The phylogenetic affinities of the bizarre Late Cretaceous Romanian theropod *Balaur bondoc* (Dinosauria, Maniraptora): dromaeosaurid or flightless bird?

Andrea Cau, Thomas Brougham, Darren Naish

The exceptionally well-preserved Romanian dinosaur *Balaur bondoc* is the most complete theropod known to date from the Upper Cretaceous of Europe. Previous studies of this remarkable taxon have included its phylogenetic interpretation as an aberrant dromaeosaurid with velociraptorine affinities. However, *Balaur* displays a combination of both apparently plesiomorphic and derived bird-like characters. Here, we analyse those features in a phylogenetic revision and show how they challenge its referral to Dromaeosauridae. Our reanalysis of two distinct phylogenetic datasets focusing on basal paravian taxa supports the reinterpretation of *Balaur* as an avialan more derived than *Archaeopteryx* but outside of Pygostylia, and as a flightless taxon within a paraphyletic assemblage of long-tailed birds. Our placement of *Balaur* within Avialae is not biased by character weighting. The placement among dromaeosaurids resulted a suboptimal alternative that cannot be rejected based on actual data. Interpreted as a dromaeosaurid, *Balaur* has been assumed to be hypercarnivorous and predatory, exhibiting a peculiar morphology influenced by island endemism. However, a dromaeosaurid-like ecology is contradicted by several details of *Balaur*'s morphology, including the loss of a third functional manual digit, the non-ginglymoid distal end of metatarsal II and a non-falciform ungual on the second pedal digit that lacks a prominent flexor tubercle. Conversely, an omnivorous ecology is better supported by *Balaur*'s morphology and is consistent with its phylogenetic placement within Avialae. Our reinterpretation of *Balaur* implies that a superficially dromaeosaurid-like taxon represents the enlarged, terrestrialised descendant of smaller and probably volant ancestors.

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Abstract

The exceptionally well-preserved Romanian dinosaur *Balaur bondoc* is the most complete theropod known to date from the Upper Cretaceous of Europe. Previous studies of this remarkable taxon have included its phylogenetic interpretation as an aberrant dromaeosaurid with velociraptorine affinities. However, *Balaur* displays a combination of both apparently plesiomorphic and derived bird-like characters. Here, we analyse those features in a phylogenetic revision and show how they challenge its referral to Dromaeosauridae. Our reanalysis of two distinct phylogenetic datasets focusing on basal paravian taxa supports the reinterpretation of *Balaur* as an avialan more derived than *Archaeopteryx* but outside of Pygostylia, and as a flightless taxon within a paraphyletic assemblage of long-tailed birds. Our placement of *Balaur* within Avialae is not biased by character weighting. The placement among dromaeosaurids resulted a suboptimal alternative that cannot be rejected based on actual data. Interpreted as a dromaeosaurid, *Balaur* has been assumed to be hypercarnivorous and predatory, exhibiting a peculiar morphology influenced by island endemism. However, a dromaeosaurid-like ecology is contradicted by several details of *Balaur*'s morphology, including the loss of a third functional manual digit, the non-ginglymoid distal end of metatarsal II and a non-falciform ungual on the second pedal digit that lacks a prominent flexor tubercle. Conversely, an omnivorous ecology is better supported by *Balaur*'s morphology and is consistent with its phylogenetic placement within Avialae. Our reinterpretation of *Balaur* implies that a superficially dromaeosaurid-like taxon represents the enlarged, terrestrialised descendant of smaller and probably volant ancestors.

Keywords: Avialae, Deinonychosauria, Homoplasy, Mesozoic, Paraves.

The theropod dinosaur *Balaur bondoc* from the Maastrichtian (latest Late Cretaceous) of Romania represents the most complete theropod dinosaur yet known from the Upper Cretaceous of Europe (Csiki et al. 2010). The remarkably well-preserved holotype specimen of *B. bondoc*, EME (Transylvanian Museum Society, Dept. of Natural Sciences, Cluj-Napoca, Romania) PV.313, was collected from red overbank floodplain sediments of the Maastrichtian Sebeş Formation in 2009 and comprises an articulated partial postcranial skeleton of a single individual, including dorsal, sacral and caudal vertebrae as well as much of the pectoral and pelvic girdles and limbs (Brusatte et al. 2013). The first phylogenetic studies incorporating *Balaur* concluded that it represents an aberrant dromaeosaurid with velociraptorine affinities, endemic to the European palaeoislands of the Late Cretaceous (Csiki et al. 2010; Turner et al. 2012; Brusatte et al. 2013). The matrices utilised in these three studies have all been versions of the Theropod Working Group (TWiG) matrix, an incrementally and independently developed large-scale matrix focusing on the interrelationships of coelurosaurian taxa (e.g., Norell et al. 2001; Makovicky et al. 2005; Turner et al. 2007; Turner et al. 2012; Brusatte et al. 2014). Comparisons made between *Balaur* and other dromaeosaurids reveals the possession of a suite of autapomorphies not present in dromaeosaurids nor in most other non-avialan theropods, such as a fused carpometacarpus, loss of a functional third manual digit, proximal fusion of the tarsometatarsus and a relatively enlarged first pedal digit (Csiki et al. 2010; Brusatte et al. 2013). Interpreted as a dromaeosaurid, *Balaur* is a strikingly odd and apparently avialan-like taxon. Recently, Godefroit et al. (2013a) included *Balaur* in a new phylogenetic analysis focusing on paravians and found it resolved as a basal avialan, more crownward than *Archaeopteryx*. A similar result was obtained independently by Foth et al. (2014) using a dataset expanded from that of Turner et al. (2012), although Foth et al. (2014) recovered it in a position relatively less crownward than in the tree obtained by Godefroit et al. (2013a), but still crownward of *Archaeopteryx*. The present study focuses on resolving these conflicting interpretations regarding the affinities of *Balaur* following examination of the holotype material (performed by TB and DN). We also present a revised phylogenetic hypothesis based on a comparison of updated versions of previously published taxon-character matrices.

Materials and methods

In order to test the competing dromaeosaurid and avialan hypotheses for the affinities of *Balaur*, we coded the holotype specimen into modified versions of two recently published theropod phylogenetic matrices: Turner et al. (2012) and Lee et al. (2014). Both of these large-scale and independently coded matrices focused on the interrelationships of basal paravian theropod dinosaurs and contain a broadly overlapping and comprehensive sampling of over 100 theropod taxa (117 and 120 taxa respectively), including many basal avialans. The two matrices differ from each other in the logical basis on character statement definitions (Sereno 2007; Brazeau 2011, see discussion below).

Turner et al. (2012) data set

We modified the Turner et al. (2012) matrix for this study to include 13 new characters and updated character states for four previously defined characters (see Electronic Supplementary Material). Characters #6, #50 and #52 were excluded from tree search, following Turner et al. (2012). All character statements considered to be ordered by Turner et al. (2012) were set accordingly. The multistate character 116, considered to be unordered by Turner et al. (2012), was set as ordered as we interpret state “1” as intermediate between states “0” and “2”. In addition, *Neuquenraptor* and the two included species of *Unenlagia* were merged as a single taxonomic unit (Turner et al. 2012, but see also Gianechini and Apesteguia 2011). *Microraptor* was re-scored based on Pei et al. (2014). The resulting data matrix (490 characters vs 113 taxa) was then analysed using the Hennig Society version of TNT v1.1 (Goloboff et al. 2008b; see Electronic Supplementary Material for further details regarding modifications to the matrix and tree search strategy).

Lee et al. (2014) data set

The dataset used by Lee at al. (2014) is an updated version of the dataset of Godefroit et al. (2013a). Character statements of the 1549 included characters and the source of score for the included 120 fossil taxa are stored at the Dryad Digital Repository (Cau et al. 2014). In our study, this dataset has been expanded including one taxonomic unit based on the extant avian *Meleagris* (ACUB 4817); accordingly, character statement 318 has been modified (see Electronic Supplementary Material). *Balaur* was re-scored based on our examination of the specimen and the incorporation of information from Brusatte et al. (2013). Lee et al. (2014) applied Bayesian inference in their analysis of this dataset and integrating the morphological information with chronostratigrafic information. In the present study, the updated morphological data matrix (1549 characters vs 121 taxa) was analysed using parsimony as the tree search strategy in TNT (see Electronic Supplementary Material).

Alternative placement test and implied weighting analyses

In our analyses of both datasets, we constrained the alternative deinonychosaurian and avialan positions for *Balaur*, measuring step changes between resultant topologies as a further indication of their relative support. The Templeton's test (Templeton 1983) was used to determine whether the step differences between the unforced and forced topologies were statistically significant. The backbone constraints used the following species: a crown avian (*Anas platyrhynchus* in the dataset of Turner et al. 2012, *Meleagris gallopavo* in the dataset of Lee et al. 2014), a dromaeosaurid (*Dromaeosaurus albertensis* in both datasets), and a troodontid (*Troodon formosus* in both datasets).

In order to test whether assumptions on character weighting influence the placement of *Balaur* among Paraves, both datasets were subjected to implied weighting analyses (IWAs, Goloboff 1993, Goloboff et al. 2008a,b; see Electronic Supplementary Material).

Institutional abbreviations

ACUB, Museo di Anatomia Comparata, University of Bologna, Bologna, Italy. *EME*,Transylvanian Museum Society, Dept. of Natural Sciences, Cluj-Napoca, Romania.

Comparative anatomy of *Balaur* and other maniraptoran theropods

Compared to other theropods, *Balaur* displays a unique and unexpected combination of characters (Brusatte et al. 2013). The phylogenetic analyses of Csiki et al. (2010) and Brusatte et al. (2013) resolved *Balaur* as a velociraptorine dromaeosaurid. Consequently, most of the unusual characters shared by *Balaur* with non-dromaeosaurid theropods were interpreted as autapomorphies, independently evolved along the lineage leading exclusively to *Balaur*. An alternative explanation is that these features may indicate a closer relationship between *Balaur* and another non-dromaeosaurid clade of maniraptorans.

Here, we list the most relevant characters that may support or challenge the alternative placements of *Balaur* within Maniraptora.

Dorsal vertebrae with stalked parapophyses

The dorsal vertebrae of *Balaur* bear distinctly stalked parapophyses (Brusatte et al. 2013). Although this feature has been reported as a deinonychosaurian synapomorphy (Turner et al. 2012), stalked parapophyses are also present in alvarezsaurids and basal avialans (Novas 1997; Chiappe et al. 1999;

Agnolín and Novas 2013).

Sacrum including at least seven fused vertebrae

The presence of five fused sacral vertebrae is the plesiomorphic condition within coelurosaurs (e.g., Brochu 2003). An independent increase in the number of fused sacral vertebrae is a widespread phenomenon within Maniraptoriformes. Six to seven sacral vertebrae are present in ornithomimids (Osmólska et al. 1972), derived oviraptorosaurs (Barsbold et al. 2000), and derived dromaeosaurids (Norell and Makovicky 1997; Turner et al. 2012; S. Brusatte pers. comm. 2014). The synsacrum is composed of seven vertebrae in derived alvarezsauroids, whereas in basal taxa it includes only five vertebrae (Choiniere et al. 2010). *Archaeopteryx* and basal paravians retain five sacral vertebrae (Hwang et al. 2002; Paul 2002; Godefroit et al. 2013b; Godefroit et al. 2013a), whereas a sacrum with at least seven vertebrae has been regarded as a synapomorphy of *Jixiangornis* and pygostylians (Turner et al. 2012). *Balaur* has at least seven sacral vertebrae: four fused and clearly discernible sacral vertebrae bearing sacral ribs are followed by three additional and co-ossified caudosacrals (Brusatte et al. 2013).

Fused scapulocoracoid

In *Balaur*, the scapula and coracoid are co-ossified and the suture is obliterated on both sides (Fig. 1a; Brusatte et al. 2013). Brusatte et al. (2013) noted that a fused scapulocoracoid is present in some dromaeosaurids (e.g., *Adasaurus*, *Microraptor*, *Velociraptor*; see Fig. 1c) but not in others (e.g., *Achillobator*, *Buitreraptor*, *Deinonychus*, *Sinornithosaurus*, *Unenlagia*). Turner et al. (2012) included fusion of the scapulocoracoid among the phylogenetically informative characters of their paravian phylogeny. Within non-avian coelurosaurs, the presence of this character state has been reported within ornithomimosaurs, therizinosauroids, alvarezsauroids, tyrannosaurids and oviraptorosaurs (Osmólska et al. 1972; Perle 1979; Perle et al. 1994; Brochu 2003; Balanoff and Norell 2012), suggesting a high degree of homoplasy. Fusion of the scapulocoracoid is also present in basal avialans (e.g., Confuciusornithidae; Chiappe et al. 1999) and flightless avians (e.g., *Struthio*; ACUB 4820).

