade definition and selected *Camptosaurus* and *Parasaurolophus* as the internal specifiers. Since the name has traditionally been used in the exact sense, we apply it to the same clade, but prefer to use *Iguanodon bernissartensis* as the second internal specifier rather than *P. walkeri* because the name *Ankylopollexia* was formed after the stiff cone-shaped thumb that characterizes *Iguanodon*-grade ornithopods. The inclusion of a different internal specifier does not change the extent of *Ankylopollexia* under any of the published phylogeny inferences. Also, even though the name derives from an apomorphy, it was never used for an apomorphy-based clade.

Ankylosauria Osborn, 1923 [converted clade name]

Registration number: 588

Definition. The largest clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Stegosaurus stenops* Marsh, 1887. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ankylosaurus magniventris* Brown, 1908 ~ *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 11 of Arbour and Currie (2016) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Thompson et al. (2012), Figure 1 of Arbour et al. (2016), Figure 3 of Brown et al. (2017), and Figure 26 of Wiersma & Irmis (2018).

Composition. Under the primary reference phylogeny, *Ankylosauria* comprises *Minmi* sp. (= *Kunbarrasaurus ieverisi*), *Mymoorapelta maysi*, and members of the clades *Ankylosauridae* and *Nodosauridae*.

Synonyms. The name *Ankylosauromorpha* Carpenter, 2001 has been recently used under an alternative systematic scheme for the same branch as *Ankylosauria*, as defined herein (Norman, 2021; see ‘Discussion’). No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ankylosauria* has been (informally) defined before (Carpenter, 1997; Sereno, 1998; Sereno, 2005). These definitions were maximum-clade and used *Ankylosaurus* (Carpenter, 1997; Sereno, 1998) or *Ankylosaurus magniventris* (Sereno, 2005) as the internal specifier and *Stegosaurus* (Carpenter, 1997; Sereno, 1998) or *Stegosaurus stenops* (Sereno, 2005) as the external specifier. Since *Ankylosauria* has been ‘traditionally’ used in this sense (though, see also ‘Discussion’), we formalize this definition. Note that Norman (2021) recently provided two phylogenetic definitions for *Ankylosauria*, a maximum-clade and a minimum-clade. In the maximum-clade definition Norman (2021) used *Euoplocephalus* and *Edmontonia* as the internal specifiers and *Scelidosaurus* as the external specifier, while in the minimum-clade definition the use of the name was anchored on *Euoplocephalus* and *Edmontonia*. See ‘Discussion’ for additional comments.

***Ankylosauridae* Brown, 1908 [converted clade name]**

Registration number: 589


Definition. The largest clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Nodosaurus textilis* Marsh, 1889. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ankylosaurus magniventris* Brown, 1908 ~ *Nodosaurus textilis* Marsh, 1889).

Reference phylogeny. Figure 11 of Arbour & Currie (2016) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Thompson et al. (2012), Figure 1 of Arbour et al. (2016), Figure 3 of Brown et al. (2017), Figure 26 of Wiersma & Irmis (2018), and Figure 9 of Zheng et al. (2018).

Composition. Under the primary reference phylogeny, *Ankylosauridae* comprises *Ahshislepelta minor*, *Aletopelta coombsi*, *Cedarpelta bilbeyhallorum*, *Chuanqilong chaoyangensis*, *Gastonia burgei*, *Liaoningosaurus paradoxus*, and members of the clades *Shamosaurinae* and *Ankylosaurinae* (the two taxon names remain formally undefined).

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ankylosauridae* has been (informally) defined before by Sereno (1998, 2005) who used *Ankylosaurus magniventris* as the internal specifier and *Panoplosaurus mirus* as the external specifier. Considering that *Ankylosauridae* has been traditionally used as a sister taxon to *Nodosauridae*, we use a definition that incorporates *Nodosaurus textilis* as the external specifier.

Ankylosaurinae Nopcsa, 1918 [converted clade name] 

Registration number: 590

Definition. The largest clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Shamosaurus scutatus* Tumanova, 1983. This is a maximum-clade definition. Abbreviated definition: $\max \nabla (Ankylosaurus\ magniventris\ Brown,\ 1908 \sim Shamosaurus\ scutatus\ Tumanova,\ 1983)$.

Reference phylogeny. Figure 11 of Arbour and Currie (2016) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Thompson et al. (2012), Figure 1 of Arbour et al. (2016), Figure 8 of Arbour & Evans (2017), Figure 26 of Wiersma & Irmis (2018), and Figure 9 of Zheng et al. (2018).

Composition. Under the primary reference phylogeny, *Ankylosaurinae* comprises *Crichtonpelta benxiensis*, *Pinacosaurus* spp., *Saichania chulsanensis*, *Tarchia kielanae*, *Tsagantegia longicranialis*, *Zaraapelta nomadis*, ‘*Zhejiangosaurus luoyangensis*’, and members of the clade *Ankylosaurini*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ankylosaurinae* was (informally) defined before (Sereno, 1998; Sereno, 2005; Vickaryous et al., 2004). All these definitions were maximum-clade and used *Ankylosaurus* (Sereno, 1998) or *Ankylosaurus magniventris* (Sereno, 2005; Vickaryous et al., 2004) as the internal specifiers and *Minmi paravertebra* and *Shamosaurus scutatus* (Sereno, 1998), *Gargoylesaurus parkpinorum*, *Minmi paravertebra*, and *Shamosaurus scutatus* (Sereno, 2005) or only *Shamosaurus scutatus* (Vickaryous et al., 2004) as the external specifiers. Owing to the dubious taxonomic status of ‘*M. paravertebra*’ (Arbour & Currie, 2016) and non-ankylosaurid affinities of *G. parkpinorum* (e.g., Arbour & Currie, 2016; Rivera-Sylva et al., 2018a; Wiersma & Irmis, 2018; Zheng et al., 2018), we formalize the definition of Vickaryous et al. (2004) in that we use a single external specifier (*Shamosaurus scutatus*).

***Ankylosaurini* Arbour & Currie, 2016 [converted clade name]**



Registration number: 592

Definition. The largest clade containing *Ankylosaurus magniventris* Brown, 1908 but not *Pinacosaurus grangeri* Gilmore, 1933 and *Saichania chulsanensis* Maryńska, 1977. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ankylosaurus magniventris* Brown, 1908 \sim *Pinacosaurus grangeri* Gilmore, 1933 & *Saichania chulsanensis* Maryńska 1977).

Reference phylogeny. Figure 11 of Arbour & Currie (2016) is treated here as the primary reference phylogeny. Additional reference phylogenies include, Figure 1 of Arbour et al. (2016), Figure 8 of Arbour & Evans (2017), Figure 26 of Wiersma & Irmis (2018), and Figure 9 of Zheng et al. (2018).

Composition. Under the primary reference phylogeny, *Ankylosaurini* comprises *Ankylosaurus magniventris*, *Anodontosaurus lambei*, *Dyoplosaurus acutosquameus*, *Euoplocephalus tutus*, *Nodocephalosaurus kirtlandensis*, *Scolosaurus cutleri*, *Talarurus plicatospineus*, and *Ziapelta sanjuanensis*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ankylosaurini* was first (informally) defined by Arbour & Currie (2016) who applied the maximum-clade definition and used *Ankylosaurus magniventris* as the internal specifier and *Pinacosaurus grangeri* and *Saichania chulsanensis* as the external specifiers. The name was used for a clade that largely includes derived North American ankylosaurines, many of which were previously synonymized with *Euoplocephalus tutus* (Arbour & Currie 2013),

although under some topologies the name may be more restricted in its use (Thompson et al., 2012).

***Aralosaurini* Prieto-Márquez et al., 2013 [converted clade name]**

Registration number: 593

Definition. The largest clade containing *Aralosaurus tuberiferus* Rozhdestvensky, 1968 and *Canardia garonnensis* Prieto-Márquez et al., 2013 but not *Lambeosaurus lambei* Parks, 1923, *Parasaurolophus walkeri* Parks, 1922, and *Tsintaosaurus spinorhinus* Young, 1958. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Aralosaurus tuberiferus* Rozhdestvensky, 1968 & *Canardia garonnensis* Prieto-Márquez et al., 2013 ~ *Lambeosaurus lambei* Parks, 1923 & *Parasaurolophus walkeri* Parks, 1922 & *Tsintaosaurus spinorhinus* Young, 1958).

Reference phylogeny. Figure 25 of Prieto-Márquez et al. (2013) is treated here as the primary reference phylogeny. Additional reference phylogeny includes Figure 11 of McDonald et al. (2021).

Composition. Under the primary reference phylogeny, *Aralosaurini* comprises *Aralosaurus tuberiferus* and *Canardia garonnensis*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name was first (informally) defined by Prieto-Márquez et al. (2013) who applied the minimum-clade definition and used *Aralosaurus tuberiferus* and *Canardia garonnensis* as the internal specifiers. Following such definition, however, *Aralosaurini* would cover the entire lambeosaurine branch under some topologies that include both of the internal specifiers (Kobayashi et al., 2019; Prieto-Márquez et al., 2019; Zhang et al., 2019; Kobayashi et al., 2021; Longrich et al., 2021). Recently, however, McDonald et al. (2021) inferred *Aralosaurini* as delimited by Prieto-Márquez et al. (2013). Therefore, we define the name but make it inapplicable under a subset of recent phylogenies.

***Brachylophosaurini* Gates et al., 2011 [converted clade name]**



Registration number: 594

Definition. The largest clade containing *Brachylophosaurus canadensis* Sternberg, 1953 but not *Edmontosaurus regalis* Lambe, 1917, *Hadrosaurus foulkii* Leidy, 1858, *Kritosaurus navajovius*

Brown, 1910, and *Saurolophus osborni* Brown, 1912. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Brachylophosaurus canadensis* Sternberg, 1953 ~ *Edmontosaurus regalis* Lambe, 1917 & *Hadrosaurus foulkii* Leidy, 1858 & *Kritosaurus navajovius* Brown, 1910 & *Saurolophus osborni* Brown, 1912).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Brachylophosaurini* comprises *Acristavus gagslarsoni*, *Brachylophosaurus canadensis*, *Maiasaura peeblesorum*, and *Probrachylophosaurus bergei* (erroneously named ‘*Probrachylophosaurus canadensis*’ in the primary reference phylogeny).

Synonyms. The name *Maiasaurini* Sereno, 2005 is an approximate synonym of *Brachylophosaurini*. To our knowledge, the name was used only in a single recent paper (McFeeters et al., 2021) that attributed the name to Horner (1992). However, this attribution was due to the adherence of the authors to the Principle of Coordination, as Horner (1992) used the name *Maiasaurinae*. Nevertheless, all recent phylogenetic studies consistently use *Brachylophosaurini* (e.g., Freedman Fowler & Horner, 2015; Cruzado-Caballero & Powell, 2017; Xing et al., 2017; Kobayashi et al., 2019; Zhang et al., 2019; Prieto-Márquez et al., 2020; Zhang et al., 2020; Kobayashi et al., 2021; McDonald et al., 2021). No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Brachylophosaurini* has been (informally) defined before (Gates et al., 2011; Freedman Fowler & Horner, 2015). These definitions were maximum-clade and used *Brachylophosaurus*, *Maiasaura*, and *Acristavus* (Gates et al., 2011) or *Brachylophosaurus*, *Probrachylophosaurus*, *Maiasaura*, and *Acristavus* (Freedman Fowler & Horner, 2015) as the internal specifiers and *Gryposaurus* and *Saurolophus* as the external specifiers. The composition of *Brachylophosaurini* and the relationships of the clade to other hadrosaurids have been stable across studies since the introduction of the name. Therefore, using more than one internal specifier is unnecessary. We use a definition that ensures *Brachylophosaurini* does not cover taxa ‘traditionally’ comprised within *Edmontosaurini*, *Kritosaurini*, and *Saurolophini*.

***Camptosauridae* Marsh, 1885 [converted clade name]**

Registration number: 595

Definition. The largest clade containing *Camptosaurus dispar* (Marsh, 1879) but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Camptosaurus dispar* [Marsh, 1879] \sim *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 13 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018) and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Camptosauridae* comprises *Camptosaurus dispar* and *Cumnoria prestwichii*. Under alternative hypotheses, however, *Camptosauridae* includes only a single unequivocal member, *Camptosaurus dispar* (e.g., Madzia et al., 2020: Fig. 12).

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Camptosauridae* was first (informally) defined by Sereno (1998: 62) who used the maximum-clade definition and selected *Camptosaurus* as the internal specifier and *Parasaurolophus* as the external specifier. We prefer to use *Iguanodon bernissartensis* as the external specifier to maintain the ‘node-branch triplet’ (‘node-stem triplet’ of Sereno [1998: 52–54]) comprising *Ankylopollexia*, *Camptosauridae*, and *Styracosterna* (all formally defined in the present paper). The inclusion of a different external specifier does not change the extent of *Camptosauridae* under any of the published phylogeny inferences.

***Centrosaurinae* Lambe, 1915 [converted clade name]**

Registration number: 596

Definition. The largest clade containing *Centrosaurus apertus* Lambe, 1904 but not *Chasmosaurus belli* (Lambe, 1902) and *Triceratops horridus* Marsh, 1889. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Centrosaurus apertus* Lambe 1904 \sim *Chasmosaurus belli* [Lambe, 1902] & *Triceratops horridus* Marsh, 1889).

Reference phylogeny. Figure 10 of Wilson et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 10 of Ryan et al. (2017), Figure 9 of

Chiba et al. (2018), and Figure 13 of Dalman et al. (2018), Figure S1 of Knapp et al. (2018), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Centrosaurinae* comprises *Achelousaurus horneri*, *Albertaceratops nesmoi*, *Avaceratops lammersi*, *Centrosaurus apertus*, *Coronosaurus brinkmani*, *Diabloceratops eatoni*, *Einiosaurus procurvicornis*, *Machairoceratops cronusi*, *Medusaceratops lokii*, *Nasutoceratops titusi*, *Pachyrhinosaurus* spp., *Stellasaurus ancillae*, *Styracosaurus albertensis*, *Styracosaurus ovatus* (?= *Styracosaurus albertensis*; see Holmes et al. [2020]), *Sinoceratops zhuchengensis*, *Spinops sternbergorum*, *Xenoceratops foremostensis*, and *Wendiceratops pinhornensis*.

Synonyms. No other taxon names are currently in use for the same or approximate clade. Although *Ceratops montanus* may fall within the largest clade containing *Centrosaurus apertus* but not *Chasmosaurus belli* and *Triceratops horridus* as well, the name *Ceratopsinae* has not been associated with the same contents as *Centrosaurinae* in the past. Therefore, *Ceratopsinae* is not considered to be an approximate synonym of *Centrosaurinae*. In any case, *C. montanus* does not seem to be diagnostic beyond *Ceratopsidae* at present (Dodson et al., 2004; Mallon et al., 2016).

Comments. The name *Centrosaurinae* has been (informally) defined before (Serenó, 1998; Dodson et al., 2004; Sereno, 2005). These definitions were maximum-clade and used *Pachyrhinosaurus* (Serenó, 1998), *Centrosaurus* (Dodson et al., 2004), or *Centrosaurus apertus* (Serenó, 2005) as the internal specifier and *Triceratops* (Serenó, 1998; Dodson et al., 2004) or *Triceratops horridus* (Serenó, 2005) as the external specifier. We apply the name *Centrosaurinae* for the same known contents; adopting the mandatory *Centrosaurus apertus* as the internal specifier and *Chasmosaurus belli* and *Triceratops horridus* as the external specifiers.

***Cerapoda* Sereno, 1986 [converted clade name]**

Registration number: 597

Definition. The smallest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Triceratops horridus* Marsh, 1889, and *Pachycephalosaurus wyomingensis* (Gilmore, 1931). This is a minimum-clade definition. Abbreviated definition: min ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889 & *Pachycephalosaurus wyomingensis* [Gilmore, 1931]).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Cerapoda* comprises members of the clades *Ornithopoda* and *Marginocephalia*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Cerapoda* has been (informally) defined before (Weishampel, 2004; Butler et al., 2008). Both types of definitions, minimum-clade as well as maximum-clade, have been proposed for the name. Weishampel (2004) preferred a maximum-clade definition and used *Triceratops* as the internal specifier and *Ankylosaurus* as the external specifier, while Butler et al. (2008) applied a minimum-clade definition, using *Triceratops horridus* and *Parasaurolophus walkeri* as the internal specifiers. Subsequent authors followed the latter definition (e.g., Bojarski, 2005; Madzia et al., 2018; Herne et al., 2019). We apply a minimum-clade definition as well and use *Iguanodon bernissartensis*, *Triceratops horridus*, and *Pachycephalosaurus wyomingensis* as the internal specifiers.

***Ceratopsia* Marsh, 1890 [converted clade name]**

Registration number: 598

Definition. The largest clade containing *Ceratops montanensis* Marsh, 1888 and *Triceratops horridus* Marsh, 1889 but not *Pachycephalosaurus wyomingensis* (Gilmore, 1931). This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ceratops montanensis* Marsh, 1888 & *Triceratops horridus* Marsh, 1889 ~ *Pachycephalosaurus wyomingensis* [Gilmore, 1931]).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure S1 of Knapp et al. (2018), Figure 1 of Dieudonné et al. (2020), Figure 3 of Yu et al. (2020), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Ceratopsia* comprises *Psittacosaurus* spp. and members of the clades *Chaoyangsauridae* and *Neoceratopsia*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ceratopsia* has been (informally) defined before (Dodson, 1997; Sereno, 1998; Sereno, 2005). These definitions were maximum-clade and used *Ceratopsidae* (Dodson,

1997), *Triceratops* (Sereno, 1998), or *Triceratops horridus* (Sereno, 2005) as the internal specifiers and *Pachycephalosauridae* (Dodson, 1997), *Pachycephalosaurus* (Sereno, 1998), or *Pachycephalosaurus wyomingensis*, *Heterodontosaurus tucki*, *Hypsilophodon foxii*, and *Ankylosaurus magniventris* (Sereno, 2005) as the external specifiers. Even though the position of *Hypsilophodon foxii* and *Heterodontosaurus tucki* is indeed somewhat unstable (see, e.g., Madzia et al. [2018] and Dieudonné et al. [2020], respectively), inclusion of these taxa among the external specifiers does not need to be necessary. We use a definition similar to that of Sereno (1998) but include the mandatory *Ceratops montanus* as a second internal specifier.

***Ceratopsidae* Marsh, 1888 [converted clade name]**

Registration number: 599

Definition. The smallest clade containing *Ceratops montanus* Marsh, 1888, *Triceratops horridus* Marsh, 1889, *Chasmosaurus belli* (Lambe, 1902), and *Centrosaurus apertus* Lambe 1904. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Ceratops montanus* Marsh, 1888 & *Triceratops horridus* Marsh, 1889 & *Chasmosaurus belli* [Lambe, 1902] & *Centrosaurus apertus* Lambe 1904).

Reference phylogeny. Figure 4 of Yu et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 14 of Mallon et al. (2016), Figure S1 of Knapp et al. (2018), Figure 10a of Fowler and Freedman Fowler (2020), Figure 10 of Wilson et al. (2020), and Figure 3 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Ceratopsidae* comprises members of the clades *Centrosaurinae* and *Chasmosaurinae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ceratopsidae* has been (informally) defined before (Sereno, 1998, Dodson et al., 2004; Sereno, 2005). These definitions were minimum-clade and used *Triceratops* and *Pachyrhinosaurus* (Sereno, 1998), *Triceratops* and *Centrosaurus* (Dodson et al., 2004), and *Triceratops horridus* and *Pachyrhinosaurus canadensis* (Sereno, 2005) as the internal specifiers. Considering that *Ceratopsidae* ‘traditionally’ contains two subclades, *Centrosaurinae* and *Chasmosaurinae*, we include the nomenclatural types of these clades, *Centrosaurus apertus* and *Chasmosaurus belli*, respectively, as the internal specifiers, and additionally add *Triceratops horridus*, a common specifier in the nomenclature of ceratopsian clades and the only taxon that

has always been used as an internal specifier in the definition of *Ceratopsidae*. Finally, we also include a fourth internal specifier, the mandatory *Ceratops montanensis*. Even though the taxon is considered a *nomen dubium* (e.g., Dodson et al., 2004; Mallon et al., 2016), its placement within the smallest clade comprising centrosaurines and chasmosaurines does not appear to be questionable (see, e.g., Mallon et al. [2016]).

***Ceratopsoidea* Hay, 1902 [converted clade name]**

Registration number: 601

Definition. The largest clade containing *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889 but not *Protoceratops andrewsi* Granger and Gregory, 1923. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ceratops montanus* Marsh, 1888 & *Triceratops horridus* Marsh, 1889 ~ *Protoceratops andrewsi* Granger and Gregory, 1923).

Reference phylogeny. Figure 4 of Yu et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure S1 of Knapp et al. (2018), Figure 10 of Morschhauser et al. (2019), and Figure 3 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Ceratopsoidea* comprises *Turanoceratops tardabilis*, *Zuniceratops christopherei*, and members of the clade *Ceratopsidae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ceratopsoidea* has been (informally) defined before by Sereno (1998, 2005) who applied a maximum-clade definition and used *Triceratops horridus* as the internal specifier and *Protoceratops andrewsi* as the external specifier. We include an additional internal specifier, the mandatory *Ceratops montanus*.

