Article

A reappraisal of *Notohypshilophodon comodorensis* (Ornithischia: Ornithopoda) from the Late Cretaceous of Patagonia, Argentina

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Abstract

The Bajo Barreal Formation (Cenomanian, Late Cretaceous; central Patagonia, Argentina) preserves an important and rich fossil record. Among the dinosaurs described, a small ornithischian, *Notohypsilophon comodorensis,* was named in the 1990s. This small-bodied dinosaur, the most complete representative of the group discovered in that formation, was described as a "hypsilophodontid" ornithopod based on close morphological affinities with other members of that group, which is currently regarded as paraphyletic. Within this context, we present a restudy of *Notohypsilophodon*. This dinosaur is considered a basal ornithopod, probably more basal than *Gasparinisaura*. Likewise, this analysis emends and provides additional unique anatomical characters that support its taxonomic validity and position. On the basis of weak evidence, *Notohypsilophodon* might share the presence of gastroliths with other basal ornithopods (*Gasparinisaura* and *Haya*), which could suggest a specific behavior in response to its food ingestion. Finally, this study increases our knowledge of the evolutionary dynamics of South American Cretaceous ornithopods, and therefore broadens our knowledge of the early Late Cretaceous continental vertebrate assemblages of central Patagonia and of the Southern Hemisphere in general.

Key words: Ornithischia, Ornithopoda, Late Cretaceous, Bajo Barreal Formation, Argentina

Introduction

The fossil record of South American ornithischians is scarce, particularly in Patagonia, and is represented predominantly by ornithopods (Coria & Calvo 2002; Novas *et al.* 2004; Coria & Cambiaso 2007; Novas 2009). However, the relatively poor diversity of South American ornithischians may be related to fossil record biases rather than their genuine absence (Coria & Cambiaso 2007). Nevertheless, although the fossil record of Patagonian ornithischians is relatively poor, this clade in general is the most diverse and geographically widespread dinosaur group (Sereno 1999; Weishampel *et al.* 2004).

Martínez (1998) named a new small ornithischian recovered from strata of the Lower Member of the Bajo Barreal Formation (Fig. 1) as *Notohypsilophodon comodorensis*. This small dinosaur, the most complete representative of the group discovered in that formation, was assigned to the "Hypsilophodontidae", based on anatomical similarities with other members of that group. However, both the fossil record and our understanding of ornithischian evolutionary history have improved in the last 15 years; consequently, some of the anatomical features, originally recognized as autapomorphic for *Notohypsilophodon*, are now known to be plesiomorphies (i.e., pronounced narrowing of the fibular shaft, astragalus with the proximal surface disposed in two levels) or widely distributed within Ornithischia (i.e., humerus with greatly reduced deltopectoral crest, ungual pedal phalanx with a flat ventral surface) (Novas *et al.* 2004; Butler *et al.* 2008; Novas 2009; Canudo *et al.* 2013). For this reason, *Notohypsilophodon* was excluded from earlier phylogenetic analyses (Butler *et al.* 2008; Makovicky *et al.* 2011; Han *et al.* 2012, among others) and was rarely included in evolutionary comparisons.
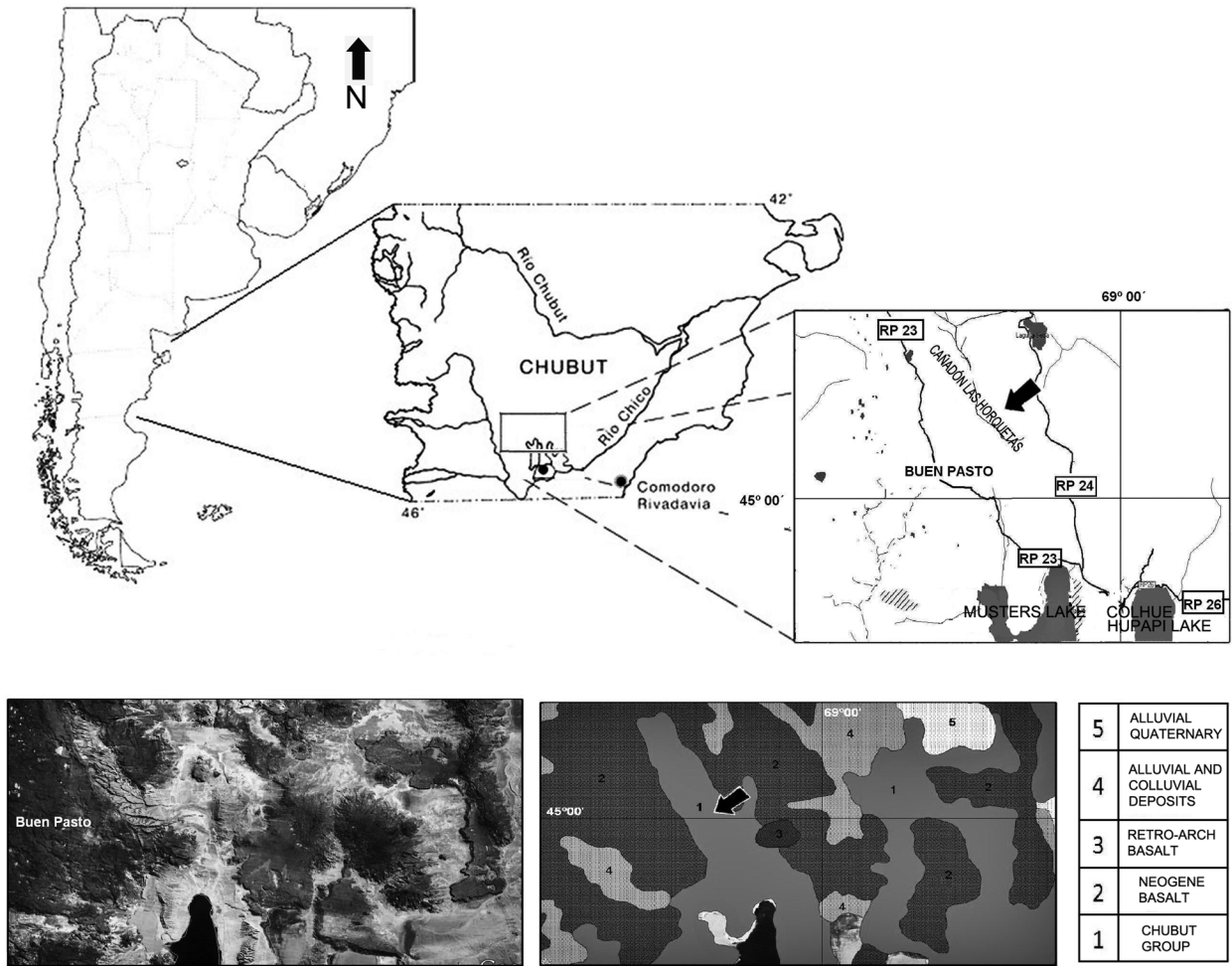
FIGURE 1. Site map showing geographical location of *Notohypsilophodon comodorensis* (UNPSJB-PV 942), denoted by the black arrow.

Therefore, here, we present an anatomical re-study of *Notohypsilophodon comodorensis* and discuss its implications for ornithopod morphological diversity and evolution. Finally, this study increases our knowledge of the Cretaceous South American ornithopod evolutionary dynamics and therefore broadens our understanding of the early Late Cretaceous continental vertebrate assemblages of central Patagonia and of the Southern Hemisphere.

Institutional abbreviation: UNPSJB, Universidad Nacional de la Patagonia, San Juan Bosco, Argentina.

Systematic Palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

***Notohypsilophodon comodorensis* Martínez, 1998**
Figs. 2–10

Holotype. UNPSJB-Pv 942 (Figs 2–10). A partial skeleton including four cervical vertebrae, seven dorsal vertebrae, four sacral vertebrae, six caudal vertebrae (all of the vertebrae are partially preserved), rib fragment, a portion of the left scapula, right coracoid, right humerus, left and right ulnae, an incomplete left femur, right tibia,

an incomplete left tibia, left fibula, an incomplete right fibula; right astragalus, left calcaneum and 13 pedal phalanges.

Emended diagnosis. A small ornithopod dinosaur distinguished from all other basal ornithopods by the following autapomorphies originally proposed by Martinez (1998) and supported in this study: Anteromedial bulge on the proximal extremity of the tibia, calcaneum with a pronounced posterodistal projection. Additionally, the following new autapomorphies are proposed: Distal tip of the sacral neural spine strongly projected posteriorly, sternal process of the coracoids markedly reduced (see below).

Locality and horizon. 28 km northeast of the town of Buen Pasto, in the central-south of Chubut Province, Patagonia, Argentina (Fig. 1). Bajo Barreal Formation, Lower Member (Late Cretaceous, Cenomanian, see Martinez & Novas 2006).
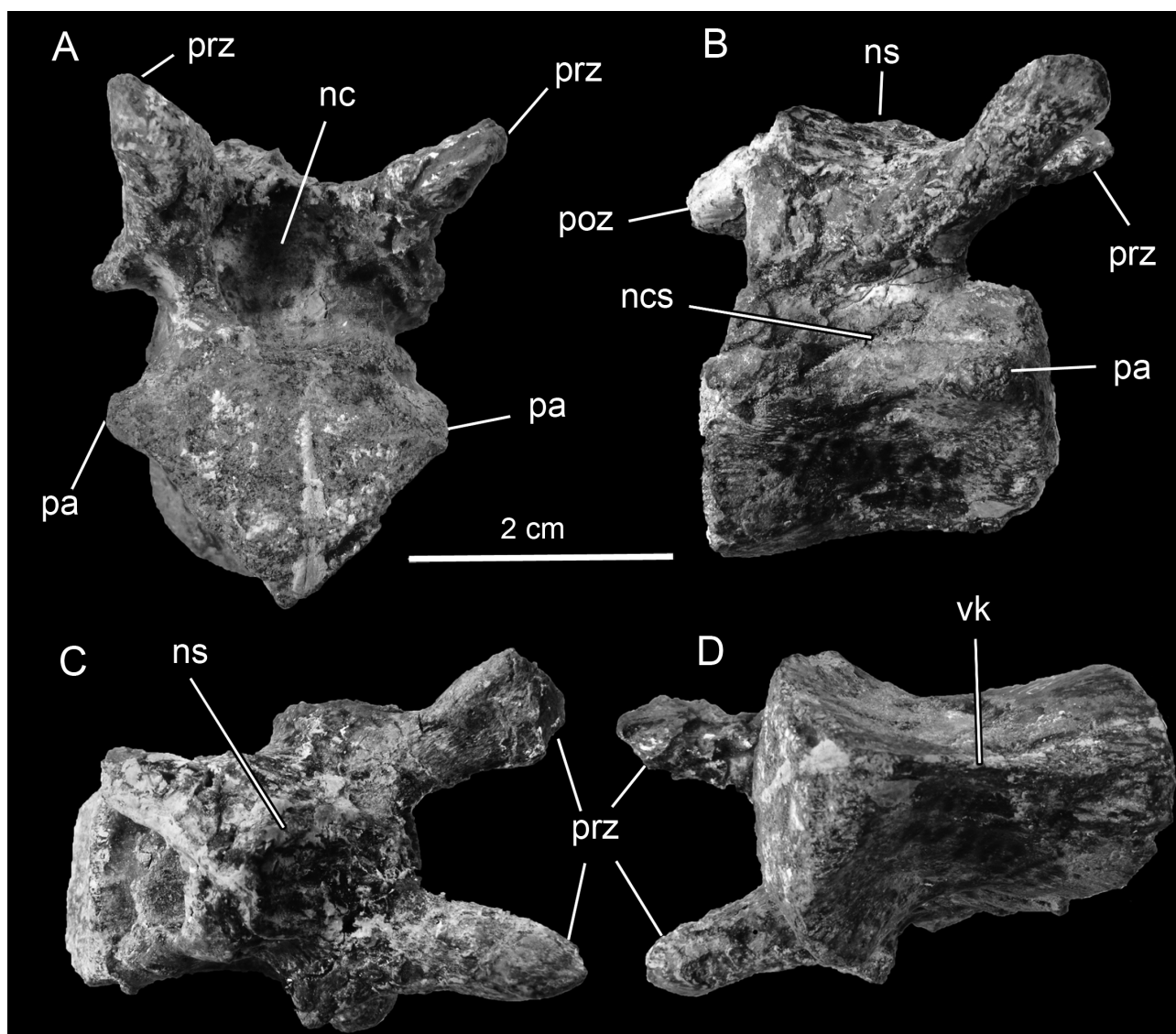

FIGURE 2. *Notohypsilophodon comodorensis*. Middle cervical vertebra (UNPSJB-PV 942/1), in anterior (A), in right lateral (B), in dorsal (C) and ventral (D) views. Abbreviations: nc, neural canal; ncs, neural central suture; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; vk, ventral keel.