Coracoid with prominent tuber placed on the anterolateral corner

The coracoid of *Balaur* bears a hypertrophied tubercle that forms the anterolateral corner of the bone and obscures the supracoracoid nerve foramen when the coracoid is observed in lateral view (Fig. 1a; Brusatte et al. 2013). Non-avialan theropods possess tubercles that are relatively smaller and more lateroventrally directed (when the scapula is oriented horizontally) than that seen in avialan theropods

(Fig. 1c; Osmólska et al. 1972; Ostrom 1976; this is the "*processus praeglenoidalis*" *sensu* Elzanowski et al. 2002). Although the coracoid tubercle of *Balaur* may appear autapomorphic among non-avialan theropods (Brusatte et al. 2013), a prominent coracoid tubercle is also present in unenlagiines (*Buitreraptor*, see Agnolin and Novas 2013), basal avialans (e.g., *Jeholornis*, *Jixiangornis*; Turner et al. 2012, fig. 82) and forms the acrocoracoid of ornithothoracines (e.g., *Apsaravis*, *Enantiophoenix*, *Enantiornis*; Clarke and Norell 2002; Baier et al. 2007; Cau and Arduini 2008; Walker and Dyke 2009; Fig. 1). A hypertrophied coracoid tubercle that obscures the supracoracoid nerve foramen in lateral view is also seen in *Sapeornis* (Zhou and Zhang 2003; Gao et al. 2012).

Humerus longer than half the combined length of tibiotarsus and tarsometatarsus

The humerus of non-avialan theropods is consistently shorter than half of the combined length of the tibiotarsus and tarsometatarsus (e.g., *Deinonychus*, *Gallimimus*, *Tyrannosaurus*, *Microraptor*; Ostrom 1969; Osmólska et al. 1972; Hwang et al. 2002; Brochu 2003). In *Balaur*, the humerus is longer than half of the combined length of the tibiotarsus and tarsometatarsus (55%) and approaches the condition seen in basal avialans (e.g., *Archaeopteryx*: 59%, *Confuciusornis*: 67%, *Jeholornis*: 77%; Chiappe et al. 1999; Elzanowski 2001; Zhou and Zhang 2002; see Brusatte et al. 2013, table 2).

Humeral condyles placed on the anterior surface of the distal end

The humerus of *Balaur* possesses distal condyles that are placed entirely on the anterior surface of the bone (Brusatte et al. 2013). As in *Balaur*, the complete anterior migration of the humeral condyles is present in therizinosauroids (e.g., Zanno 2010), basal pygostylians (e.g., *Confuciusornis*, *Limenavis*, *Enantiornis*; Chiappe et al. 1999; Clarke and Chiappe 2001; Walker and Dyke 2009) and extant birds (e.g., *Dromaius*, *Meleagris*, *Struthio*; ACUB 3131; 4817; 4820). All other known dromaeosaurids (e.g., *Deinonychus*; Ostrom 1969), most non-avialan theropods (e.g., *Gallimimus*, *Allosaurus*, *Tyrannosaurus*; Osmólska et al. 1972; Madsen 1976; Brochu 2003) and the basalmost avialans (e.g., *Archaeopteryx*; Berlin specimen) bear the condyles in a more distal position, with a limited, if not absent, extent onto the anterior surface of bone. In the analysis of Turner et al. (2012), *Balaur* was scored as retaining the primitive condition (*contra* Brusatte et al. 2013). Following Brusatte et al. (2013), we re-scored character 371, describing the placement of the humeral condyles in the dataset of Turner et al. (2012), as 371.1.

Deep and elongate triangular brachial fossa on humerus

The humerus of *Balaur* has a prominent triangular fossa on the anterior surface of the distal end of the humerus (Brusatte et al. 2013, fig. 12). This fossa is bordered both laterally and medially by raised crests confluent with the epicondyles. The same configuration defines the brachial fossa present in birds (e.g., *Confuciusornis*, *Limenavis*, *Apsaravis*; Chiappe et al. 1999; Clarke and Chiappe 2001; Clarke and Norell 2002). This fossa is also variably developed within dromaeosaurids (e.g., *Bambiraptor*; Turner et al. 2012; Brusatte et al. 2013).

Ulna with brachial depression

The proximal third of *Balaur*'s ulna bears a shallow, elongate depression on the medial surface termed the "proximal fossa" (Brusatte et al. 2013, fig. 14). This character is topographically equivalent to the brachial fossa present in pygostylians (Baumel and Witmer 1993; Clarke and Chiappe 2001; Walker and Dyke 2009). The ulna of most non-avialan theropods lacks a brachial depression or possesses a poorly developed one (e.g., *Allosaurus*, *Tyrannosaurus*; Madsen 1976; Brochu 2003). However, the structure is well developed in some dromaeosaurids (e.g., *Bambiraptor*, *Buitreraptor*; Burnham 2004; Agnolín and Novas 2011; Agnolín and Novas 2013).

Distal carpals fused to proximal end of metacarpals

The manus of *Balaur* displays co-ossification of the distal carpals with the proximal ends of the metacarpals (Fig. 2a; Brusatte et al. 2013), unlike the dromaeosaurid condition in which no such fusion in present (Fig. 2d). The fusion between the distal carpals and the metacarpals is present in a few non-avialan theropod lineages (e.g., *Avimimus*, *Mononykus*; Kurzanov 1981; Perle et al. 1993) and in derived avialans (e.g., *Confuciusornis*, *Xiangornis*; Chiappe et al. 1999; Hu et al. 2012). In particular, the pattern of proximal fusion among the carpometacarpal elements in *Balaur* is shared by most basal pygostylians (e.g., *Confuciusornis*, *Sinornis*, *Sapeornis*, *Pengornis*, *Enantiornis*, *Zhouornis*; Chiappe et al. 1999; Sereno et al. 2002; Zhou and Zhang 2003; Zhou et al. 2008; Walker and Dyke 2009; Zhang et al. 2013; see Fig. 2b-c, Fig. S1). Most ornithurines and some enantiornithines display a complete distal fusion between metacarpals II and III in addition to the aforementioned proximal fusion of the carpometacarpus as seen in *Balaur* (e.g., *Apsaravis*, *Teviornis*, *Xiangornis*; Clarke and Norell 2002; Kurochkin et al. 2002; Hu et al. 2012).

Semilunate carpal shifted laterally and first metacarpal sloped proximolaterally

In *Balaur*, the semilunate carpal overlaps the whole proximal ends of both metacarpals II and III (Fig. 2a, Fig. S1). Furthermore, the proximal end of the first metacarpal in *Balaur* is mediolaterally narrower than the distal end, producing a proximolaterally sloping medial margin of the metacarpus. In

Archaeopteryx and most non-avialan maniraptorans, the proximal end of the first metacarpal is not constricted compared to the distal end, and the semilunate carpal overlaps most of metacarpal I; whereas the overlap on metacarpal III is absent or limited to the medialmost margin of the bone (Fig. 2d; Ostrom 1976, fig. 10; Xu et al. 2014). Therefore, the position of the semilunate carpal of *Balaur* represents a lateral shift when compared to other non-avialan maniraptorans, and recalls the condition in long-tailed and pygostylian birds where the semilunate carpal has a reduced or absent overlap on metacarpal I and extensively covers both metacarpals II and III (e.g., *Confuciusornis*, *Sinornis*, *Sapeornis*, *Enantiornis*, *Zhouornis*; Chiappe et al. 1999; Sereno et al. 2002; Zhou and Zhang 2003; Walker and Dyke 2009; Zhang et al. 2013; see also Xu et al. 2014; see Fig. 2b-c). As in *Balaur*, pygostylian birds show a mediolateral constriction of the proximal end of the first metacarpal, and a medial margin ("anterior margin", using *Nomina Anatomica Avium* nomenclature, see Harris 2004) that is variably sloped proximolaterally in extensor view.

Distal condyles of metacarpals I-II restricted to the distal and ventral surfaces of the metacarpals

Metacarpals I and II of *Balaur* bear distal condyles that are restricted to the distal and ventral surfaces of the metacarpals, and are excluded from the extensor surfaces (Brusatte et al. 2013). The dromaeosaurid condition (e.g., *Deinonychus*, *Velociraptor*, *Graciliraptor*; Ostrom 1969; Norell and Makovicky 1999; Xu and Wang 2003), in which the distal condyles are expanded along the extensor surface of the metacarpals, is present in most non-avialan theropods (e.g., *Acrocanthosaurus*, *Allosaurus*, *Australovenator*, *Berberosaurus*, *Dilophosaurus*, *Patagonykus*, *Rapator*; Madsen 1976; Welles 1984; Novas 1997; Senter and Robins 2005; Allain et al. 2007; White et al. 2013). The condition present in the metacarpals of *Balaur* is also present in pygostylians (e.g., *Teviornis*, *Sinornis*, *Enantiornis*; Kurochkin et al. 2002; Sereno et al. 2002; Walker and Dyke 2009) and extant birds (e.g., *Dromaius*; *Meleagris*, *Struthio*; ACUB 3131; 4817; 4820). Furthermore, the ventral surface of the metacarpals of *Balaur* are excavated by a wide flexor sulcus but lack distinct flexor pits at the distal end, similar to the condition present in avialans (e.g., *Teviornis*; Kurochkin et al. 2002) but differing from that of dromaeosaurids and most non-avialan theropods that do bear a distinct flexor pit (e.g., *Allosaurus*, *Acrocanthosaurus*, *Mahakala*, *Velociraptor*; Madsen 1976; Senter and Robins 2005; Turner et al. 2011).

Metacarpal II with an intermetacarpal ridge running along the dorsolateral edge of the bone and closed intermetacarpal space between metacarpals II and III

Balaur possesses a distinct web of bone that extends along the dorsolateral edge of metacarpal II and contacts metacarpal III distally, and a distally closed intermetacarpal space between metacarpals II and III (Brusatte et al. 2013). Within basal avialans, the extent of the contact between metacarpals II and III displays some variation, ranging from the close contact of a straight metacarpal III to metacarpal II with no intermetacarpal space (e.g., *Sapeornis*; Zhou and Zhang 2003; Gao et al. 2012; see Fig. 2, Fig. S1), an appressed distal contact but not fusion of metacarpal III to metacarpal II (the condition as seen in *Balaur* and many basal avialans, including *Jeholornis*, *Enantiornis*, *Confuciusornis*, *Zhouornis*, and *Piscivoravis*; Zhou and Zhang 2002; Walker and Dyke 2009; Zhang et al. 2009; Zhang et al. 2013; Zhou et al. 2014), to distal obliteration of the contact between metacarpals II and III due to complete fusion between the bones (e.g., *Teviornis*, *Xiangornis, Meleagris*; Kurochkin et al. 2002; Hu et al. 2012; ACUB 4817). A closed intermetacarpal space is present in *Confuciusornis* (Chiappe et al. 1999; Zhang et al. 2009), some long-tailed birds (e.g., *Jeholornis*, *Jixiangornis*; Zhou and Zhang 2002), and ornithothoracines (e.g., *Enantiornis*, *Xiangornis*, *Zhouornis*; Walker and Dyke 2009; Hu et al. 2012; Zhang et al. 2013; see Fig. 2b). Derived euornithines differ from *Balaur* and most avialans in having a more distally placed intermetacarpal space relative to a more shortened metacarpal I (e.g., *Teviornis*; Kurochkin et al. 2002).

Distal end of metacarpal III unexpanded and not divided into separated condyles

The third metacarpal of *Balaur* bears a simple distal end that lacks distinct condyles. Dromaeosaurids share with most non-avialan theropods the presence of well-defined distal metacarpal condyles separated by an intercondylar sulcus (e.g., *Allosaurus*, *Bambiraptor*, *Deinocheirus, Deinonychus*, *Dilophosaurus*, *Gallimimus*; Ostrom 1969; Osmólska and Roniewicz 1970; Osmólska et al. 1972; Madsen 1976; Welles 1984; Burnham 2004). The condition present in the third metacarpal of *Balaur* is shared by derived tyrannosauroids (e.g., *Tyrannosaurus*; Lipkin and Carpenter 2008, fig. 10.10), basal pygostylians (e.g., *Confuciusornis*, *Enantiornis*, *Sinornis*, *Teviornis*, *Xiangornis, Zhouornis*; Chiappe et al. 1999; Kurochkin et al. 2002; Sereno et al. 2002; Walker and Dyke 2009; Hu et al. 2012; Zhang et al. 2013) and crown avians (e.g., *Meleagris*, *Struthio*; ACUB 4817; 4820). This character is not obviously linked with the reduction in the number of phalanges in digit III (see below), since *Confuciusornis* shows the derived metacarpal condition (i.e., simple distal end of metacarpal III) yet retains a full set of four functional phalanges in digit III.

Third manual digit bearing less than three phalanges

The third manual digit of *Balaur* is extremely reduced and lacks the distal phalanges, including the ungual (Fig. 2a; Brusatte et al. 2013). The only known phalanx in the third manual digit of *Balaur* has a tapering distal end with a small distal articular surface, suggesting the presence of a possible additional phalanx of very small size. Such a reduction is unknown in dromaeosaurids, which have three non-ungual phalanges on manual digit III and a fully functional ungual (Fig. 2d), but are commonly found in non-confuciusornithid pygostylians, where the third manual digit is usually reduced to two or fewer phalanges with a tapering distal end and poorly defined articular surfaces (e.g., *Sinornis*, *Sapeornis*, *Zhouornis*, *Piscivoravis*; Sereno et al. 2002; Gao et al. 2012; Zhang et al. 2013; Zhou et al. 2014; see Fig. 2b-c, Fig. S1).