***Chaoyangsauridae* Zhao et al., 1999 [converted clade name]**

Registration number: 602

Definition. The largest clade containing *Chaoyangsaurus youngi* Zhao et al., 1999 but not *Triceratops horridus* Marsh, 1889 and *Psittacosaurus mongoliensis* Osborn, 1923. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Chaoyangsaurus youngi* Zhao et al., 1999 ~ *Triceratops horridus* Marsh, 1889 & *Psittacosaurus mongoliensis* Osborn, 1923).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Chaoyangsauridae* comprises *Chaoyangsaurus youngi*, *Hualianceratops wucaiwansensis*, *Xuanhuaceratops niei*, and *Yinlong downsi*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Chaoyangsauridae* has been (informally) defined before by Han et al. (2015) who applied a maximum-clade definition and used *Chaoyangsaurus youngi* as the internal specifier and *Triceratops horridus* and *Psittacosaurus mongoliensis* as the external specifiers. This definition is formalized here.

***Chasmosaurinae* Lambe, 1915 [converted clade name]**

Registration number: 603

Definition. The largest clade containing *Chasmosaurus belli* (Lambe, 1902) and *Triceratops horridus* Marsh, 1889 but not *Centrosaurus apertus* Lambe 1904. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Chasmosaurus belli* [Lambe, 1902] & *Triceratops horridus* Marsh, 1889 ~ *Centrosaurus apertus* Lambe 1904).

Reference phylogeny. Figure 10a of Fowler and Freedman Fowler (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 14 of Mallon et al. (2016), Figure S1 of Knapp et al. (2018), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Chasmosaurinae* comprises *Agujaceratops mariscalensis*, *Anchiceratops ornatus*, *Arrhinoceratops brachyops*, *Bravoceratops polyphemus*, *Chasmosaurus* spp., *Coahuilaceratops magnacuerna*, *Eotriceratops xerinsularis*, *Kosmoceratops richardsoni*, *Navajoceratops sullivani*, *Nedoceratops hatcheri*, *Ojoceratops fowleri*, *Pentaceratops sternbergii*, *Terminocavus sealyi*, *Torosaurus* spp., *Triceratops* spp., *Utahceratops gettyi*, and *Vagaceratops irvinensis*.

Synonyms. The taxon *Ceratops montanus* may also fall within the largest clade containing *Chasmosaurus belli* and *Triceratops horridus* but not *Centrosaurus apertus* (see, e.g., Mallon et al., 2016). In such case, *Ceratopsinae* would be an approximate synonym. Though the name has been advocated to be the proper name for the clade (it has been [informally] defined by Sereno [1998] and Sereno [2005]), it was actually introduced four years later than *Chasmosaurinae*. Note that the Principle of Coordination, which would make *Ceratopsinae* attributable to Marsh (1888), rather than to Abel (1919), does not apply under the ICPN (see Note 9.15A.3).

Therefore, *Ceratopsinae* would not have priority over *Chasmosaurinae* under the ICPN. Anyway, *C. montanus* does not seem to be diagnostic beyond *Ceratopsidae* at present (Mallon et al., 2016).

Comments. The name *Chasmosaurinae* has been (informally) defined before by Dodson et al. (2004) who applied a maximum-clade definition and used *Triceratops* as the internal specifier and *Centrosaurus* as the external specifier. We apply the name *Chasmosaurinae* for the same known contents; adopting *Triceratops horridus* and the mandatory *Chasmosaurus belli* as the internal specifiers and *Centrosaurus apertus* as the external specifier.

***Clypeodonta* Norman, 2014 [converted clade name]**

Registration number: 604

Definition. The smallest clade within *Ornithopoda* containing *Hypsilophodon foxii* Huxley, 1869 and *Edmontosaurus regalis* Lambe, 1917. This is a minimum-clade definition. Abbreviated definition: $\min \nabla \in \textit{Ornithopoda} (\textit{Hypsilophodon foxii}$ Huxley, 1869 & *Edmontosaurus regalis* Lambe, 1917).

Reference phylogeny. Figure 50 of Norman (2015) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 25 of Herne et al. (2019) and Figure 2 of Dieudonné et al. (2020).

Composition. Under the primary reference phylogeny, *Clypeodonta* comprises a clade formed by *Hypsilophodon foxii*, *Rhabdodontidae*, and *Tenontosaurus* spp., and a clade uniting *Dryosauridae* and *Ankylopollexia* (termed *Iguanodontia* in Norman [2015]). However, see ‘Comments’ below for discussion of potential alternative composition of *Clypeodonta*.

Synonyms. No other taxon names are currently in use for the same or approximate clade. *Iguanodontia*, as reconstructed, for example, by Madzia et al. (2020) covers a similar taxic composition; though the topology of Madzia et al. (2020) differs from that of the primary reference phylogeny of *Clypeodonta* significantly.

Comments. The name *Clypeodonta* was claimed as being new in two different studies (Norman, 2014: 29; Norman, 2015: 102), although Norman (2015: 170) also cites Norman (2014) as the establishing reference. The use of the name *Clypeodonta* differed across studies. Originally, Norman (2014, 2015) intended to use it for a subclade of *Ornithopoda* that (approximately) comprises *Hypsilophodon foxii* and its relatives, and ornithopods more derived than *H. foxii*, and

(informally) defined the name as pertaining to either, the branch of “*Parasaurolophus walkeri* and all taxa more closely related to *P. walkeri* than to *Thescelosaurus neglectus*” (Norman, 2014: 29) and the node of “*Hypsilophodon foxii*, *Edmontosaurus regalis*, their most recent common ancestor, and all of its descendants” (Norman, 2015: 170). In both these studies, *Clypeodonta* is said (Norman, 2014: 29) or figured (Norman, 2015: Fig. 50) to cover the same known contents although neither of the studies included taxa in their analyses that would fall outside the clade (except for *Lesothosaurus diagnosticus*). Madzia et al. (2018) followed the definition of Norman (2015). In their phylogenetic analysis, however, the name covers a much broader contents as one of the internal specifiers of *Clypeodonta*, *Hypsilophodon foxii*, is reconstructed outside *Cerapoda* in that study (Madzia et al. 2018: Fig. 4). Still, Madzia et al. (2018: Appendix 1) stated that as *Clypeodonta* was a relatively new name with no ‘traditional’ meaning, they saw no reason for its redefinition. They also noted, though, that “given the unstable position of *H. foxii* among neornithischians, the name might have only limited utility” Madzia et al. (2018: Appendix 1). Here we define the name *Clypeodonta* using the minimum-clade definition of Norman (2015). However, by including the part “within *Ornithopoda*” in the definition, we restrict the use of *Clypeodonta* to the node only when *H. foxii* represents an ornithopod (see Article 11.14 of the ICPN), following the original intent of Norman (2014, 2015).

***Coronosauria* Sereno, 1986 [converted clade name]**

Registration number:

Definition. The smallest clade containing *Triceratops horridus* Marsh, 1889 and *Protoceratops andrewsi* Granger and Gregory, 1923. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Triceratops horridus* Marsh, 1889 & *Protoceratops andrewsi* Granger and Gregory, 1923).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Coronosauria* comprises members of the clades *Protoceratopsidae* and *Ceratopsoidea*. Additional reference phylogenies include Figure S1 of Knapp et al. (2018) and Figure 4 of Yu et al. (2020).

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Coronosauria* has been (informally) defined before by Sereno (1998, 2005) who applied the minimum-clade definition and used *Triceratops horridus* and *Protoceratops andrewsi* as the internal specifiers. This definition is formalized here.

***Dryomorpha* Sereno, 1986 [converted clade name]**

Registration number: 606

Definition. The smallest clade containing *Dryosaurus altus* (Marsh, 1878) and *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Dryosaurus altus* [Marsh, 1878] & *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 2 of Dieudonné et al. (2020), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Dryomorpha* comprises members of the clades *Dryosauridae* and *Ankylopollexia*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Dryomorpha* was first (informally) defined by Sereno (2005) who attributed the name to “[t]he most inclusive clade containing *Dryosaurus altus* (Marsh 1878) and *Parasaurolophus walkeri* Parks 1922”. However, due to the use of ‘most’, rather than ‘least’, such definition makes the name inapplicable. Boyd (2015) later corrected the wording and proposed a minimum-clade definition using the same taxa as the internal specifiers. Here we use the same type of definition but replace *P. walkeri* with *I. bernissartensis*. This taxon has always been considered a part of *Dryomorpha*.

***Dryosauridae* Stefano, 1903 [converted clade name]**



Registration number: 607

Definition. The largest clade containing *Dryosaurus altus* (Marsh, 1878) but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Dryosaurus altus* [Marsh, 1878] ~ *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 57 of Barta & Norell (2021), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Dryosauridae* comprises *Callovosaurus leedsi*, ‘*Camptosaurus*’ *valdensis*, *Dryosaurus altus*, *Dysalotosaurus lettowvorbecki*, *Elrhazosaurus nigeriensis*, *Eousdryosaurus nanohallucis*, and *Valdosaurus canaliculatus*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. *Dryosauridae* was first (informally) defined by Sereno (1998: 61) who used the maximum-clade definition and *Dryosaurus altus* as the internal specifier and *Parasaurolophus walkeri* as the external specifier. Here we use the same type of definition but replace *P. walkeri* with *I. bernissartensis*. This taxon has always been considered outside *Dryosauridae*.

***Edmontosaurini* Glut, 1997 [converted clade name]**

Registration number: 608

Definition. The largest clade containing *Edmontosaurus regalis* Lambe, 1917 but not *Brachylophosaurus canadensis* Sternberg, 1953, *Hadrosaurus foulkii* Leidy, 1858, *Kritosaurus navajovius* Brown, 1910, and *Saurolophus osborni* Brown, 1912. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Edmontosaurus regalis* Lambe, 1917 ~ *Brachylophosaurus canadensis* Sternberg, 1953 & *Hadrosaurus foulkii* Leidy, 1858 & *Kritosaurus navajovius* Brown, 1910 & *Saurolophus osborni* Brown, 1912).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Edmontosaurini* comprises *Edmontosaurus* spp., *Kerberosaurus manakini*, *Kundurosaurus nagorny*, and *Shantungosaurus giganteus*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Edmontosaurini* has been (informally) defined before (Sereno, 2005; Xing et al., 2014). Sereno (2005) applied the maximum-clade definition and used *Edmontosaurus regalis* as the internal specifier and *Maiasaura peeblesorum* and *Saurolophus*

osborni as the external specifiers. In turn, Xing et al. (2014) applied a minimum-clade definition, with *Edmontosaurus* and *Kerberosaurus* as the internal specifiers. We formalize a maximum-clade definition similar to that of Sereno (2005) but replace *M. peeblesorum* with *Brachylophosaurus canadensis*, as the representative of *Brachylophosaurini*, and further add *Kritosaurus navajovius* and *Hadrosaurus foulkii*.

***Elasmaria* Calvo et al., 2007 [converted clade name]**

Registration number: 609

Definition. The smallest clade containing *Talenkauen santacrucensis* Novas et al., 2004 and *Macrogryphosaurus gondwanicus* Calvo et al., 2007, provided that it does not include *Hypsilophodon foxii* Huxley, 1869, *Iguanodon bernissartensis* Boulenger in Beneden, 1881, or *Thescelosaurus neglectus* Gilmore, 1913. This is a minimum-clade definition. Abbreviated definition: $\min \nabla$ (*Talenkauen santacrucensis* Novas et al., 2004 & *Macrogryphosaurus gondwanicus* Calvo et al., 2007 | \sim *Hypsilophodon foxii* Huxley, 1869 \vee *Iguanodon bernissartensis* Boulenger in Beneden, 1881 \vee *Thescelosaurus neglectus* Gilmore, 1913).

Reference phylogeny. Figure 31 of Rozadilla et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 26 of Herne et al. (2019), Figure 2 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Elasmaria* comprises *Anabisetia saldiviai*, *Atlascopcosaurus loadsi*, *Fulgurotherium austral*, *Gasparinisaura cincosaltensis*, *Kangnasaurus coetzeei*, *Macrogryphosaurus gondwanicus*, *Morrosaurus antarcticus*, *Notohypsilophodon comodorensis*, *Quantassaurus intrepidus*, and *Trinisaura santamartaensis*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Elasmaria* has been (informally) defined before (Calvo et al., 2007; Herne et al., 2019). The definition proposed by Calvo et al. (2007) was minimum-clade, while the definition of Herne et al. (2019) was maximum-clade. However, both studies used *Talenkauen santacrucensis* and *Macrogryphosaurus gondwanicus* as the internal specifiers. Herne et al. (2019) proposed to add *Iguanodon bernissartensis* and *Hypsilophodon foxii* as the external specifiers to maintain the use of the name *Elasmaria* to the ‘traditional’ contents under a hypothesis in which one of the internal specifiers was reconstructed, for example, closer to

iguanodontians. We keep the use of a minimum-clade definition (as first proposed for the name). However, even though all phylogenetic analyses consistently reconstruct close relationships between *T. santacrucensis* and *M. gondwanicus*, we follow Herne et al. (2019) in that the unsettled placement of elasmarians on the neornithischian phylogenetic tree warrants addition of external specifiers. We include *Iguanodon bernissartensis* and *Hypsilophodon foxii* as the external specifiers (following Herne et al. [2019]) and further add a third external specifier, *Thescelosaurus neglectus*, to reflect that elasmarians were already inferred as a clade within *Thescelosaurinae*, as the sister taxon to *Thescelosaurus* spp. (Boyd, 2005).

***Euceratopsia* [new clade name]**

Registration number: 610

Definition. The smallest clade containing *Leptoceratops gracilis* Brown, 1914, *Protoceratops andrewsi* Granger & Gregory, 1923, and *Triceratops horridus* Marsh, 1889. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Leptoceratops gracilis* Brown, 1914 & *Protoceratops andrewsi* Granger & Gregory, 1923 & *Triceratops horridus* Marsh, 1889).

Etymology. Derived from the Greek *eu-* (true) and formed to show its association to members of *Ceratopsia*. Note that *Euceratopsia* does not derive from the name *Ceratops montanus* Marsh, 1888, and, as such, the taxon does not have to be the internal specifier in the used definition.

Reference phylogeny. Figure 4 of Yu et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure S1 of Knapp et al. (2018), Figure 10 of Morschhauser et al. (2019), and Figure 3 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Euceratopsia* comprises members of the clades *Leptoceratopsidae* and *Coronosauria*.

Synonyms. The name *Coronosauria* Sereno, 1986 covers the same contents under the topology of You & Dodson (2004). However, see ‘Comments’. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Euceratopsia* is established for the well-supported node uniting the three most derived clades of ceratopsians – *Leptoceratopsidae*, *Protoceratopsidae*, and *Ceratopsioidea*. The monophyly of the grouping is supported by all recently published phylogenies that infer *Euceratopsia* to branch into two clades – leptoceratopsids and coronosaurs (protoceratopsids + ceratopsoids). Both these clades comprise representatives that are very close or survived to the

Cretaceous/Paleogene mass extinction event (Fowler, 2017: S1 Table). It is worth noting that You & Dodson (2004) reconstructed leptoceratopsids to be the sister taxon to *Ceratopsoidea*, and *Protoceratopsidae* to be the sister taxon to *Leptoceratopsidae* + *Ceratopsoidea*. Under such topology, *Euceratopsia* becomes a heterodefinitional synonym of *Coronosauria*, with the latter having priority.

***Euhadrosauria* Weishampel et al., 1993 [converted clade name]**

Registration number: 611

Definition. The smallest clade containing *Saurolophus osborni* Brown, 1912 and *Lambeosaurus lambei* Parks, 1923, provided that it does not include *Hadrosaurus foulkii* Leidy, 1858. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Saurolophus osborni* Brown, 1912 & *Lambeosaurus lambei* Parks, 1923 | \sim *Hadrosaurus foulkii* Leidy, 1858).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 7 of Kobayashi et al. (2021), Figure 10 of Longrich et al. (2021), and Figure 11 of McDonald et al. (2021).

Composition. *Euhadrosauria* comprises members of the clades *Saurolophinae* and *Lambeosaurinae*.

Synonyms. The name *Hadrosauridae* Cope, 1869 is an approximate synonym of *Euhadrosauria*. If *Hadrosaurus foulkii* nests within the smallest clade containing *Saurolophus osborni* and *Lambeosaurus lambei*, and within the ‘*Saurolophus* branch’ of the clade (see the entry for the name *Saurolophinae*), the name *Hadrosauridae* is used for the node instead, and *Euhadrosauria* becomes inapplicable. Additionally, the name *Saurolophidae* has been used for the same contents as well (see ‘Comments’).

Comments. The history and application of *Euhadrosauria* is complicated and has been thoroughly described and discussed by Madzia et al. (2020: 14–16). We therefore refer to that study for details.

***Euiguanodontia* Coria & Salgado, 1996 [converted clade name]**

Registration number: 612

Definition. The smallest clade containing *Gasparinisaura cincosaltensis* Coria & Salgado, 1996, *Dryosaurus altus* (Marsh, 1878), and *Camptosaurus dispar* (Marsh, 1879), provided that it does not include *Tenontosaurus tilletti* Ostrom, 1970. This is a minimum-clade definition.

Abbreviated definition: $\min \nabla$ (*Gasparinisaura cincosaltensis* Coria and Salgado, 1996 & *Dryosaurus altus* [Marsh, 1878] & *Camptosaurus dispar* [Marsh, 1879] | \sim *Tenontosaurus tilletti* Ostrom, 1970).

Reference phylogeny. Figure 13 of Coria and Salgado (1996) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Euiguanodontia* comprises *Gasparinisaura* and members of the clades *Dryosauridae* and *Ankylopollexia*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Euiguanodontia* is applicable only on the condition that *G. cincosaltensis*, *D. altus*, and *C. dispar* form a clade exclusive of *T. tilletti*, as originally used by Coria and Salgado (1996). We follow the definition advocated by Madzia et al. (2018: Appendix 1) and refer to that study for additional comments. Note also that *Euiguanodontia* must be a subclade of *Iguanodontia* under the proposed definition because *T. tilletti* is an internal specifier in the definition of the name.

***Euornithopoda* Sereno, 1986 [converted clade name]**

Registration number: 613

Definition. The largest clade within *Ornithopoda* containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Heterodontosaurus tucki* Crompton and Charig, 1962. This is a maximum-clade definition. Abbreviated definition: $\max \nabla \in$ *Ornithopoda* (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 \sim *Heterodontosaurus tucki* Crompton and Charig, 1962).

Reference phylogeny. Figure 1 of Sereno (1999) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Euornithopoda* comprises *Tenontosaurus* spp. and members of the clades *Ankylopollexia*, *Dryosauridae*, and *Hypsilophodontidae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Euornithopoda* has been (informally) defined before (Sereno, 1998; Sereno, 2005). These definitions were maximum-clade and used *Parasaurolophus* as the internal specifier and *Heterodontosaurus tucki*, *Pachycephalosaurus wyomingensis*, *Triceratops horridus*, and *Ankylosaurus magniventris* (Sereno, 2005) as the external specifiers. Here we define the name *Euornithopoda* using a similar maximum-clade definition as that of Sereno (1998) but replace *Parasaurolophus* with *Iguanodon bernissartensis*. Also, by including the part “within *Ornithopoda*” in the definition, we restrict the use of *Euornithopoda* to the branch only when *Heterodontosaurus tucki* represents an ornithopod (see Article 11.14 of the *ICPN*), thus maintaining the ‘traditional’ use (Sereno, 1998; Sereno, 2005).

***Eurypoda* Sereno, 1986 [converted clade name]**

Registration number: 614

Definition. The smallest clade containing *Ankylosaurus magniventris* Brown, 1908 and *Stegosaurus stenops* Marsh, 1887. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Ankylosaurus magniventris* Brown, 1908 & *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 3 of Thompson et al. (2012) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018) and Figure 1 of Dieudonné et al. (2020).

Composition. Under the primary reference phylogeny, *Eurypoda* comprises members of the clades *Ankylosauria* and *Stegosauria*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Eurypoda* has been (informally) defined before by Sereno (1998) who used *Ankylosaurus* and *Stegosaurus* as the internal specifiers. Since *Eurypoda* has never been proposed an alternative use, we formalize this definition.

***Genasauria* Sereno, 1986 [converted clade name]**

Registration number: 615

Definition. The smallest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Triceratops horridus* Marsh, 1889, *Ankylosaurus magniventris* Brown, 1908, and *Stegosaurus stenops* Marsh, 1887. This is a minimum-clade definition. Abbreviated definition:

min ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889 & *Ankylosaurus magniventris* Brown, 1908 & *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 16 of Han et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Genasauria* comprises members of the clades *Neornithischia* and *Thyreophora*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Genasauria* has been (informally) defined before (Currie and Padian, 1997; Sereno, 1998; Sereno, 2005; Butler et al., 2008). These definitions were minimum-clade and used *Thyreophora* and *Cerapoda* (Currie and Padian, 1997), *Ankylosaurus* and *Triceratops* (Sereno, 1998), *Ankylosaurus magniventris*, *Triceratops horridus*, and *Parasaurolophus walkeri* (Sereno, 2005), and *Ankylosaurus magniventris*, *Stegosaurus stenops*, *Triceratops horridus*, *Parasaurolophus walkeri*, and *Pachycephalosaurus wyomingensis* (Butler et al., 2008) as the internal specifiers. In order to maintain the ‘node-branch triplet’ (‘node-stem triplet’ of Sereno [1998: 52–54]) comprising *Genasauria*, *Neornithischia*, and *Thyreophora* (all formally defined in the present paper), the internal specifiers in the definition of *Genasauria* are used from among the taxa representing the two four major subclades – *Ornithopoda* (*Iguanodon bernissartensis*), *Marginocephalia* (*Triceratops horridus*), *Ankylosauria* (*Ankylosaurus magniventris*), and *Stegosauria* (*Stegosaurus stenops*). Addition of *P. wyomingensis* as another internal specifier (to include representatives of both marginocephalian clades – *Ceratopsia* and *Pachycephalosauria*) is considered unnecessary because pachycephalosaurs have always been inferred to be part of *Genasauria* as defined herein.