Description and comparisons. As mentioned by Martínez (1998), the morphology of the material clearly differs from that seen in the most derived ornithopods (i.e., hadrosaurids). Likewise, the material does not possess synapomorphies or anatomical similarities of marginocephalians (i.e., pachycephalosaurs and ceratopsians). For this reason, members of both groups were excluded from our comparisons. Therefore, in order to ascertain the evolutionary affinities of *Notohypsilophodon* within Ornithischia, we compared the specimen to the following genera: basal neornithischians - *Hexinlusaurus* (Barrett *et al.* 2005) and *Yandusaurus* (He 1979; He & Cai 1984);

basal (non-iguanodontian) ornithopods - *Changchunsaurus* (Zan *et al.* 2005; Butler *et al.* 2011), *Gasparinisaura* (Coria & Salgado 1996; Salgado *et al.* 1997), *Gideonmantellia* (Ruiz-Omeñaca *et al.* 2012), *Haya* (Makovicky *et al.* 2011), *Hypsilophodon* (Galton 1974a; Torres & Viera 1994), *Jeholosaurus* (Xu *et al.* 2000; Han *et al.* 2012), *Koreanosaurus* (Huh *et al.* 2010), *Orodromeus* (Horner & Weishampel 1988), *Oryctodromeus* (Varricchio *et al.* 2007), *Parksosaurus* (Parks 1926; Galton 1973), *Thescelosaurus* (Gilmore 1915; Galton 1974b; Boyd *et al.* 2009), *Trinisaura* (Coria *et al.* 2013), and *Yueosaurus* (Zheng *et al.* 2012); non-hadrosaurid iguanodontians - *Anabisetia* (Coria & Calvo 2002), *Camptosaurus dispar*; *Camptosaurus prestwichii = Cumnoria prestwichii*, *Camptosaurus aphanoecetes = Uteodon aphanoecetes* [Gilmore 1909; Galton and Powell 1980; Carpenter & Wilson 2008, see McDonald 2011), *Dryosaurus* (Janensch 1955; Galton 1981), *Iguanodon* (Norman 1980), *Macrogryphosaurus* (Calvo *et al.* 2007), *Mantellisaurus* (Hooley 1925; Norman 1986; Paul 2006, 2008; McDonald 2012), *Mochlodon* (Ösi *et al.* 2012), *Ouranosaurus* (Taquet 1976), *Talenkauen* (Novas *et al.* 2004), *Tenontosaurus* (Forster 1990; Winkler *et al.* 1997), *Valdosaurus* (Galton & Taquet 1982; Galton 2009; Barrett *et al.* 2011), and *Zalmoxes* (Nopcsa 1900; Weishampel *et al.* 2003). Additionally, other specimens (e.g., the Australian ornithopods) as well as isolated and partially perservered materials are also used in the present comparison (see below).
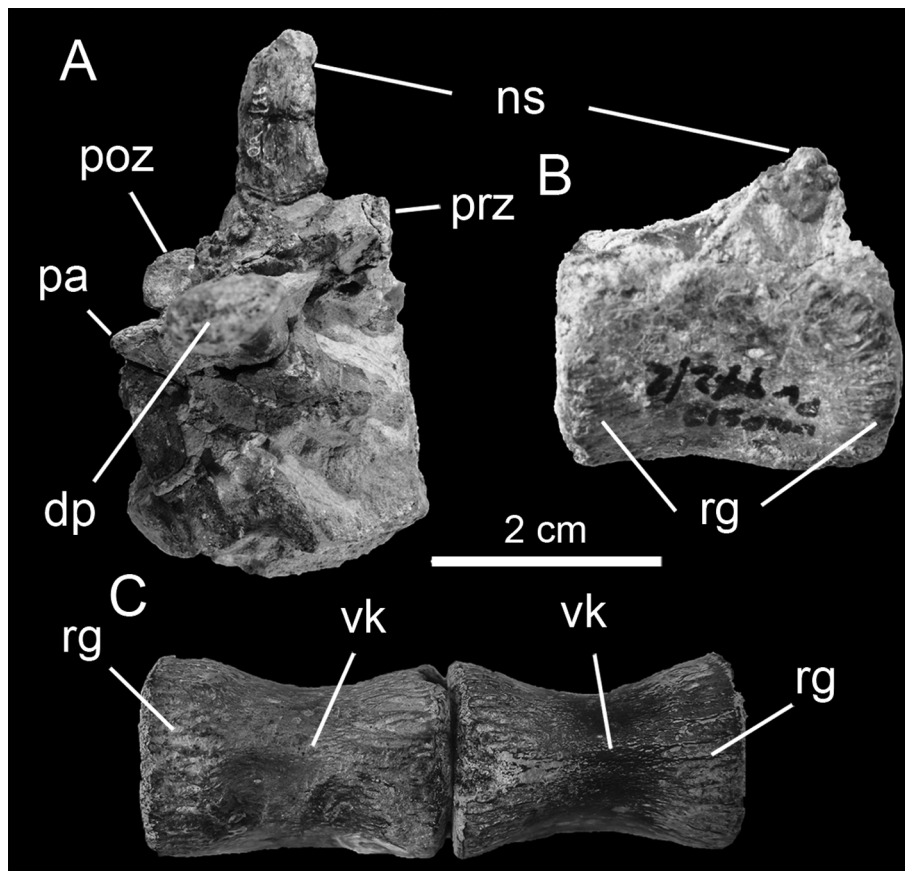

FIGURE 3. *Notohypsilophodon comodorensis*. Anterior dorsal vertebrae (UNPSJB-PV 942/5,6,7 respectively), in right lateral (A and B) and ventral (C) views. Abbreviations: dp, diapophysis; ns, neural spine; pa, parapophysis; prz, prezygapophysis; rg, rugosities; vk, ventral keel.

Cervical vertebrae. The cervical vertebrae (Fig. 2) of *Notohypsilophodon comodorensis*, based on the morphology of the centra and the portions of the neural arches preserved are presumably middle cervicals. The centra are amphyplatian as in *Haya, Hypsilophodon* and *Jeholosaurus*. In more derived ornithopods (e.g., *Camptosaurus*, *Cumnoria*, *Dryosaurus*, *Tenontosaurus*, *Valdosaurus* and *Zalmoxes*), on the other hand, the cervical centra are slightly opisthocoelous or amphicoelous, as in *Macrogryphosaurus*. The centra of *Notohypsilophodon* are slightly wider than tall, as is the case in most basal neornithischians and basal ornithopods (e.g., *Changchunsaurus*, *Hypsilophodon*, *Yueosaurus*). In ornithopods more derived than *Camptosaurus* (see Galton 2009: fig. 20), *Macrogryphosaurus* and *Talenkauen*, the cervical centra are anteroposteriorly longer than tall. In lateral view, the centra are "divided" in two slightly concave surfaces as in basal ornithopods due to the presence of

the longitudinal ridge at approximately centrum midheight. Ventrally, the cervical vertebrae of *Notohypsilophodon* exhibit a thin midline keel similar to those seen in *Anabisetia*, *Changchunsaurus*, *Gasparinisaura*, *Hypsilophodon*, *Macrogryphosaurus*, and *Valdosaurus* (see Barrett *et al*. 2011: fig. 2) and unlike the thicker, rugose ventral keels, present in some basal iguanodontids (e.g., *Camptosaurus*, *Cumnoria, Tenontosaurus*, *Uteodon*, *Zalmoxes*: Carpenter & Wilson 2008; Norman 2004). In anterior view, the cervical vertebrae have pentagonal articular surfaces with an acute ventral apex as the rhabdodontid ornithopod *Zalmoxes* (Weishampel *et al*. 2003: fig. 15) and the basal ornithopod *Yueosaurus* (Zheng *et al.* 2012: fig. 3); however, in the latter, the ventral apex is more pronounced than in *Notohypsilophodon* and *Zalmoxes*. The neural canal is proportionally large and ovoid in outline (a feature which could be related to the juvenile status of *Notohypsilophodon,* see below). The articular facets of the prezygapophyses are subcircular in outline and project strongly anterodorsally as in *Hypsilophodon*. Based on the preserved portion of the cervical neural spines, they appear to be notably reduced, a condition also reported in the basal ornithopods *Hypsilophodon*, *Gasparinisaura* and the basal iguanodontian *Talenkauen*. In lateral view, the centra exhibit an open neurocentral suture, indicating that *Notohypsilophodon* was not somatically mature (as Martinez 1998, pointed out in his original study, see below). A parapophysis located just below the neurocentral suture is also present in *Tenontosaurus* and *Thescelosaurus*.