Dorsal margin of manual unguals does not arch dorsally above level of articular facet and flexor tubercles not expanded ventrally

Senter (2007a) argued that in dromaeosaurid manual unguals, the dorsal margins arch higher than the articular facets when the latter is held vertically, and that this feature differentiates dromaeosaurid manual unguals from those of other theropods. The derived condition is present in microraptorines and eudromaeosaurs but is absent in unenlagiines (Senter 2007a; Senter 2007b; Currie and Paulina Carabajal 2012; Fig. S1A-B). Furthermore, the manual unguals in both dromaeosaurids and troodontids bear prominent and dorsoventrally expanded flexor tubercles. In *Balaur*, the dorsal margins of the manual unguals do not arch higher than the articular facet, and the flexor tubercles are relatively low, more elongate proximodistally than dorsoventrally (Brusatte et al. 2013 figs. 21-22, figs. 21-22; Fig. S1C). Reduction in both curvature and development of the flexor tubercles is widespread among the manual unguals of basal avialans (e.g., *Sinornis*, *Sapeornis*, *Zhouornis*, *Piscivoravis*; Sereno et al. 2002; Gao et al. 2012; Zhang et al. 2013; Zhou et al. 2014; see Fig. 2b-c).

Complete coossification of pelvic bones

Balaur displays coossification of the pelvic bones such that both the iliopubic and ilioischial sutures are obliterated (Brusatte et al. 2013, Fig. S2A). In most tetanuran theropods, including basalmost avialans, the pelvic elements do not completely coossify (e.g., *Allosaurus*, *Jeholornis*, *Patagonykus*, *Sapeornis*, *Tyrannosaurus*; Madsen 1976; Novas 1997; Zhou and Zhang 2002; Brochu 2003; Zhou and Zhang 2003). This contrasts with ceratosaurian-grade theropods (Tykoski and Rowe 2004), some non-avialan coelurosaurs (e.g., *Avimimus*; Kurzanov 1981) and derived avialans (e.g., *Apsaravis*, cf. *Enantiornis*, *Patagopteryx*, *Qiliania*, *Sinornis*; Chiappe 2002; Chiappe and Walker 2002; Clarke and Norell 2002; Sereno et al. 2002; Ji et al. 2011, Fig. S2D) in which the pelvic bones fuse completely. Although coossification of the ilium to the pubis is present in the only known specimen of the microraptorine dromaeosaurid *Hesperonychus*, the pelvic coossification differs from *Balaur* and avialans as the ilioischial articulation remains unfused (Longrich and Currie 2009).

Ridge bounding the cuppedicus fossa confluent with the acetabular rim

In the ilium of *Balaur*, the ridge that dorsally bounds the cuppedicus fossa is extended posteriorly on the lateral surface of the pubic peduncle and is confluent with the acetabular rim (Brusatte et al. 2013; Fig. S2A). This feature is a compound character formed by the presence of a ridge bounding the cuppedicus fossa, which is a neotetanuran synapomorphy (Hutchinson 2001; Novas 2004), and the posterior extension of the cuppedicus fossa on the lateral surface of the pubic peduncle, which is a derived feature of paravians (Hutchinson 2001, figs. 4-6). The combination of features present in *Balaur* is shared by *Anchiornis* and *Xiaotingia* (Turner et al. 2012), *Unenlagia* and *Rahonavis* (Novas 2004), *Velociraptor* (Norell and Makovicky 1999) and enantiornithines (e.g., Sereno et al. 2002, fig. 8.4; Walker and Dyke 2009, Fig. S2D). The presence and extent of the cuppedicus fossa is difficult to determine in most Mesozoic avialans because of the two-dimensional preservation of most specimens (Novas 2004). Furthermore, the character statements relative to the ridge bounding the cuppedicus fossa in phylogenetic analyses are marked as ‘inapplicable’ in those taxa lacking a distinct cuppedicus fossa (Hutchinson 2001; e.g., *Mahakala*, *Patagopteryx*, Ornithurae; Turner et al. 2011), a scoring strategy followed by both Turner et al. (2012) and Godefroit et al. (2013a).

Pubis and ischium projected strongly posteroventrally and subparallel

Balaur has a posteroventrally directed pubis, subparallel to the ischium (Csiki et al. 2010; Fig. S2A). Although Brusatte et al. (2013) acknowledged that the extreme posterior inclination of the pubis may partially be the result of taphonomic distortion, they confirmed the genuine posteroventral orientation of this bone. Within Theropoda, retroversion of the pubis (opisthopuby) is known in therizinosauroids, parvicursorine alvarezsaurids, dromaeosaurids and pygostylians. Therizinosauroids more derived than *Falcarius* show a posteroventrally directed pubis that articulates with the obturator process of the ischium (Zanno 2010). Opisthopuby is present in many parvicursorines (e.g., *Mononykus*; Perle et al. 1994), but absent in more basal alvarezsauroids (e.g., *Haplocheirus*, *Patagonykus*; Novas 1997; Choiniere et al. 2010). A retroverted pubis is absent in basal paravians – they instead display a vertically oriented (‘mesopubic’) pubis – and is present in some dromaeosaurids (e.g., *Adasaurus* and *Velociraptor*; Norell and Makovicky 1999; Xu et al. 2010; Turner et al. 2012) but absent in others (e.g., *Achillobator*, *Utahraptor*; Perle et al. 1999; Senter et al. 2012). It is also a common feature in pygostylian birds (e.g., *Confuciusornis*, *Patagopteryx*, *Sapeornis*; Chiappe et al. 1999; Hutchinson 2001; Chiappe 2002; Chiappe and Walker 2002; Zhou and Zhang 2003).

Broad pelvic canal with laterally convex pubes and abrupt distal narrowing of interpubic distance

Brusatte et al. (2013) noted as an autapomorphy of *Balaur* an interpubic distance that is proportionally greater than that present in other dromaeosaurids (e.g., *Velociraptor*; Norell and Makovicky 1997; Norell and Makovicky 1999). The gap between the laterally bowed pubes of *Balaur* only begins to narrow abruptly in the distalmost third of the bone (Fig. 3b, Fig. S2B; Brusatte et al. 2013, fig. 56). This condition differs from that seen in most theropods (e.g., *Avimimus*, *Sinraptor*, *Tyrannosaurus*; Currie and Zhao 1993; Vickers-Rich et al. 2002; Brochu 2003), including *Velociraptor* (Fig. 3d, Fig. S2C; Norell and Makovicky 1999; Brusatte et al. 2013), *Bambiraptor* (Burnham 2004) and *Archaeopteryx* (Norell and Makovicky 1999, fig. 25), where the narrowing is more gradual over the length of the pubes and the pubis is not bowed laterally in anteroposterior view. Brusatte et al. (2013) noted that the condition in *Balaur* is somewhat similar to the condition in therizinosaurids (Zanno 2010). The combination of a relatively broad pelvic canal, bounded by laterally convex pubes and with an abrupt distal narrowing of the interpubic distance, is also seen in pygostylian birds (e.g., *Concornis*, *Dapingfangornis*, *Piscivoravis*, *Sapeornis*, *Yanornis*; Sanz et al. 1995; Zhou and Zhang 2003; Li et al. 2006; Zhou et al. 2014; Zheng et al. 2014; see Figs. 3c, Fig. S2E).

Ischial tuberosity

The ischium of *Balaur* bears a well-developed obturator tuberosity (*ischial tuberosity* of Hutchinson 2001) on the proximal end of its anterior margin that contacts or nearly contacts the pubis ventrally (Brusatte et al. 2013). This feature was determined to be a synapomorphy of the velociraptorine subclade including *Balaur* by Turner et al. (2012). However, almost all non-velociraptorine taxa were scored by them as either unknown for or lacking an ischial tuberosity (char. 176 in Turner et al. 2012), with only *Adasaurus*, *Anchiornis*, *Deinonychus* and *Velociraptor* scored as bearing that feature. Nevertheless, a prominent ischial tuberosity is also present in avialans, in particular in large-bodied flightless taxa (e.g., *Patagopteryx*; Hutchinson 2001). The ischial tuberosity of birds approaches and eventually contacts the pubis (e.g., *Dromaius*; ACUB 3131), and is the case in *Balaur*.

Ischium with proximodorsal flange

The ischium of *Balaur* bears a process along the proximal half of its dorsal surface (Brusatte et al. 2013, fig. 27A: “dorsal flange of proximal ischium”). This process is topographically equivalent to the proximal dorsal ischial tuberosity of other reptiles (Hutchinson 2001). This structure is variably developed on the ischia of many paravians (e.g., Novas and Puerta 1997; Forster 1998; Xu et al. 1999;

Agnolín and Novas 2013). In unenlagiines and microraptorines, the ischium bears a tuber-like proximodorsal process (Novas and Puerta 1997; Agnolín and Novas 2013, figs. 3.5c-e) which is absent in known velociraptorines (Norell and Makovicky 1999; Agnolín and Novas 2013; Brusatte et al. 2013) except for a *Velociraptor*-like taxon from Mongolia (Norell and Makovicky 1999, fig 24). In basal avialans, the ischial tuberosity is developed as a prominent trapezoidal flange which is more proximodistally expanded than it is in other paravians and which resembles the condition present in *Balaur* (e.g., *Confuciusornis*, cf. *Enantiornis*, *Jeholornis*, *Patagopteryx*, *Sapeornis*, *Sinornis*; Chiappe et al. 1999; Hutchinson 2001; Sereno et al. 2002; Zhou and Zhang 2002; Zhou and Zhang 2003; Walker and Dyke 2009; see Agnolín and Novas 2013; Fig. S2D, F).

Fibula fused to tibia proximally

In *Balaur*, the tibia and the fibula are fused proximally (Brusatte et al. 2013), a condition not seen in dromaeosaurids or most non-avialan theropods. Among coelurosaurs, a more extensive proximal fusion between tibia and fibula is present in pygostylian birds (e.g., *Qiliania*; Ji et al. 2011).

Tuber and ridge along lateral surface of the distal end of the tibiotarsus

The distal end of the tibiotarsus of *Balaur* bears a pronounced anteroposteriorly oriented lateral ridge. The ridge is most pronounced anteriorly, where it terminates at a discrete rounded tubercle located at the point where the lateral condyle and shaft merge. The ridge is kinked at its midpoint where it forms a second, ventrally directed tubercle positioned laterodistally relative to the first tubercle (Brusatte et al. 2013, fig. 35). Brusatte et al. (2013) suggested that the first tubercle may represent the distal end of the fibula, fused to the tibiotarsus, whereas no interpretation of the second tubercle was provided. A raised ridge along the anterolateral margin of the distal end of the tibiotarsus at the point of fusion between the tibia and the proximal tarsals is also present in *Qiliania* (Ji et al. 2011) and in the enigmatic Haţeg taxon *Bradycneme* (Harrison and Walker 1975). Based on comparison with birds, we interpret the second tubercle and the corresponding kinked ridge as the fibular facet of the calcaneum. According to our interpretation, the other tubercle, more proximally placed, is topographically equivalent to the *tuberculum retinaculi M. fibularis* of birds (Baumel and Witmer 1993).

Complete distal co-ossification of the tibiotarsus

The distal end of the tibia and the proximal tarsals of *Balaur* are coossified, forming a tibiotarsus where the sutures are obliterated (Brusatte et al. 2013). Turner et al. (2012) considered the fusion between the calcaneum and astragalus, but not the tibia and tarsals, to be a synapomorphy of Paraves.

Fusion involving the proximal tarsals and the distal end of the tibia is a condition seen in some basal neotheropods (Tykoski and Rowe 2004). Within non-avialan coelurosaurs, coossification of the proximal tarsals and the distal end of the tibia is observed in alvarezsaurids (e.g., *Albinykus*, *Mononykus*; Perle et al. 1994; Nesbitt et al. 2011) and some oviraptorosaurs (e.g., *Avimimus*, *Elmisaurus*; Osmólska 1981; Vickers-Rich et al. 2002). Within Avialae, the presence of a fully coossified tibiotarsus is present in taxa more crownward than *Archaeopteryx* (e.g., *Apsaravis*, *Confuciusornis*, *Hollanda*; Chiappe et al. 1999; Clarke and Norell 2002; Bell et al. 2010).

Deep extensor groove on distal tibiotarsus

Balaur bears a deep and prominent extensor groove on the distal end of the tibiotarsus (Brusatte et al. 2013). Within dromaeosaurids, this feature has otherwise been reported only in *Buitreraptor* and is homoplastically present in other maniraptoran lineages (e.g., *Apsaravis*, *Hollanda*, *Mononykus*; Perle et al. 1994; Clarke and Norell 2002; Bell et al. 2010).