***Hadrosauridae* Cope, 1869 [converted clade name]**

Registration number: 616

Definition. The smallest clade containing *Hadrosaurus foulkii* Leidy, 1858, *Saurolophus osborni* Brown, 1912, and *Lambeosaurus lambei* Parks, 1923. This is a minimum-clade definition.

Abbreviated definition: min ∇ (*Hadrosaurus foulkii* Leidy, 1858 & *Saurolophus osborni* Brown, 1912 & *Lambeosaurus lambei* Parks, 1923).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Hadrosauridae* comprises *Hadrosaurus foulkii*, *Eotrachodon orientalis*, *Latirhinus uitstlani*, *Aquilarhinus palimentus*, and members of the clades *Saurolophinae* and *Lambeosaurinae*.

Synonyms. Several taxon names have been historically or recently used as approximate synonyms of *Hadrosauridae*. Of these, only the names *Saurolophidae* and *Euhadrosauria* have recently been attributed to a clade of the same or a similar composition (e.g., Prieto-Márquez, 2010; Verdú et al., 2018; Zhang et al., 2019; Madzia et al., 2020; Prieto-Márquez et al., 2020; Zhang et al., 2020; Kobayashi et al., 2021; Verdú et al., 2021). See ‘Comments’ below.

Comments. The use of *Hadrosauridae* and other names applied to the same or similar clades (*Saurolophidae* and *Euhadrosauria*) have been thoroughly described and discussed by Madzia et al. (2020: 14–16) who recommended to use *Hadrosauridae* for the smallest clade containing *H. foulkii*, *S. osborni*, and *L. lambei*; *Euhadrosauria* for the smallest clade containing *S. osborni* and *L. lambei*; and to abandon *Saurolophidae*. Note that under some phylogenies, in which *H. foulkii* is reconstructed within the smallest clade containing *S. osborni* and *L. lambei*, the names *Hadrosauridae* and *Euhadrosauria*, as (informally) defined by Madzia et al. (2020), become heterodefinitional synonyms. Although such option may still be viewed acceptable, we decided to apply a minimum-clade definition for *Euhadrosauria* that makes the name inapplicable under such hypothesis.



***Hadrosauriformes* Sereno, 1997 [converted clade name]**

Registration number: 617

Definition. The smallest clade containing *Hadrosaurus foulkii* Leidy, 1858 and *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Hadrosaurus foulkii* Leidy, 1858 & *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 8

of Słowiak et al. (2020), Figure 11 of McDonald et al. (2021), and Figure 9 of Verdú et al. (2021).

Composition. *Hadrosauriformes* comprises members of the clades *Iguanodontidae* and *Hadrosauroidea*.

Synonyms. If *Hypselospinus fittoni* nests within the smallest clade containing *Hadrosaurus foulkii* and *Iguanodon bernissartensis*, the name *Hadrosauriformes* is a potential heterodefinitional synonym of *Neoiguanodontia*. In such case, the name *Hadrosauriformes* should have priority.

Comments. The name *Hadrosauriformes* has been (informally) defined before (Serenó, 1998; Norman, 2015; Madzia et al. 2020). However, only Madzia et al. (2020: Table 1) included the mandatory *H. foulkii* as the internal specifier. We formalize the definition of Madzia et al. (2020).

***Hadrosaurinae* Lambe, 1918 [converted clade name]**

Registration number: 618

Definition. The largest clade containing *Hadrosaurus foulkii* Leidy, 1858 but not *Lambeosaurus lambei* Parks, 1923. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Hadrosaurus foulkii* Leidy, 1858 \sim *Lambeosaurus lambei* Parks, 1923).

Reference phylogeny. Figure 5 of Kobayashi et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 13 of Cruzado-Caballero & Powell (2017), Figure 20 of Xing et al. (2017), Figure 5 of Zhang et al. (2020), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Hadrosaurinae* comprises *Hadrosaurus foulkii* and members of the clades *Brachylophosaurini*, *Edmontosaurini*, *Kritosaurini*, and *Saurolophini*.

Synonyms. The name *Saurolophinae* Brown, 1914a has been recently used for the same clade (under the hypothesis in which *H. foulkii* is nested outside the smallest clade containing *Saurolophus osborni* and *Lambeosaurus lambei*). See the entry for the name *Saurolophinae*.

Comments. The name *Hadrosaurinae* has been (informally) defined before by (Serenó, 1998; Sereno, 2005). Sereno (1998) applied the maximum-clade definition and used *Saurolophus* as the internal specifier and *Parasaurolophus* as the external specifier. In turn, Sereno (2005),

apparently erroneously, defined *Hadrosaurinae* as pertaining to “[t]he most inclusive taxon containing *Saurolophus osborni* Brown 1912 and *Parasaurolophus walkeri* Parks 1922 and including *Hadrosaurus foulkii* Leidy 1858”. Our formal maximum-clade definition was formed to make *Hadrosaurinae* applicable regardless of whether the taxon lies outside or within the smallest clade containing *Saurolophus osborni* and *Lambeosaurus lambei*.

***Hadrosauroidea* von Huene, 1952 [converted clade name]**



Registration number: 619

Definition. The largest clade containing *Hadrosaurus foulkii* Leidy, 1858 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Hadrosaurus foulkii* Leidy, 1858 ~ *Iguanodon bernissartensis* Boulenger in Beneden, 1881).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 8 of Słowiak et al. (2020), Figure 11 of McDonald et al. (2021), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Hadrosauroidea* comprises *Altirhinus kurzanovi*, *Batyrosaurus rozhdestvenskyi*, *Bolong yixianensis*, *Equijubus normani*, *Gongpoquansaurus mazongshanensis*, *Jinzhousaurus yangi*, *Koshisaurus katsuyama*, *Mantellisaurus atherfieldensis*, *Morelladon beltrani*, *Ouranosaurus nigeriensis*, *Penelopognathus weishampeli*, *Proa valdearinnoensis*, *Probactrosaurus gobiensis*, *Ratchasimasaurus suranareae*, *Sirindhorna khoratensis*, *Xuwulong yueluni*, *Zuoyunlong huangi*, and members of the clade *Hadrosauromorpha*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Hadrosauroidea* was first (informally) defined by Sereno (1998: 62) who used the maximum-clade definition and *Parasaurolophus walkeri* as the internal specifier and *Iguanodon bernissartensis* as the external specifier. We formalize the definition of Madzia et al. (2020: Table 1) who replaced *P. walkeri* with *H. foulkii*.

***Hadrosauromorpha* Norman, 2014 [converted clade name]**

Registration number: 620

Definition. The largest clade containing *Hadrosaurus foulkii* Leidy, 1858 but not *Probactrosaurus gobiensis* Rozhdestvensky, 1967. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Hadrosaurus foulkii* Leidy, 1858 ~ *Probactrosaurus gobiensis* Rozhdestvensky, 1967).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 7 of Kobayashi et al. (2021), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Hadrosauromorpha* comprises *Bactrosaurus johnsoni*, *Datonglong tianzhenensis*, *Eolambia caroljonesa*, *Gilmoresaurus mongoliensis*, *Jeyawati rugoculus*, *Jintasaurus meniscus*, *Levnesovia transoxiana*, *Nanyangosaurus zhugeii*, ‘*Orthomerus dolloi*’, *Plesiohadros djadokhtaensis*, *Protohadros byrdi*, *Tanius sinensis*, *Tethyshadros insularis*, *Shuangmiaosaurus gilmorei*, *Zhanghenglong yangchengensis*, and members of the clade *Hadrosauridae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. *Hadrosauromorpha* was first (informally) defined by Norman (2014: 32) who used the maximum-clade definition and *Parasaurolophus walkeri* as the internal specifier and *Probactrosaurus gobiensis* as the external specifier. We formalize the definition of Madzia et al. (2020: Table 1) who replaced *P. walkeri* with *H. foulkii*.

***Heterodontosauridae* Romer, 1966 [converted clade name]**

Registration number: 622

Definition. The largest clade containing *Heterodontosaurus tucki* Crompton and Charig, 1962 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Triceratops horridus* Marsh, 1889, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), and *Stegosaurus stenops* Marsh, 1887. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Heterodontosaurus tucki* Crompton and Charig, 1962 ~ *Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889 & *Pachycephalosaurus wyomingensis* [Gilmore, 1931] & *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 25 of Herne et al. (2019) and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Heterodontosauridae* comprises *Abrictosaurus consors*, *Echinodon becklesii*, *Eocursor parvus*, *Fruitadens haagarorum*, *Heterodontosaurus tucki*, *Lycorhinus angustidens*, *Manidens condorensis*, *Pegomastax africana*, and *Tianyulong confuciusi*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Heterodontosauridae* has been (informally) defined before (Serenó, 1998; Sereno, 2005). These definitions were maximum-clade and used *Heterodontosaurus* as the internal specifier and *Parasaurolophus* (Serenó, 1998) or *Parasaurolophus walkeri*, *Pachycephalosaurus wyomingensis*, *Triceratops horridus*, and *Ankylosaurus magniventris* (Serenó, 2005) as the external specifiers. We apply the name *Heterodontosauridae* for the same known contents; adopting the mandatory *Heterodontosaurus tucki* as the internal specifier and representatives of all major ornithischian lineages, *Ceratopsia* (*Triceratops horridus*), *Ornithopoda* (*Iguanodon bernissartensis*), *Pachycephalosauria* (*Pachycephalosaurus wyomingensis*), and *Thyreophora* (*Stegosaurus stenops*), as the external specifiers.

***Huayangosauridae* Dong et al., 1982 [converted clade name]**

Registration number: 623

Definition. The largest clade containing *Huayangosaurus taibaii* Dong et al., 1982 but not *Stegosaurus stenops* Marsh, 1887. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Huayangosaurus taibaii* Dong et al., 1982 ~ *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 12 of Maidment et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 11 of Maidment et al. (2008) and Figure 1 of Raven and Maidment (2017).

Composition. Under the primary reference phylogeny, *Huayangosauridae* comprises *Chungkingosaurus jiangbeiensis* and *Huayangosaurus taibaii*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Huayangosauridae* was first (informally) defined by Galton and Upchurch (2004: 358) who used the maximum-clade definition and selected *Huayangosaurus* as the internal specifier and *Stegosaurus* as the external specifier. We formalize this definition.

***Hypsilophodontia* Cooper, 1985 [converted clade name]**

Registration number: 624

Definition. The smallest clade within *Ornithopoda* containing *Hypsilophodon foxii* Huxley, 1869 and *Tenontosaurus tilletti* Ostrom, 1970, provided that it does not include *Iguanodon bernissartensis* Boulenger in Beneden, 1881. This is a minimum-clade definition. Abbreviated definition: $\min \nabla \in \textit{Ornithopoda} (\textit{Hypsilophodon foxii}$ Huxley, 1869 & *Tenontosaurus tilletti* Ostrom, 1970 | $\sim \textit{Iguanodon bernissartensis}$ Boulenger in Beneden, 1881).

Reference phylogeny. Figure 50 of Norman (2015) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Hypsilophodontia* comprises a clade formed by *Hypsilophodon foxii*, *Rhabdodontidae*, and *Tenontosaurus* spp. However, see ‘Comments’ below for discussion of potential alternative composition of *Clypeodonta*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Hypsilophodontia* was (informally) defined as pertaining to “*Hypsilophodon foxii*, *Tenontosaurus tilletti*, their most recent common ancestor, and all of its descendants” (Norman, 2015: 171). However, such definition does not reflect alternative topologies that do not show *Hypsilophodontia* as reconstructed by Norman (2015), making it applicable for markedly different contents (see, e.g., Madzia et al. 2018: Fig. 4). Here we define the name *Hypsilophodontia* using a similar minimum-clade definition as that of Norman (2015) but by including the part “within *Ornithopoda*” in the definition, and adding an external specifier, we restrict the use of *Hypsilophodontia* to the node only when *H. foxii* represents an ornithopod (see Article 11.14 of the ICPN) and when *Hypsilophodon foxii* and *Tenontosaurus tilletti* are more closely related to each other than either is to *I. bernissartensis*, following the original intent of Norman (2015).

***Hypsilophodontidae* Dollo, 1882 [converted clade name]**

Registration number: 625

Definition. The largest clade containing *Hypsilophodon foxii* Huxley, 1869 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881 and *Rhabdodon priscus* Matheron, 1869. This is a maximum-clade definition. Abbreviated definition: $\max \nabla (\textit{Hypsilophodon foxii}$ Huxley, 1869 $\sim \textit{Iguanodon bernissartensis}$ Boulenger in Beneden, 1881 & *Rhabdodon priscus* Matheron, 1869).

Reference phylogeny. Figure 2 of Dieudonné et al. (2020) is treated here as the primary reference phylogeny.

Composition. Under the primary reference phylogeny, *Hypsilophodontidae* comprises *Hypsilophodon foxii*, *Gasparinisaura cincosaltensis*, and *Parksosaurus warreni*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. *Hypsilophodontidae* was first (informally) defined by Sereno (1998: 61) who used the maximum-clade definition and *Hypsilophodon foxii* as the internal specifier and *Parasaurolophus walkeri* as the external specifier. Here we use the same type of definition but replace *P. walkeri* with *I. bernissartensis*. This taxon has always been considered outside *Hypsilophodontidae*. Additionally, we include *Rhabdodon priscus* as a second external specifier to prevent the inclusion of *Rhabdodontidae* within *Hypsilophodontidae* under the topology of Norman (2015: Fig. 48)

***Iguanodontia* Baur, 1891 [converted clade name]**

Registration number: 626

Definition. The smallest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Dryosaurus altus* (Marsh, 1878), *Rhabdodon priscus* Matheron, 1869, and *Tenontosaurus tilletti* Ostrom, 1970. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Dryosaurus altus* [Marsh, 1878] & *Rhabdodon priscus* Matheron, 1869 & *Tenontosaurus tilletti* Ostrom, 1970).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure 20 of Verdú et al. (2018), Figure 25 of Herne et al. (2019), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Iguanodontia* comprises members of the clade *Rhabdodontomorpha*, *Tenontosaurus* spp., and *Dryomorpha*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Clypeodonta, as reconstructed by Norman (2015) covers a similar taxic composition; though the topology of Norman (2015) differs from that of the primary phylogeny of *Iguanodontia* significantly.

Comments. The application of *Iguanodontia* has been described and discussed by Madzia et al. (2018: Appendix 1) and Madzia et al. (2020: Table 1). We therefore refer to these studies for details.

***Iguanodontidae* Bonaparte, 1850 [converted clade name]**

Registration number: 627

Definition. The largest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Hadrosaurus foulkii* Leidy, 1858. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 ~ *Hadrosaurus foulkii* Leidy, 1858).

Reference phylogeny. Figure 13 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Madzia et al. (2018), Figure 20 of Verdú et al. (2018), and Figure 7 of Kobayashi et al. (2021).

Composition. Under the primary reference phylogeny, *Iguanodontidae* comprises *Barilium dawsoni*, *Iguanodon bernissartensis*, *Iguanodon galvensis*, and *Lurdusaurus arenatus*.

Synonyms. The name *Iguanodontoidea* Hay, 1902 is an approximate synonym of *Iguanodontidae* (see, e.g., Figure 20 of Verdú et al. [2018]). Both these names have been used for various sets of taxa thought or reconstructed to be more closely related to *Iguanodon bernissartensis* than to hadrosaurids. Considering that significant differences exist between phylogeny reconstructions of *Iguanodon*-grade ornithopods (e.g., Madzia et al., 2018; Verdú et al., 2018; Madzia et al., 2020; McDonald et al., 2021), it is difficult to link either of the names to a certain, stable composition. Here, we prefer to apply the name *Iguanodontidae* because it is more frequent in the literature and because it was coined 52 years before *Iguanodontoidea*.

Comments. The name *Iguanodontidae* was first (informally) defined by Sereno (1998, 2005) who applied the maximum-clade definition and used *Iguanodon bernissartensis* as the internal specifier and *Parasaurolophus walkeri* as the external specifier. We apply a similar definition but replace *P. walkeri* with *H. foulkii*.

***Jeholosauridae* Han et al., 2012 [converted clade name]**

Registration number: 628

Definition. The largest clade outside *Hypsilophodontidae* or *Thescelosauridae* containing *Jeholosaurus shangyuanensis* Xu et al., 2000 but not *Hypsilophodon foxii* Huxley, 1869, *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Triceratops horridus* Marsh, 1889, *Pachycephalosaurus wyomingensis* (Gilmore, 1931), and *Thescelosaurus neglectus* Gilmore, 1913. This is a maximum-clade definition. Abbreviated definition: $\max \nabla \notin \textit{Hypsilophodontidae} \vee \textit{Thescelosauridae}$ (*Jeholosaurus shangyuanensis* Xu et al., 2000 \sim *Hypsilophodon foxii* Huxley, 1869 & *Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889 & *Pachycephalosaurus wyomingensis* [Gilmore, 1931] & *Thescelosaurus neglectus* Gilmore, 1913).

Reference phylogeny. Figure 25 of Herne et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 16 of Han et al. (2018), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Jeholosauridae* comprises *Changchunsaurus parvus*, *Haya griva*, and *Jeholosaurus shangyuanensis*. Under alternative hypotheses, however, *Jeholosauridae* includes *Jeholosaurus shangyuanensis* and *Yueosaurus tiantaiensis* (e.g., Madzia et al., 2018: Fig. 4; Barta & Norell, 2021: Fig. 57).

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. We use a maximum-clade definition similar to that of Han et al. (2012), which is the only definition (informally) used for *Jeholosauridae*. Our definition differs in that we replaced the original representative of *Ceratopsia* (*Protoceratops andrewsi*) with a taxon that is widely used in phylogenetic definitions of ornithischian clade names (*Triceratops horridus*). Additionally, our definition prevents the use of *Jeholosauridae* under the potential hypotheses in which *Jeholosaurus* is inferred as part of *Hypsilophodontidae* or *Thescelosauridae*.

***Kritosaurini* Glut, 1997 [converted clade name]**

Registration number: 629

Definition. The largest clade containing *Kritosaurus navajovius* Brown, 1910 but not *Brachylophosaurus canadensis* Sternberg, 1953, *Edmontosaurus regalis* Lambe, 1917, *Hadrosaurus foulkii* Leidy, 1858, and *Saurolophus osborni* Brown, 1912. This is a maximum-clade definition. Abbreviated definition: $\max \nabla$ (*Kritosaurus navajovius* Brown, 1910 \sim

Brachylophosaurus canadensis Sternberg, 1953 & *Edmontosaurus regalis* Lambe, 1917 & *Hadrosaurus foulkii* Leidy, 1858 & *Saurolophus osborni* Brown, 1912).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny *Kritosaurini* comprises *Gryposaurus* spp., *Kritosaurus* spp., *Rhinorex condrupus*, *Secernosaurus koernereri*, and the specimen ‘Big Bend UTEP 37.7’.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The study of Lapparent & Lavocat (1955) has been cited to be the reference establishing the name *Kritosaurini* (e.g., Prieto-Márquez, 2014). However, Lapparent & Lavocat (1955) used ‘Kritosaurinés’ rather than ‘Kritosaurini’. The name *Kritosaurini* was then used by Brett-Surman (1989) and by Glut (1997). Since Brett-Surman (1989) is an unpublished doctoral dissertation, we consider Glut (1997) to be the earliest publication to spell the name *Kritosaurini*. The name was first (informally) defined by Prieto-Márquez (2014) who applied the minimum-clade definition and used *Kritosaurus navajovius*, *Gryposaurus notabilis*, and *Naashoibitosaurus ostromi* as the internal specifiers. We preserve the original intent of Prieto-Márquez (2014) but prefer to apply the maximum-clade definition. *Kritosaurus navajovius* is used as the internal specifier and *Hadrosaurus foulkii*, and representatives of *Brachalophosaurini* (*Brachylophosaurus canadensis*), *Edmontosaurini* (*Edmontosaurus regalis*), and *Saurolophini* (*Saurolophus osborni*), as the external specifiers.

***Lambeosaurinae* Parks, 1923 [converted clade name]**

Registration number: 630

Definition. The largest clade containing *Lambeosaurus lambei* Parks, 1923 but not *Hadrosaurus foulkii* Leidy, 1858 and *Saurolophus osborni* Brown, 1912. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Lambeosaurus lambei* Parks, 1923 ~ *Hadrosaurus foulkii* Leidy, 1858 & *Saurolophus osborni* Brown, 1912).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al.