Dorsal vertebrae. The dorsal vertebrae (Fig. 3) are slightly amphicoelous and hourglass-shaped in ventral view as a consequence of their lateral compression. There are strongly-developed longitudinal striations around the margins of each of the articular surfaces, probably related to the insertion of soft tissues (i.e., the dorsal hypaxial musculature: Butler *et al*. 2010; Butler *et al*. 2011; Zheng *et al*. 2012). These longitudinal striations are comparable to those observed in many ornithopods, such as *Camptosaurus*, *Dryosaurus*, *Macrogryphosaurus*, *Tenontosaurus*, *Thescelosaurus* and a set of dorsal vertebrae recovered in Cretaceous outcrops of the Bajo Barreal Formation (Cenomanian-Turonian; UNPSJB-PV 960 see Ibiricu *et al.* 2010). Ventrally, the centra of *Notohypsilophodon* bear a midline keel as in the cervical vertebrae; however, this structure is not as sharp or as well defined as in the cervicals. A similar ventral keel is also seen in *Changchunsaurus*, *Hypsilophodon*, *Trinisaura* and *Yueosaurus*, whereas non-hadrosaurid iguanodontians (e.g., *Cumnoria*, *Iguanodon*, *Mantellisaurus*, *Tenontosaurus*, *Zalmoxes* and UNPSJB-PV 960) have centrum ventral surfaces that lack keels and which are more concave and rounded. The posterior surfaces of the centra are suboval in outline, a feature present in basal neornithischians (e.g., *Hexinlusaurus* and *Yandusaurus*) and basal iguanodontians (e.g., *Camptosaurus*, *Iguanodon* and *Mantellisaurus*). The transverse processes preserved in *Notohypsilophodon* project laterally, at approximately the same level as the zygapophyses, as is characteristic of basal ornithopods (Norman 2004; Makovicky *et al*. 2011). The preserved dorsal neural spine appears to be relatively low and anteroposteriorly narrow. This feature is comparable to the anatomy of basal ornithopods and differs from that seen in the more derived members of the group (i.e., non-hadrosaurid iguanodontians), where the dorsal neural spines are elevated and rectangular in shape (Norman *et al*. 2004).

Sacral vertebrae. Due to the disarticulated nature of the sacral vertebrae, it is difficult to determine with confidence the positions of two of the sacral vertebrae recovered. Nevertheless, the sacral vertebra possessing a posterior articular surface that is laterally wider than its anterior counterpart is considered the dorsosacral (Fig. 4, also see Butler *et al.* 2011). Unfortunately, it is not possible to determine the full sacral number (including the sacrodorsal vertebra) due to the absence of complete articulation. However, based on the preserved elements, we considered a putative number of five or six, as also known in many other ornithischians (e.g., *Dryosaurus*, *Gasparinisaura*, *Haya*, *Hexinlusaurus*, *Hypsilophodon*: also see Galton 1974a). On the other hand, with the exception of *Oryctodromeus* (Varricchio *et al.*, 2007), some derived ornithopods, such as rhabdodontids (e.g., *Zalmoxes* and probably *Mochlodon;* see Ösi *et al.* 2012) and derived iguanodontians, possess more than six sacral vertebrae.

Of the two sets of sacral vertebrae recovered with *Notohypsilophodon*, three vertebrae, probably representing the anterior ones, are co-ossified (Fig. 4A–C–E), whereas the other set, of two sacral vertebrae, are articulated but not co-ossified (Fig. 4B–D–F). The sacral rib preserved (which is considered to be the first true sacral rib) is robust. The centra are slightly laterally compressed and are cotton-reel-shaped in ventral view. Circumscribing the articular surfaces, well-developed longitudinal striations are present. These striations continue onto the ventral surfaces of the centra, where they become more pronounced. The preserved sacral neural spine is wider anteroposteriorly than transversely. The distal end of the neural spine is posteriorly extended. In ventral view, the centra are comparable to those in *Gasparinisaura*, in possessing slightly concave ventral surfaces, whereas in many other basal ornithopods a longitudinal keel or ridge is present (e.g., *Changchunsaurus* and *Haya*).
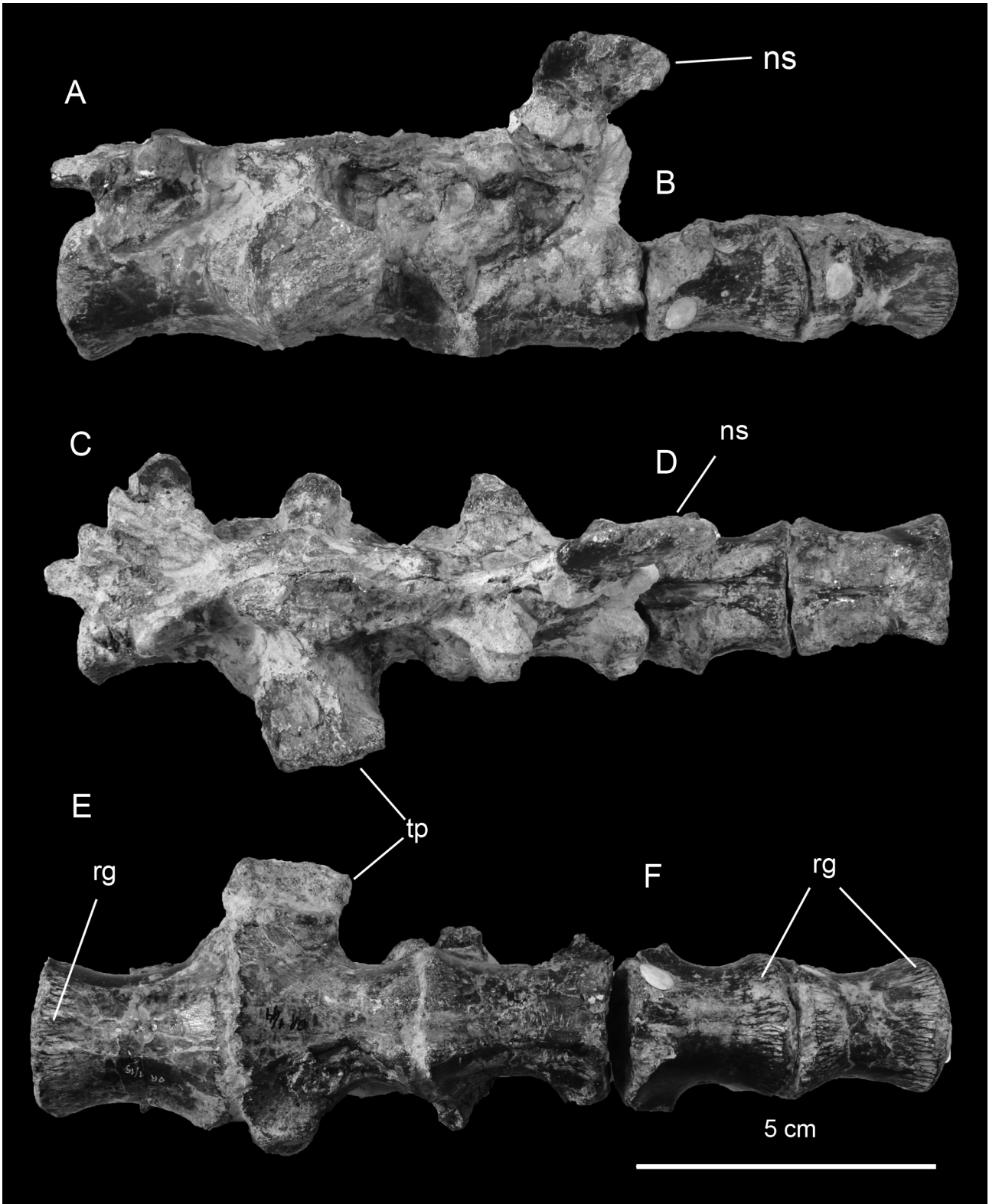
FIGURE 4. *Notohypsilophodon comodorensis*. Sacral vertebrae (UNPSJB-PV 942/12,13,14,15,16 respectively), in left lateral (A and B), in dorsal (C and D) and ventral (E and F) views. Abbreviations: ns, neural spine; rg, rugosities; tp, transverse process.

Caudal vertebrae. The caudal vertebral centra (Fig. 5) are slightly amphicoelous, as in *Gideonmantellia* and UNPSJB-PV 960, and they are significantly longer anteroposteriorly than wide transversely. Additionally, comparisons with well-preserved caudal sequences (e.g., *Hypsilophodon*, *Tenontosaurus*) demonstrate that these

caudal vertebrae were located in the anterior portion of the tail. *Notohypsilophodon* possesses subrectangular intercentral articular surfaces, a feature shared with *Tenontosaurus* and UNPSJB-Pv 960. There are relatively well-developed longitudinal striations toward each lateral and ventral margin. This feature may be related to the insertion of soft tissue (e.g., the caudofemoralis musculature). Ventrally, the caudal centra of *Notohypsilophon* exhibit a marked longitudinal groove and well-developed facets for the insertion of the haemal arches. These last two features are also seen in several basal ornithopods and basal non-hadrosaurid iguanodontians (e.g., *Gasparinisaura*, *Hypsilophodon*, *Macrogryphosaurus*, *Zalmoxes,* UNPSJB-Pv 960 and, although less developed, in the basal ornithopod *Jeholosaurus*). The presence of the marked longitudinal groove could be related to either ontogenetic status (Han *et al.* 2012) or sexual dimorphism (Nopcsa 1929; Ibiricu *et al.* 2010). No ossified tendons are preserved in *Notohypsilophodon*, which may be related to preservation rather than genuine absence.
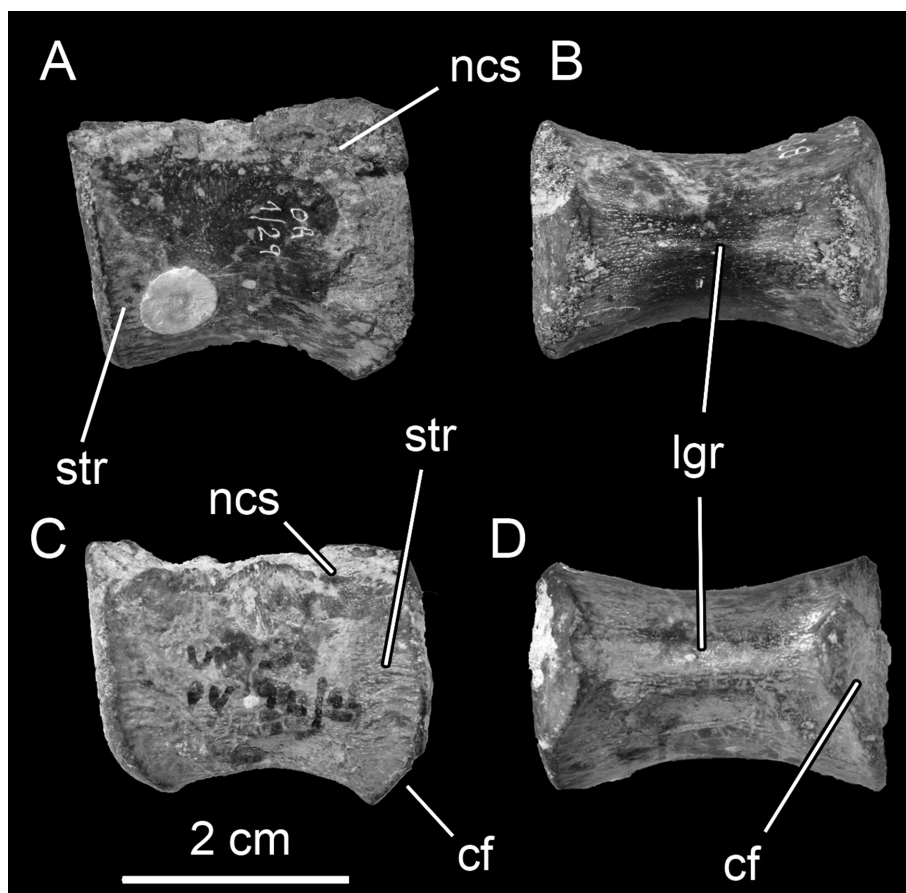

FIGURE 5. *Notohypsilophodon comodorensis*. Anterior caudal vertebrae (UNPSJB-PV 942/17,18), in right lateral (A and C) and ventral (B and D) views. Abbreviations: cf, chevron facet; lgr, longitudinal groove; ncs, neurocentral suture; str, striations. Scale bar equals 2 cm.