Tibiotarsus with intercondylar sulcus extended along the posterior surface

The distal end of *Balaur*'s tibiotarsus is saddle-shaped due to the presence of a large and distinct intercondylar sulcus (Brusatte et al. 2013). The latter feature is restricted not only to the anterodistal end of the bone but also extends along the distal end of the posterior surface as a flexor sulcus. This feature is also present in basal avialans known from three-dimensionally preserved specimens (e.g., *Apsaravis*, *Hollanda*; Clarke and Norell 2002; Bell et al. 2010).

Deep circular pit on medial surface of distal tibiotarsus

The medial surface of the distal end of *Balaur*'s tibiotarsus is excavated by a deep subcircular pit which was described as being deeper than are the homologous depressions variably present in the astragali of some dromaeosaurids (Brusatte et al. 2013). A pit comparable in depth to that present in *Balaur* is also present in avialans more crownward than *Archaeopteryx* (*depressio epicondylaris medialis*, Baumel and Witmer 1993) and has been considered a phylogenetically informative feature (see O'Connor et al. 2011).

Extensive coossification of tarsometatarsus

The tarsometatarsal elements of *Balaur* display extensive coossification (Fig. 4a, Figs. S3-4; Brusatte et al. 2013), in contrast to most non-avian theropods in which no such fusion is present (e.g., *Velociraptor*; see Fig. 4b, Fig. S4A). Many maniraptoran lineages display coossification of the distal tarsals to the proximal ends of the metatarsals (e.g., *Avimimus*, *Adasaurus*, *Albinykus, Elmisaurus*; Kurzanov 1981; Osmólska 1981; Nesbitt et al. 2011; Turner et al. 2012). However, the extensive coossification of the metatarsal shafts is a character present only in *Balaur* and pygostylians (e.g., *Bauxitornis*, *Confuciusornis*, *Evgenavis*, *Hollanda*, *Patagopteryx*, *Vorona*, *Yungavolucris*; Chiappe 1993; Chiappe et al. 1999; Chiappe 2002; Forster et al. 2002; Bell et al. 2010; Dyke and Ősi 2010; O'Connor et al. 2014; see Fig. 4c, Fig. S3, Fig. S4C-D).

Metatarsals with one or more longitudinal eminences on the dorsal surface of the shafts

The shafts of *Balaur*'s second to fourth metatarsals are dorsoventrally deep in cross-section, being strongly convex along the extensor surfaces except for the area of contact between metatarsals II and III. Here, the lateral edge of metatarsal II and the medial edge of metatarsal III form dorsoventrally shallow, longitudinally arranged flanges that, together, form a depressed region between the remainder of the metatarsal shafts. This unusual character combination, which is not observed in non-avialan theropods, was considered to be an autapomorphy of *Balaur* by Brusatte et al. (2013). However, comparable features are present in several Mesozoic avialans. *Vorona* possesses two distinct ridges that extend along the distal halves of the extensor surfaces of both metatarsals III and IV, delimiting a depressed intermetatarsal space (Forster et al. 2002). A depressed area between metatarsals II and III is also present in *Patagopteryx* (Chiappe 2002). The extensor surfaces of metatarsals II and III are markedly convex transversely in many avisaurids with depressed areas present between the metatarsal shafts (e.g., *Avisaurus*, *Bauxitornis*; Chiappe 1993; Dyke and Ősi 2010; Fig. S3H). *Yungavolucris* is reported to lack a dorsally convex third metatarsal; however, the shaft's extensor surface at the proximal end of metatarsal III bears a centrally positioned, longitudinally oriented eminence comparable to the condition in *Balaur* (Chiappe 1993). Finally, the enigmatic avialan *Mystiornis* also bears distinct longitudinal ridges along the extensor surfaces of metatarsals II-IV (Kurochkin et al. 2010).

Enlarged extensor fossa on distal end of metatarsal II

In most theropods, the distal end of metatarsal II bears an extensor fossa proximal to the articular end. This fossa usually appears as a pit delimited by distinct margins and does not extend mediolaterally across the entire extensor surface (e.g., *Allosaurus*, *Deinonychus*, *Tyrannosaurus*; Ostrom 1969; Madsen 1976; Brochu 2003). In *Balaur*, the extensor fossa of metatarsal II is enlarged and extends across the whole distal surface, bounded laterally by a raised ridge converging with the trochlea

(Brusatte et al. 2013; Fig. S3B). A large, proximodistally enlarged extensor fossa is present on the second metatarsal of *Evgenavis* (O'Connor et al. 2014; Fig. S3F). An enlarged extensor fossa on metatarsal II, lacking distinct margins and bounded laterally by a raised margin, is also present in *Parabohaiornis* (Wang et al. 2014a) and *Yungavolucris* (Chiappe 1993; Fig. S3E).

Metatarsal II with plantarly projected medial condyle

Balaur bears a plantarly projected medial condyle on the distal end of metatarsal II, visible in medial view as a distinct ventral projection of the distal end (Brusatte et al. 2013; Fig. S3A). In most theropods, including dromaeosaurids, the medial condyle of metatarsal II does not project plantarly more than the lateral condyle (e.g., *Deinonychus*, *Eustreptospondylus*, *Falcarius*, *Garudimimus*, *Sinraptor, Talos*, *Tyrannosaurus, Zuolong*; Ostrom 1969; Currie and Zhao 1993; Brochu 2003; Kirkland et al. 2004; Kobayashi and Barsbold 2005; Sadleir et al. 2008; Choiniere et al. 2010; Zanno et al. 2011). Many avialans bear a plantarly unexpanded medial condyle on metatarsal II and hence resemble other theropods (e.g., *Avisaurus*, *Mystiornis*, *Yungavolucris*; Chiappe 1993; Kurochkin et al. 2010). However, a plantarly projected medial condyle like that present in *Balaur* is present in the basal pygostylians *Confuciusornis* and *Evgenavis* (O'Connor et al. 2014; Fig. S3G, I) and in the ornithuromorph *Apsaravis* (Clarke and Norell 2002).

Metatarsal II lacks prominent ginglymoid distal end

The presence of a prominent extensor sulcus on the second metatarsal is regarded as a synapomorphy of Dromaeosauridae (Turner et al. 2012). *Balaur* possesses a broadly convex distal end of metatarsal II that lacks a ginglymoid distal articulation with a well-developed extensor sulcus (Fig. 4a; see Norell and Makovicky 1997; Brusatte et al. 2013; Fig. S3B). Some avialan taxa also bear a distinct extensor sulcus on metatarsal II like that present in dromaeosaurids (e.g., *Avisaurus*, *Yungavolucris*; Chiappe 1993; Fig. S3C, E) whereas others bear a broadly convex articular facet and hence resemble *Balaur* (e.g., *Bauxitornis*, *Evgenavis*; Dyke and Ősi 2010; O'Connor et al. 2014; Fig. S3D, F).

Distal articular surface of metatarsal II narrower than maximum width of its distal end

The width of the distal articular surface of metatarsal II in *Balaur* is less than the width of the entire distal end of the metatarsal (Brusatte et al. 2013; Fig. S3B). In extensor view, a large non-articular region is present both lateral and medial to the articular surface. The metatarsals of derived therizinosauroids show a similar condition (e.g., *Segnosaurus*; Perle 1979). The same feature also occurs in the second metatarsal of some avisaurid avialans, where distinct non-articular mediolateral expansions are present proximal to the distal articular surface (*Avisaurus archibaldi*, *A. gloriae*; Chiappe 1993; Varricchio and Chiappe 1995; Fig. S3C).

Shaft of metatarsal IV anteroposteriorly compressed and mediolaterally widened

In most theropods, the mid-length cross section of metatarsal IV is subcircular, or anteroposteriorly thicker than wide. In *Balaur*, the mid-length cross section of metatarsal IV is anteroposteriorly compressed and mediolaterally expanded (Brusatte et al. 2013), a characteristic that is also seen in both velociraptorine (e.g., *Deinonychus*, *Velociraptor* and *Adasaurus*) and dromaeosaurine dromaeosaurids (e.g., *Utahraptor*) as well as basal troodontids (Turner et al. 2012). However, an anteroposteriorly compressed metatarsal IV with a flat cross section is also present in basal avialans (e.g., *Avisaurus*, *Mystiornis*, *Evgenavis*, *Yungavolucris*; Brett-Surman and Paul 1985; Chiappe 1993; Kurochkin et al. 2010; O'Connor et al. 2014; Fig. S3E, H).

Short and robust metatarsal V

Dromaeosaurids bear a slender and elongate metatarsal V that is at least 40% of metatarsal III's length (Fig 5c; Norell and Makovicky 1999; Hwang et al. 2002; Brusatte et al. 2013). *Balaur* possesses a shorter and stouter metatarsal V that is less than 30% of metatarsal III's length (Fig 5a, Fig. S3A, S4B; Brusatte et al. 2013): it is thus more similar to the condition present in basal avialans (e.g., *Evgenavis, Sapeornis*, *Vorona*; Forster et al. 2002; Zhou and Zhang 2003; O'Connor et al. 2014) and most non-avialan coelurosaurs (e.g., *Khaan*, *Segnosaurus*, *Tyrannosaurus*; Perle 1979; Brochu 2003; Balanoff and Norell 2012).

Hallux unreduced compared to other toes and functional

Balaur possesses a hallux that cannot be considered reduced in size compared to the other pedal digits (Brusatte et al. 2013, Fig. S4B). Most non-avialan theropods, including dromaeosaurids, possess a relatively small first pedal ungual (e.g., *Allosaurus*, *Microraptor*, *Velociraptor*; Madsen 1976; Norell and Makovicky 1997; Hwang et al. 2002; Fig. S4A). However, a large and falciform first pedal ungual that is not reduced compared to the other pedal unguals, as seen in *Balaur*, is also present in many basal birds (e.g., *Confuciusornis*, *Jixiangornis*, *Patagopteryx*, *Sapeornis*, *Zhouornis*; Chiappe et al. 1999; Chiappe 2002; Ji et al. 2002; Zhou and Zhang 2003; Zhang et al. 2013; Fig. S4D). Furthermore, the first phalanx in *Balaur*'s hallux is subequal in length compared to the proximal phalanges of pedal digits II-IV, a condition present in basal avialans (e.g., *Jixiangornis*, *Sapeornis*, *Zhouornis*; Ji et al. 2002; Zhou and Zhang 2003; Zhang et al. 2013; Fig. S4) but not in non-avialan theropods. The distal placement of the articular end of metatarsal I in *Balaur* relative to the trochlea of metatarsal II is more similar to that of the basal avialans (e.g., *Confuciusornis*, *Patagopteryx*; Chiappe et al. 1999; Chiappe 2002) than the more proximally placed trochlea of metatarsal I in dromaeosaurids (e.g., *Microraptor*, *Deinonychus*, *Velociraptor*; Norell and Makovicky 1997; Hwang et al. 2002; Fowler et al. 2011) and other non-avialan theropods (e.g., *Khaan*, Balanoff and Norell 2012). In addition, the well-developed articular surfaces indicate that the hallux of *Balaur* was dextrous, mobile and fully functional (Brusatte et al. 2013). This is also the condition present in birds but contrasts with that of most non-avialan theropods, including dromaeosaurids (Norell and Makovicky 1997).

Enlarged pedal ungual II lacking both marked falciform shape and prominent flexor tubercle

Balaur bears a hypertrophied second pedal ungual that is larger than the third and fourth pedal unguals, similar to that seen in most deinonychosaurs (Turner et al. 2012; Brusatte et al. 2013). However, Brusatte et al. (2013) noted that the second pedal ungual of *Balaur* does not show the marked falciform shape and prominent flexor tubercle seen in most dromaeosaurids (e.g., Ostrom 1969; Turner et al. 2012). A robust second pedal digit with an enlarged and moderately recurved ungual, comparable to the condition in *Balaur*, is also present among several avialans (e.g., *Bohaiornis*, *Fortunguavis*, *Jixiangornis*, *Parabohaiornis*, *Patagopteryx*, *Qiliania*, *Sulcavis*, *Zhouornis*; Chiappe 2002; Ji et al. 2002; Hu et al. 2011; Ji et al. 2011; O'Connor et al. 2013; Zhang et al. 2013; Wang et al. 2014b; Wang et al. 2014A; Fig. S4D).

Penultimate phalanges of pedal digit III longer than 1.2 times that of the preceding phalanx

In most theropods, including dromaeosaurids, the penultimate phalanx of the third pedal digit is subequal to or shorter than the length of the preceding phalanges (e.g., *Gallimimus*, *Khaan*, *Tyrannosaurus*, *Velociraptor*; Osmólska et al. 1972; Norell and Makovicky 1997; Brochu 2003; Balanoff and Norell 2012; Brusatte et al. 2013, table 7). However, *Balaur* bears a relatively elongate penultimate phalanx on pedal digit III that is 1.2 times longer than the preceding phalanx (Brusatte et al. 2013; Fig. S4B). This condition is similar to that seen in many basal avialans (e.g., *Concornis*, *Sapeornis*, *Zhouornis*; Sanz et al. 1995; Zhou and Zhang 2003; Zhang et al. 2013; Fig. S4D) and unlike that of dromaeosaurids and most non-avialan theropods.