(2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Lambeosaurinae* comprises *Aralosaurus tuberiferus*, *Canardia garonnensis*, *Jaxartosaurus aralensis*, and members of the clades *Lambeosaurini*, *Parasaurolophini*, and *Tsintaosaurini*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Lambeosaurinae* has been (informally) defined before (Sereno, 1998; Sereno, 2005; Prieto-Márquez, 2010). These definitions were maximum-clade and used *Parasaurolophus* (Sereno, 1998) or *Lambeosaurus lambei* (Prieto-Márquez, 2010) as the internal specifiers and *Saurolophus* (Sereno, 1998) or *Hadrosaurus foulkii*, *Saurolophus osborni*, and *Edmontosaurus regalis* (Prieto-Márquez, 2010) as the external specifiers. Sereno (2005), apparently erroneously, defined *Lambeosaurinae* as pertaining to “[t]he most inclusive taxon containing *Saurolophus osborni* Brown 1912 but not *Parasaurolophus walkeri* Parks 1922 and including *Lambeosaurus lambei* Parks 1923”. Our formal maximum-clade definition is similar to that of Prieto-Márquez (2010) though we have removed *E. regalis* from the external specifiers because the taxon is consistently inferred outside *Lambeosaurinae* (Kobayashi et al., 2019; Prieto-Márquez et al., 2019; Prieto-Márquez et al., 2020; Zhang et al., 2019; Zhang et al., 2020; Kobayashi et al., 2021; Longrich et al., 2021).

***Lambeosaurini* Sullivan et al., 2011 [converted clade name]**

Registration number: 631

Definition. The largest clade containing *Lambeosaurus lambei* Parks, 1923 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Parasaurolophus walkeri* Parks, 1922, and *Tsintaosaurus spinorhinus* Young, 1958. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Lambeosaurus lambei* Parks, 1923 ~ *Aralosaurus tuberiferus* Rozhdestvensky, 1968 & *Parasaurolophus walkeri* Parks, 1922 & *Tsintaosaurus spinorhinus* Young, 1958).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Lambeosaurini* comprises *Amurosaurus riabinini*, *Arenysaurus ardevoli*, *Blasisaurus canudo*, *Corythosaurus* spp., *Hypacrosaurus stebingeri*, *Hypacrosaurus altispinus*, *Lambeosaurus* spp., *Magnapaulia laticaudus*, *Olorotitan arharensis* (misspelled as ‘*ararhensis*’ in the primary reference phylogeny), *Sahaliyana elunchunorum*, and *Velafrons coahuilensis*.

Synonyms. The name *Corythosaurini* Glut, 1997 is an approximate synonym of *Lambeosaurini* (e.g., Evans & Reisz, 2007; Gates et al., 2007; Pereda-Suberbiola et al., 2009). However, its use has been discouraged (Prieto-Marquéz et al., 2013) and all recent phylogenetic studies preferred to use *Lambeosaurini* instead (e.g., Xing et al., 2017; Kobayashi et al., 2019; Prieto-Márquez et al., 2019; Zhang et al., 2020; Kobayashi et al., 2021; Longrich et al., 2021). No other taxon names are currently in use for the same or approximate clade.

Comments. Even though Sullivan et al. (2011) did not explicitly formulate the definition of their newly proposed name *Lambeosaurini*, they noted that their “definition of the *Lambeosaurini* would be equivalent to node 38 of Prieto-Márquez (2010a: fig. 9)” (Sullivan et al., 2011: p. 417). The name *Lambeosaurini* was first (informally) defined by Prieto-Márquez et al. (2013) who applied the maximum-clade definition and used *Lambeosaurus lambei* as the internal specifier and *Parasaurolophus walkeri*, *Tsintaosaurus spinorhinus*, and *Aralosaurus tuberiferus* as the external specifier. Such defined, the use of *Lambeosaurini* adheres to the original intent of Sullivan et al. (2011). We formalize this definition.

***Leptoceratopsidae* Nopcsa, 1923 [converted clade name]**

Registration number: 632

Definition. The largest clade containing *Leptoceratops gracilis* Brown, 1914b but not *Triceratops horridus* Marsh, 1889. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Leptoceratops gracilis* Brown, 1914b ~ *Triceratops horridus* Marsh, 1889).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure S1 of Knapp et al. (2018), Figure 10 of Morschhauser et al. (2019), Figure 3 of Yu et al. (2020), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Leptoceratopsidae* comprises *Cerasinops hodgskissi*, *Gryphoceratops morrisoni*, *Helioceratops brachygnathus*, *Ischioceratops*

zhuchengensis, *Koreaceratops hwaseongensis*, *Leptoceratops gracilis*, *Montanoceratops cerorhynchus*, *Prenoceratops pieganensis*, *Udanoceratops tchizhovi*, *Unescoceratops kopelhusae*, and *Zhuchengceratops inexpectus*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Leptoceratopsidae* has been (informally) defined before by Makovicky (2001) who used *Leptoceratops gracilis* as the internal specifier and *Triceratops horridus* as the external specifier. Since *Leptoceratopsidae* has never been proposed an alternative use, we formalize this definition.

***Marginocephalia* Sereno, 1986 [converted clade name]**

Registration number: 633

Definition. The smallest clade containing *Ceratops montanus* Marsh, 1888, *Triceratops horridus* Marsh, 1889 and *Pachycephalosaurus wyomingensis* (Gilmore, 1931). This is a minimum-clade definition. Abbreviated definition: min ∇ (*Ceratops montanus* Marsh, 1888 & *Triceratops horridus* Marsh, 1889 & *Pachycephalosaurus wyomingensis* [Gilmore, 1931]).

Reference phylogeny. Figure 16 of Han et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Marginocephalia* comprises members of the clades *Ceratopsia* and *Pachycephalosauria*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Marginocephalia* has been (informally) defined before (Currie and Padian, 1997; Sereno, 1998; Sereno, 2005; Madzia et al., 2018; Herne et al., 2019). These definitions, except for that of Herne et al. (2019), were minimum-clade and used *Ceratopsia* and *Pachycephalosauria* (Currie and Padian, 1997) or *Triceratops horridus* and *Pachycephalosaurus wyomingensis* (Sereno, 1998; Sereno, 2005; Madzia et al., 2018) as the internal specifiers. Madzia et al. (2018) further included *Ceratops montanus* as a third internal specifier, stating that “[t]he first definition of *Marginocephalia* was node-based and used ‘*Ceratopsia*’ and ‘*Pachycephalosauria*’ as the internal specifiers [...]. To follow the definition, and adhere to the ICPN (Art. 11), we have to use name-bearing species or their type specimens as specifiers which

makes the name to be anchored on the types of *Ceratops montanus* and *Pachycephalosaurus wyomingensis*. Even if *C. montanus* may be a *nomen dubium*, its type specimen is unequivocally nested deeply within Ceratopsia and thus its use does not change the extent of the name” (Madzia et al. [2018: Appendix 1]). In turn, Herne et al. (2019) preferred a maximum-clade definition with *T. horridus* and *P. wyomingensis* as the internal specifiers and *Parasaurolophus walkeri* as the external specifier, arguing that “[previous] definitions [were] not complementary with present definitions of Cerapoda and Ornithopoda within a node-stem triplet arrangement of clades” and that “re-definition of Marginocephalia as a stem now mirrors its sister stem clade, Ornithopoda, within a node-based Cerapoda. As a result, this stabilization of definition allows for the definitive assignment of all cerapodan OTUs either as ornithopods or marginocephalians” (Herne et al. [2019: Supplemental Text S1: 4]). However, *Marginocephalia* has never formed such ‘triplet’. Actually, when its use in a ‘node-branch triplet’ is considered, it is more closely tied with *Ceratopsia* and *Pachycephalosauria* rather than with *Cerapoda* and *Ornithopoda*. Here, the internal specifiers in the definition of *Marginocephalia* are used from among the taxa representing the two major subclades – *Ceratopsia* (*Ceratops montanus* and *Triceratops horridus*) and *Pachycephalosauria* (*Pachycephalosaurus wyomingensis*).



***Neoceratopsia* Sereno, 1986 [converted clade name]**

Registration number: 634

Definition. The largest clade containing *Triceratops horridus* Marsh, 1889 but not *Psittacosaurus mongoliensis* Osborn, 1923 and *Chaoyangsaurus youngi* Zhao et al., 1999. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Triceratops horridus* Marsh, 1889 ~ *Psittacosaurus mongoliensis* Osborn, 1923 & *Chaoyangsaurus youngi* Zhao et al., 1999).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure S1 of Knapp et al. (2018), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Neoceratopsia* comprises *Aquilops americanus*, *Archaeoceratops oshimai*, *Asiaceratops salsopaludalis*, *Auroraceratops rugosus*, ZPAL MgD-I/156 (= *Graciliceratops mongoliensis*), *Liaoceratops yanzigouensis*, *Mosaiceratops azumai*, *Stenopelix valdensis*, *Yamaceratops dorn gobiensis*, and members of the clades *Leptoceratopsidae* and *Coronosauria*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Neoceratopsia* has been (informally) defined before by Sereno (1998, 2005) who applied a maximum-clade definition and used *Triceratops horridus* as the internal specifier and *Psittacosaurus mongoliensis* as the external specifiers. We further include a second external specifier, *Chaoyangsaurus youngi*, to ensure that *Chaoyangsauridae*, a clade usually reconstructed as some of the basalmost ceratopsians (e.g., Han et al., 2018; Knapp et al., 2018; Yu et al., 2020), are maintained outside *Neoceratopsia*.

***Neoiguanodontia* Norman, 2014 [converted clade name]**

Registration number: 635

Definition. The smallest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881, *Hypselospinus fittoni* (Lydekker, 1889), and *Parasaurolophus walkeri* Parks 1922. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Hypselospinus fittoni* [Lydekker, 1889] & *Parasaurolophus walkeri* Parks 1922).

Reference phylogeny. Figure 2.26 of Norman (2014) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 48 of Norman (2015) and Figure 11 of McDonald et al. (2021).

Composition. Under the primary reference phylogeny, *Neoiguanodontia* comprises *Hypselospinus fittoni* and members of the clades *Iguanodontidae* and *Hadrosauroidea*.

Synonyms. *Neoiguanodontia* is a potential heterodefinitional synonym of *Hadrosauriformes*. If *Hypselospinus fittoni* nests within the smallest clade containing *Hadrosaurus foulkii* and *Iguanodon bernissartensis* (e.g., Verdú et al., 2018), the name *Hadrosauriformes* should have priority.

Comments. The application of *Neoiguanodontia* has been described and discussed by Madzia et al. (2020: Table 1). We therefore refer to that study for details.

***Neornithischia* Cooper, 1985 [converted clade name]**

Registration number: 636

Definition. The largest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 and *Triceratops horridus* Marsh, 1889 but not *Ankylosaurus magniventris* Brown, 1908 and

Stegosaurus stenops Marsh, 1887. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889 ~ *Ankylosaurus magniventris* Brown, 1908 & *Stegosaurus stenops* Marsh, 1887).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Neornithischia* comprises *Agilisaurus louderbacki*, *Hexinlusaurus multidentis*, *Hypsilophodon foxii*, *Kulindadromeus zabaikalicus*, *Leaellynasaura amicagraphica*, *Lesothosaurus diagnosticus*, *Othnielosaurus consors* (= *Nanosaurus agilis*; see Carpenter and Galton [2018]) *Yandusaurus hongheensis*, and members of the clades *Cerapoda*, *Jeholosauridae*, and *Thescelosauridae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Neornithischia* has been (informally) defined before (Serenó, 1998; Sereno, 2005; Butler et al., 2008; Herne et al., 2019). These definitions were maximum-clade and used *Triceratops horridus* (Serenó, 1998), *Parasaurolophus walkeri* (Butler et al., 2008) or both, *T. horridus* and *P. walkeri* (Serenó, 2005; Herne et al., 2019) as the internal specifiers, and *Ankylosaurus magniventris* (Serenó, 1998; Sereno, 2005; Herne et al., 2019) or *A. magniventris* and *Stegosaurus stenops* (Butler et al., 2008) as the external specifiers. In order to maintain the ‘node-branch triplet’ (‘node-stem triplet’ of Sereno [1998: 52–54]) comprising *Genasauria*, *Neornithischia*, and *Thyreophora* (all formally defined in the present paper), the internal specifiers in the definition of *Neornithischia* are used from among the taxa representing the two major subclades – *Ornithopoda* (*Iguanodon bernissartensis*) and *Marginocephalia* (*Triceratops horridus*) – and the external specifiers are used from among the taxa representing the thyreophoran clades *Ankylosauria* (*Ankylosaurus magniventris*) and *Stegosauria* (*Stegosaurus stenops*).

***Nodosauridae* Marsh, 1890 [converted clade name]**

Registration number: 637

Definition. The largest clade containing *Nodosaurus textilis* Marsh, 1889 but not *Ankylosaurus magniventris* Brown, 1908. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Nodosaurus textilis* Marsh, 1889 ~ *Ankylosaurus magniventris* Brown, 1908).

Reference phylogeny. Figure 5 of Rivera-Sylva et al. (2018a) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Thompson et al. (2012), Figure 11 of Arbour and Currie (2016), Figure 1 of Arbour et al. (2016), Figure 3 of Brown et al. (2017).

Composition. Under the primary reference phylogeny, *Nodosauridae* comprises *Dongyangopelta yangyanensis*, *Gastonia burgei*, *Gargoyleosaurus parkpinorum*, and members of the clades *Nodosaurinae* and *Polacanthinae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Nodosauridae* has been (informally) defined before by Sereno (1998, 2005) who used *Panoplosaurus mirus* (Sereno, 1998) or *P. mirus* and *Nodosaurus textilis* Sereno (2005) as the internal specifiers and *Ankylosaurus magniventris* as the external specifier. Considering that all phylogeny reconstructions that include *P. mirus* and *N. textilis* indicate that these taxa are more closely related to each other than either is to *A. magniventris* (or placed outside the *Ankylosauridae* + *Nodosauridae* node), we use a definition that incorporates *Nodosaurus textilis* as the sole internal specifier.

***Nodosaurinae* Abel, 1919 [converted clade name]**

Registration number: 638

Definition. The largest clade containing *Nodosaurus textilis* Marsh, 1889, but not *Hylaeosaurus armatus* Mantell, 1833, *Mymoorapelta maysi* Kirkland & Carpenter, 1994, and *Polacanthus foxii* Fox, 1866. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Nodosaurus textilis* Marsh, 1889 ~ *Hylaeosaurus armatus* Mantell, 1833 & *Mymoorapelta maysi* Kirkland & Carpenter, 1994 & *Polacanthus foxii* Fox, 1866).

Reference phylogeny. Figure 5 of Rivera-Sylva et al. (2018a) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Thompson et al. (2012), Figure 11 of Arbour and Currie (2016), Figure 1 of Arbour et al. (2016), and Figure 3 of Brown et al. (2017).

Composition. Under the primary reference phylogeny, *Nodosaurinae* comprises *Acantholipan gonzalezi*, *Ahshislepelta minor*, *Niobrarasaurus coleii*, *Nodosaurus textilis*, *Peloroplites cedrimontanus*, *Sauropelta edwardsi*, *Silvisaurus condrayi*, *Taohelong jinchengensis*,

Tatankacephalus cooneyorum, members of the clades *Panoplosaurini* and *Struthiosaurini*, and the specimen CPC 273.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Nodosaurinae* has been (informally) defined before (Sereno, 1998; Sereno, 2005). Both these definitions were maximum-clade and used *Panoplosaurus* (Sereno, 1998) or *Panoplosaurus mirus* and *Nodosaurus textilis* as the internal specifiers and *Sarcolestes* and *Hylaeosaurus* (Sereno, 1998) or *Polacanthus foxii*, *Hylaeosaurus armatus*, and *Mymoorapelta maysi* as the external specifiers.

***Ornithischia* Seeley, 1888 [converted clade name]**

Registration number: 639

Definition. The largest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Allosaurus fragilis* Marsh, 1877b and *Camarasaurus supremus* Cope, 1877. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 \sim *Allosaurus fragilis* Marsh, 1877b & *Camarasaurus supremus* Cope, 1877).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 2 of Boyd (2015), Figure 1 of Baron et al. (2017a), Figure 1 of Baron et al. (2017b), and Figure 1 of Langer et al. (2017).

Composition. Under the primary reference phylogeny, *Ornithischia* comprises *Pisanosaurus mertii* and members of the clades *Heterodontosauridae* and *Genasauria*. Note, however, that the early evolution and basal branching of *Ornithischia* is currently unsettled. For example, *P. mertii*, may represent either a basal ornithischian (recently, e.g., Desojo et al. 2020) or a (non-dinosaur) silesaurid dinosauriform (Agnolín & Rozadilla 2018, Baron 2019). The same may be true for members of *Silesauridae*, a group often reconstructed as the sister taxon to *Dinosauria* (e.g., Nesbitt et al., 2010; Peacock et al., 2013; Ezcurra, 2016; Cau, 2018; Ezcurra et al., 2020), that have recently been inferred to represent basal representatives of *Ornithischia* (Pacheco et al., 2019; Müller & Garcia, 2020).

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ornithischia* has been (informally) defined before (Padian & May, 1993; Sereno, 1998; Weishampel, 2004; Norman et al., 2004a; Sereno, 2005; Baron et al., 2017a). These definitions were maximum-clade and used *Triceratops horridus* (Padian & May, 1993;

Sereno, 1998; Weishampel, 2004; Sereno, 2005; Baron et al., 2017a) or *Iguanodon bernissartensis* (Norman et al., 2004a) as the internal specifiers. In turn, “birds” (Padian & May, 1993), *Neornithes* (Sereno, 1998), *Tyrannosaurus* (Weishampel, 2004), *Cetiosaurus* (Norman et al., 2004a), *Passer domesticus* and *Saltasaurus loricatus* (Sereno, 2005), and *Passer domesticus* and *Diplodocus carnegii* (Baron et al., 2017a) were used as the external specifiers. Although both, *I. bernissartensis* and *T. horridus*, are clearly ‘traditional’ members of *Ornithischia*, we have selected the former as the internal specifier and *Allosaurus fragilis* and *Camarasaurus supremus* as the external specifiers. These specifiers are preferred because (a) they represent deeply nested taxa within their respective clades (*Ornithischia*, *Theropoda*, and *Sauropodomorpha*), (b) they have been historically associated with these clades, thus being their ‘traditional’ members, and (c) their phylogenetic placements are stable across studies. Two external specifiers, instead of one, are used due to the alternative topologies of dinosaur relationships (see, e.g., Baron et al., 2017a; Langer et al., 2017). Additionally, *Iguanodon bernissartensis* was used as the internal specifier in the formal definition of *Dinosauria* (Langer et al., 2020), considered therein as a ‘traditional’ representative of *Ornithischia*, and the external specifier in the formal definition of *Sauropodomorpha* (Fabbri et al., 2020), again considered therein as a ‘traditional’ representative of *Ornithischia*; *A. fragilis* was used as the internal specifier in the formal definitions of *Theropoda* (Naish et al. 2020) and *Saurischia* (Gauthier et al., 2020), and as the external specifier in the formal definition of *Sauropodomorpha* (Fabbri et al., 2020), considered in the latter two contributions as a ‘traditional’ representative of *Theropoda*; and *Camarasaurus supremus* was used as the internal specifier in the formal definition of *Saurischia* (Gauthier et al., 2020) and considered therein as a ‘traditional’ representative of *Sauropodomorpha*.

***Ornithopoda* Marsh, 1881 [converted clade name]**

Registration number: 640

Definition. The largest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Triceratops horridus* Marsh, 1889 and *Pachycephalosaurus wyomingensis* (Gilmore, 1931). This is a maximum-clade definition. Abbreviated definition: max ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 ~ *Triceratops horridus* Marsh, 1889 & *Pachycephalosaurus wyomingensis* [Gilmore, 1931]).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 16 of Han et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Ornithopoda* comprises *Burianosaurus augustai*, *Gideonmantellia amosanjuananae*, and members of the clades *Elasmaria* and *Iguanodontia*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Ornithopoda* has been (informally) defined before (Sereno, 1998; Norman et al., 2004b; Sereno, 2005; Butler et al. 2008; Herne et al. 2019). Two of these definitions were minimum-clade (Sereno, 1998; Sereno, 2005) and used *Parasaurolophus walkeri* and *Heterodontosaurus tucki* as the internal specifiers. Sereno (2005) further restricted the name to a hypothesis in which *P. walkeri* and *H. tucki* were more closely related to each other than either was to *Pachycephalosaurus wyomingensis*, *Triceratops horridus*, and *Ankylosaurus magniventris*. In turn, Norman et al. (2004b), Butler et al. (2008), and Herne et al. (2019) defined *Ornithopoda* as pertaining to the largest clade containing *Edmontosaurus regalis* (in Norman et al. [2004b]) or *P. walkeri* (in Butler et al. [2008] and Herne et al. [2019]) than to *T. horridus*. Herne et al. (2019) additionally included a second external specifier (*P. wyomingensis*). We selected a definition that follows Herne et al. (2019) in that it includes two external specifiers (*T. horridus* and *P. wyomingensis*, representatives of two clades closely related to ornithopods; i.e., *Ceratopsia* and *Pachycephalosauria*, respectively). However, we prefer to use *Iguanodon bernissartensis* as the internal specifier rather than *P. walkeri*, because the former is among the few taxa that have been considered a part of *Ornithopoda* when the name was being introduced in the literature (e.g., Marsh, 1882). The inclusion of a different internal specifier does not change the extent of *Ornithopoda* under any of the published phylogeny inferences.