Scapula. The left scapula of *Notohypsilophodon* (Fig. 6A–B; Table 1) preserves the proximal end and a portion of shaft, which is transversally narrow as in *Gasparinisaura*. The scapula and coracoids are unfused as in the majority of small ornithischians (Han *et al.* 2012), and unlike *Koreanosaurus* and *Oryctodromeus*. The proximal end is expanded as in basal ornithopods (e.g., *Gasparinisaura*, *Hypsilophodon*) and basal iguanodontians (e.g., *Dryosaurus*, *Tenontosaurus*). The acromial process is not complete; therefore, it cannot be determined if it process was well developed, as in *Anabisetia*, or only moderately developed, as in *Gasparinisaura* (Coria & Calvo 2002). In dorsal view, the scapula of *Notohypsilophodon* exhibits two asymmetrical surfaces, the glenoid fossa and the coracoid articulation. The former is concave, whereas the latter is gently convex. The glenoid fossa is subrectangular in outline. Likewise, dorsally to this fossa, a marked concavity (= supraglenoid fossa; Zheng *et al.* 2012) is also present. This last feature is shared with various ornithischians including: *Hexinlusaurus*, *Hypsilophodon*, *Lesothosaurus* (Thulborn 1972), *Thescelosaurus*, *Tenontosaurus*, *Uteodon*, and *Yueosaurus*. However, the supraglenoid fossa in *Notohypsilophodon* is more pronounced than in all of these taxa with the exception of *Tenontosaurus*, whose fossa is similar to that seen in *Notohypsilophodon* (Martinez 1998).

TABLE 1. Selected measurements (in mm) of *Notohypsilophodon comodorensis* (UNPSJB-PV 942).

| Element		Measurement
Humerus	Total length	127.3
Ulna	Total length	91.3
Femur (proximal end)	Maximun anteroposterior width	44.9
	Maximun lateral width	47.7
Femur (distal end)	Maximun anteroposterior width	45.5
Tibia	Total length	211.5
	Greatest proximal width	56.5
	Greatest distal width	45.5
Fibula	Total length	192
	Greatest proximal width	29.6
	Greatest distal width	14.1
Phalanx (?-1)	Total length	36.1
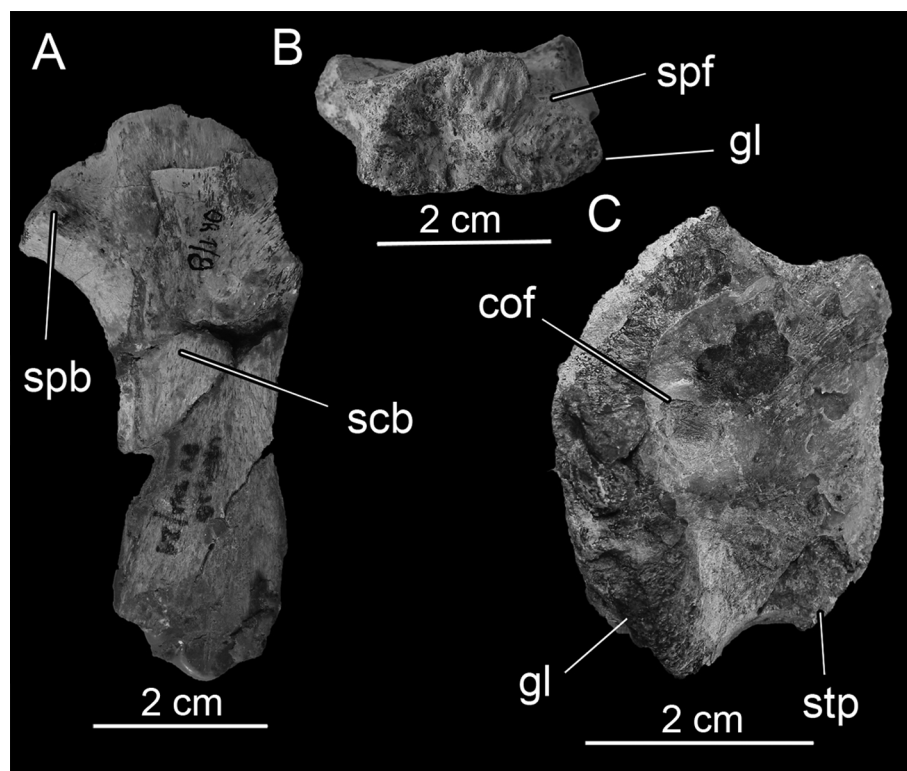
FIGURE 6. *Notohypsilophodon comodorensis*. Left scapula (UNPSJB-PV 942/23), in lateral (A) and proximal (B) views. Right coracoids (UNPSJB-PV 942/24), in lateral view (C). Abbreviation: cof, coracoids foramen; gl, glenoid; scb, scapular blade; spb, supraglenoidal buttress; spf, supraglenoid fossa; stp, sternal process.

Coracoids. The semicircular shape of the right coracoid (Fig. 6C), with a slightly convex lateral surface and medially concave surface, is comparable to that of *Gasparinisaura*, *Hypsilophodon* and *Yandusaurus*. Conversely, in *Changchunsaurus*, *Jeholosaurus* and *Koreanosaurus*, the coracoids are sub-rectangular in shape with flat surfaces. In *Trinisaura*, the coracoid is semicircular in outline, as in *Notohypsilophodon*; however, in the former the dorsal margin is interrupted by a marked concavity (see Coria *et al.* 2013: fig. 3). The sternal process, in *Notohypsilophodon* is not as well-developed as those of *Anabisetia*, *Gasparinisaura*, *Haya*, *Koreanosaurus*, *Tenontosaurus* or *Trinisaura*. Although, it is taphonomically affected on its lateral size, in *Notohypsilophodon* the sternal process is markedly more reduced than in those ornithopods (see below).
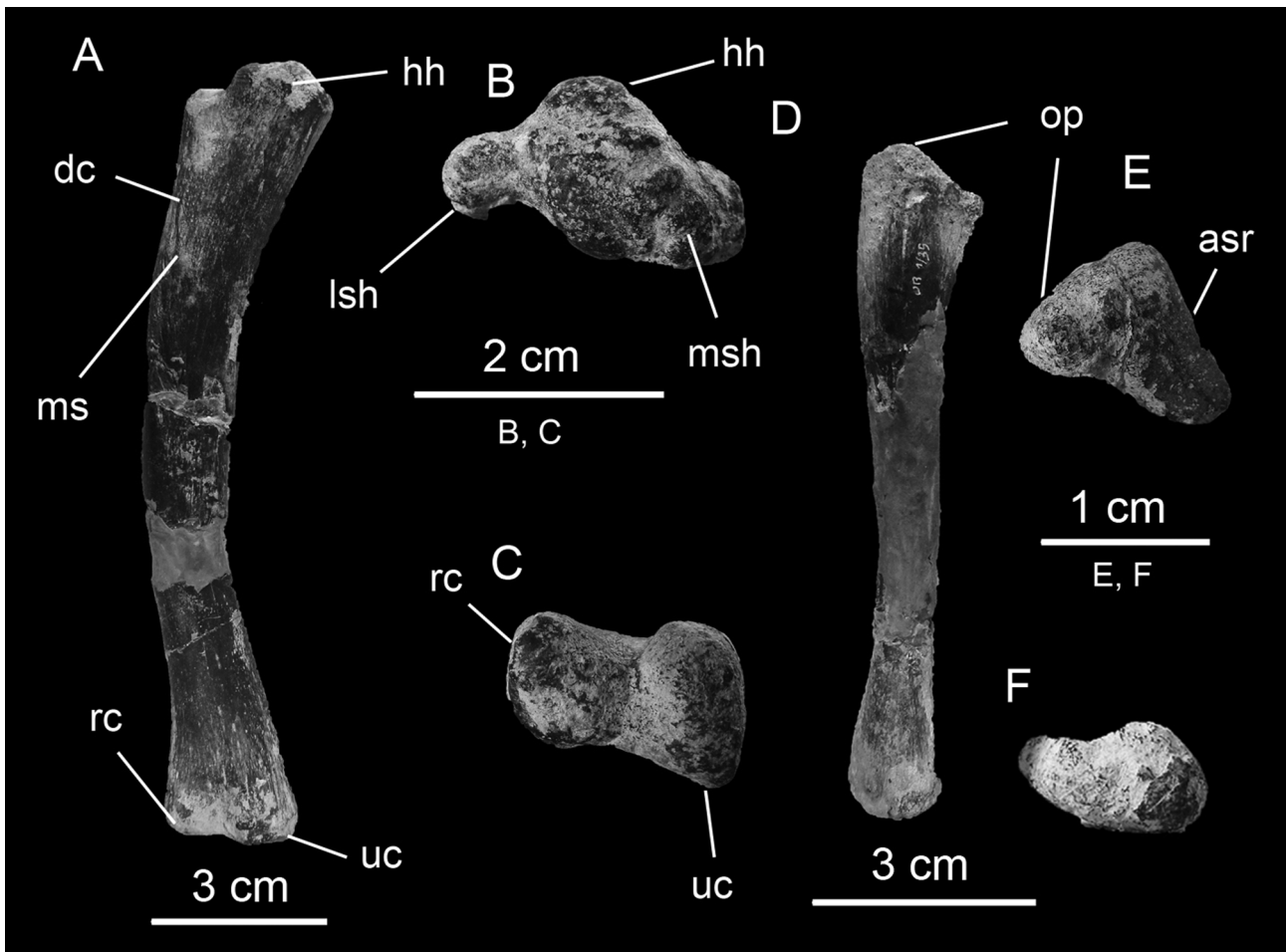
FIGURE 7. *Notohypsilophodon comodorensis*. Right humerus (UNPSJB-PV 942/25), in anterior (A), proximal (B) and distal (C) views. Left ulna (UNPSJB-PV 942/27), in medial (D), proximal (E) and distal (F) views. Abbreviation: asr, articular surface radius; dc, deltopectoral crest; hh, humeral head; lsh, lateral shoulder; ms, muscle scars; msh, medial shoulder; op, olecranon process; rc, radial condyle; uc, ulnar condyle.

The coracoid foramen is circular in outline, proportionately large and completely enclosed. The coracoid foramen in *Notohypsilophodon* is placed well above the scapula-coracoid suture (i.e., there is no contact between the foramen and scapula). The shape and position of the coracoid foramen is similar to those of *Anabisetia*, *Gasparinisaura*, *Trinisaura* and *Tenontosaurus* (see Winkler *et al.* 1997: fig. 16a), and unlike that observed in *Hypsilophodon*. In the latter taxon, the foramen is positioned close to the suture and connected to the scapula by a groove (Galton 1974a; Huh *et al.* 2010). In more basal forms (e.g., *Changchunsaurus*, *Koreanosaurus*), the foramen is smaller than in *Notohypsilophodon* and located more towards the center of the coracoid plate.