Pedal ungual IV reduced in size

Balaur's fourth pedal ungual, although distally incomplete in the holotype specimen, is the smallest of the pedal unguals (about 60% the size of pedal ungual III, see Brusatte et al. 2013; Fig. S4B). This condition differs from dromaeosaurids, *Sapeornis* and some troodontids that have fourth pedal unguals that are more than 85% the length of the third pedal ungual (e.g., *Borogovia* 140%, *Sapeornis* 100%; Osmólska 1987; Brusatte et al. 2013, table 7; Pu et al. 2013) but resembles the condition of ornithothoracine birds (e.g., *Bohaiornis* 59%, *Parabohaiornis* 60%, *Qiliania* 76%, *Zhouornis* 66%; Hu et al. 2011; Ji et al. 2011; Zhang et al. 2013; Fig. S4C-D). The relative length of the fourth pedal ungual of most maniraptorans is intermediate between *Balaur* and dromaeosaurids, being 70-85% the length of pedal ungual III (e.g., *Archaeopteryx* 77-78%, *Khaan*, *Jixiangornis*, *Sinornithoides* and *Zhongjianornis* 80%; Elzanowski 2001; Currie and Dong 2001; Ji et al. 2002; Zhou and Li 2010; Balanoff and Norell 2012, fig. 33).

Results

Modified Turner et al. (2012) analysis

The modified Turner et al. (2012) analysis produced >999,999 shortest cladograms of 2085 steps each (CI = 0.2998, RI = 0.7389). In all shortest trees found, *Balaur* was recovered as an avialan, as the sister-taxon of *Sapeornis* and not as a member of Dromaeosauridae. The '*Balaur* + *Sapeornis'* clade resolved as the sister-taxon of a clade including Pygostylia, *Jixiangornis* and *Jeholornis*. Exploration of the alternative topologies found indicated that *Epidendrosaurus* and *Pedopenna* acted as 'wildcard' taxa among Maniraptora, as in Turner et al. (2012), and these taxa were pruned *a posteriori* from the results of the analyses to improve resolution within basal paravian taxa. After pruning the 'wildcard' taxa from the strict consensus topology (Fig. 5), *Archaeopteryx* resolved as the basalmost avialan.

Unambiguous synapomorphies for the sister taxon relationships between *Balaur* and *Sapeornis* are: anterior surface of deltopectoral crest with distinct muscle scar near lateral edge along distal end of crest for insertion of biceps muscle (141.1, homoplastic among maniraptorans); third manual digit with two or less phalanges (150.2, convergently developed among ornithothoracines); humerus condyles placed on anterior surface (371.1, convergently developed among therizinosauroids and most avialans); metacarpal III anteroposterior diameter less than 50% same diameter of metacarpal II (391.1); length of first phalanx of pedal digit I > 66% of first pedal phalanx of pedal digit III (483.1, convergently developed among derived avialans).

Furthermore, all three versions of the dataset that used implied weighting recovered *Balaur* as an avialan and sister-taxon of *Sapeornis* (see Figure S5).

Modified Lee et al. (2014) analysis

The modified Lee et al. (2014) analysis recovered 1152 shortest trees of 6350 steps each (CI = 0.2672, RI = 0.5993). The strict consensus of the shortest trees found is in general agreement with the Maximum Clade Credibility Tree recovered by Lee et al. (2014), the most relevant difference being the unresolved polytomy among *Aurornis*, *Jinfengopteryx*, Dromaeosauridae, Troodontidae and Avialae (Fig. 6). The *a posteriori* pruning of the two above mentioned genera does not resolve the polytomy among the three suprageneric clades. It is noteworthy that an unresolved polytomy among the main paravian lineages was also obtained by Brusatte et al. (2014) using an expanded version of Turner et al.'s (2012) dataset. In all trees found, *Balaur* was resolved as a basal avialan and as the sister taxon of Pygostylia (the '*Zhonjianornis* + (*Sapeornis* + more derived avialans)' clade), in agreement with the results of previous versions of this matrix (i.e., Godefroit et al. 2013b). The character states unambiguously supporting this placement for *Balaur* are: (1) presence of fusion between metacarpal II and the distal carpals (char. 311.1); presence of a mediolaterally slender third metacarpal (char. 322.1); absence of the mediodorsal process on the ischium (char. 423.0); presence of an elongate first phalanx of pedal digit I (char. 499.0); presence of a completely fused tibiotarsus (char. 580.1). Nodal support for this placement was low (Decay Index = 1). Nevertheless, higher nodal support values for more basal nodes along the basal part of Avialae support the placement of *Balaur* in this clade. This interpretation is further supported by the implied weighting analyses of the data set: as discussed above, these analyses consistently recovered *Balaur* as a non-pygostylian member of Avialae, located less crownward within Avialae than was the case in the unweighted analysis, and bracketed by *Archaeopteryx* and all other avialans (see Figure S6).

Templeton tests

We re-analysed Turner et al.'s (2012) original dataset enforcing the following backbone constraint: ((*Balaur*, *Anas*), *Troodon*, *Dromaeosaurus*) (i.e., enforcing the analysis to retain only those topologies where *Balaur* is closer to modern birds than both troodontids and dromaeosaurids, thus by definition forcing it to be a member of Avialae; see Electronic Supplementary Material). The shortest enforced topologies that resulted were 2054 steps long, five steps less parsimonious than the shortest unconstrained topologies that recovered *Balaur* among Dromaeosauridae. This difference was not statistically significant based on the Templeton test (p>0.490, N>49).

We also re-analysed Turner et al.'s (2012) modified dataset, this time enforcing *Balaur* as a dromaeosaurid using the following backbone constraint: ((*Balaur*, *Dromaeosaurus*), *Troodon*, *Anas*).

The shortest enforced topologies that resulted were 2087 steps long, two steps less parsimonious than the shortest unconstrained topologies were *Balaur* was recovered within Avialae. This difference was not statistically significant based on the Templeton test (*p*>0.750, N>37).

Using the dataset modified from Lee et al. (2014), we enforced a dromaeosaurid placement for *Balaur*, using the following backbone constraint: ((*Balaur*, *Dromaeosaurus*), *Troodon*, *Meleagris*). The shortest trees found using that constraint are nine steps longer than the shortest unforced topologies, and placed *Balaur* as the basalmost dromaeosaurid, excluded from the ((Eudromaeosauria + Microraptoria) + Unenlagiinae) clade. This difference was not statistically significant based on the Templeton test (*p*>0.440, N>125).

Finally, we also tested a velociraptorine placement for *Balaur*, using the following backbone constraint: ((*Balaur*, *Velociraptor*), *Dromaeosaurus*, *Troodon*). The shortest trees found using that constraint are 14 steps longer than the shortest unforced topologies, and placed *Balaur* as the basalmost velociraptorine. This difference was not statistically significant based on the Templeton test (*p*>0.158, N>89).

Discussion

Balaur possesses a unique and bizarre mix of characters, many of which were previously considered exclusive to Deinonychosauria or Avialae, and which may challenge its placement in either of the aforementioned clades. Godefroit et al. (2013b, Electronic Supplementary Material) tested alternative placements of *Balaur* among Paraves, and recovered the dromaeosaurid placement for that taxon as a suboptimal solution. Here, we have shown that an avialan placement for *Balaur* using the original dataset of Turner et al. (2012) is a suboptimal solution that cannot be rejected using that dataset.

Although the most parsimonious results of the two updated phylogenetic analyses presented here concur in resolving *Balaur* within Avialae, the deinonychosaurian placement for this taxon discussed by Brusatte et al. (2013) can be only tentatively rejected based on current information. The most parsimonious placement was recovered under both equally weighted and implied weighting analyses, suggesting that the avialan placement of *Balaur* was not biased by *a priori* assumptions on character weighting. Nevertheless, in assuming an avialan placement for *Balaur*, a significant amount of homoplasy, due to both convergences and reversals, is required to explain its unique morphology.

The sister taxon relationships between *Balaur* and the short-tailed *Sapeornis* resulted by the analysis of the dataset modied from Turner et al. (2012) is quite unexpected, and may be partially biased by the placement of the long-tailed *Jeholornis* and *Jixiangornis* as closer to other short-tailed birds than *Sapeornis* (a relationships also recovered by the original dataset, Turner et al. 2012). According to that topology, the short pygostyle-bearing tail of *Sapeornis* evolved independently to the same condition in more crown-ward birds. The topology resulted by the dataset modified from Lee et al. (2014) is more 'traditional' as it depicts a single origin of the pygostylian tail among birds. Topological discrepancies and alternative placements of problematic taxa may be influenced by artefacts in coding practice, or by the logical basis of character statement definition followed by different authors (Brazeau 2011). The datasets of Turner et al. (2012) and Lee et al. (2014) differ from each other in the logical basis of their respective character statements and definitions. The definitions of many characters used in the analysis of Turner et al. (2012) impose congruence by linking more than one variable character to a particular state (see Brazeau 2011 and references therein), or by mixing together neomorphic and transformational characters as alternative states of the same character statements (see Sereno 2007) – a decision made such that contingent characters may be ordered so that absence is not "counted twice". Character statements and definitions in the analysis of Lee et al. (2014) followed the recommendations outlined by Sereno (2007) and Brazeau (2011); consequently, each character statement describes a single variable character, and neomorphic and transformational characters were included as separate character statements. To avoid the creation of spurious transformational optimizations under some topologies, the characters in the analysis of Lee et al. (2014) were therefore atomized in such a way as to capture both the presence or absence of the feature in addition to the states of the feature (Brazeau 2011). Taxa scored as lacking a particular neomorphic character were scored as 'unknown' for the transformational characters describing different conditions of the same neomorphic feature.

We therefore consider it likely that some discrepancies between the updated analyses of Turner et al. (2012) and Lee et al. (2014) – including the alternative placements of *Balaur* and *Sapeornis* among basal avialans – reflect artefacts of coding rather than actual conflict in the data. Nevertheless, it is noteworthy that even using distinct datasets, alternative character weighting hypotheses and different logical bases for character definitions, *Balaur* was consistently recovered as a basal avialan.

Furthermore, the phylogenetic analysis of Foth et al. (2014), which used the dataset of Turner et al. (2012) as their basis and which included an expanded set of characters, independently found *Balaur* to be a basal avialan more crownward than *Archaeopteryx*, but in a less crownward position than that presented here. In conclusion, we consider the consensus among the results of these alternative tests (i.e., *Balaur* as a non-pygostylian basal avialan) as the phylogenetic framework for the discussion on its evolution and palaeoecology.

Implications for the palaeoecology of Balaur

In the absence of both extrinsic data on diet and craniodental remains there is no direct evidence pertaining to the ecology and trophic adaptations of *Balaur*. Although not explicitly stated, Brusatte et al.'s (2013) inferences about the ecology and diet of *Balaur* rest entirely on their favoured phylogenetic placement of the taxon within the predatory deinonychosaurian clade Velociraptorinae (see Carpenter 1998). However, some aspects of *Balaur*'s morphology do not support the hypothesis that its ecomorphology was similar to that of dromaeosaurids. While there exists evidence that dromaeosaurids employed both their hands and feet in predation (see Carpenter 1998), the reduction in length and functionality of the third manual digit and the poor development or absence of the pedal characters linked with predatory behaviour in deinonychosaurs (i.e., ginglymoid distal end of metatarsal II allowing extensive hyperextension, falciform second ungual with prominent flexor tubercle; Ostrom 1969; Fowler et al. 2011), challenge the notion of a specialised, dromaeosaurid-like predatory ecology for *Balaur*. Brusatte et al. (2013) interpreted these unusual traits of *Balaur* as the result of insularism, although they acknowledged that comparable morphological changes in insular taxa have so far not been reported in predatory species. We are not aware of the reduction or loss of predatory adaptations in any insular predatory taxon, and therefore consider it unlikely that the unique morphology of *Balaur*, in particular the appendicular characters considered to be predatory adaptations among dromaeosaurids, could be sufficiently accounted for by the 'island effect'.

Most of the features considered to be autapomorphies of *Balaur* by Csiki et al. (2010) and Brusatte et al. (2013) are reinterpreted here as avialan synapomorphies. Consequently, these traits were inherited by *Balaur* from its bird-like ancestors before its lineage was isolated in the Haţeg environment. Since our analyses place *Balaur* among a grade of non-predatory avialans including herbivorous and/or omnivorous species (Zhou and Zhang 2002; Dalsätt et al. 2006; Zanno and Makovicky 2011), our preferred scenario does not necessitate a hypothesis of a carnivorous ecology for this taxon and is thus more consistent with the absence of the aforementioned predatory adaptations. Furthermore, in assuming a herbivorous or omnivorous ecology for *Balaur*, the amount of morphological changes, particularly in limb shapes and proportions, is comparable to that reported in several insular herbivorous and omnivorous taxa, including both mammals (Sondaar 1977; Caloi and Palombo 1994; van der Geer et al. 2011) and dinosaurs (e.g., Dalla Vecchia 2009). In particular, the presence in *Balaur* of a relatively broad pelvic canal, the short and broad metatarsus with mediolaterally expanded distal ends relative to the articular surfaces, and the presence of an enlarged first pedal digit is a combination of features convergently acquired only by the non-predatory clade Therizinosauridae among Mesozoic theropods (Zanno 2010; Zanno and Makovicky 2011).