Orodrominae Brown et al., 2013 [converted clade name]

Registration number: 641

Definition. The largest clade within *Hypsilophodontidae* ∨ *Thescelosauridae* containing *Orodromeus makelai* Horner & Weishampel, 1988 but not *Hypsilophodon foxii* Huxley, 1869 and *Thescelosaurus neglectus* Gilmore, 1913. This is a maximum-clade definition. Abbreviated

definition: $\max \nabla \in \textit{Hypsilophodontidae} \vee \textit{Thescelosauridae}$ (*Orodromeus makelai* Horner & Weishampel, 1988 ~ *Hypsilophodon foxii* Huxley, 1869 & *Thescelosaurus neglectus* Gilmore, 1913).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 25 of Herne et al. (2019) and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Orodrominae* comprises *Albertadromeus syntarsus*, *Changchunsaurus parvus*, *Haya griva*, *Koreanosaurus boseongensis*, *Orodromeus makelai*, *Oryctodromeus cubicularis*, *Zephyrosaurus schaffi*, and the ‘Kaiparowits orodromine’.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Orodrominae* has been (informally) defined before (Brown et al., 2013; Boyd, 2015). Both these definitions were maximum-clade and used *Orodromeus makelai* as the internal specifier and *Thescelosaurus neglectus* (Brown et al., 2013) or *Thescelosaurus neglectus* and *Parasaurolophus walkeri* (Boyd, 2015) as the external specifiers. Considering the ‘traditional concept’ of *Orodrominae*, as a subclade of *Thescelosauridae*/‘hypsilophodonts’, and keeping in mind the unstable phylogenetic position of *H. foxii* (e.g., Madzia et al., 2018), we apply *Orodrominae* only when it is inferred either within *Thescelosauridae* or *Hypsilophodontidae* (see Article 11.14 of the ICPN).

***Pachycephalosauria* Maryńska & Osmólska, 1974 [converted clade name]**

Registration number: 642

Definition. The largest clade containing *Pachycephalosaurus wyomingensis* (Gilmore, 1931) but not *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889. This is a maximum-clade definition. Abbreviated definition: $\max \nabla (\textit{Pachycephalosaurus wyomingensis}$ [Gilmore, 1931] ~ *Ceratops montanus* Marsh, 1888 & *Triceratops horridus* Marsh, 1889).

Reference phylogeny. Figure 27 of Schott and Evans (2017) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Evans et al. (2013), Figure 16 of Han et al. (2018), and Figure 1 of Dieudonné et al. (2020).

Composition. Under the primary reference phylogeny, *Pachycephalosauria* comprises *Wannanosaurus yanshiensis* and members of the clade *Pachycephalosauridae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Pachycephalosauria* has been (informally) defined before (Sereno, 1998; Maryańska et al., 2004; Sereno, 2005). These definitions were maximum-clade and used *Pachycephalosaurus* (Sereno, 1998) or *Pachycephalosaurus wyomingensis* (Maryańska et al., 2004; Sereno, 2005) as the internal specifiers and *Triceratops* (Sereno, 1998), *Triceratops horridus* (Maryańska et al., 2004), or *Triceratops horridus*, *Heterodontosaurus tucki*, *Hypsilophodon foxii*, and *Ankylosaurus magniventris* (Sereno, 2005) as the external specifiers. Even though the position of *Hypsilophodon foxii* and *Heterodontosaurus tucki* is indeed somewhat unstable (see, e.g., Madzia et al. [2018] and Dieudonné et al. [2020], respectively), and, for example, *Heterodontosauridae* were inferred to be more closely related to *P. wyomingensis* than to *T. horridus* (Dieudonné et al., 2020: Fig. 1), inclusion of these taxa among the external specifiers does not need to be necessary as it can be expected that *Pachycephalosauria*, as traditionally defined, may cover taxa that are markedly different from the Late Cretaceous members of the clade. We use a definition similar to that of Maryańska et al. (2004) but include *Ceratops montanus* as a second external specifier.

***Pachycephalosauridae* Sternberg, 1945 [converted clade name]**

Registration number: 643

Definition. The smallest clade containing *Pachycephalosaurus wyomingensis* (Gilmore, 1931) and *Stegoceras validum* Lambe, 1902, provided that it does not include *Heterodontosaurus tucki* Crompton and Charig, 1962. This is a minimum-clade definition. Abbreviated definition: min ∇ (*Pachycephalosaurus wyomingensis* [Gilmore, 1931] & *Stegoceras validum* Lambe, 1902 | ~ *Heterodontosaurus tucki* Crompton and Charig, 1962).

Reference phylogeny. Figure 27 of Schott and Evans (2017) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Evans et al. (2013) and Figure 3 of Williamson and Brusatte (2016).

Composition. Under the primary reference phylogeny, *Pachycephalosauridae* comprises *Acrotholus audeti*, *Alaskacephale gongloffii*, *Amtiocephale gobiensis*, *Colepiocephale lambei*, *Dracorex hogwartsia*, *Foraminacephale brevis*, *Goyocephale lattimorei*, *Hanssuesia sternbergi*, *Homalocephale calathocercos*, *Pachycephalosaurus wyomingensis*, *Prenocephale prenes*, *Sphaerotholus buchholtzae*, *Sphaerotholus goodwini*, *Stegoceras novomexicanum*, *Stegoceras validum*, *Stygimoloch spinifer*, and *Tylocephale gilmorei*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Pachycephalosauridae* has been (informally) defined before by Sereno (1998, 2005) who applied the minimum-clade definition and used *Pachycephalosaurus wyomingensis* and *Stegoceras validum* as the internal specifiers. This definition is followed here though we also include *Heterodontosaurus tucki* as an external specifier. Even though no phylogenetic analysis has ever reconstructed *H. tucki* or any other ‘traditional’ heterodontosaurid to be within the smallest clade containing *P. wyomingensis* and *S. validum*, *Heterodontosauridae* were inferred to be basal pachycephalosaurs (Dieudonné et al., 2020). The addition of *H. tucki* as an external specifier will therefore ensure that *Pachycephalosauridae* will never comprise *Heterodontosauridae*.

***Panoplosaurini* [new clade name]**

Registration number: 644

Definition. The largest clade containing *Panoplosaurus mirus* Lambe, 1919 but not *Nodosaurus textilis* Marsh, 1889 and *Struthiosaurus austriacus* Bunzel, 1871. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Panoplosaurus mirus* Lambe, 1919 ~ *Nodosaurus textilis* Marsh, 1889 & *Struthiosaurus austriacus* Bunzel, 1871).

Etymology. Derived from the stem of *Panoplosaurus* Lambe, 1919, the name of an included taxon, which combines the Greek words *pan* (all), *hoplon* (type of shield), and *sauros* (lizard, reptile).

Reference phylogeny. Figure 5 of Rivera-Sylva et al. (2018a) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 1 of Arbour et al. (2016), Figure 3 of Brown et al. (2017), and Figure 9 of Zheng et al. (2018).

Composition. Under the primary reference phylogeny, *Panoplosaurini* comprises *Animantarx ramaljonesi*, ‘*Denversaurus*’ *schlessmani*, *Edmontonia longiceps*, *Edmontonia rugosidens*, *Panoplosaurus mirus*, *Texasetes pleurohalio*, and the Argentinian ankylosaur.

Synonyms. The name *Panoplosaurinae* Nopcsa, 1929 has been recently suggested for the same clade (e.g., Rivera-Sylva et al., 2018a; see also ‘Comments’ below). Additionally, Bakker (1988) coined the name *Edmontoniinae* for *Edmontonia rugosidens*, *Edmontonia longiceps*, and *Denversaurus schlessmani* and *Edmontoniidae* to include *Edmontoniinae* and *Panoplosaurinae*;

no phylogenetic definition was proposed for either and neither clade name has been widely used since.

Comments. The grouping, here covered under the name *Panoplosaurini*, has previously been suggested to be named *Panoplosaurinae* (Rivera-Sylva et al., 2018a). No (informal) phylogenetic definition for *Panoplosaurinae* has ever been published in the peer-reviewed literature, though Burns (2015) proposed “all Late Cretaceous nodosaurids more closely related to *Panoplosaurus* than to *Pawpawsaurus*” in his dissertation, and the name itself has not been widely used. Bakker (1988) provided a diagnosis of *Panoplosaurinae*, as nodosaurids with lumpy armor and expanded internarial bridges, which contained the two species of *Panoplosaurus* he recognized (*Panoplosaurus mirus* and *Panoplosaurus* sp. 1, represented by ROM 1215). Alpha taxonomic reviews of the Campanian-Maastrichtian North American nodosaurids generally recognize *Panoplosaurus mirus*, *Edmontonia rugosidens*, and *Edmontonia loripiceps* as valid taxa (e.g., Carpenter, 2001) and these typically form a derived clade (e.g. Kirkland et al., 1998, Vickaryous et al., 2004; Thompson et al., 2012; Yang et al. 2013), sometimes with additional taxa such as *Texasetes* (Arbour et al., 2016; Rivera-Sylva et al., 2018a) or *Animantarx* (Hill et al., 2003). Rivera-Sylva et al. (2018a) noted that the grouping *Animantarx*, ‘*Denversaurus*’, *Edmontonia*, *Panoplosaurus*, *Texasetes*, and an unnamed Argentinian ankylosaur could bear the name *Panoplosaurinae*. In several recent analyses *Edmontonia* and *Panoplosaurus* are found as the sister clade to a clade containing *Struthiosaurus* (Arbour et al., 2016; Brown et al., 2017; Rivera-Sylva et al., 2018a), here named *Struthiosaurini* (see the name entry). Owing to the fact that the ‘*Panoplosaurus* clade’ is nested within *Nodosaurinae*, we prefer to use a name that implies a lesser inclusiveness. The suffix *-inae* (as in *Panoplosaurinae*) is typically associated with the rank of ‘subfamily’ under the ICZN. Therefore, the use of *Panoplosaurinae*, without discussing the phylogenetic context, may suggest that *Panoplosaurinae* represents a clade outside *Nodosaurinae*. When the widely used suffix *-ini* (typically associated with the rank of ‘tribe’) is applied, such confusion is eliminated.

***Parasaurolophini* Glut, 1997 [converted clade name]**

Registration number: 645

Definition. The largest clade containing *Parasaurolophus walkeri* Parks, 1922 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Lambeosaurus lambei* Parks, 1923 and

1597 *Tsintaosaurus spinorhinus* Young, 1958. This is a maximum-clade definition. Abbreviated
1598 definition: max ∇ (*Parasaurolophus walkeri* Parks, 1922 ~ *Aralosaurus tuberiferus*
1599 Rozhdestvensky, 1968 & *Lambeosaurus lambei* Parks, 1923 & *Tsintaosaurus spinorhinus*
1600 Young, 1958).

1601 **Reference phylogeny.** Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary
1602 reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al.
1603 (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of
1604 Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

1605 **Composition.** Under the primary reference phylogeny, *Parasaurolophini* comprises
1606 *Charonosaurus jiayinensis* and *Parasaurolophus* spp.

1607 **Synonyms.** No other taxon names are currently in use for the same or approximate clade.

1608 **Comments.** The name was first (informally) defined by Prieto-Márquez et al. (2013) who
1609 applied the maximum-clade definition and used *Parasaurolophus walkeri* as the internal
1610 specifier and *Lambeosaurus lambei*, *Tsintaosaurus spinorhinus*, and *Aralosaurus tuberiferus* as
1611 the external specifiers. We formalize this definition.

1612

1613 ***Polacanthinae* Lapparent & Lavocat, 1955 [converted clade name]**

1614 **Registration number:** 646

1615 **Definition.** The largest clade within *Ankylosauridae* or *Nodosauridae* containing *Polacanthus*
1616 *foxii* Fox, 1866 but not *Ankylosaurus magniventris* Brown, 1908 and *Nodosaurus textilis* Marsh,
1617 1889. This is a maximum-clade definition. Abbreviated definition: max $\nabla \in$ *Ankylosauridae* \vee
1618 *Nodosauridae* (*Polacanthus foxii* Fox, 1866 ~ *Ankylosaurus magniventris* Brown, 1908 &
1619 *Nodosaurus textilis* Marsh, 1889).

1620 **Reference phylogeny.** Figure 9 of Yang et al. (2013) is treated here as the primary reference
1621 phylogeny. Additional reference phylogenies include Figure 3 of Kirkland et al. (1998), Figure 2
1622 of Thompson et al. (2012), Figure 1 of Arbour et al. (2016), Figure 5 of Rivera-Sylva et al.
1623 (2018a), and Figure 9 of Zheng et al. (2018).

1624 **Composition.** Under the primary reference phylogeny, *Polacanthinae* comprises *Polacanthus*
1625 *foxii* and *Taohelong jinchengensis*.

1626 **Synonyms.** Wieland (1911) proposed the name *Polacanthidae* to include ankylosaurs that
1627 appeared intermediate between *Ankylosauridae* and *Nodosauridae*. Kirkland et al. (1998) were

the first to test this using cladistic methods and found ‘polacanthids’ to be a clade of basal ankylosaurids, and as such should preferably be called *Polacanthinae* rather than *Polacanthidae*, to eliminate the possible confusion that *Ankylosauridae* and *Polacanthidae* refer to mutually exclusive clades. Carpenter (2001) argued that *Polacanthidae* was instead valid and defined the name as all ankylosaurs closer to *Gastonia* than to *Edmontonia* or *Euoplocephalus*.

Comments. The name *Polacanthinae* was (informally) defined before by Yang et al. (2013), who used *Polacanthus foxii* as the internal specifier and *Ankylosaurus magniventris* and *Panoplosaurus mirus* as the external specifiers. Kirkland et al. (1998) diagnosed *Polacanthinae* as comprising ankylosaurs with an ankylosaurid-like skulls, nearly straight and parallel tooth rows, long basipterygoid processes, well-developed acromion arising from dorsal margin of scapula, ventrally flexed ischia, coossified pelvic osteoderms forming pelvic shield, pectoral osteoderms elongate spikes with posterior grooves, and caudal osteoderms large, elongate laterally directed, and with hollow bases. Kirkland et al. (1998) initially found *Polacanthinae* at the base of *Ankylosauridae* including *Gastonia*, *Polacanthus*, and *Mymoorapelta* and also referred *Hoplitosaurus* and *Hylaeosaurus* to the clade. Arbour et al. (2016), Rivera-Sylva et al. (2018a), and Zheng et al. (2018) inferred what could be called *Polacanthinae* at the base of *Nodosauridae*, including *Polacanthus foxii* and *Hoplitosaurus marshi*. *Polacanthinae* is poorly supported in most phylogenetic analyses yet frequently referenced in the literature. Taxa typically referred to as ‘polacanthines’ most often form a grade of basal nodosaurids (e.g., Thompson et al. 2012; Brown et al. 2017). Additional taxonomic and phylogenetic revisions are needed to provide an assessment of *Polacanthinae*. We define the name here to ensure that it is applicable either within *Ankylosauridae* or *Nodosauridae*. If the ‘*Polacanthus* clade’ is reconstructed outside the *Ankylosauridae* + *Nodosauridae* node, the name *Polacanthinae* becomes inapplicable and the preferred name for the grouping should probably be *Polacanthidae* (not defined here).

***Protoceratopsidae* Granger & Gregory, 1923 [converted clade name]**

Registration number: 647

Definition. The largest clade containing *Protoceratops andrewsi* Granger & Gregory, 1923 but not *Ceratops montanus* Marsh, 1888 and *Triceratops horridus* Marsh, 1889. This is a maximum-

clade definition. Abbreviated definition: max ∇ (*Protoceratops andrewsi* Granger & Gregory, 1923 ~ *Ceratops montanus* Marsh, 1888 & *Triceratops horridus* Marsh, 1889).

Reference phylogeny. Figure 10 of Morschhauser et al. (2019) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure S1 of Knapp et al. (2018), Figure 10 of Morschhauser et al. (2019), Figure 3 of Yu et al. (2020), and Figure 4 of Yu et al. (2020).

Composition. Under the primary reference phylogeny, *Protoceratopsidae* comprises *Bagaceratops rozhdestvenskyi*, *Magnirostris dodsoni* (?= *Bagaceratops rozhdestvenskyi*; see Czepiński [2020]), and *Protoceratops* spp.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Protoceratopsidae* has been (informally) defined before by Sereno (1998, 2005) who applied a maximum-clade definition and used *Protoceratops andrewsi* as the internal specifier and *Triceratops horridus* as the external specifier. We include an additional external specifier, *Ceratops montanus*, because the name *Protoceratopsidae* has been traditionally applied to the sister taxon of *Ceratopsoidea*.

***Rhabdodontidae* Weishampel et al., 2003 [converted clade name]**

Registration number: 648

Definition. The smallest clade containing *Rhabdodon priscus* Matheron, 1869 and *Zalmoxes robustus* (Nopcsa, 1900). This is a minimum-clade definition. Abbreviated definition: min ∇ (*Rhabdodon priscus* Matheron, 1869 & *Zalmoxes robustus* [Nopcsa, 1900]).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 3 of Madzia et al. (2018), Figure 20 of Verdú et al. (2018), Figure 25 of Herne et al. (2019), Figure 2 of Dieudonné et al. (2020), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Rhabdodontidae* comprises *Rhabdodon priscus*, *Zalmoxes robustus*, *Zalmoxes shqiperorum*, *Mochlodon suessi*, and *Mochlodon vorosi*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Rhabdodontidae* was first (informally) defined by Weishampel et al. (2003: 69) who used the minimum-clade definition and selected *Rhabdodon priscus* and *Zalmoxes robustus* as the internal specifiers. Sereno (2005) later used a maximum-clade

definition, using *Rhabdodon priscus* as the internal specifier and *Parasaurolophus walkeri* as the external specifier. We formalize the former, minimum-clade, definition. A definition similar in effect to that of Sereno (2005) is applied to *Rhabdodontomorpha*.

***Rhabdodontomorpha* Dieudonné et al., 2016 [converted clade name]**

Registration number: 649

Definition. The largest clade containing *Rhabdodon priscus* Matheron, 1869 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881 and *Hypsilophodon foxii* Huxley, 1869. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Rhabdodon priscus* Matheron, 1869 \sim *Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Hypsilophodon foxii* Huxley, 1869).

Reference phylogeny. Figure 2 of Dieudonné et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 25 of Herne et al. (2019), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Rhabdodontomorpha* comprises *Muttaburrasaurus langdoni*, *Fostoria dhimbangunmal*, the ‘Vegagete ornithopod’, and members of the clade *Rhabdodontidae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The application of *Rhabdodontomorpha* has been described, and (informally) proposed definitions have been discussed, by Madzia et al. (2018: Appendix 1) and Madzia et al. (2020: Table 1). We therefore refer to these studies for details. Our formalized maximum-clade definition is similar to that of Madzia et al. (2020) in that it uses *Rhabdodon priscus* as the internal specifier and *Iguanodon bernissartensis* as the external specifier. We have further added a second external specifier, *Hypsilophodon foxii*, to prevent its inclusion to *Rhabdodontomorpha* under phylogenies similar to that of Norman (2015: Fig. 48).

***Saurolophinae* Brown, 1914a [converted clade name]**

Registration number: 650

Definition. The largest clade containing *Saurolophus osborni* Brown, 1912 but not *Lambeosaurus lambei* Parks, 1923, provided that it does not include *Hadrosaurus foulkii* Leidy, 1858. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Saurolophus osborni* Brown, 1912 \sim *Lambeosaurus lambei* Parks, 1923 | \sim *Hadrosaurus foulkii* Leidy, 1858).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Saurolophinae* comprises ?*Gryposaurus alsatei*, *Naashoibitosaurus ostromi*, members of the clades *Brachylophosaurini*, *Edmontosaurini*, *Kritosaurini*, and *Saurolophini*, and the specimen ‘PASAC 1 (‘Sabinosaur’)’.

Synonyms. Following the widespread application of the Principle of Coordination, under which *Hadrosaurinae* has to be attributed to Cope (1869), the name *Hadrosaurinae* is generally considered to have priority over *Saurolophinae*, even though the latter was coined four years earlier. In recent years, both *Hadrosaurinae* and *Saurolophinae*, have been used for the sister taxon of *Lambeosaurinae*. The selection of the proper name has traditionally depended on whether the clade includes *Hadrosaurus foulkii* or not (**Fig. 2**). In the cases in which *H. foulkii* falls within the smallest clade containing *Saurolophus osborni* and *Lambeosaurus lambei*, and within the ‘*Saurolophus* branch’, the name *Hadrosaurinae* is preferred (e.g., Cruzado-Caballero & Powell, 2017; Xing et al., 2017; Kobayashi et al., 2019; Zhang et al., 2020). However, when *H. foulkii* falls outside the clade, the name *Saurolophinae* is used (e.g., Prieto-Márquez et al., 2019; Prieto-Márquez et al., 2020; Kobayashi et al., 2021; McDonald et al., 2021).

Comments. The name *Saurolophinae* has been (informally) defined before by Prieto-Márquez (2010) who applied a maximum-clade definition and used *Saurolophus osborni* as the internal specifier and *Lambeosaurus lambei* and *Hadrosaurus foulkii* as the external specifiers. Here, we formalize a maximum-clade definition of *Saurolophinae* that applies the name to the sister clade of *Lambeosaurinae* only on the condition that it does not contain *H. foulkii*. In turn, the name *Hadrosaurinae* is defined to be used for the ‘*Saurolophus* branch’ when *H. foulkii* falls within the clade. Although our definition may be considered similar to that of Prieto-Márquez (2010) it differs substantially because under our definition, the name *Saurolophinae* may become inapplicable.