Humerus. The right humerus (Fig. 7A–C; Table 1) of *Notohypsilophodon* is gracile (1.5 cm, measurement of the shaft taken in anterior view below the deltopectoral crest) as in *Anabisetia*, *Gasparinisaura*, *Talenkauen* and *Trinisaura*, whereas in the rhabdodontid *Zalmoxes* (approximately 3 cm, measurement taken from Weishampel *et al.* 2003: fig. 20d) and the basal iguanodontian *Tenontosaurus*, the humerus is robust (Norman *et al.* 2004). The shaft is slightly twisted, as is characteristic of a variety of basal ornithopods (Norman *et al.* 2004). Nevertheless, the rotation of the humeral shaft appears to be less than in *Hypsilophodon* (Galton 1974a: figs. 38–39) and resembles the condition of *Anabisetia*. In anterior view, the shaft is bowed as in *Yandusaurus* and unlike those of *Anabisetia* and *Trinisaura* where the bowing is less marked. The deltopectoral crest is reduced (i.e., to shallow rugosities for the pectoral muscle insertions) and is positioned in the proximal portion of the humerus as in *Anabisetia*, *Bugenasaura* (Norman *et al.* 2004), *Gasparinisaura*, *Talenkauen* and *Trinisaura*. By contrast, the deltopectoral crests of basal neornithischians and ornithopods (e.g., *Haya*, *Hypsilophodon*, *Jeholosaurus*, *Koreanosaurus*, *Yandusaurus*, among others) are well developed and angular in outline. Likewise, the deltopectoral crest in basal (non-hadrosaurid) iguanodontians is robust and it occupies approximately 50% of total humerus

length (Norman *et al.* 2004). The proximal end of the humeral head is transversally expanded as in *Anabisetia* and *Gasparinisaura,* and exhibits a marked tuberosity, similar to that described in *Dryosaurus* (Martínez 1998). Thus, the proximal end is wider than the distal end as in *Anabisetia* and *Trinisaura*. Conversely, in *Hypsilophodon*, *Yandusaurus* and basal iguanodontians (e.g., *Tenontosaurus*), the proximal and distal ends of the humerus are approximately equal in mediolateral width. The distal end of the humerus exhibits moderately developed radial and ulnar condyles, as well as an intercondylar groove (=fossa) on its anterior surface. This condition differs from that seen in *Hypsilophodon*, *Thescelosaurus* and non-hadrosaurid iguanodontians (e.g., *Camptosaurus*, *Iguanodon*, *Mantellisaurus*) where the condyles and the groove are more strongly developed. The lateral radial condyle is expanded anteroposteriorly and the medial ulnar condyle is rounded, both of which are features that *Notohypsilophodon* shares with basal neornithischians and ornithopods such as *Yandusaurus* and *Koreanosaurus*.

Ulna. The ulna (Fig. 7D–E–F; Table 1) of *Notohypsilophodon* is slender, as in *Hypsilophodon*, in contrast to the more robust ulnae of non-hadrosaurid iguanodontians. In proximal view, the ulna is triangular in outline (formed by the head of the ulna and the lateral and medial processes according to Butler *et al.* 2011) with the lateral border convex, the medial slightly concave and the articular surface for the radius gently concave. The olecranon process is reduced, and comparable to that observed in *Hypsilophodon* and *Parksosaurus*. *Anabisetia*, *Dryosaurus* and a variety of basal ornithopods (Huh *et al.* 2010; Makovicky *et al.* 2011) possess relatively prominent olecranon processes that are more pronounced than that present in *Notohypsilophodon*, but reduced in comparison with those of heterodontosaurids (Norman *et al.* 2004). The shaft of the ulna is narrow toward the medial section and slightly expanded distally. The ulna is approximately 75% of the length of the humerus. These last two features in *Notohypsilophodon* are shared with basal ornithopods.

Femur. The proximal and distal ends of the left femur (Fig. 8, Table 1), and a portion of the shaft, have been recovered in *Notohypsilophodon*. The preserved portion of the shaft strongly suggests that it was slender (a constricted neck is present) as in *Gasparinisaura* and other basal ornithopods such as *Hypsilophodon*, *Jeholosaurus*, *Koreanosaurus* and *Yueosaurus*. The femoral head is bulbous (i.e., with a well-developed spherical articular condyle), a feature shared with *Gasparinisaura*. In *Notohypsilophodon*, as in *Orodromeus*, the femoral head is oriented slightly dorsally with respect to the shaft, forming an angle greater than 100°, unlike the angle of approximately 90° found in most basal ornithopods (Norman *et al.* 2004). On the other hand, overall, the femora of basal iguanodontians (see Naish & Martill 2001: figs. 1-3), including rhabdodontids and ankylopollexians, are more robust than those of *Notohypsilophodon*, with the exception of those in dryosaurids, which are slender (e.g., *Callovosaurus* [see Ruiz-Omeñaca *et al.* 2007], *Dryosaurus* and *Valdosaurus* [see Barrett *et al.* 2011]). In proximal view, the head is compressed anteroposteriorly and the trochanters are expanded anteroposteriorly, as in *Changchunsaurus*. The femoral head is separated from the trochanters by a shallow depression, the *fossa trochanteris*. This fossa is absent in basal ornithischians such as *Hexinlusaurus* and heterodontosaurids, whereas it is usually present in cerapodans (Butler *et al.* 2011). Likewise, in proximal view, a well-marked convexity (i.e., "tuberosity" of Novas 1996) and a shallow notch (=sulcus, sensu Butler *et al.* 2011) for the *ligamentum capitis femoris* are present in *Notohypsilophodon*. The greater trochanter is anteroposteriorly expanded and its dorsal surface is slightly convex, whereas the "finger-like" lesser (=anterior) trochanter is also gently convex in the same direction. The greater and lesser trochanters are unfused and separated by a marked cleft (the intertrochanteric cleft for some authors, for the m. *iliofemoralis* insertion: Hutchinson & Gatesy 2000), a feature that occurs in *Gideonmantellia*, *Hexinlusaurus*, *Hypsilophodon*, *Valdosaurus* and *Yandusaurus* (Norman *et al.* 2004; Barrett *et al.* 2011; Ruiz- Omeñaca *et al.* 2012). Additionally, this feature is variable in *Hypsilophodon* (P. M. Barrett, pers. comm., December 2013). In contrast, in *Gasparinisaura*, *Koreanosaurus*, and *Yueosaurus*, the greater and lesser trochanters are fused. Although in *Anabisetia*, *Trinisaura* (see Coria *et al.* 2013), a cleft separating those trochanters is present, it is narrow in comparison with that seen in *Notohypsilophodon*. In lateral view, the tip of the lesser trochanter is set below the level of the greater trochanter, as in most basal ornithischians (Agnolin *et al.* 2010). This differs, for example, from those see in *Anabisetia*, *Changchunsaurus*, *Jeholosaurus*, *Koreanosaurus* and dryosaurids (both trochanters are nearly to the same level, also see Naish & Martill 2001: fig. 1-6, plate 8). The distal end of the femur in *Notohypsilophodon* exhibits two asymmetrical condyles, the tibial (medial) and fibular (lateral). The former is larger than the latter and the rounded articular surfaces are covered with well-developed rugosities for soft tissue insertions. The lateral condyle projects slightly laterally, like those of *Gasparinisaura* and *Trinisaura*. Lateral to the medial condyle, a marked and slightly concave surface is present, as in *Hypsilophodon* (i.e., the extension of the medial surface occupies all the lateral aspect of the tibial condyle). *Notohypsilophodon*
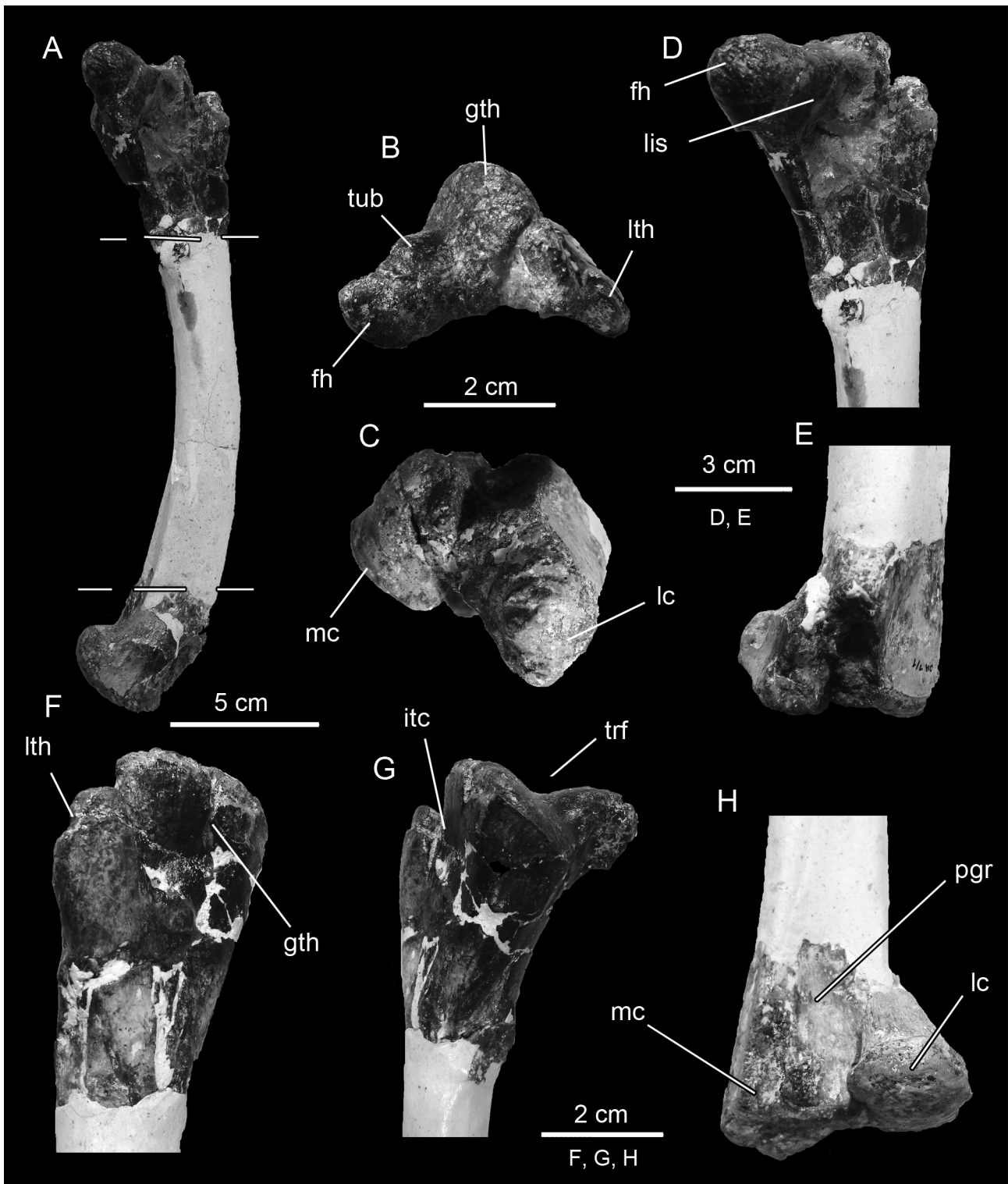
FIGURE 8. *Notohypsilophodon comodorensis*. Left femur (UNPSJB-PV 942/28), in medial (A- D), proximal (B), distal (C), posterolateral (E), lateral (F), anterior (G) and posterior (H) views. Abbreviation: fh, femoral head; gth, greater trochanter; ict, intertrochanteric cleft; lc, lateral condyle; lis, ligament sulcus; lth, lesser trochanter; mc, medial condyle; pgr, posterior groove; tub, tubercle. Note: dotted lines delimit the reconstructed femoral shaft.