However, we agree with previous authors that, regardless of its position within Paraves, the morphology of *Balaur* includes a unique and unexpected combination of features, otherwise seen in distinct maniraptoran lineages. Interestingly, *Balaur* independently evolved a series of features previously reported in more crownward bird lineages, such as a deep *depressio epicondylaris medialis* in the tibiotarsus, a hypertrophied extensor fossa in the second metatarsal, and dorsally convex metatarsals with expanded distal ends (characters elsewhere seen in some ornithothoracines). A possible role of insularism in the origin of some of these traits is acknowledged even in our preferred phylogenetic scenario. In particular, the results of our analyses indicate that *Balaur* is phylogenetically bracketed by taxa showing relatively more elongate forelimbs (humeral lengths usually more than 60% of the tibiotarsus + tarsometatarsus length) and more robust forearms (ulna as thick as or thicker than the tibiotarsus). Accordingly, we interpret the forelimb of *Balaur* as secondarily reduced.

Flightlessness has also been inferred in the ornithurine *Gargantuavis* from the Campanian-Maastrichtian of southern France (Buffetaut and Loeuff 1998), indicating that distinct avialan lineages endemic to Late Cretaceous Europe reduced or lost their flight adaptations. Several bird clades independently evolved flightlessness during the Cenozoic as a result of their exploitation of insular environments and the taxa concerned typically displayed apomorphic reduction of the forelimbs compared to those of their closest relatives (Paul 2002; Naish 2012). Therefore, the reduced forelimb of *Balaur* may be interpreted as the result of insularism.

Finally, existing skeletal and life reconstructions of *Balaur* have interpreted it as a velociraptorine-like dromaeosaurid (Csiki et al. 2010; Brusatte et al. 2013). Does our re-interpretation of this taxon as a member of Avialae require that previous hypotheses about its appearance should be modified? By combining the known elements of *Balaur* with those of other paravians, a new skeletal reconstruction has been produced (Fig. 7). As our knowledge of Mesozoic paravian diversity has improved, it has become ever clearer that early members of the deinonychosaurian and avialan lineages were highly similar in proportions, detailed anatomy and life appearance: consequently, an ‘avialan interpretation’ of *Balaur* does not result in an animal obviously different from a ‘dromaeosaurid interpretation’. This conclusion has been supported by recent quantitative analyses that demonstrate a significant degree of shared morphospace between basal avialan taxa and their closest paravian relatives (e.g., Brusatte et al.

2014). Nevertheless, we suggest that *Balaur* may have been proportionally shorter-tailed and with a less raptorial-looking foot than previously depicted (Csiki et al. 2010; Brusatte et al. 2013). Clearly, details of its cranial and dental anatomy are speculative. We assume that, like other paravians, *Balaur* was extensively feathered.

Conclusions

The Maastrichtian paravian theropod *Balaur bondoc* is reinterpreted here as a basal avialan rather than as a dromaeosaurid. Features supporting its placement among Avialae include the hypertrophied coracoid tubercle, the anterior placement of the distal condyles of the humerus, the proximally fused carpometacarpus with a laterally shifted semilunate carpal, the closed intermetacarpal space, the reduced condyles on metacarpals I-II, the slender metacarpal III, the reduced phalangeal formula of the third digit, the extensively fused tibiotarsus, the extensively fused tarsometatarsus, the distal placement of the articular end of first metatarsal, the large size of the hallux, and the elongation of the penultimate phalanges of the pes. The absence of dromaeosaurid synapomorphies (e.g., non-ginglymoid metatarsals II and III, short metatarsal V) is thus interpreted as plesiomorphic and not as reversals. Both its phylogenetic bracketing within basal avialans and the absence of predatory adaptations concur in indicating that *Balaur* was herbivorous or omnivorous, not predatory. The reduced forelimb of *Balaur* represents one of the most compelling pieces of evidence for insular adaptation in a Mesozoic bird. Furthermore, with its unique combination of features shared by distinct paravian clades and its possible placement as one of the closest relatives of Pygostylia, *Balaur* may represent a pivotal taxon in future investigations of Mesozoic bird interrelationships.

The hypothesis that some Mesozoic paravians represent the flightless descendants of volant, *Archaeopteryx*-like ancestors, most vigorously promoted by Paul (1988, 2002), has not been supported by recent phylogenetic hypotheses (e.g., Senter 2007b; Turner et al. 2012; Agnolín and Novas 2013). Furthemore, phylogenetic analyses that incorporate sufficient character data are able to differentiate the members of such paravian lineages as Dromaeosauridae, Troodontidae and Avialae, as demonstrated by our present study. Nevertheless, reinterpretation of *Balaur* as a flightless avialan reinforces the point that at least some Mesozoic paravian taxa, highly similar in general form and appearance to dromaeosaurids, may indeed be the enlarged, terrestrialised descendants of smaller, flighted ancestors, and that the evolutionary transition involved may have required relatively little in the way of morphological or trophic transformation.

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Figure captions

Figure 1. Comparison of the scapulocoracoid of (a) *Balaur* (lateral view) to that of (b) the pygostylian *Enantiophoenix* (medial view); and (c) the dromaeosaurid *Velociraptor* (lateral view); (a) after Csiki et al. (2010, fig. 1); (b) modified after Cau and Arduini (2003, fig. 2); (c) after Norell and Makovicky (1999, fig. 4). All scapulocoracoids are drawn with the proximal half of the scapular blade oriented horizontally. Abbreviations: ac, acromion; ct, coracoid tubercle; snf, supracoracoid nerve foramen.

Figure 2. Comparison of the manus of (a) *Balaur* to those of (b) the enantiornithine *Zhouornis*; (c) the pygostylian *Sapeornis*; and (d) the dromaeosaurid *Deinonychus*, showing bird-like features of *Balaur*. (a) after Csiki et al. (2010, fig. 1, mirrored from original); (b) after Zhang et al. (2013, fig. 7); (c) after Zhou and Zhang (2003, fig. 7); (d) after Wagner and Gauthier (1999, fig. 2). All drawn at the same metacarpal II length. Abbreviations: cis, closed intermetacarpal space; cmc, carpometacarpus; d3, reduced third digit; drc, distally restricted condyles; lsc, laterally shifted semilunate carpal; pnm, proximally narrow metacarpal I.

Figure 3. Pelvis of *Balaur* in lateral view (a). Comparison of the pubes of *Balaur* in anteroventral view (b) to those of the pygostylian *Sapeornis* in anterior view (c), and the dromaeosaurid *Velociraptor* in posterior view (d). (c) after Zhou and Zhang (2003, fig. 8); (d) after Norell and Makovicky (1999, fig. 19).

Figure 4. Comparison of the metatarsus and pes of (b) *Balaur* to that of (a) the dromaeosaurid *Velociraptor*; and (c) the pygostylian *Zhouornis*. (a) after Norell and Makovicky (1997 figs. 6); (c) after Zhang et al. (2013, fig. 8, mirrored from original). Abbreviations: mt I, metatarsal I; U II: pedal ungual I.

Figure 5. Reduced strict consensus of the shortest trees from the analysis of the modified Turner et al. (2012) matrix after pruning the ‘wildcard’ taxa *Epidendrosaurus* and *Pedopenna.* Numbers adjacent to nodes indicate Decay Index values >1.

Figure 6. Strict consensus tree of the shortest trees from the analysis of the modified Lee et al. (2014) matrix. Filled circle indicates Avialae. Numbers adjacent to nodes indicate Decay Index values.

Figure 7. Speculative skeletal reconstruction for *Balaur bondoc*, showing known elements in white and unknown elements in grey. Note that the integument would presumably have substantially altered the outline of the animal in life. Produced by Jaime Headden, used with permission.

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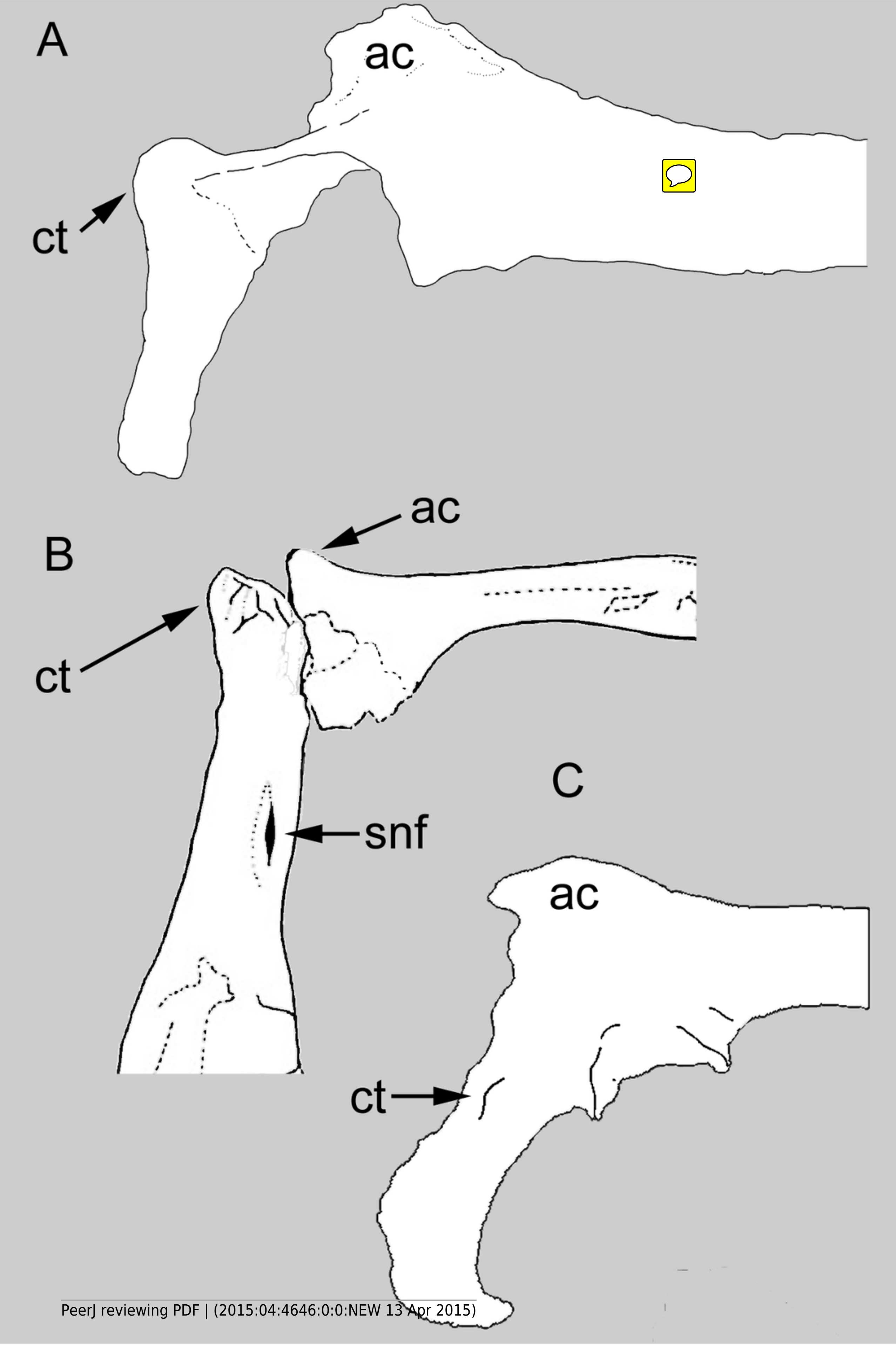
1

Comparison between the scapulocoracoid of *Balaur* and other paravians.