***Saurolophini* Glut, 1997 [converted clade name]**

Registration number: 651

Definition. The largest clade containing *Saurolophus osborni* Brown, 1912 but not *Brachylophosaurus canadensis* Sternberg, 1953, *Edmontosaurus regalis* Lambe, 1917, *Hadrosaurus foulkii* Leidy, 1858, and *Kritosaurus navajovius* Brown, 1910. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Saurolophus osborni* Brown, 1912 ~ *Brachylophosaurus canadensis* Sternberg, 1953 & *Edmontosaurus regalis* Lambe, 1917 & *Hadrosaurus foulkii* Leidy, 1858 & *Kritosaurus navajovius* Brown, 1910).

Reference phylogeny. Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 9 of Zhang et al. (2019), Figure 5 of Zhang et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 10 of Longrich et al. (2021).

Composition. Under the primary reference phylogeny, *Saurolophini* comprises *Augustynolophus morrisoni*, *Prosaurolophus maximus*, and *Saurolophus* spp.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Saurolophini* has been (informally) defined before (Sereno, 2005; Prieto-Márquez et al., 2014). Both these definitions were maximum-clade and used *Saurolophus osborni* as the internal specifier and *Edmontosaurus regalis* and *Maiasaura peeblesorum* (Sereno, 2005) or *Brachylophosaurus canadensis*, *Edmontosaurus regalis*, *Kritosaurus navajovius*, and *Lambeosaurus lambei* (Prieto-Márquez et al., 2014) as the external specifiers. Here we apply a definition similar to that of Prieto-Márquez et al. (2014) but remove *L. lambei* and instead add *Hadrosaurus foulkii*.

***Shamosaurinae* Tumanova, 1983 [converted clade name]**

Registration number: 652

Definition. The largest clade containing *Shamosaurus scutatus* Tumanova, 1983 and *Gobisaurus domoculus* Vickaryous et al., 2001 but not *Ankylosaurus magniventris* Brown, 1908. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Shamosaurus scutatus* Tumanova, 1983 & *Gobisaurus domoculus* Vickaryous et al., 2001 ~ *Ankylosaurus magniventris* Brown, 1908).

Reference phylogeny. Figure 11 of Arbour & Currie (2016) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 1 of Arbour et al. (2016), Figure 8 of Arbour & Evans (2017), and Figure 5 of Rivera-Sylva et al. (2018a).

Composition. Under the primary reference phylogeny, *Shamosaurinae* comprises *Gobisaurus domoculus* and *Shamosaurus scutatus*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. Tumanova (1987) described *Shamosaurinae* based on a list of diagnostic features; shamosaurines were ankylosaurids with narrow anterior snouts, angle of the orbital plane with the skull axis less than 25°, anterior wall of the pterygois inclined posteriorly, occipital condyle a wide oval, pterygoids fused with the basisphenoid, small interpterygoid fenestra, and orbits at the midlength of the skull. *Shamosaurinae* is not reconstructed in all recent phylogenetic analyses, as *Shamosaurus* and *Gobisaurus* are sometimes inferred as successive outgroups to *Ankylosaurinae* rather than as a clade (e.g. Thompson et al., 2012; Wiersma & Irmis, 2018). We provide a maximum-clade definition that makes *Shamosaurinae* applicable only under the topologies in which *Shamosaurus* and *Gobisaurus* are closely related to each other than either is to *Ankylosaurus*.

***Stegosauria* Marsh, 1877a [converted clade name]**

Registration number: 653

Definition. The largest clade containing *Stegosaurus stenops* Marsh, 1887 but not *Ankylosaurus magniventris* Brown, 1908. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Stegosaurus stenops* Marsh, 1887 ~ *Ankylosaurus magniventris* Brown, 1908).

Reference phylogeny. Figure 12 of Maidment et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 11 of Maidment et al. (2008), Figure 1 of Raven and Maidment (2017), and Figure 1 of Dieudonné et al. (2020).

Composition. Under the primary reference phylogeny, *Stegosauria* comprises *Isaberrysaura mollensis*, *Gigantspinosaursichuanensis*, and members of the clades *Stegosauridae* and *Huayangosauridae*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Stegosauria* has been (informally) defined before (Galton, 1997; Sereno, 1998; Galton and Upchurch, 2004; Sereno, 2005) using *Stegosaurus* (Galton, 1997; Sereno, 1998; Galton and Upchurch, 2004) or *Stegosaurus stenops* (Sereno, 2005) as the internal specifier and *Ankylosaurus* (Galton, 1997; Sereno, 1998), *Ankylosauria* (Galton and Upchurch, 2004), or *Ankylosaurus magniventris* (Sereno, 2005) as the external specifiers. Since *Stegosauria*

has never been proposed an alternative use, we use *S. stenops* as the internal specifier and *A. magniventris* as the external specifier.

***Stegosauridae* Marsh, 1880 [converted clade name]**

Registration number: 654

Definition. The largest clade containing *Stegosaurus stenops* Marsh, 1887 but not *Huayangosaurus taibaii* Dong et al., 1982. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Stegosaurus stenops* Marsh, 1887 \sim *Huayangosaurus taibaii* Dong et al., 1982).

Reference phylogeny. Figure 12 of Maidment et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 11 of Maidment et al. (2008) and Figure 1 of Raven and Maidment (2017).

Composition. Under the primary reference phylogeny, *Stegosauridae* comprises *Adratiklit boulahfa*, *Alcovasaurus longispinus*, *Dacentrurus armatus*, *Hesperosaurus mjosi*, *Jiangjunosaurus junggarensis*, *Kentrosaurus aethiopicus*, *Loricatosaurus priscus*, *Miragaia longicollum*, *Paranthodon africanus*, *Stegosaurus homheni*, *Stegosaurus stenops*, and *Tuojiangosaurus multispinus*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Stegosauridae* was first (informally) defined by Sereno (1998, 2005) who used the maximum-clade definition and selected *Stegosaurus stenops* as the internal specifier and *Huayangosaurus taibaii* as the external specifier. We formalize this definition.

***Struthiosaurini* [new clade name]**

Registration number: 655

Definition. The largest clade containing *Struthiosaurus austriacus* Bunzel, 1871 but not *Nodosaurus textilis* Marsh, 1889 and *Panoplosaurus mirus* Lambe, 1919. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Struthiosaurus austriacus* Bunzel, 1871 \sim *Nodosaurus textilis* Marsh, 1889 & *Panoplosaurus mirus* Lambe, 1919).

Etymology. Derived from the stem of *Struthiosaurus* Bunzel, 1871, the name of an included taxon, which combines the Latin words *struthio* (ostrich) and Greek *sauros* (lizard, reptile).

Reference phylogeny. Figure 5 of Rivera-Sylva et al. (2018a) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 1 of Arbour et al. (2016), Figure 3 of Brown et al. (2017), and Figure 9 of Zheng et al. (2018).

Composition. Under the primary reference phylogeny, *Struthiosaurini* comprises *Europelta carbonensis*, *Hungarosaurus tormai*, *Pawpawsaurus campbelli*, *Stegopelta landerensis*, and *Struthiosaurus* spp.

Synonyms. The name *Struthiosaurinae* Nopcsa, 1923 has been recently used for an approximate clade (Kirkland et al., 2013; Blows & Honeysett, 2014; Villanueva-Amadoz et al., 2015). No other taxon names are currently in use for the same or approximate clade.

Comments. A grouping similar to that covered here under the name *Struthiosaurini* has previously been named *Struthiosaurinae* (Kirkland et al., 2013). The name *Struthiosaurinae* was (informally) defined by Kirkland et al. (2013) who applied the maximum-clade definition and used *Europelta* as the internal specifier and *Cedarpelta*, *Peloroplites*, *Sauropelta*, and *Edmontonia* as the external specifiers. *Struthiosaurinae* was considered to represent the clade of Late Cretaceous European nodosaurids. However, Kirkland et al. (2013) did not include a character matrix or phylogenetic analysis in their study and have not yet published a follow-up paper with results indicating the extent of their *Struthiosaurinae*. They provided, however, a list of diagnostic characters. According to Kirkland et al. (2013), *Struthiosaurinae* includes nodosaurid ankylosaurs with narrow prementaries, nearly horizontal and unfused quadrates, quadrate condyls that are 3 times transversely wider than long, premaxillary teeth and dentary teeth that are near the prementary symphysis, dorsally arched sacra, an acromion process dorsal to the midpoint of the scapulocoracoid suture, straight ischia with a straight dorsal margin, long slender limbs, a sacral shield, and erect sacral osteoderms with flat bases. This suite of characters was considered to unite *Anoplosaurus*, *Europelta*, *Hungarosaurus*, and *Struthiosaurus*, but many of these characters have a broad distribution in *Ankylosauria* and *Nodosauridae* (Ösi, 2015). Arbour et al. (2016) reconstructed a clade containing *Ahshislepelta*, *Europelta*, *Hungarosaurus*, *Niobrarasaurus*, *Nodosaurus*, *Pawpawsaurus*, *Stegopelta*, *Struthiosaurus*, and the ‘Paw Paw juvenile’ as the sister clade to that containing *Edmontonia*, which would thus be considered *Struthiosaurinae*. Brown et al. (2017) added *Borealopelta* to Arbour et al. (2016) and reconstructed a clade of *Borealopelta*, *Europelta*, *Hungarosaurus*, and *Pawpawsaurus*; *Stegopelta* and *Struthiosaurus* were outside of this clade and sister to *Edmontonia*,

‘*Denversaurus*’, and *Panoplosaurus*. As was the case with *Panoplosaurinae*, owing to the fact that the ‘*Struthiosaurus* clade’ is nested within *Nodosaurinae*, we prefer to use a name that implies a lesser inclusiveness (that is, *-ini* rather than *-inae*). The use of *Struthiosaurinae*, without discussing the phylogenetic context, may suggest that *Struthiosaurinae* and *Nodosaurinae* are mutually exclusive clades. When the suffix *-ini* is applied, such confusion is eliminated. Note that the recent use of *Struthiosaurinae* has been largely limited to mentions of Kirkland et al.’s (2013) application of the name (Blows & Honeysett, 2014; Villanueva-Amadoz et al., 2015).

***Styracosterna* Sereno, 1986 [converted clade name]**

Registration number: 656

Definition. The largest clade containing *Iguanodon bernissartensis* Boulenger in Beneden, 1881 but not *Camptosaurus dispar* (Marsh, 1879). This is a maximum-clade definition. Abbreviated definition: max ∇ (*Iguanodon bernissartensis* Boulenger in Beneden, 1881 \sim *Camptosaurus dispar* [Marsh, 1879]).

Reference phylogeny. Figure 12 of Madzia et al. (2020) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 20 of Verdú et al. (2018), Figure 11 of McDonald et al. (2021), and Figure 9 of Verdú et al. (2021).

Composition. Under the primary reference phylogeny, *Styracosterna* comprises *Cedrorestes crichtoni*, *Cumnoria prestwichii*, *Dakotadon lakotaensis*, *Draconyx loureioi*, *Fukuisaurus tetoriensis*, *Hippodraco scutodens*, *Iguanacolossus fortis*, *Lanzhousaurus magnidens*, *Muttaburrasaurus langdoni*, *Osmakasaurus depressus*, *Owenodon hoggii*, *Planicoxa venenica*, *Theiophytalia kerri*, *Uteodon aphanoecetes*, *Yunganglong datongensis*, and members of the clade *Hadrosauriformes*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Styracosterna* was first (informally) defined by Sereno (1998: 62) who used the maximum-clade definition and selected *Parasaurolophus* as the internal specifier and *Camptosaurus* as the external specifier. We prefer to use *Iguanodon bernissartensis* as the external specifier to maintain the ‘node-branch triplet’ (‘node-stem triplet’ of Sereno [1998: 52–54]) comprising *Ankylopollexia*, *Camptosauridae*, and *Styracosterna* (all formally defined in the

present paper). The inclusion of a different external specifier does not change the extent of *Styracosterna* under any of the published phylogeny inferences.

***Thescelosauridae* Sternberg, 1937 [converted clade name]**

Registration number: 657

Definition. The largest clade containing *Thescelosaurus neglectus* Gilmore, 1913 and *Orodromeus makelai* Horner & Weishampel, 1988 but not *Iguanodon bernissartensis* Boulenger in Beneden, 1881, provided that it does not include *Hypsilophodon foxii* Huxley, 1869. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Thescelosaurus neglectus* Gilmore, 1913 & *Orodromeus makelai* Horner & Weishampel, 1988 \sim *Iguanodon bernissartensis* Boulenger in Beneden, 1881 | \sim *Hypsilophodon foxii* Huxley, 1869).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 25 of Herne et al. (2019) and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Thescelosauridae* comprises members of the clades *Thescelosaurinae* and *Orodrominae*.

Synonyms. The name *Parksosauridae* Buchholz, 2002 has been used recently for the same contents (Boyd, 2015; Rivera-Sylva et al., 2018b). No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Thescelosauridae* has been (informally) defined before (Brown et al., 2013; Madzia et al., 2018). Both these definitions were minimum-clade and used *Thescelosaurus neglectus* and *Orodromeus makelai* as the internal specifiers. Madzia et al. (2018) further added one external specifier, *Iguanodon bernissartensis*, to ensure that the name is applicable under multiple phylogenetic hypotheses (see Madzia et al. [2018: Appendix 1] for details). We apply a complex maximum-clade definition, rather than a minimum-clade definition similar to those proposed before, to ensure that *Thescelosauridae* is not inferred within *Hypsilophodontidae* under a topology in which *Hypsilophodon* is the sister taxon to the *Thescelosaurinae* + *Orodrominae* node. Even though no such phylogenetic hypothesis has been proposed, the placements of taxa ‘traditionally’ dubbed the ‘hypsilophodonts’ is highly pliable across studies (Han et al., 2018; Madzia et al., 2018; Herne et al., 2019; Dieudonné et al., 2020) and often differ significantly even under different tree-search methods of a single dataset. Therefore, it can be

expected that phylogeny inferences of the rootward neornithischian-ornithomimid transitional segment of the ornithischian phylogenetic trees may result in such topology at some point.

***Thescelosaurinae* Sternberg, 1940 [converted clade name]**

Registration number: 658

Definition. The largest clade within *Hypsilophodontidae* or *Thescelosauridae* containing *Thescelosaurus neglectus* Gilmore, 1913 but not *Hypsilophodon foxii* Huxley, 1869 and *Orodromeus makelai* Horner & Weishampel, 1988. This is a maximum-clade definition. Abbreviated definition: $\max \nabla \in \text{Hypsilophodontidae} \vee \text{Thescelosauridae}$ (*Thescelosaurus neglectus* Gilmore, 1913 \sim *Hypsilophodon foxii* Huxley, 1869 & *Orodromeus makelai* Horner & Weishampel, 1988).

Reference phylogeny. Figure 4 of Madzia et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 25 of Herne et al. (2019) and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Thescelosaurinae* comprises *Notohypsilophodon comodorensis*, *Parksosaurus warreni*, and *Thescelosaurus* spp.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Thescelosaurinae* has been (informally) defined before (Brown and Druckenmiller, 2011; Boyd, 2015). Both these definitions were maximum-clade and used *Thescelosaurus neglectus* as the internal specifier and *Orodromeus makelai* and *Hypsilophodon foxii* (Brown and Druckenmiller, 2011) or *Orodromeus makelai* and *Parasaurolophus walkeri* (Boyd, 2015) as the external specifiers. Considering the ‘traditional concept’ of *Thescelosaurinae*, as a subclade of *Thescelosauridae*/‘hypsilophodonts’, and keeping in mind the unstable phylogenetic position of *H. foxii* (e.g., Madzia et al., 2018), we apply *Thescelosaurinae* only when it is inferred either within *Thescelosauridae* or *Hypsilophodontidae* (see Article 11.14 of the ICPN).

***Thyreophora* Nopcsa, 1915 [converted clade name]**

Registration number: 659

Definition. The largest clade containing *Ankylosaurus magniventris* Brown, 1908 and *Stegosaurus stenops* Marsh, 1887 but not *Iguanodon bernissartensis* Boulenger in Beneden,

1881 and *Triceratops horridus* Marsh, 1889. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Ankylosaurus magniventris* Brown, 1908 & *Stegosaurus stenops* Marsh, 1887 ~ *Iguanodon bernissartensis* Boulenger in Beneden, 1881 & *Triceratops horridus* Marsh, 1889).

Reference phylogeny. Figure 16 of Han et al. (2018) is treated here as the primary reference phylogeny. Additional reference phylogenies include Figure 4 of Madzia et al. (2018), Figure 25 of Herne et al. (2019), Figure 1 of Dieudonné et al. (2020), and Figure 57 of Barta & Norell (2021).

Composition. Under the primary reference phylogeny, *Thyreophora* comprises *Scutellosaurus lawleri*, *Emausaurus ernsti*, *Scelidosaurus harrisonii*, and members of the clade *Eurypoda*.

Synonyms. No other taxon names are currently in use for the same or approximate clade.

Comments. The name *Thyreophora* has been (informally) defined before (Serenó, 1998; Sereno, 2005; Norman, 2021). All these definitions were maximum-clade. The definitions of Sereno (1998; 2005) used *Ankylosaurus magniventris* as the internal specifiers, and *Triceratops horridus* (Serenó, 1998) or *T. horridus*, *Parasaurolophus walkeri*, and *Pachycephalosaurus wyomingensis* (Serenó, 2005) as the external specifiers. In turn, Norman (2021) defined *Thyreophora* using *Euoplocephalus* and *Stegosaurus* as the internal specifiers and *Hypsilophodon* as the external specifier. In order to maintain the ‘node-branch triplet’ (‘node-stem triplet’ of Sereno [1998: 52–54]) comprising *Genasauria*, *Neornithischia*, and *Thyreophora* (all formally defined in the present paper), the internal specifiers in the definition of *Thyreophora* are used from among the taxa representing the two major subclades – *Ankylosauria* (*Ankylosaurus magniventris*) and *Stegosauria* (*Stegosaurus stenops*) – and the external specifiers are used from among the taxa representing the neornithischian clades *Ornithopoda* (*Iguanodon bernissartensis*) and *Marginocephalia* (*Triceratops horridus*).

***Tsintaosaurini* Prieto-Márquez et al., 2013 [converted clade name]**

Registration number: 660

Definition. The largest clade containing *Tsintaosaurus spinorhinus* Young, 1958 and *Pararhabdodon isonensis* Casanovas Cladellas et al., 1993 but not *Aralosaurus tuberiferus* Rozhdestvensky, 1968, *Lambeosaurus lambei* Parks, 1923 and *Parasaurolophus walkeri* Parks, 1922. This is a maximum-clade definition. Abbreviated definition: max ∇ (*Tsintaosaurus spinorhinus* Young, 1958 & *Pararhabdodon isonensis* Casanovas Cladellas et al., 1993 ~

1996 *Aralosaurus tuberiferus* Rozhdestvensky, 1968 & *Lambeosaurus lambei* Parks, 1923 &
1997 *Parasaurolophus walkeri* Parks, 1922).

1998 **Reference phylogeny.** Figure 18 of Prieto-Márquez et al. (2020) is treated here as the primary
1999 reference phylogeny. Additional reference phylogenies include Figure 20 of Xing et al. (2017),
2000 Figure 5 of Kobayashi et al. (2019), Figure 11 of Prieto-Márquez et al. (2019), Figure 5 of Zhang
2001 et al. (2020), Figure 7 of Kobayashi et al. (2021), and Figure 11 of McDonald et al. (2021).

2002 **Composition.** Under the primary reference phylogeny, *Tsintaosaurini* comprises
2003 *Pararhabdodon isonensis* and *Tsintaosaurus spinorhinus*.

2004 **Synonyms.** No other taxon names are currently in use for the same or approximate clade.

2005 **Comments.** The name was first (informally) defined by Prieto-Márquez et al. (2013) who
2006 applied the minimum-clade definition and used *Pararhabdodon isonensis* and *Tsintaosaurus*
2007 *spinorhinus* as the internal specifiers. We preserve the original intent of Prieto-Márquez et al.
2008 (2013) but prefer to use the maximum-clade definition. *Pararhabdodon isonensis* and
2009 *Tsintaosaurus spinorhinus* are used as the internal specifiers and representatives of *Aralosaurini*
2010 (*Aralosaurus tuberiferus*), *Lambeosaurini* (*Lambeosaurus lambei*), and *Parasaurolophini*
2011 (*Parasaurolophus walkeri*), as the external specifiers. The name *Tsintaosaurini* is inapplicable
2012 under some recent phylogenies (Prieto-Márquez et al., 2019; Longrich et al., 2021).

2013

2014 Discussion

2015 Phylogeny reconstructions of some ornithischian clades currently face challenges that have an
2016 impact on the construction of the phylogenetic definitions of several taxon names. Below, we
2017 provide discussion of some topological conflicts.