possesses a shallow anterior (extensor) groove as in basal euornithopods (Norman *et al.* 2004). This groove is absent in some other taxa (e.g., *Gasparinisaura*) but well-developed in *Anabisetia*, *Muttaburrasaurus* (Bartholomai & Molnar 1981; Molnar 1996 also see Agnolin *et al.* 2010) and *Trinisaura*. The posterior (flexor) intercondylar groove is comparable to those observed in basal ornithopods (Norman *et al.* 2004), whereas in basal

non-hadrosaurid iguanodontians it is wider. Lastly, the distal end of the "Victoria femur type I" (Rich & Rich 1999) is similar in morphology to that of *Notohypsilophodon*, in having a laterally placed fibular condyle, transverse compression and a medial condyle that is markedly larger than the lateral (Agnolin *et al.* 2010). However, these features probably are due to taphonomic aspects rather than genuine anatomical characteristics (P. M. Barrett, pers. comm., December 2013).
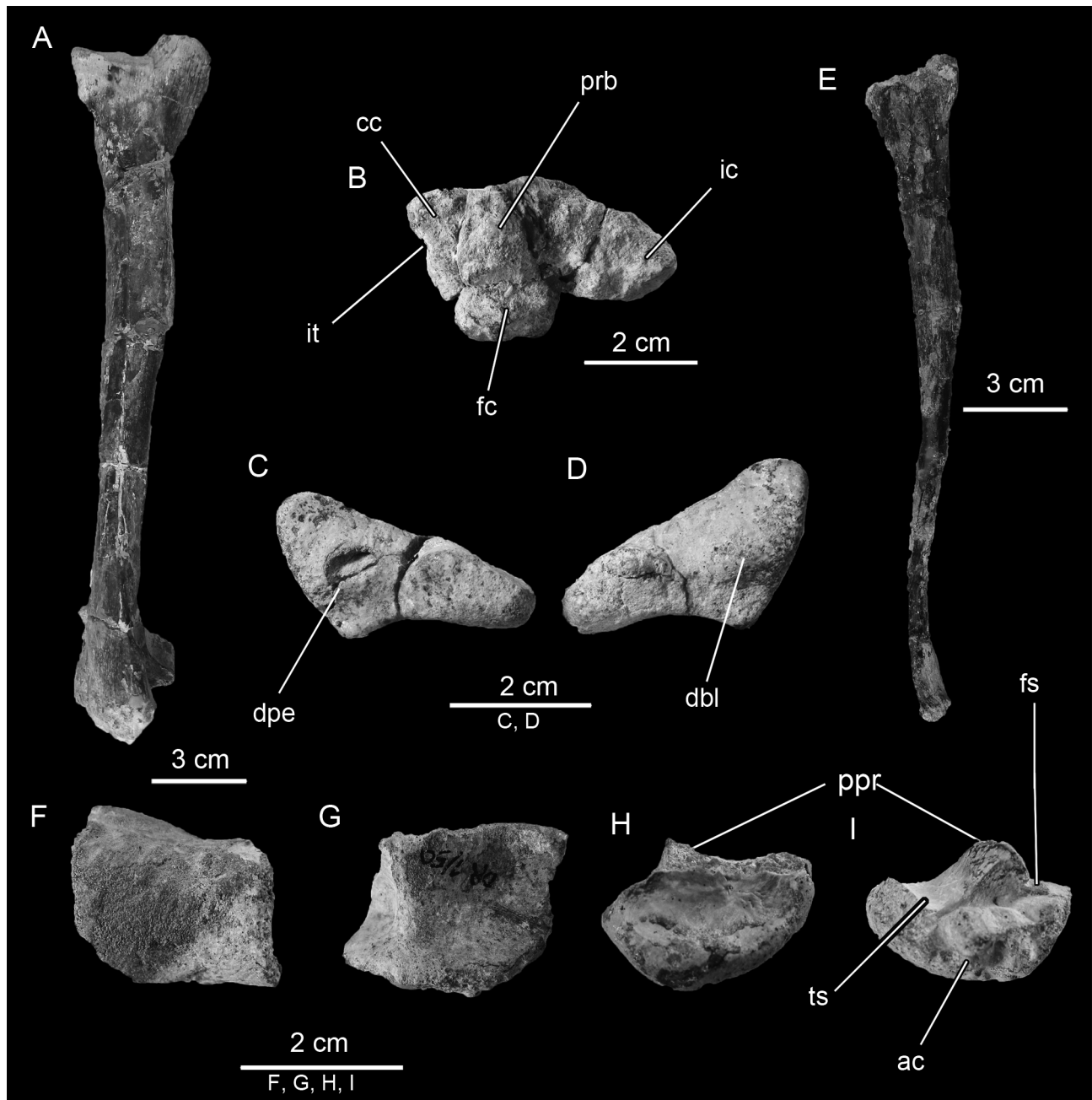

FIGURE 9. *Notohypsilophodon comodorensis*. Left tibia (UNPSJB-PV 942/29), in medial (A), proximal (B) and distal (C) views. Right tibia (UNPSJB-PV 942/30), in distal (D) view. Left fibula (UNPSJB-PV 942/32), in medial (E) view. Right astragalus (UNPSJB-PV 942/33), in posterior (F) and anterior (G) views. Left calcaneum (UNPSJB-PV 942/34), in lateral (H) and medial (I) views. Abbreviation: ac, astragalar contact; cc, cnemial crest; dbl, distal bulge; dpe, distal perforation; fc, fibular condyle; fs, fibular surface; ic, inner condyle; it, incisura tibialis; ppr, proximal process; prb, proximal bulge; ts, tibial surface.

Tibia. The straight right tibia (Fig. 9A–B–C–D; Table 1) of *Notohypsilophodon* is slender, a feature shared with a variety of ornithopods (e.g., *Anabisetia*, *Gasparinisaura*, *Gideonmantellia*, *Hypsilophodon*, *Yueosaurus*, among others). The proximal end is anteroposteriorly expanded as in *Changchunsaurus* and *Gasparinisaura*. The cnemial crest is modestly developed and slightly laterally and dorsally projected as is usual in basal ornithopods

(Huh *et al.* 2010). The cnemial crest is separated from the fibular condyle by a groove (the *incisura tibialis* see Butler *et al.* 2011) as in *Koreanosaurus*, *Jeholosaurus* and *Hypsilophodon*. Both condyles of *Notohypsilophodon*, the rounded inner and fibular are anteroposteriorly expanded, particularly the latter. The proximal expansion of the condyles is more strongly developed than in basal forms such as *Haya* and *Koreanosaurus*. Proximally, the tibial surface exhibits a well-developed bulge. The distal end of the tibia in *Notohypsilophodon*, is subtriangular in outline as in *Dryosaurus* and *Yueosaurus*. Additionally, it is transversely expanded as in basal ornithischians (Makovicky *et al.* 2011). The outer malleolus is larger than the inner malleolus, a condition reported in basal ornithopods (Zheng *et al.* 2012) and unlike the subequally-sized malleoli in *Gasparinisaura*. With regard to the distal end, the subtriangular shape, prominently extended anteromedial flange, presence of a shallow lateral groove, and the similarly-shaped astragalar articular surface, are features that *Notohypsilophodon* shares with *Dryosaurus altus* (see Novas 1996: fig. 4I). Also in distal view, the articular surface of the tibia exhibits a well-developed perforation similar to that drawn in *Dryosaurus* (see Novas 1996: fig. 4I). This sub-oval distal perforation, which could be related with insertion of soft tissue (probably variable ossification of the cartilage capping the tibia), is placed closer to the external margin of the inner malleolus than the outer malleolus. Likewise, its counterpart, in the same position, exhibits a well-developed distal bulge (Fig. 9C and D).

Fibula. The left fibula (Fig. 9E) of *Notohypsilophodon* is slender. Its proximal end is anteroposteriorly expanded and its surface is slightly concave. The shaft narrows somewhat to the mid-length of the bone. At this point, the shaft exhibits a thin well-developed flange (flange on medial surface of fibula according to Butler *et al.* 2011) that extends medially. This flange reaches the distal end of the fibula. The distal end is moderately expanded.

Astragalus. The partially preserved right astragalus (Fig. 9F–G) has a sub-rectangular shape. In distal view, it is convex, whereas in dorsal view, it is concave and divided into two articular surfaces divided by a ridge. The surface that received the distal end of tibia is wide, whereas the laterally placed surface for contact with the calcaneum is small. The ascending process is sub-triangular in shape and it is moderately developed, as also described in other basal ornithopods (Norman *et al.* 2004).

Calcaneum. The left calcaneum (Fig. 9H–I) is semicircular in shape, slightly concave laterally, and mediolaterally compressed. The articular surfaces for contact with the distal ends of tibia and fibula are divided by a moderately developed and partially oblique proximal projection. The fibular and tibial articular surfaces are concave. The tibial articular surface is open medially. In contrast, the fibular surface is delimited by a thin lip. The medial surface of the calcaneum displays a well-developed astragalar process or contact, as well as a medial groove. Distally, this element exhibits well-developed rugosities indicating soft tissue insertions. The semicircular shape is shared with other ornithopods including *Camptosaurus*, *Cumnoria*; *Gasparinisaura*, *Hypsilophodon*, *Iguanodon*, *Ouranosaurus*, *Valdosaurus*, *Zalmoxes*, and UNPSJB-PV 960, among others. Likewise, the proximal ridge that separates the fibular and tibial articular surfaces, the well-developed astragalar process, and the medial groove are also anatomical characteristics shared with these other ornithopods. However, by contrast, the medial surface of the calcaneum in *Changchunsaurus* is flat, lacking the groove and process. The tibial articular surface in *Notohypsilophodon* is concave in lateral view and it may have distally enveloped the anterior portion of the tibial lateral malleolus, this condition, when in natural articulation, is comparable to those seen in *Gasparinisaura*, *Hypsilophodon*, *Ouranosaurus* and UNPSJB-PV 960. In *Notohypsilophodon* there is a marked difference in size between the fibular and tibial articular surfaces, the former being smaller than the latter in lateral view. This feature is shared with *Gasparinisaura* and UNPSJB-PV 960, but in *Camptosaurus*, *Hexinlusaurus*, *Hypsilophodon* and *Zalmoxes* these fossae are subequal in size in the same view. Likewise, in iguanodontians such as *Iguanodon* and *Mantellisaurus*, the fibular articular surface is clearly longer than the tibial (see Ibiricu *et al.* 2010), unlike the condition in *Notohypsilophodon*.