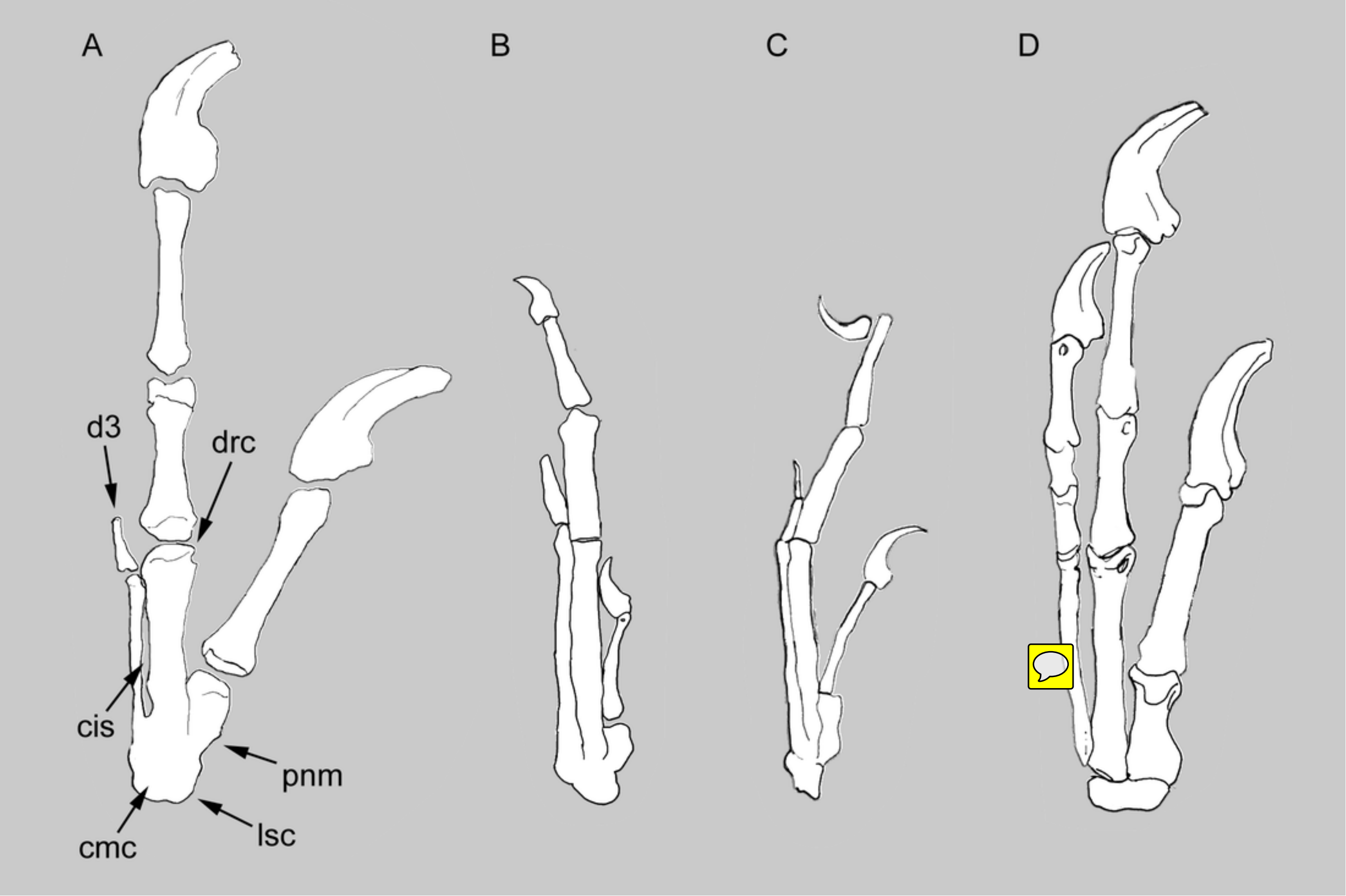
Comparison of the scapulocoracoid of (a) *Balaur* (lateral view) to that of (b) the pygostylian *Enantiophoenix* (medial view); and (c) the dromaeosaurid *Velociraptor* (lateral view); (a) after Csiki et al. (2010, fig. 1); (b) modified after Cau and Arduini (2003, fig. 2); (c) after Norell and Makovicky (1999, fig. 4). All scapulocoracoids are drawn with the proximal half of the scapular blade oriented horizontally. Abbreviations: ac, acromion; ct, coracoid tubercle; snf, supracoracoid nerve foramen.


A
ac
ct
B
ac
ct
snf
C
ac
ct

2

Comparison between the manus of *Balaur* and other paravians.

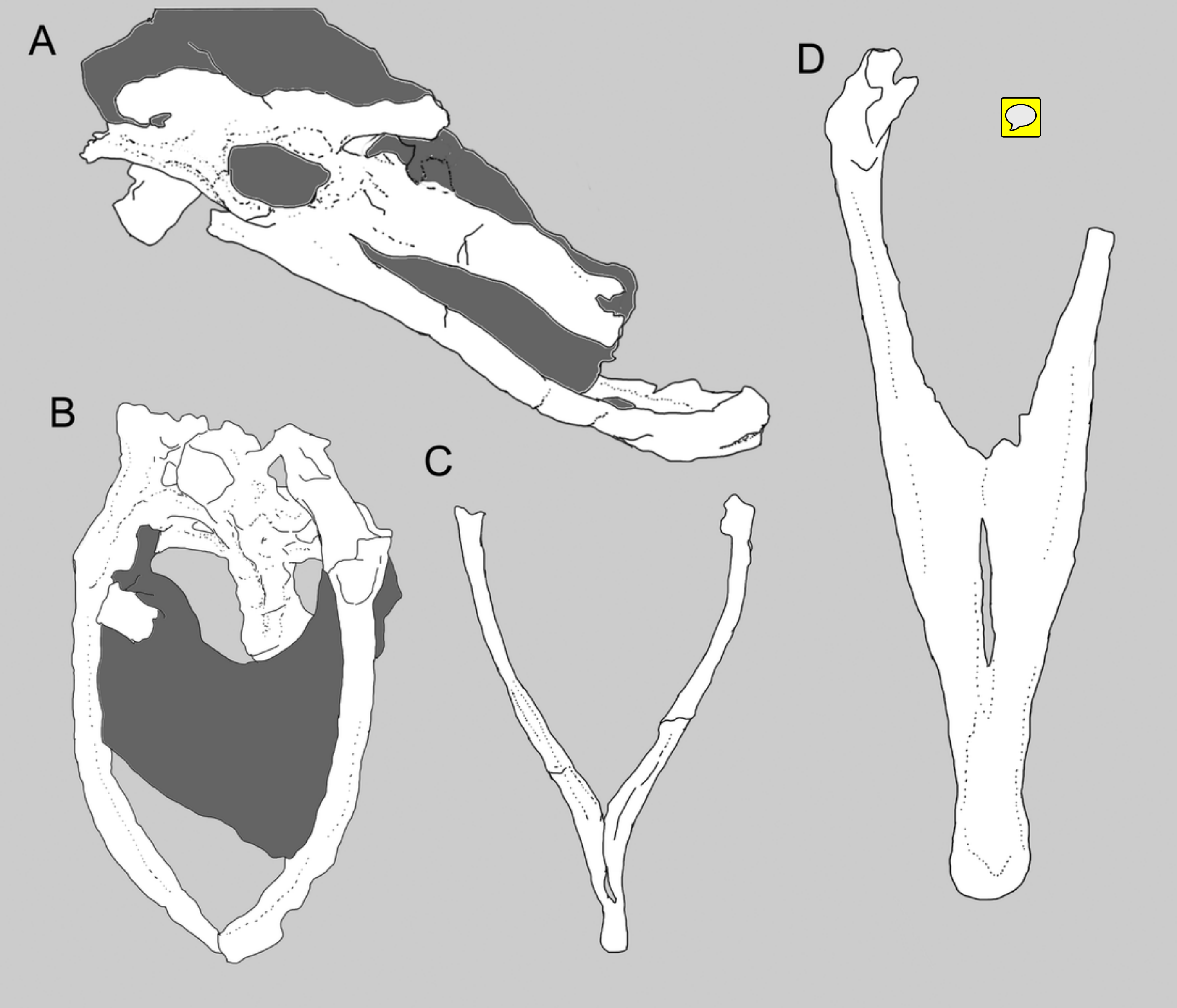
Comparison of the manus of (a) *Balaur* to those of (b) the enantiornithine *Zhouornis*; (c) the pygostylian *Sapeornis*; and (d) the dromaeosaurid *Deinonychus*, showing bird-like features of Balaur. (a) after Csiki et al. (2010, fig. 1, mirrored from original); (b) after Zhang et al. (2013, fig. 7); (c) after Zhou and Zhang (2003, fig. 7); (d) after Wagner and Gauthier (1999, fig. 2). All drawn at the same metacarpal II length. Abbreviations: cis, closed intermetacarpal space; cmc, carpometacarpus; d3, reduced third digit; drc, distally restricted condyles; lsc, laterally shifted semilunate carpal; pnm, proximally narrow metacarpal I.



3

Comparison between the pelvis of *Balaur* and other paravians.

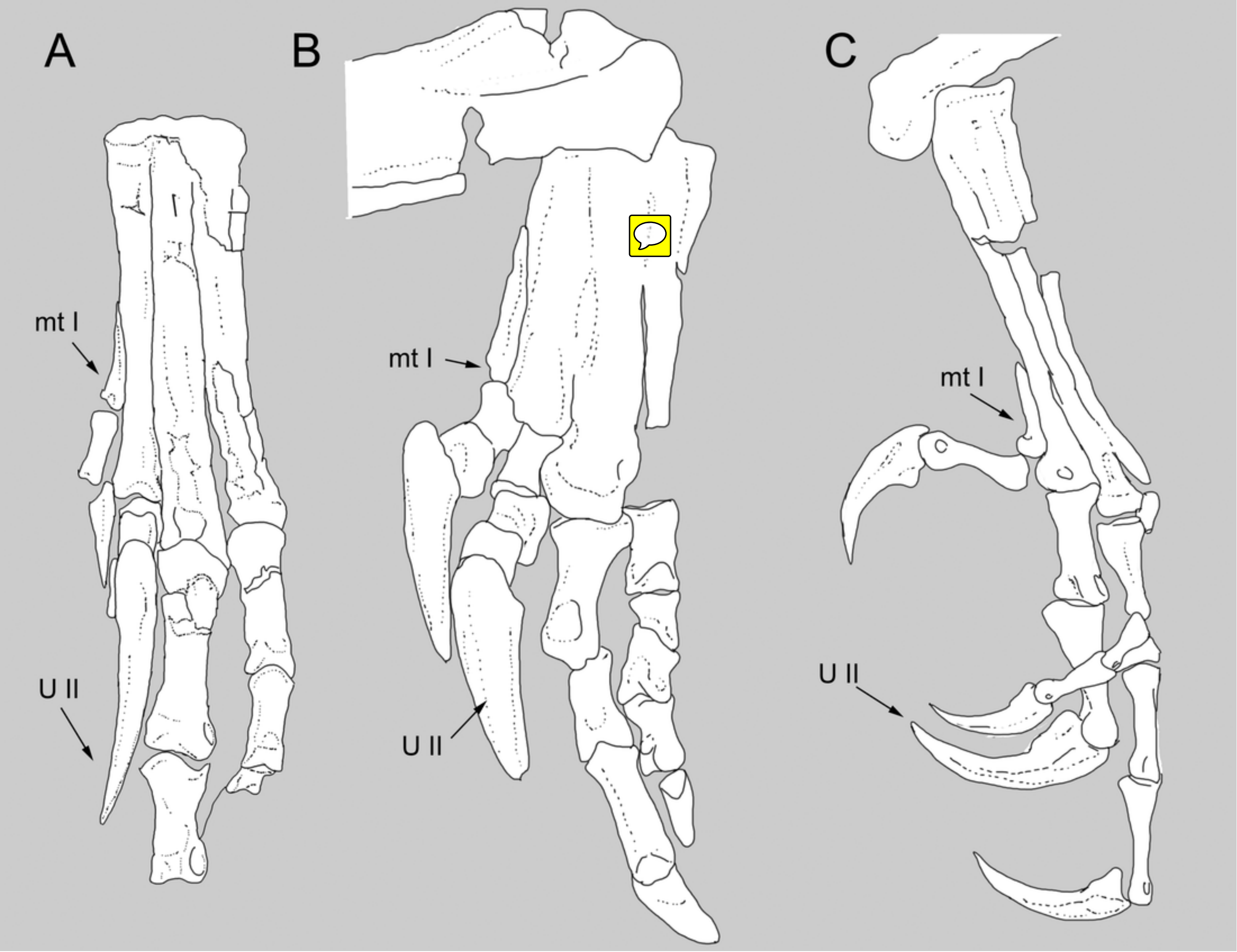
Pelvis of *Balaur* in lateral view (a). Comparison of the pubes of *Balaur* in anteroventral view (b) to those of the pygostylian *Sapeornis* in anterior view (c), and the dromaeosaurid *Velociraptor* in posterior view (d). (c) after Zhou and Zhang (2003, fig. 8); (d) after Norell and Makovicky (1999, fig. 19).



4

Comparison between the metatarsus of *Balaur* and other paravians.