2018

2019 The phylogeny of early-diverging ornithischians



2020 The early evolution of *Ornithischia* and the phylogenetic relationships of taxa nested near the
2021 base of the clade are currently contentious, particularly with respect to the potential Triassic
2022 members of the clade. Ornithischians have been ‘traditionally’ represented by a single
2023 undisputed Triassic taxon, *Pisanosaurus mertii* Casamiquela, 1967. Recent reassessments of the
2024 type specimen of *P. mertii* showed, however, that the morphological features of the taxon are
2025 rather difficult to interpret and that it may represent either, a non-dinosaur dinosauriform from

the clade *Silesauridae* (Agnolín & Rozadilla, 2018, Baron, 2019) or a basal ornithischian (Desojo et al., 2020). Even if *P. mertii* turns out to be a silesaurid, however, it may still represent an early-diverging ornithischian dinosaur as a few studies have proposed that silesaurids, a group of Anisian–?Rhaetian (Middle and Late Triassic) dinosauriforms that are usually inferred to be the sister group to dinosaurs (e.g., Nesbitt et al., 2010; Peacock et al., 2013; Ezcurra, 2016; Cau, 2018; Ezcurra et al., 2020), may form an early clade of ornithischians (Langer and Ferigolo, 2013; Cabreira et al., 2016; Pacheco et al., 2019) or a paraphyletic assemblage of taxa successively acquiring the ‘early ornithischian’ body plan (Müller and Garcia, 2020). Such placement of the silesaurid taxa would have considerable implications for the early evolution of dinosaurs as a whole because neither of the two other major dinosaur clades, theropods and sauropodomorphs, are known from the Middle Triassic. Pending additional studies, more focused on the basal dinosauriform-dinosaur transition, we do not define neither *Silesauridae* Langer et al., 2010 nor the recently proposed name *Sulcimentisauria* Martz and Small, 2019. If formal definitions for the names are to be proposed in the future, the definitions should comply with all recently proposed phylogenies, including the possible paraphyletic ‘dissolution’ of *Silesauridae* (Müller and Garcia, 2020) that would make *Sulcimentisauria*, as (informally) defined by Martz and Small (2019), applicable to a clade containing the vast majority of ‘traditional’ silesaurids and all ‘core’ ornithischians. One option is to restrict the use of *Sulcimentisauria* for a clade only when inferred within *Silesauridae* (e.g., ‘ $\max \nabla \in Silesauridae$ (*Silesaurus opolensis* Dzik, 2003 ~ *Asilisaurus kongwe* Nesbitt et al., 2010)’), as originally intended by Martz and Small (2019).

The phylogenetic placement of *Heterodontosauridae*


The members of *Heterodontosauridae* have long been treated as early-diverging ornithomorphs (e.g., Sereno, 1986, 1998, 1999). The last two decades have shown, however, that heterodontosaurids represent some of the more problematic ornithischian groups; with some studies inferring them as non-ornithomorph neornithischians (Butler, 2005), as the sister group to *Marginocephalia* (Xu et al., 2006), near the base of *Ornithischia* (e.g., Butler et al., 2008; Boyd, 2005; Sereno, 2012; Dieudonné et al., 2016; Han et al., 2018; Madzia et al., 2018; Herne et al., 2019), and within *Pachycephalosauria* (Dieudonné et al., 2020). The recent reconstruction of

heterodontosaurids as basal pachycephalosaurs by Dieudonné et al. (2020) is particularly puzzling, given that such placement would also substantially prolong some other ornithischian lineages, including *Ornithopoda* and *Ceratopsia*, to the Early Jurassic. It is worth noting, however, that *Heterodontosauridae*, as reconstructed in Dieudonné et al. (2020), are not paraphyletic (*contra* Dieudonné et al. [2020]). Even though some taxa that are usually inferred as members of *Heterodontosauridae* (*Echinodon becklesii* and *Tianyulong confuciusi*) are placed more closely to pachycephalosaurids in Dieudonné et al. (2020: Fig. 1), *Heterodontosauridae* still form a clade, comprising *Abriotosaurus consors*, *Fruitadens haagarorum*, *Heterodontosaurus tucki*, and *Lycorhinus angustidens*. Similarly, under the topology of Xu et al. (2006), heterodontosaurids and marginocephalians were inferred as the sister taxa, forming a clade named *Heterodontosauriformes*. Such topology has not been supported in more recent studies (see studies cited above). While the name may prove useful in the future, it is currently of little use and is not defined here.


Regardless of which of the hypotheses will gain further support in subsequent studies, the definition of the name *Heterodontosauridae* needs to reflect each of them. Therefore, the applied phylogenetic definition of the name includes representatives of all major ornithischian lineages, *Ceratopsia* (*Triceratops horridus*), *Ornithopoda* (*Iguanodon bernissartensis*), *Pachycephalosauria* (*Pachycephalosaurus wyomingensis*), and *Thyreophora* (*Stegosaurus stenops*).

The early-diverging thyreophorans and ankylosaurs

The ‘armored’ dinosaurs, *Thyreophora*, comprise two major clades, *Ankylosauria* and *Stegosauria*, and other taxa that are more closely related to members of the two species-rich lineages than to ornithopods and marginocephalians. These include *Emausaurus ernsti*, *Scelidosaurus harrisonii*, and *Scutellosaurus lawleri* (e.g., Han et al., 2018; Herne et al., 2019; Madzia et al., 2018; Dieudonné et al., 2020), and some other, more problematic taxa, such as the dubious ‘*Tatisaurus oehleri*’ (Norman et al., 2007) and ‘*Bienosaurus lufengensis*’ (Raven et al., 2019). Additionally, *Lesothosaurus diagnosticus* and *Laquintasaura venezuelae* have previously been inferred as basal thyreophorans as well (e.g., Butler et al. [2008] and Baron et al. [2017c], respectively). More recent studies, however, place *Le. diagnosticus* as an early neornithischian (e.g., Madzia et al., 2018; Herne et al., 2019) or a basal ornithischian in general (e.g., Han et al.,

2088 2018; Dieudonné et al., 2020), and *La. venezuelae* as a basal ornithischian (e.g., Han et al., 2018;
 2089 Dieudonné et al., 2020).
 2090 Following his thorough redescription of *Scelidosaurus harrisonii* (Norman, 2020a, 2020b,
 2091 2020c), Norman (2021) assessed the phylogenetic relationships of early-diverging thyreophorans
 2092 and reconstructed *E. ernsti*, *Sce. harrisonii*, and *Scu. lawleri* as the basalmost
 2093 ankylosauromorphs (*Ankylosauria sensu* this study), restricting the name *Ankylosauria* to a more
 2094 inclusive clade, approximately comprising ankylosaurids and nodosaurids (two definitions – one
 2095 minimum-clade and one maximum-clade – were provided; both applying the name to the same
 2096 known contents). Norman (2021: 70) further noted that the node comprising ankylosaurids and
 2097 nodosaurids “has the potential to become the new taxon Euankylosauria but this additional clade
 2098 name is neither essential nor particularly desirable”.
 2099 When applying a minimum-clade definition (e.g., ‘min ∇ (*Ankylosaurus magniventris* Brown,
 2100 1908 & *Nodosaurus textilis* Marsh, 1889)’), the name *Euankylosauria* may indeed be useful in
 2101 the future, especially if further studies support the placement of some taxa, such as
 2102 *Mymoorapelta maysi* and *Kunbarrasaurus ieveresi* (as in Arbour and Currie [2016]), or *E. ernsti*,
 2103 *Sce. harrisonii*, and *Scu. lawleri* (as in Norman [2020c]), as non-ankylosaurid/non-nodosaurid
 2104 ankylosaurs. However, there is no need to replace *Ankylosauria* with *Ankylosauromorpha* as the
 2105 name for the maximum-clade taxon containing *A. magniventris* but not *Stegosaurus stenops*. The
 2106 branch has long been named *Ankylosauria* and it has always been expected that it may contain
 2107 taxa with characters that are absent in ‘traditional’ ankylosaurs (i.e., ankylosaurids and
 2108 nodosaurids). We suggest that the name *Ankylosauromorpha* is abandoned. 

2110 **Problematic clades within *Ankylosauria***

2111 Comprehensive alpha taxonomic reviews and phylogenetic analyses of *Ankylosauridae* in recent
 2112 years have clarified many of the interrelationships within this clade (e.g., Arbour & Currie 2013;
 2113 Arbour & Currie 2016). However, similar reviews for *Nodosauridae* have not been undertaken in
 2114 recent years, and phylogenetic resolution within *Nodosauridae* is often poor and inconsistent
 2115 between different phylogenies (e.g., Thompson et al., 2012; Arbour et al., 2016; Brown et al.,
 2116 2017), in part because many recent ankylosaur phylogenetic analyses are modified from Arbour
 2117 & Currie (2016) which was designed to test relationships within *Ankylosauridae*, not 
 2118 *Nodosauridae*. Additionally, many names for clades within *Nodosauridae* have been introduced

by various authors based on proposed diagnostic characters rather than phylogenetic hypotheses, and have not been defined phylogenetically. In particular, the validity of *Polacanthidae* or *Polacanthinae*, *Sauropeltinae*, *Struthiosaurinae*, and *Stegopeltinae*, and the contents of *Edmontiniinae* or *Panoplosaurinae*, are unclear. In this manuscript we provide formal definitions of *Polacanthinae*, and revise the use of *Struthiosaurinae* and *Panoplosaurinae*, as the names have been mentioned recently with some frequency and have had informal definitions proposed previously. Ford (2000) introduced the names *Sauropeltinae* and *Stegopeltinae* and provided diagnostic characters but did not test their contents phylogenetically; *Sauropeltinae* included *Sauropelta edwardsorum* and *Silvisaurus condrayi* and *Stegopeltinae* included *Aletopelta coombsi*, *Glyptodontopelta mimus*, and *Stegopelta landerensis*. *Sauropelta* and *Silvisaurus* do not form a clade in any recent analyses, nor do *Stegopelta*, *Glyptodontopelta*, and *Aletopelta*. As such, we do not provide formal definitions for *Sauropeltinae* or *Stegopeltinae* at this time.

The origin of *Ornithopoda*

The understanding of the origin and early evolution of *Ornithopoda* is tightly connected with the knowledge of the character distribution among rootward neornithischians. With that respect, the basal neornithischian-ornithopod transition is among the poorest known stages of the ornithischian evolutionary history, as recent phylogenetic studies that focused on that particular tree segment provided strikingly conflicting topologies (e.g., Boyd, 2005; Dieudonné et al., 2016; Han et al., 2018; Madzia et al., 2018; Herne et al., 2019; Dieudonné et al., 2020). Substantial conflicts are apparent especially with regards to the phylogenetic placements of taxa ‘traditionally’ dubbed the ‘hypsilophodonts’ (compare, e.g., Boyd [2015], Han et al. [2018], and Herne et al. [2019]), including *Hypsilophodon foxii* itself (e.g., Madzia et al., 2018). Phylogeny reconstructions of ornithopods provide more stable results around the node marking the origin of *Iguanodontia* (e.g., Madzia et al., 2018; Madzia et al., 2020), although alternative hypotheses of early iguanodontian phylogenetic relationships exist as well (e.g., Norman, 2015). The names of non-cerapod neornithischian and rootward ornithopod clades are defined here to reflect these uncertainties though we recognize that some potential topologies may still render issues. For example, if *Hypsilophodon* forms a clade with thescelosaurids but falls outside the *Thescelosaurus* + *Orodromeus* node, *Hypsilophodontidae* would cover *Thescelosauridae* if the latter name was defined using a minimum-clade definition (as in Brown et al. [2013] and Madzia

et al. [2018]). We do not include *T. neglectus* as an external specifier in the definition of *Hypsilophodontidae* because under the scenario, in which *H. foxii* would be inferred within the *Thescelosaurus* + *Orodromeus* node, the names *Thescelosauridae*, *Thescelosaurinae*, and *Orodrominae* would be all inapplicable, while *Hypsilophodontidae* could effectively remain in use only for *H. foxii*. The definitions we propose ensure that if *H. foxii* is component of the *Thescelosaurus* + *Orodromeus* clade, *Thescelosauridae* becomes inapplicable, while *Thescelosaurinae* and *Orodrominae* still remain in use. The potential issue with *Hypsilophodontidae* covering *Thescelosauridae* under a topology in which *Hypsilophodon* is the sister taxon to the *Thescelosaurus* + *Orodromeus* node was solved by providing *Thescelosauridae* with a maximum-clade definition that makes it inapplicable under such scenario.

Hadrosaurid ingroup relationships

Hadrosaurids are some of the most intensively researched ornithischians, with thoroughly explored phylogenetic relationships. Recent studies almost uniformly infer seven major hadrosaurid clades: *Brachylophosaurini*, *Edmontosaurini*, *Kritosaurini*, *Lambeosaurini*, *Parasaurolophini*, *Saurolophini*, and *Tsintaosaurini* (e.g., Freedman Fowler & Horner, 2015; Prieto-Márquez et al., 2016; Xing et al., 2017; Kobayashi et al., 2019; Prieto-Márquez et al., 2019; Prieto-Márquez et al., 2020; Zhang et al., 2020; Kobayashi et al., 2021; Longrich et al., 2021; McDonald et al., 2021). Longrich et al. (2021) recently introduced a new clade name, *Arenysaurini*, for a diverse grouping of mostly European lambeosaurines, resulting, at the same time, in that *Tsintaosaurini* (as originally used and as defined here) becomes inapplicable. The study of Longrich et al. (2021) was first to infer such topology. Other phylogenetic studies usually place *Arenysaurus ardevoli* either deeply within *Lambeosaurini* (e.g., Prieto-Márquez et al., 2016; Prieto-Márquez et al., 2019; Zhang et al., 2019; Prieto-Márquez et al., 2020) or as the sister taxon to the clade uniting *Lambeosaurini* and *Parasaurolophini* (e.g., Cruzado-Caballero & Powell, 2017; Xing et al., 2017; Kobayashi et al., 2019; Zhang et al., 2020). Owing to the fact that the consensus regarding the placement of *Arenysaurus ardevoli* among lambeosaurines has yet to be reached, and that other ‘arenysaurins’ of Longrich et al. (2021) are distributed across the lambeosaurine tree in other studies, we do not define *Arenysaurini* here. If future studies support the results of Longrich et al. (2021), *Arenysaurini* should probably

be defined so that it becomes inapplicable if inferred within *Lambeosaurini*. The easiest way to obtain such effect would be to define *Arenysaurini* through a maximum-clade definition using *Arenysaurus ardevoli* and at least one another internal specifier that would make the name applicable only in the case *Arenysaurus* is inferred outside *Lambeosaurini*. The taxon *Adynomosaurus arcanus* is a possible candidate, if such solution is preferred. In turn, *Blasisaurus canudo* should be avoided as this taxon has been inferred as the sister taxon of *A. ardevoli* in some analyses (e.g., Prieto-Márquez et al., 2019; Prieto-Márquez et al., 2020). Another option is to apply a clause similar to that we used in the definitions of *Clypeodonta*, *Euornithopoda*, *Hypsilophodontia*, *Orodrominae*, and *Thescelosaurinae*. That is, by using the set theory symbol \notin , meaning “not element of”, the name *Arenysaurini* could be applicable only under the condition that the clade for which the name was intended was reconstructed outside *Lambeosaurini*. Such definition could be abbreviated as follows: $\max \nabla \notin \textit{Lambeosaurini}$ (*Arenysaurus ardevoli* Pereda-Suberbiola et al., 2009 ~ *Lambeosaurus lambei* Parks, 1923 & *Parasaurolophus walkeri* Parks, 1922).

Conclusions

Ornithischian dinosaurs were a major clade of globally distributed Mesozoic archosaurs that achieved substantial taxic diversity and apparent morphological disparity, expressed especially through their cranial features and the body armor of some of their most distinctive members. Throughout their two-century-long research history, ornithischians have been thoroughly assessed both taxonomically and phylogenetically, which have led to the recognition of numerous clades. Following the pivotal studies establishing the theoretical foundation of the phylogenetic nomenclature in the 1980s and early 1990s, many names of the ornithischian clades have been provided phylogenetic definitions, some of which have proven useful and have not been changed since their introduction. However, following the 2020 establishment of the *International Code of Phylogenetic Nomenclature (ICPN)*, or the *PhyloCode*, all of the definitions proposed before the implementation of the Code are treated as formally ineffective. We have reconsidered the utility of previously proposed phylogenetic definitions of established ornithischian taxon names and provide definitions for 71 names of ornithischian clades, three of

which are newly proposed here, as specified by the Articles of the *ICPN*, thus marking the first step towards the formal phylogenetic nomenclature of ornithischian dinosaurs.

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Figure 1. Specifier-based phylogeny of *Ornithischia*. Subclade topologies reflect those of the primary reference phylogenies: *Ankylosauria* (Figure 11 of Arbour & Currie [2016]; Figure 5 of Rivera-Sylva et al. [2018a]), *Hadrosauridae* (Figure 25 of Prieto-Márquez et al. [2013], Figure 18 of Prieto-Márquez et al. [2020]), *Marginocephalia* (Figure 27 of Schott and Evans [2017], Figure 10 of Morschhauser et al. [2019], Figure 4 of Yu et al. [2020]), non-ankylosaur *Thyreophora* (Figure 16 of Han et al. [2018]), non-cerapod *Neornithischia* (Figure 4 of Madzia et al. [2018]), non-genasaur *Ornithischia* (Figure 4 of Madzia et al. [2018]), non-hadrosaurid *Ornithopoda* (Figure 2.26 of Norman [2014], Figure 4 of Madzia et al. [2018], Figure 12 of Madzia et al. [2020]). Abbreviations: *Cd.* – *Ceratopsidae*; *Hd.* – *Hadrosauridae*; *Ni.* – *Neoiguanodontia*; *Pd.* – *Pachycephalosauridae*; *Rh.* – *Rhabdodontomorpha*; *Rd.* – *Rhabdodontidae*; and *Sh.* – *Shamosaurinae*. Majority of the silhouettes were obtained from phylopic.org: *Ankylosaurinae* (Andrew A. Farke, CC BY 3.0), *Camptosauridae* (Tasman Dixon, public domain), *Chaoyangsauridae* (Andrew A. Farke, CC BY 3.0), *Chasmosaurinae* (Jagged Fang Designs, public domain), *Dryosauridae* (Gereth Monger, CC BY 3.0), *Heterodontosauridae* (Scott Hartman, CC BY 3.0), *Iguanodontidae* (Tasman Dixon, public domain), *Lambeosaurinae* (Dmitry Bogdanov, CC BY 3.0), *Nodosaurinae* (Scott Hartman, public domain), *Polacanthinae* (FunkMonk, public domain), *Protoceratopsidae* (Andrew A. Farke, CC BY 3.0), *Rhabdodontidae* (Scott Hartman, CC BY 3.0), *Stegosauria* (Scott Hartman, CC BY 3.0). We have further added silhouettes for *Elasmaria* (Victoria M. Arbour, CC BY 4.0), *Pachycephalosauria* (Victoria M. Arbour, CC BY 4.0), *Saurolophinae* (Victoria M. Arbour, CC BY 4.0), and *Thescelosauridae* (Victoria M. Arbour, CC BY 4.0).

Figure 2. Specifier-based phylogeny of *Hadrosauridae* showing alternative placements of *Hadrosaurus foulkii*. The silhouette of *Lambeosaurinae* was obtained from phylopic.org (Dmitry Bogdanov, CC BY 3.0). The silhouette of *Saurolophinae* was prepared by Victoria M. Arbour (CC BY 4.0).

Table 1 (on next page)

Phylogenetic definitions of ornithischian dinosaur clade names.

Clade name	Authorship	Definition type	Abbreviated definition	Primary reference phylogeny
<i>Ankylopollexia</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Camptosaurus dispar</i> [Marsh, 1879] & <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 12 of Madzia et al. (2020)
<i>Ankylosauria</i>	Osborn, 1923	maximum-clade	max ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 ~ <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 11 of Arbour & Currie (2016)
<i>Ankylosauridae</i>	Brown, 1908	maximum-clade	max ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 ~ <i>Nodosaurus textilis</i> Marsh, 1889)	Figure 11 of Arbour & Currie (2016)
<i>Ankylosaurinae</i>	Nopcsa, 1918	maximum-clade	max ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 ~ <i>Shamosaurus scutatus</i> Tumanova, 1983)	Figure 11 of Arbour and Currie (2016)
<i>Ankylosaurini</i>	Arbour & Currie, 2016	maximum-clade	max ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 ~ <i>Pinacosaurus grangeri</i> Gilmore, 1933 & <i>Saichania chulsanensis</i> Maryńska 1977)	Figure 11 of Arbour and Currie (2016)
<i>Aralosaurini</i>	Prieto-Márquez et al., 2013	maximum-clade	max ∇ (<i>Aralosaurus tuberiferus</i> Rozhdestvensky, 1968 & <i>Canardia garonnensis</i> Prieto-Márquez et al., 2013 ~ <i>Lambeosaurus lambei</i> Parks, 1923 & <i>Parasaurolophus walkeri</i> Parks, 1922 & <i>Tsintaosaurus spinorhinus</i> Young, 1958)	Figure 25 of Prieto-Márquez et al. (2013)
<i>Brachylophosaurini</i>	Gates et al., 2011	maximum-clade	max ∇ (<i>Brachylophosaurus canadensis</i> Sternberg, 1953 ~ <i>Edmontosaurus regalis</i> Lambe, 1917 & <i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Kritosaurus navajovius</i> Brown, 1910 & <i>Saurolophus osborni</i> Brown, 1912)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Camptosauridae</i>	Marsh, 1885	maximum-clade	max ∇ (<i>Camptosaurus dispar</i> [Marsh, 1879] ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 13 of Madzia et al. (2020)
<i>Centrosaurinae</i>	Lambe, 1915	maximum-clade	max ∇ (<i>Centrosaurus apertus</i> Lambe 1904 ~ <i>Chasmosaurus belli</i> [Lambe, 1902] & <i>Triceratops horridus</i> Marsh, 1889)	Figure 10 of Wilson et al. (2020)
<i>Cerapoda</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Iguanodon bernissartensis</i> Boulenger in	Figure 4 of Madzia et al.