Non-ungual phalanx. One of the best-preserved proximal non-ungual phalanges (Fig. 10A–B–C), probably the first phalanx, exhibits a concave surface for articulation with the metatarsal. The shaft is slightly constricted as in *Gasparinisaura*. The distal articulation of the phalanx possesses two almost symmetrical condyles. These are separated by a marked intercondylar groove. The phalanx has ovoid collateral ligament pits on the external surfaces of the lateral and medial condyles (although the latter is not as strongly developed as the former). Another well preserved non-ungual phalanx (Fig. 10D–E; a second phalanx) is shorter than the previously described phalanx. The proximal articular surface is divided by a marked sagittal ridge (= intercondylar ridge, according to Zheng *et al.* 2012). This strong dorsal process delimits two concave surfaces. This suggests that it is not a proximal phalanx [(based on anatomical comparisons with well represented pedes; e.g., *Changchunsaurus* and *Yueosaurus*), probably

phalanx ?-2]. The well-developed collateral ligament pits and the presence of dorsal and sagittal ridges on the proximal end of the non-proximal phalanx are features that are common to all basal neornithischians and basal ornithopods (Zheng *et al.* 2012).

Ungual phalanges. The ungual phalanges are subtriangular in shape (Fig. 10F–G–H). They bear well-developed grooves on both the lateral and medial sides and the ventral surface is planar. The elongate grooves extend for almost the full length of the unguals. The morphology of these elements resembles to those described in MOZ-PV 020 (Canudo *et al.* 2013). In contrast, those seen in styracosternans are dorsoventrally flattened and spade-shaped.
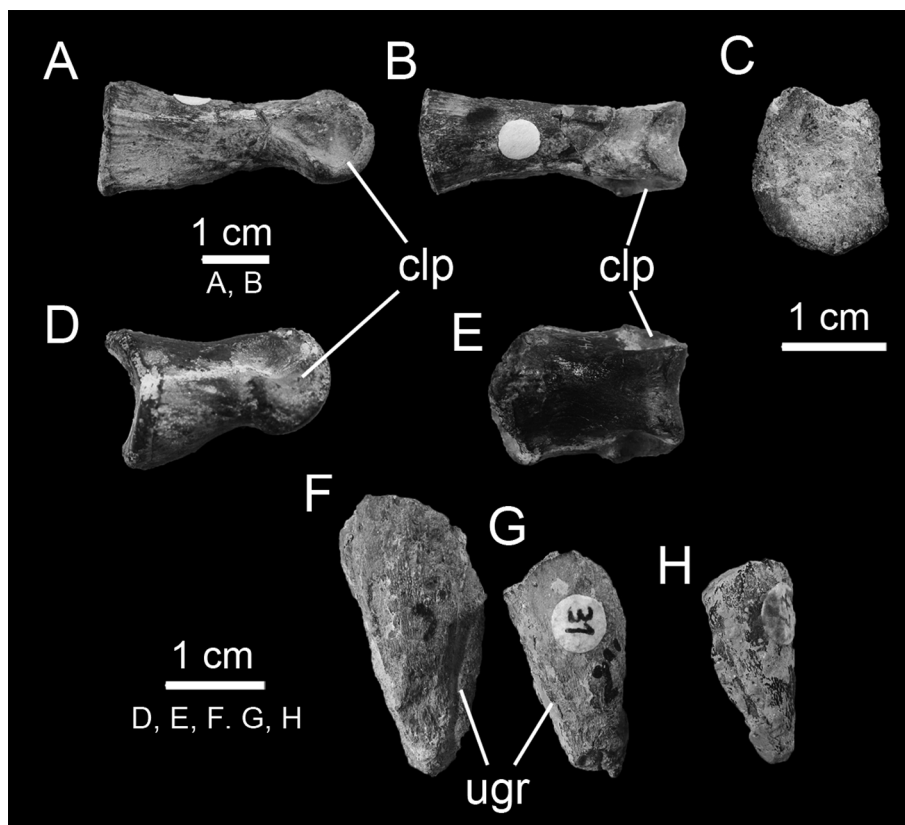

FIGURE 10. *Notohypsilophodon comodorensis.* Non-ungual phalanx (UNPSJB-PV 942/35), in medial (A), dorsal (B) and proximal (C) views. Non-ungual phalanx (UNPSJB-PV 942/37), in medial (B) view. Non-ungual phalanx (UNPSJB-PV 942/39), in dorsal (C) view. Ungual phalanges (UNPSJB-PV 942/45,46,47), in dorsal view. Abbreviation: clp, collateral ligament pit; ugr, ungula groove.

Discussion

Ontogenetic stage and body size. The lack of complete fusion between the vertebral centra and their respective neural arches suggests that *Notohypsilophodon* was not fully skeletally mature at death (Brochu 1996; Irmis 2007; Butler *et al.* 2010). However, a histological study is necessary to determine the precise ontogenetic stage and growth strategy of the specimen (see Horner *et al.* 2009 and Cerda & Chinsamy 2012).

Ornithischians show a large diversity of body sizes. Species with small adult sizes (< 1 m) include the heterodontosaurids *Fruitadens haagarorum* (Butler *et al.* 2010) and *Manidens condorensis* (Pol *et al.* 2011). In basal ornithopods (e.g., *Hypsilophodon*), the length (i.e., from the skull to the end of the tail) is approximately 1.4 m (although all known *Hypsilophodon* individuals are probably juveniles; Butler *et al.* 2010). In some non-hadrosaurid "Patagonian" iguanodontians, body sizes are estimated between 7–8 meters (see Ibiricu *et al.* 2010) and *Iguanodon* can reach 9–10 meters. As mentioned, *Notohypsilophodon* is, at present, considered to be a juvenile and its size and proportions could change in tandem with some morphologic aspects (i.e., ontogenetic variation).

Significance for ornithopod morphology and evolutionary affinities. Owing to the incomplete preservation

of *Notohypsilophodon*, inclusion of holotype in a phylogenetic analysis leads to incongruent results. For example, when *Notohypsilophodon* is codified in the matrix of Han *et al.* (2012), based on that originally proposed by Butler *et al.* (2008), and analyzed using TNT (Goloboff *et al.* 2008) the phylogenetic position of *Notohypsilophodon* is recovered as highly unstable. Additionally, when the instability of its phylogenetic position is quantified by evaluating the amount of missing data or levels of character conflict (see Pol & Escapa 2009), missing data seems to be the main cause for the uncertain phylogenetic position of *Notohypsilophodon*. Therefore, without the discovery of additional material, better resolution of basal ornithopod relationships, or the addition of new characters (which is beyond the scope of the current work), the precise phylogenetic position of *Notohypsilophodon* will remain elusive.

Notohypsilophodon displays synapomorphic characters that can be used to identify the specimen as a neornithischian: strongly transversally expanded distal end of the tibia (char. 206, Butler *et al.* 2008, also see Makovicky *et al.* 2011; Zheng *et al.* 2012); the lesser trochanter exhibits reduced anteroposterior width, although, it is not closely appressed to the expanded greater trochanter. Likewise, *Notohypsilophodon* exhibits a marked cleft separating the lesser and greater trochanters, a feature seen in basal neornithischians (Zheng *et al.* 2012). The well-marked cleft, is also present in dryosaurids (e.g., *Callovosaurus*, *Dryosaurus*, *Valdosaurus*), although in these taxa, the deep cleft, in addition to the overall long bone morphology (e.g., the tibia elongated relative to the femur), could have related to the bipedal cursorial abilities of both groups (Butler *et al.* 2007; Ruiz-Omeñaca *et al.* 2007).

As mentioned above, the *Notohypsilophodon* postcranium greatly resembles those of basal ornithopods (including "hypsilophodont-grade" taxa). However, because of the absence of skull material and the pelvic girdle, ornithopod synapomorphies cannot be recognized in the material at present. Nevertheless, several morphological features displayed by *Notohypsilophodon*, particularly in the long bones, strongly suggest that the specimen is related to basal ornithopod dinosaurs. The morphological characters which support this can be summarized as: the humeral shaft is slightly twisted (feature also shared with some basal ornithischians, see Butler *et al.* 2007); the humerus lateral radial condyle is expanded anteroposteriorly and the medial ulnar condyle is rounded; the length of the ulna is approximately 75% of the length of the humerus; the lesser trochanter of the femur is placed more distally than the expanded greater trochanter (an anatomical characteristic also present in some basal ornithischians); the anterior (extensor) groove is shallow or weakly developed. In addition, the cnemial crest is modestly developed and slightly laterally and dorsally projected as is usual in basal ornithopods (Huh *et al.* 2010). The outer malleolus of the tibia is larger than the inner malleolus, a condition reported in basal ornithopods (Zheng *et al.* 2012). The ascending process of the astragalus is subtriangular in shape and it is moderately developed as described in basal ornithopods (Norman *et al.* 2004). Lastly, the pointed ungual phalanx is another of the morphological characteristics suggesting that *Notohypsilophodon* may be considered a putative basal representative of Ornithopoda.

The taxonomic validity of *Notohypsilophodon comodorensis* is supported based on the following autapomorphies proposed originally by Martinez (1998) and currently sustained in this study: anteromedial bulge on the proximal extremity of the tibia, calcaneum with a pronounced posterodistal projection. In addition to that set of diagnostic features, this small bodied ornithopod exhibits the following new autapomorphies which distinguish *Notohypsilophodon* from other basal ornithopods: The distal tip of the sacral neural spine is strongly projected posteriorly (Fig. 11), and the sternal process of the coracoids is markedly reduced compared to other ornithopods (Fig. 12).