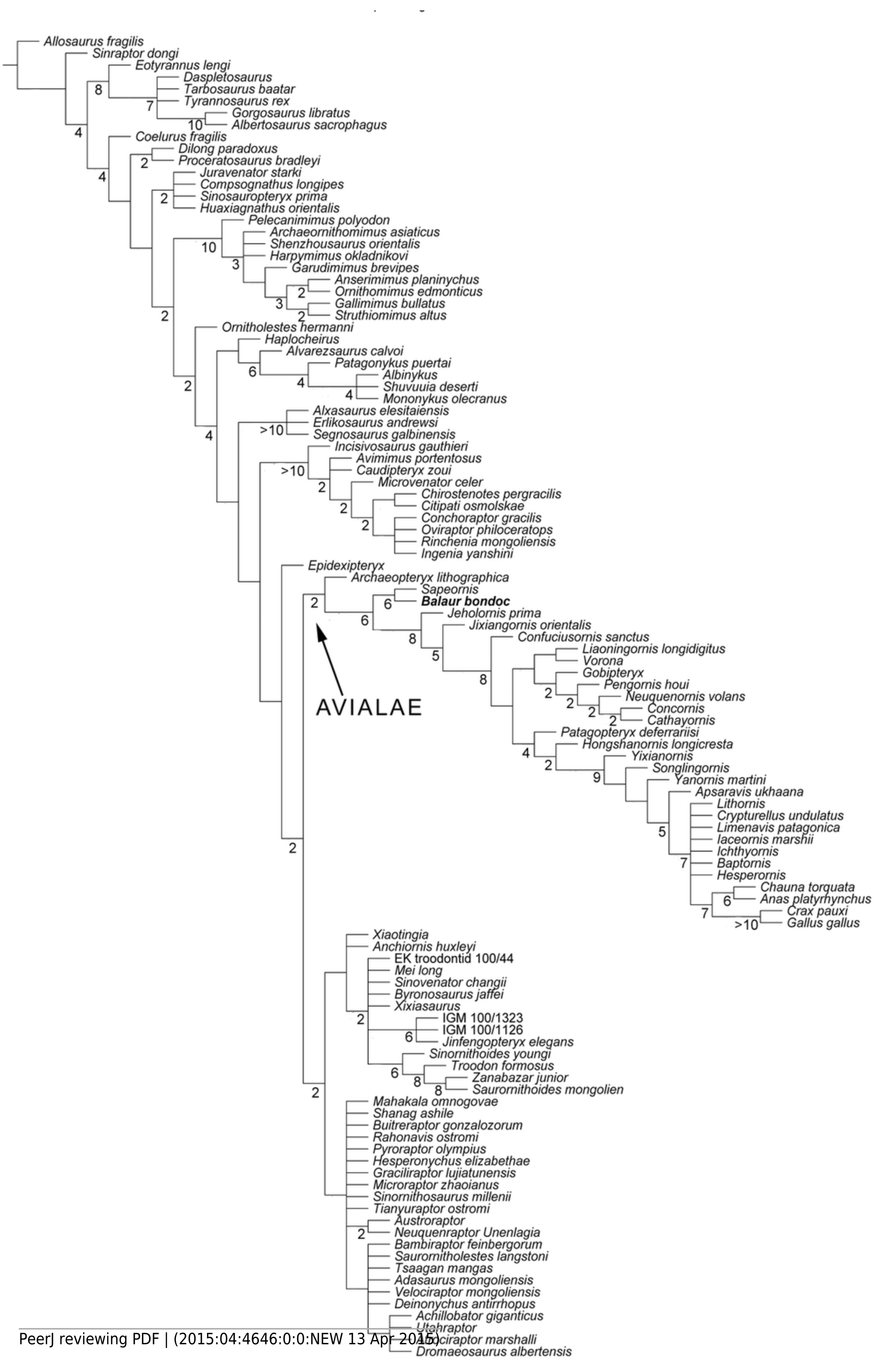
Pelvis of *Balaur* in lateral view (a). Comparison of the pubes of *Balaur* in anteroventral view (b) to those of the pygostylian *Sapeornis* in anterior view (c), and the dromaeosaurid *Velociraptor* in posterior view (d). (c) after Zhou and Zhang (2003, fig. 8); (d) after Norell and Makovicky (1999, fig. 19).



5

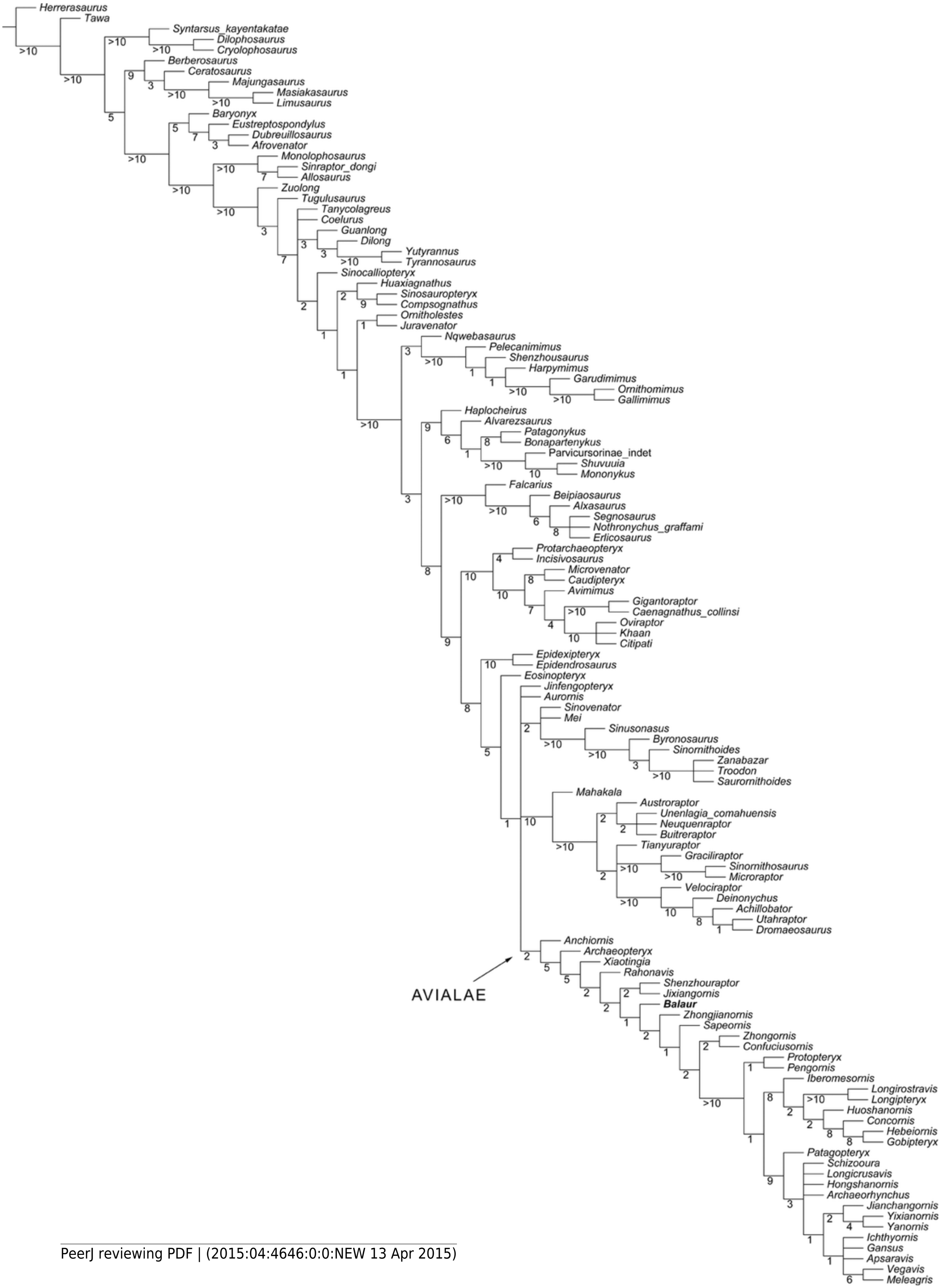
Updated dataset of Turner et al. (2012)

Reduced strict consensus of the shortest trees from the analysis of the modified Turner et al. (2012) matrix after pruning the ‘wildcard’ taxa *Epidendrosaurus* and *Pedopenna*. Numbers adjacent to nodes indicate Decay Index values >1.


Allosaurus fragilis
Sinraptor dongi
Eotyrannus lengi
8
Daspletosaurus
Tarbosaurus baatar
Tyrannosaurus rex
7
Gorgosaurus libratus
10
Albertosaurus sacrophagus
4
Coelurus fragilis
Dilong paradoxus
2
Proceratosaurus bradleyi
4
Juravenator starki
Compsognathus longipes
2
Sinosauropteryx prima
Huaxiagnathus orientalis
Pelecanimimus polyodon
Archaeornithomimus asiaticus
10
Shenzhousaurus orientalis
Harpymimus okladnikovi
3
Garudimimus brevipes
Anserimimus planinychus
2
Ornithomimus edmonticus
3
Gallimimus bullatus
2
Struthiomimus altus
2
Ornitholestes hermanni
Haplocheirus
Alvarezsaurus calvoi
6
Patagonykus puertai
4
Albinykus
4
Shuvuuia deserti
Mononykus olecranus
2
Alxasaurus elesitaiensis
Erlikosaurus andrewsi
>10
Segnosaurus galbinensis
4
Incisivosaurus gauthieri
>10
Avimimus portentosus
Caudipteryx zoui
2
Microvenator celer
2
Chirostenotes pergracilis
Citipati osmolskae
2
Conchoraptor gracilis
Oviraptor philoceratops
Rinchenia mongoliensis
Ingenia yanshini
Epidexipteryx
Archaeopteryx lithographica
2
Sapeornis
6
Balaur bondoc
6
Jeholornis prima
Jixiangornis orientalis
8
Confuciusornis sanctus
5
Liaoningornis longidigitus
Vorona
8
Gobipteryx
Pengornis houi
2
Neuquenornis volans
2
Concornis
2
2
Cathayornis
AVIALAE
Patagopteryx deferrariisi
4
Hongshanornis longicresta
2
Yixianornis
9
Songlingornis
Yanornis martini
Apsaravis ukhaana
Lithornis
Crypturellus undulatus
5
Limenavis patagonica
Iaceornis marshii
Ichthyornis
7
Baptornis
Hesperornis
Chauna torquata
6
Anas platyrhynchus
7
Crax pauxi
>10
Gallus gallus
2
Xiaotingia
Anchiornis huxleyi
EK troodontid 100/44
Mei long
Sinovenator changii
Byronosaurus jaffei
Xixiasaurus
2
IGM 100/1323
IGM 100/1126
6
Jinfengopteryx elegans
Sinornithoides youngi
6
Troodon formosus
8
Zanabazar junior
8
Saurornithoides mongolien
2
Mahakala omnogovae
Shanag ashile
Buitreraptor gonzalozorum
Rahonavis ostromi
Pyroraptor olympius
Hesperonychus elizabethae
Graciliraptor lujiatunensis
Microraptor zhaoianus
Sinornithosaurus millenii
Tianyuraptor ostromi
Austroraptor
2
Neuquenraptor Unenlagia
Bambiraptor feinbergorum
Saurornitholestes langstoni
Tsaagan mangas
Adasaurus mongoliensis
Velociraptor mongoliensis
Deinonychus antirrhopus
Achillobator giganticus
Utahraptor
Atrociraptor marshalli
Dromaeosaurus albertensis

6

Updated dataset of Lee et al. (2014)


Herrerasaurus
Tawa
Syntarsus_kayentakatae
Dilophosaurus
Cryolophosaurus
Berberosaurus
Ceratosaurus
Majungasaurus
Masiakasaurus
Limusaurus
Baryonyx
Eustreptospondylus
Dubreuillosaurus
Afrovenator
Monolophosaurus
Sinraptor_dongi
Allosaurus
Zuolong
Tugulusaurus
Tanycolagreus
Coelurus
Guanlong
Dilong
Yutyrannus
Tyrannosaurus
Sinocalliopteryx
Huaxiagnathus
Sinosauropteryx
Compsognathus
Ornitholestes
Juravenator
Nqwebasaurus
Pelecanimimus
Shenzhousaurus
Harpymimus
Garudimimus
Ornithomimus
Gallimimus
Haplocheirus
Alvarezsaurus
Patagonykus
Bonapartenykus
Parvicursorinae_indet
Shuvuuia
Mononykus
Falcarius
Beipiaosaurus
Alxasaurus
Segnosaurus
Nothronychus_graffami
Erlicosaurus
Protarchaeopteryx
Incisivosaurus
Microvenator
Caudipteryx
Avimimus
Gigantoraptor
Caenagnathus_collinsi
Oviraptor
Khaan
Citipati
Epidexipteryx
Epidendrosaurus
Eosinopteryx
Jinfengopteryx
Aurornis
Sinovenator
Mei
Sinusonasus
Byronosaurus
Sinornithoides
Zanabazar
Troodon
Saurornithoides
Mahakala
Austroraptor
Unenlagia_comahuensis
Neuquenraptor
Buitreraptor
Tianyuraptor
Graciliraptor
Sinornithosaurus
Microraptor
Velociraptor
Deinonychus
Achillobator
Utahraptor
Dromaeosaurus
Anchiornis
Archaeopteryx
Xiaotingia
Rahonavis
Shenzhouraptor
Jixiangornis
Balaur
Zhongjianornis
Sapeornis
Zhongornis
Confuciusornis
Protopteryx
Pengornis
Iberomesornis
Longirostravis
Longipteryx
Huoshanornis
Concornis
Hebeiornis
Gobipteryx
Patagopteryx
Schizooura
Longicrusavis
Hongshanornis
Archaeorhynchus
Jianchangornis
Yixianornis
Yanornis
Ichthyornis
Gansus
Apsaravis
Vegavis
Meleagris
AVIALAE

7

Skeletal reconstruction of *Balaur*.

Speculative skeletal reconstruction for *Balaur bondoc*, showing known elements in white and unknown elements in grey. Note that the integument would presumably have substantially altered the outline of the animal in life. Produced by Jaime Headden, used with permission.