			Beneden, 1881 & <i>Triceratops horridus</i> Marsh, 1889 & <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931])	(2018)
<i>Ceratopsia</i>	Marsh, 1890	maximum-clade	max ∇ (<i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889 ~ <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931])	Figure 10 of Morschhauser et al. (2019)
<i>Ceratopsidae</i>	Marsh, 1888	minimum-clade	min ∇ (<i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889 & <i>Chasmosaurus belli</i> [Lambe, 1902] & <i>Centrosaurus apertus</i> Lambe 1904)	Figure 4 of Yu et al. (2020)
<i>Ceratopsoidea</i>	Hay, 1902	maximum-clade	max ∇ (<i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889 ~ <i>Protoceratops andrewsi</i> Granger & Gregory, 1923)	Figure 4 of Yu et al. (2020)
<i>Chaoyangsauridae</i>	Zhao et al., 1999	maximum-clade	max ∇ (<i>Chaoyangsaurus youngi</i> Zhao et al., 1999 ~ <i>Triceratops horridus</i> Marsh, 1889 & <i>Psittacosaurus mongoliensis</i> Osborn, 1923)	Figure 10 of Morschhauser et al. (2019)
<i>Chasmosaurinae</i>	Lambe, 1915	maximum-clade	max ∇ (<i>Chasmosaurus belli</i> [Lambe, 1902] & <i>Triceratops horridus</i> Marsh, 1889 ~ <i>Centrosaurus apertus</i> Lambe 1904)	Figure 10a of Fowler & Freedman Fowler (2020)
<i>Clypeodonta</i>	Norman, 2014	minimum-clade	min $\nabla \in$ <i>Ornithopoda</i> (<i>Hypsilophodon foxii</i> Huxley, 1869 & <i>Edmontosaurus regalis</i> Lambe, 1917)	Figure 50 of Norman (2015)
<i>Coronosauria</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Triceratops horridus</i> Marsh, 1889 & <i>Protoceratops andrewsi</i> Granger & Gregory, 1923)	Figure 10 of Morschhauser et al. (2019)
<i>Dryomorpha</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Dryosaurus altus</i> [Marsh, 1878] & <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 12 of Madzia et al. (2020)
<i>Dryosauridae</i>	Stefan  1903	maximum-clade	max ∇ (<i>Dryosaurus altus</i> [Marsh, 1878] ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 12 of Madzia et al. (2020)
<i>Edmontosaurini</i>	Glut, 1997	maximum-clade	max ∇ (<i>Edmontosaurus regalis</i> Lambe, 1917 ~ <i>Brachylophosaurus canadensis</i> Sternberg, 1953 & <i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Kritosaurus navajovius</i> Brown, 1910 & <i>Saurolophus osborni</i>	Figure 18 of Prieto-Márquez et al. (2020)

			Brown, 1912)	
<i>Elasmaria</i>	Calvo et al., 2007	minimum-clade	min ∇ (<i>Talenkauen santacrucensis</i> Novas et al., 2004 & <i>Macrogyphosaurus gondwanicus</i> Calvo et al., 2007 ~ <i>Hypsilophodon foxii</i> Huxley, 1869 \vee <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 \vee <i>Thescelosaurus neglectus</i> Gilmore, 1913)	Figure 31 of Rozadilla et al. (2019)
<i>Euceratopsia</i>	new	minimum-clade	min ∇ (<i>Leptoceratops gracilis</i> Brown, 1914 & <i>Protoceratops andrewsi</i> Granger & Gregory, 1923 & <i>Triceratops horridus</i> Marsh, 1889)	Figure 4 of Yu et al. (2020)
<i>Euhadrosauria</i>	Weishampel et al., 1993	minimum-clade	min ∇ (<i>Saurolophus osborni</i> Brown, 1912 & <i>Lambeosaurus lambei</i> Parks, 1923 ~ <i>Hadrosaurus foulkii</i> Leidy, 1858)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Euiguanodontia</i>	Coria & Salgado, 1996	minimum-clade	min ∇ (<i>Gasparinisaura cincosaltensis</i> Coria & Salgado, 1996 & <i>Dryosaurus altus</i> [Marsh, 1878] & <i>Camptosaurus dispar</i> [Marsh, 1879] ~ <i>Tenontosaurus tilletti</i> Ostrom, 1970)	Figure 13 of Coria & Salgado (1996)
<i>Euornithopoda</i>	Sereno, 1986	maximum-clade	max $\nabla \in$ <i>Ornithopoda</i> (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 ~ <i>Heterodontosaurus tucki</i> Crompton & Charig, 1962)	Figure 1 of Sereno (1999)
<i>Eurypoda</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 & <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 3 of Thompson et al. (2012)
<i>Genasauria</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Triceratops horridus</i> Marsh, 1889 & <i>Ankylosaurus magniventris</i> Brown, 1908 & <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 16 of Han et al. (2018)
<i>Hadrosauridae</i>	Cope, 1869	minimum-clade	min ∇ (<i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Saurolophus osborni</i> Brown, 1912 & <i>Lambeosaurus lambei</i> Parks, 1923)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Hadrosauriformes</i>	Sereno, 1997	minimum-clade	min ∇ (<i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 12 of Madzia et al. (2020)

<i>Hadrosaurinae</i>	Lambe, 1918	maximum-clade	max ∇ (<i>Hadrosaurus foulkii</i> Leidy, 1858 ~ <i>Lambeosaurus lambei</i> Parks, 1923)	Figure 5 of Kobayashi et al. (2019)
<i>Hadrosauroidea</i>	von Huene, 1952	maximum-clade	max ∇ (<i>Hadrosaurus foulkii</i> Leidy, 1858 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 12 of Madzia et al. (2020)
<i>Hadrosauromorpha</i>	Norman, 2014	maximum-clade	max ∇ (<i>Hadrosaurus foulkii</i> Leidy, 1858 ~ <i>Probactrosaurus gobiensis</i> Rozhdestvensky, 1967)	Figure 12 of Madzia et al. (2020)
<i>Heterodontosauridae</i>	Romer, 1966	maximum-clade	max ∇ (<i>Heterodontosaurus tucki</i> Crompton & Charig, 1962 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Triceratops horridus</i> Marsh, 1889 & <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931] & <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 4 of Madzia et al. (2018)
<i>Huayangosauridae</i>	Dong et al., 1982	maximum-clade	max ∇ (<i>Huayangosaurus taibaii</i> Dong et al., 1982 ~ <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 12 of Maidment et al. (2020)
<i>Hypsilophodontia</i>	Cooper, 1985	minimum-clade	min $\nabla \in$ <i>Ornithopoda</i> (<i>Hypsilophodon foxii</i> Huxley, 1869 & <i>Tenontosaurus tilletti</i> Ostrom, 1970 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881)	Figure 50 of Norman (2015)
<i>Hypsilophodontidae</i>	Dollo, 1882	maximum-clade	max ∇ (<i>Hypsilophodon foxii</i> Huxley, 1869 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Rhabdodon priscus</i> Matheron, 1869)	Figure 2 of Dieudonné et al. (2020)
<i>Iguanodontia</i>	Baur, 1891	minimum-clade	min ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Dryosaurus altus</i> [Marsh, 1878] & <i>Rhabdodon priscus</i> Matheron, 1869 & <i>Tenontosaurus tilletti</i> Ostrom, 1970)	Figure 12 of Madzia et al. (2020)
<i>Iguanodontidae</i>	Bonaparte, 1850	maximum-clade	max ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 ~ <i>Hadrosaurus foulkii</i> Leidy, 1858)	Figure 13 of Madzia et al. (2020)
<i>Jeholosauridae</i>	Han et al., 2012	maximum-clade	max $\nabla \notin$ <i>Hypsilophodontidae</i> \vee <i>Thescelosauridae</i> (<i>Jeholosaurus shangyuanensis</i> Xu et al., 2000 ~ <i>Hypsilophodon foxii</i> Huxley, 1869 & <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 &	Figure 25 of Herne et al. (2019)

			<i>Triceratops horridus</i> Marsh, 1889 & <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931] & <i>Thescelosaurus neglectus</i> Gilmore, 1913)	
<i>Kritosaurini</i>	Glut, 1997	maximum-clade	max ∇ (<i>Kritosaurus navajovius</i> Brown, 1910 ~ <i>Brachylophosaurus canadensis</i> Sternberg, 1953 & <i>Edmontosaurus regalis</i> Lambe, 1917 & <i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Saurolophus osborni</i> Brown, 1912)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Lambeosaurinae</i>	Parks, 1923	maximum-clade	max ∇ (<i>Lambeosaurus lambei</i> Parks, 1923 ~ <i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Saurolophus osborni</i> Brown, 1912)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Lambeosaurini</i>	Sullivan et al., 2011	maximum-clade	max ∇ (<i>Lambeosaurus lambei</i> Parks, 1923 ~ <i>Aralosaurus tuberiferus</i> Rozhdestvensky, 1968 & <i>Parasaurolophus walkeri</i> Parks, 1922 & <i>Tsintaosaurus spinorhinus</i> Young, 1958)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Leptoceratopsidae</i>	Nopcsa, 1923	maximum-clade	max ∇ (<i>Leptoceratops gracilis</i> Brown, 1914b ~ <i>Triceratops horridus</i> Marsh, 1889)	Figure 10 of Morschhauser et al. (2019)
<i>Marginocephalia</i>	Sereno, 1986	minimum-clade	min ∇ (<i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889 & <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931])	Figure 16 of Han et al. (2018)
<i>Neoceratopsia</i>	Sereno, 1986	maximum-clade	max ∇ (<i>Triceratops horridus</i> Marsh, 1889 ~ <i>Psittacosaurus mongoliensis</i> Osborn, 1923 & <i>Chaoyangsaurus youngi</i> Zhao et al., 1999)	Figure 10 of Morschhauser et al. (2019)
<i>Neoiguanodontia</i>	Norman, 2014	minimum-clade	min ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Hypselospinus fittoni</i> [Lydekker, 1889] & <i>Parasaurolophus walkeri</i> Parks 1922)	Figure 2.26 of Norman (2014)
<i>Neornithischia</i>	Cooper, 1985	maximum-clade	max ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Triceratops horridus</i> Marsh, 1889 ~ <i>Ankylosaurus magniventris</i> Brown, 1908 & <i>Stegosaurus stenops</i> Marsh, 1887)	Figure 4 of Madzia et al. (2018)

<i>Nodosauridae</i>	Marsh, 1890	maximum-clade	max ∇ (<i>Nodosaurus textilis</i> Marsh, 1889 ~ <i>Ankylosaurus magniventris</i> Brown, 1908)	Figure 5 of Rivera-Sylva et al. (2018a)
<i>Nodosaurinae</i>	Abel, 1919	maximum-clade	max ∇ (<i>Nodosaurus textilis</i> Marsh, 1889 ~ <i>Hylaeosaurus armatus</i> Mantell, 1833 & <i>Mymoorapelta maysi</i> Kirkland & Carpenter, 1994 & <i>Polacanthus foxii</i> Fox, 1866)	Figure 5 of Rivera-Sylva et al. (2018a)
<i>Ornithischia</i>	Seeley, 1888	maximum-clade	max ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 ~ <i>Allosaurus fragilis</i> Marsh, 1877a & <i>Camarasaurus supremus</i> Cope, 1877)	Figure 4 of Madzia et al. (2018)
<i>Ornithopoda</i>	Marsh, 1881	maximum-clade	max ∇ (<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 ~ <i>Triceratops horridus</i> Marsh, 1889 & <i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931])	Figure 4 of Madzia et al. (2018)
<i>Orodrominae</i>	Brown et al., 2013	maximum-clade	max ∇ ∈ <i>Hypsilophodontidae</i> ∨ <i>Thescelosauridae</i> (<i>Orodromeus makelai</i> Horner & Weishampel, 1988 ~ <i>Hypsilophodon foxii</i> Huxley, 1869 & <i>Thescelosaurus neglectus</i> Gilmore, 1913)	Figure 4 of Madzia et al. (2018)
<i>Pachycephalosauria</i>	Maryańska & Osmólska, 1974	maximum-clade	max ∇ (<i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931] ~ <i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889)	Figure 27 of Schott & Evans (2017)
<i>Pachycephalosauridae</i>	Sternberg, 1945	minimum-clade	min ∇ (<i>Pachycephalosaurus wyomingensis</i> [Gilmore, 1931] & <i>Stegoceras validum</i> Lambe, 1902 ~ <i>Heterodontosaurus tucki</i> Crompton & Charig, 1962)	Figure 27 of Schott & Evans (2017)
<i>Panoplosaurini</i>	new	maximum-clade	max ∇ (<i>Panoplosaurus mirus</i> Lambe, 1919 ~ <i>Nodosaurus textilis</i> Marsh, 1889 & <i>Struthiosaurus austriacus</i> Bunzel, 1871)	Figure 5 of Rivera-Sylva et al. (2018a)
<i>Parasaurolophini</i>	Glut, 1997	maximum-clade	max ∇ (<i>Parasaurolophus walkeri</i> Parks, 1922 ~ <i>Aralosaurus tuberiferus</i> Rozhdestvensky, 1968 & <i>Lambeosaurus lambei</i> Parks, 1923 & <i>Tsintaosaurus spinorhinus</i> Young, 1958)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Polacanthinae</i>	Lapparent &	maximum-clade	max ∇ ∈ <i>Ankylosauridae</i> ∨ <i>Nodosauridae</i> (<i>Polacanthus</i>	Figure 9 of Yang et al. (2013)

	Lavocat, 1955		<i>foxii</i> Fox, 1866 ~ <i>Ankylosaurus magniventris</i> Brown, 1908 & <i>Nodosaurus textilis</i> Marsh, 1889)	
<i>Protoceratopsidae</i>	Granger & Gregory, 1923	maximum-clade	max ∇ (<i>Protoceratops andrewsi</i> Granger & Gregory, 1923 ~ <i>Ceratops montanus</i> Marsh, 1888 & <i>Triceratops horridus</i> Marsh, 1889)	Figure 10 of Morschhauser et al. (2019)
<i>Rhabdodontidae</i>	Weishampel et al., 2003	minimum-clade	min ∇ (<i>Rhabdodon priscus</i> Matheron, 1869 & <i>Zalmoxes robustus</i> [Nopcsa, 1900])	Figure 4 of Madzia et al. (2018)
<i>Rhabdodontomorpha</i>	Dieudonné et al., 2016	maximum-clade	max ∇ (<i>Rhabdodon priscus</i> Matheron, 1869 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Hypsilophodon foxii</i> Huxley, 1869)	Figure 2 of Dieudonné et al. (2020)
<i>Saurolophinae</i>	Brown, 1914a	maximum-clade	max ∇ (<i>Saurolophus osborni</i> Brown, 1912 ~ <i>Lambeosaurus lambei</i> Parks, 1923 ~ <i>Hadrosaurus foulkii</i> Leidy, 1858)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Saurolophini</i>	Glut, 1997	maximum-clade	max ∇ (<i>Saurolophus osborni</i> Brown, 1912 ~ <i>Brachylophosaurus canadensis</i> Sternberg, 1953 & <i>Edmontosaurus regalis</i> Lambe, 1917 & <i>Hadrosaurus foulkii</i> Leidy, 1858 & <i>Kritosaurus navajovius</i> Brown, 1910)	Figure 18 of Prieto-Márquez et al. (2020)
<i>Shamosaurinae</i>	Tumanova, 1983	maximum-clade	max ∇ (<i>Shamosaurus scutatus</i> Tumanova, 1983 & <i>Gobisaurus domoculus</i> Vickaryous et al., 2001 ~ <i>Ankylosaurus magniventris</i> Brown, 1908)	Figure 11 of Arbour & Currie (2016)
<i>Stegosauria</i>	Marsh, 1877a	maximum-clade	max ∇ (<i>Stegosaurus stenops</i> Marsh, 1887 ~ <i>Ankylosaurus magniventris</i> Brown, 1908)	Figure 12 of Maidment et al. (2020)
<i>Stegosauridae</i>	Marsh, 1880	maximum-clade	max ∇ (<i>Stegosaurus stenops</i> Marsh, 1887 ~ <i>Huayangosaurus taibaii</i> Dong et al., 1982)	Figure 12 of Maidment et al. (2020)
<i>Struthiosaurini</i>	new	maximum-clade	max ∇ (<i>Struthiosaurus austriacus</i> Bunzel, 1871 ~ <i>Nodosaurus textilis</i> Marsh, 1889 & <i>Panoplosaurus mirus</i> Lambe, 1919)	Figure 5 of Rivera-Sylva et al. (2018a)
<i>Styracosterna</i>	Sereno, 1986	maximum-clade	max ∇ (<i>Iguanodon bernissartensis</i> Boulenger in	Figure 12 of Madzia et al.

			Beneden, 1881 ~ <i>Camptosaurus dispar</i> [Marsh, 1879])	(2020)
<i>Thescelosauridae</i>	Sternberg, 1937	maximum-clade	max ∇ (<i>Thescelosaurus neglectus</i> Gilmore, 1913 & <i>Orodromeus makelai</i> Horner & Weishampel, 1988 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 ~ <i>Hypsilophodon foxii</i> Huxley, 1869)	Figure 4 of Madzia et al. (2018)
<i>Thescelosaurinae</i>	Sternberg, 1940	maximum-clade	max $\nabla \in$ <i>Hypsilophodontidae</i> \vee <i>Thescelosauridae</i> (<i>Thescelosaurus neglectus</i> Gilmore, 1913 ~ <i>Hypsilophodon foxii</i> Huxley, 1869 & <i>Orodromeus makelai</i> Horner & Weishampel, 1988)	Figure 4 of Madzia et al. (2018)
<i>Thyreophora</i>	Nopcsa, 1915	maximum-clade	max ∇ (<i>Ankylosaurus magniventris</i> Brown, 1908 & <i>Stegosaurus stenops</i> Marsh, 1887 ~ <i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881 & <i>Triceratops horridus</i> Marsh, 1889)	Figure 16 of Han et al. (2018)
<i>Tsintaosaurini</i>	Prieto-Márquez et al., 2013	maximum-clade	max ∇ (<i>Tsintaosaurus spinorhinus</i> Young, 1958 & <i>Pararhabdodon isonensis</i> Casanovas Cladellas et al., 1993 ~ <i>Aralosaurus tuberiferus</i> Rozhdestvensky, 1968 & <i>Lambeosaurus lambei</i> Parks, 1923 & <i>Parasaurolophus walkeri</i> Parks, 1922)	Figure 18 of Prieto-Márquez et al. (2020)

Figure 1

Specifier-based phylogeny of *Ornithischia*.

Subclade topologies reflect those of the primary reference phylogenies: *Ankylosauria* (Figure 11 of Arbour & Currie [2016]; Figure 5 of Rivera-Sylva et al. [2018a]), *Hadrosauridae* (Figure 25 of Prieto-Márquez et al. [2013], Figure 18 of Prieto-Márquez et al. [2020]),

Marginocephalia (Figure 27 of Schott and Evans [2017], Figure 10 of Morschhauser et al. [2019], Figure 4 of Yu et al. [2020]), non-ankylosaur *Thyreophora* (Figure 16 of Han et al. [2018]), non-cerapod *Neornithischia* (Figure 4 of Madzia et al. [2018]), non-genasaur

Ornithischia (Figure 4 of Madzia et al. [2018]), non-hadrosaurid *Ornithopoda* (Figure 2.26 of Norman [2014], Figure 4 of Madzia et al. [2018], Figure 12 of Madzia et al. [2020]).

Abbreviations: *Cd.* – *Ceratopsidae*; *Hd.* – *Hadrosauridae*; *Ni.* – *Neoiguanodontia*; *Pd.* – *Pachycephalosauridae*; *Rh.* – *Rhabdodontomorpha*; *Rd.* – *Rhabdodontidae*; and *Sh.* –

Shamosaurinae. Majority of the silhouettes were obtained from phylopic.org: *Ankylosaurinae* (Andrew A. Farke, CC BY 3.0), *Camptosauridae* (Tasman Dixon, public domain),

Chaoyangsauridae (Andrew A. Farke, CC BY 3.0), *Chasmosaurinae* (Jagged Fang Designs, public domain), *Dryosauridae* (Gereth Monger, CC BY 3.0), *Heterodontosauridae* (Scott Hartman, CC BY 3.0), *Iguanodontidae* (Tasman Dixon, public domain), *Lambeosaurinae*

(Dmitry Bogdanov, CC BY 3.0), *Nodosaurinae* (Scott Hartman, public domain), *Polacanthinae* (FunkMonk, public domain), *Protoceratopsidae* (Andrew A. Farke, CC BY 3.0), *Rhabdodontidae*

(Scott Hartman, CC BY 3.0), *Stegosauria* (Scott Hartman, CC BY 3.0). We have further added silhouettes for *Elasmaria* (Victoria M. Arbour, CC BY 4.0), *Pachycephalosauria* (Victoria M.

Arbour, CC BY 4.0), *Saurolophinae* (Victoria M. Arbour, CC BY 4.0), and *Thescelosauridae*

(Victoria M. Arbour, CC BY 4.0).

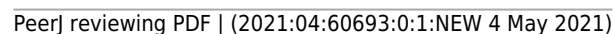


Figure 2

Specifier-based phylogeny of *Hadrosauridae* showing alternative placements of *Hadrosaurus foulkii*.

The silhouette of *Lambeosaurinae* was obtained from phylopic.org (Dmitry Bogdanov, CC BY 3.0). The silhouette of *Saurolophinae* was prepared by Victoria M. Arbour (CC BY 4.0).