Remains of basal ornithopods are known from the Middle Jurassic until the latest Cretaceous in both Gondwanan and Laurasian landmasses. Representative non-iguanodontian euornithopods have been recovered in Asia, Europe, North America, South America, Antarctica and Australia (Norman *et al.* 2004). Therefore, basal ornithopod dinosaurs attained a global to near-global distribution. Currently, basal ornithopods known from Patagonia ranged from the early Late to the latest Cretaceous (Wilf *et al.* 2013). In this regard, *Notohypsilophodon* from the Cenomanian, is the oldest representative of the group in South American Cretaceous outcrops (Novas 2009). This highlights the importance of this small ornithopod dinosaur. Finally, whether or not, *Notohypsilophodon* supports some type (e.g., climate-driven, see Benson *et al.* 2012) of provincialism in the ornithopod fauna in particular or among dinosaurs in general in the Gondwanan landmasses (particularly among Antarctica, Australia, New Zealand and South America) remain unsolved, but plausible pending new discoveries and better phylogenetic resolution among basal ornithopods.
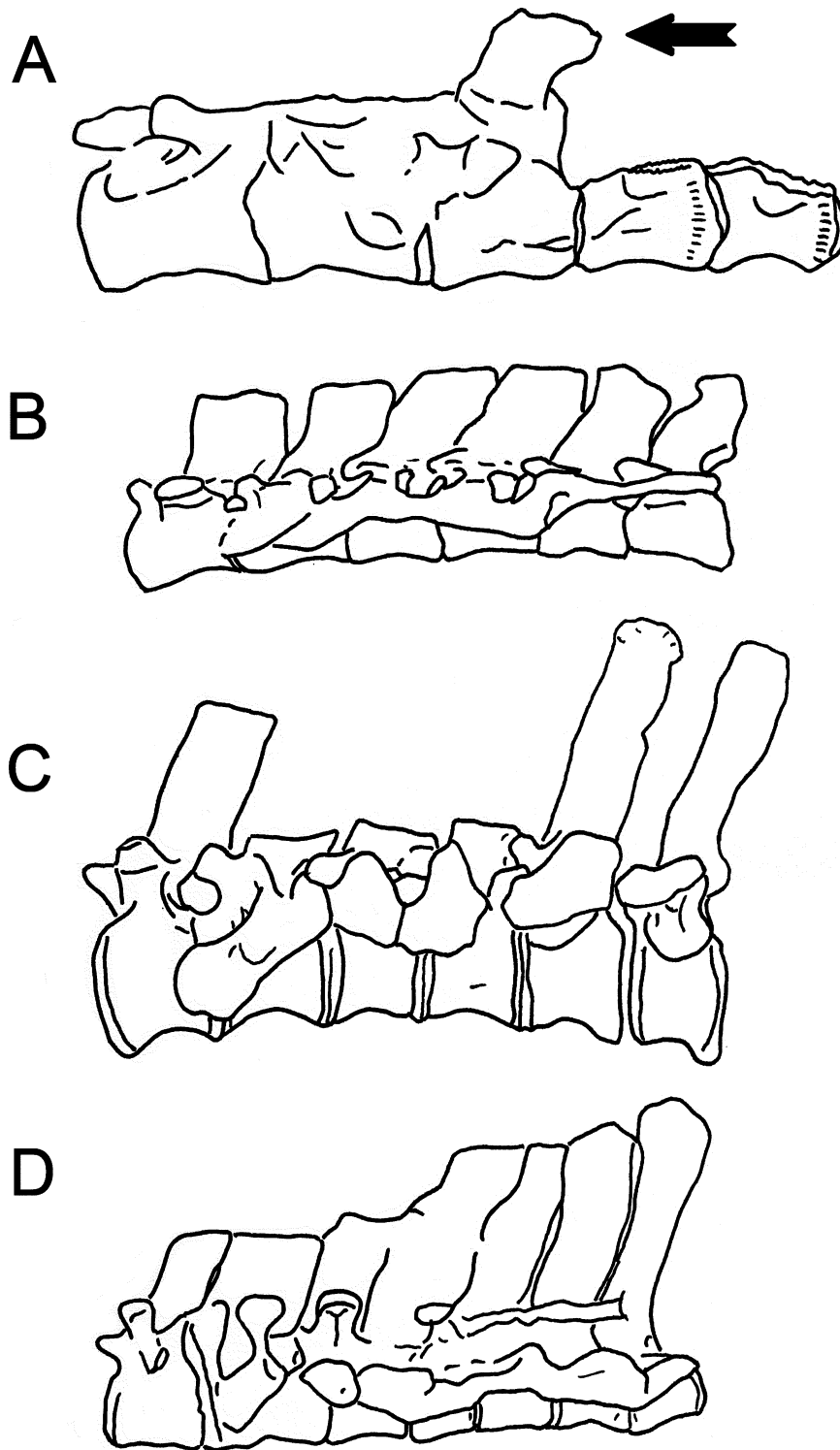
FIGURE 11. Comparisons of the sacral vertebrae in lateral view of (A), *Notohypsilophodon comodorensis*; (B) *Hypsilophodon* (after Galton 1974); (C) *Tenontosaurus* (after Forster 1990) and (D) *Iguanodon* (after Norman 1980). Black arrow denotes the new proposes autapomorphy (distal tip of the sacral neural spine, strongly projected posteriorly, see text). Not to scale.

Probable gastroliths in *Notohypsilophodon*. Gastroliths ("stomach stones") have been unambiguously recovered in three ornithischian taxa (Makovicky *et al.* 2011). These pebbles are related to the mechanical processing of food (see Wings 2004; Wings & Sander 2007; Cerda 2008; Makovicky *et al.* 2011). Within Ornithopoda, only two basal ornithopods, *Gasparinisaura* (Cerda 2008) and *Haya* (Makovicky *et al.* 2011), possess gastroliths. In these taxa, a substantial accumulation of stones was found near to the abdominal area.

Likewise, both specimens are almost complete and articulated. In addition, several taphonomic attributes can be recognized supporting the relationship of these stomach stones with their respective bone associations (see Cerda 2008). Therefore, these inorganic materials represent unequivocal evidence of true gastroliths and support the strategy of lithophagy in Ornithopoda or at least some members of the group.
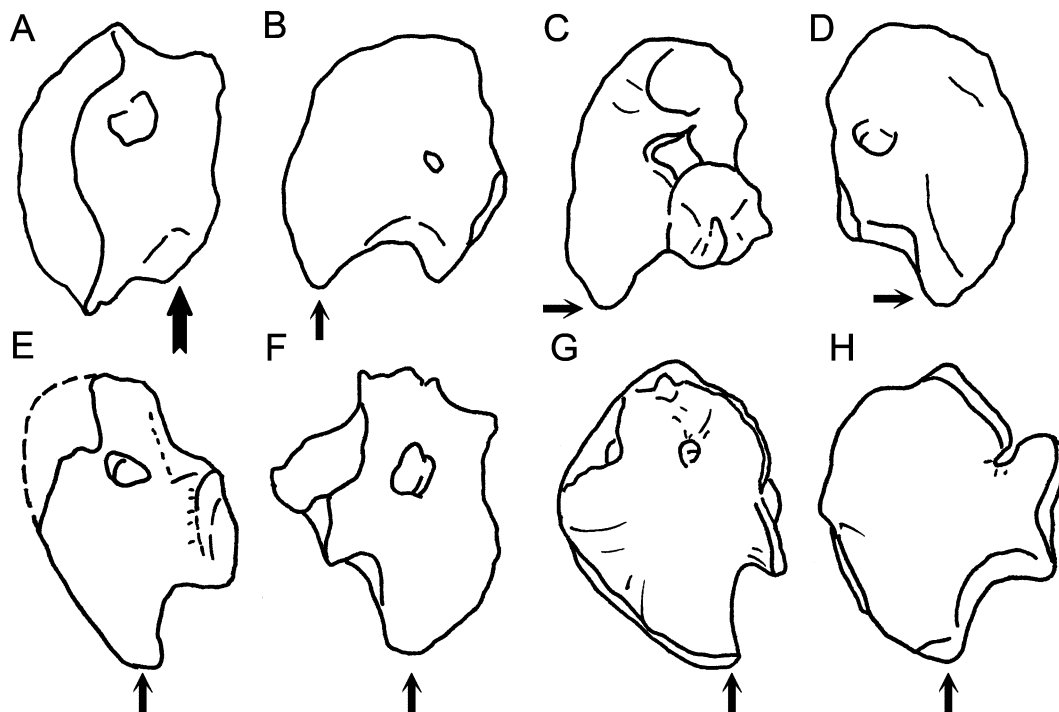

FIGURE 12. Comparisons of the coracoids in lateral view of (A), *Notohypsilophodon comodorensis* (right coracoid); (B) *Hypsilophodon* (left coracoid, reversed, after Galton 1974); (C) *Thescelosaurus* (left coracoid, reversed, after Gilmore 1913); (D) *Gasparinisaura* (right coracoid, after Coria & Salgado 1996); (E) *Anabisetia* (left coracoid, reversed, after Coria & Calvo 2002); (F) *Trinisaura* (right coracoid, after Coria *et al.* 2013); (G) *Tenontosaurus* (left coracoid, reversed, after Forster 1990); (H) *Iguanodon* (left coracoid, reversed, after Norman 1980). The black large arrow denotes the markedly reduced sternal processes in *Notohypsilophodon* (the new proposed autapomorphy, see text), whereas the black small arrows denote the sternal process in the remaining ornithopods. Not to scale.

During the extraction of *Notohypsilophodon*, during the early 1990s, some indeterminate material was collected (Fig. 13). On the basis of the texture (polished), color (light brown with dull surface), composition (quartz), form (sub-rounded), size (8 mm), and comparisons with the material described by Wings (2007), Cerda (2008) and Makovicky *et al.* (2011), this material (Fig. 13) is preliminarily interpreted as a gastrolith mass. Likewise, some of the sedimentologic criteria for gastrolith identification proposed by Wings (2004, see also Cerda 2008) could be inferred in *Notohypsilophodon*. For example, the matrix surrounding *Notohypsilophodon* lacks similar stones, either isolated or in clusters, and there is no evidence of isolated or clustered stones in the outcrops where *Notohypsilophodon* was recovered. However, some of the criteria for gastrolith identification (Wings 2004, 2007) cannot be applied. For example, the stones were not found in situ in the abdominal area of the skeleton, *Notohypsilophodon* is not represented for an almost complete and articulated skeleton, and the potential gastroliths were not recovered as an accumulation. Another of the possibilities is that *Notohypsilophodon* accidentally ingested them with its food supply as occurs in some extant vertebrates (Wings 2007). In summary, although the evidence is weak, it is important to highlight that *Notohypsilophodon* probably shared this feature with some other basal ornithopods (i.e., *Gasparinisaura* and *Haya*) and that the presence of gastroliths might suggest a specific behavior in response to a particular set of environmental conditions (Makovicky *et al.* 2011).
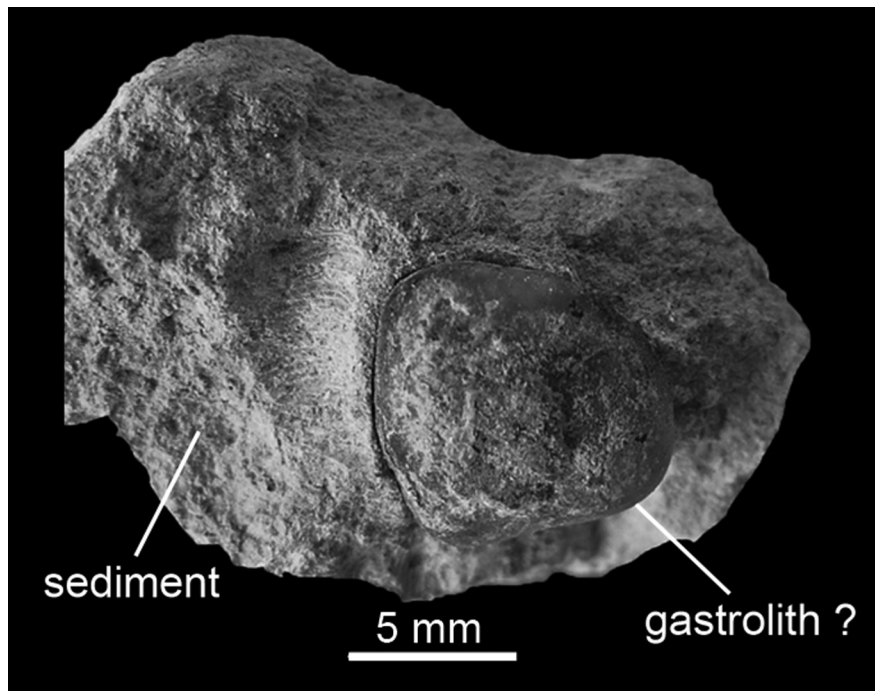
FIGURE 13. A detailed view of a probable gastrolith (UNPSJB-PV 942/52).

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