

OSTEOLOGY AND RELATIONSHIPS OF A NEW THEROPOD DINOSAUR FROM THE MIDDLE JURASSIC OF PATAGONIA

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Abstract: A new taxon of theropod dinosaur is described as *Condorraptor currumili* gen. et sp. nov., from the Middle Jurassic (Callovian) Cañadón Asfalto Formation of Chubut Province, Argentinean Patagonia. The taxon is represented by a single fragmentary postcranial skeleton. Although incompletely known, *Condorraptor* is the second most complete theropod from the Middle Jurassic of Gondwana. The new taxon is characterized by the absence of a posterior incision between the fibular condyle and the medial side of the proximal articular end of the tibia, the pleurocoels in the

anterior cervicals being situated posteroventral to the parapophyses, and the presence of a pronounced ‘step’ between the distal articular facet and shaft of Mt IV. Pneumatic features of the vertebral column show strong variation between the left and right side. *Condorraptor* gen. nov. can be referred to the Tetanurae and is a representative of a global radiation of basal tetanurans in the Early to Mid Jurassic.

Key words: South America, Cañadón Asfalto Formation, Callovian, Argentina, Theropoda, Tetanurae.

THE Jurassic saw an important radiation of theropod dinosaurs, including the origin and/or early radiation of many important groups. Unfortunately, however, little is still known of Middle Jurassic theropod faunas. This is especially true for the Southern Hemisphere, from where only two Middle Jurassic theropod taxa have been named so far. One of these, *Ozraptor subotaii*, from the Bajocian Colalura Sandstone of Western Australia, is based on a single bone fragment (Long and Molnar 1998), and the theropod identity of this element is questionable (Molnar, pers. comm. 2002). The second theropod from the Middle Jurassic of Gondwana, *Piatnitzkysaurus floresii*, is based on two partial skeletons, including parts of the skull (Bonaparte 1979, 1986), and is therefore the most completely known theropod from the Middle–Late Jurassic of the Southern Hemisphere.

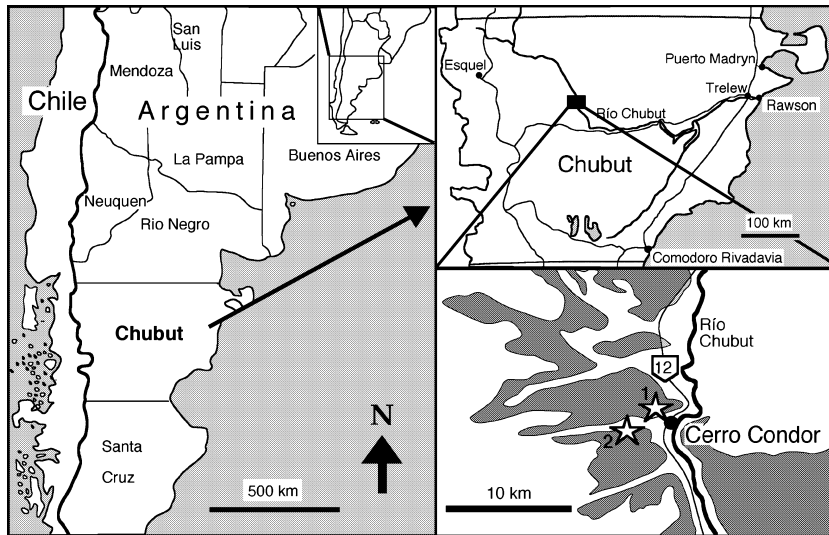
Piatnitzkysaurus is derived from the mainly lacustrine Cañadón Asfalto Formation of Chubut Province, Argentinean Patagonia (Text-fig. 1). This formation is usually dated as Callovian (Tasch and Volkheimer 1970; Musacchio *et al.* 1990; Figari and Courtade 1993; Page *et al.* 1999). Recent fieldwork in the Cañadón Asfalto Formation by the Museo Paleontológico Egidio Feruglio, Trelew, Argentina, led to the discovery of a wealth of new vertebrate material (Rauhut and Puerta 2001; Rauhut *et al.* 2001). Among this material were numerous remains of dinosaurs, including a fragmentary postcranial skeleton of

a new theropod from the vicinity of the village of Cerro Cándor. This specimen is described herein, and its systematic position is discussed.

GEOLOGICAL AND PALAEOONTOLOGICAL CONTEXT

The Cañadón Asfalto Formation is a series of mainly lacustrine sediments with frequent basaltic intercalations (Stipanovic *et al.* 1968; Tasch and Volkheimer 1970; Figari and Courtade 1993; Cortiñas 1996; Page *et al.* 1999). In the area of Cerro Cándor (Text-fig. 1), the sediments are dominated by organic limestones (Volkheimer *in* Tasch and Volkheimer 1970; Cabaleri and Armella 1999), with frequent intercalations of tuffites, marls, conglomerates and breccias. This sequence represents a synrift phase of the basin evolution (Figari and Courtade 1993), with the conglomerates and breccias representing gravity flows into the lake resulting from tectonic activity.

The Cañadón Asfalto Formation has yielded a wealth of invertebrate, plant and vertebrate fossils. Lacustrine algal limestones are very abundant, mainly formed by stromatolites (Cabaleri and Armella 1999). The most frequent invertebrates are conchostracans (Tasch *in* Tasch and Volkheimer 1970), but bivalves are also common in some layers. Apart from the dinosaurs, the rich vertebrate



TEXT-FIG. 1. Geographical position of the localities mentioned in the text. Shaded areas in the enlarged part indicate outcrops of Middle and Late Jurassic continental units. Localities: 1, Cerro C6ndor south, type locality of *Piatnitzkysaurus floresi* Bonaparte, 1979; 2, Las Chacritas, type locality of *Condorraptor currumili* gen. et sp. nov.

fauna includes remains of fishes, anurans, turtles, lepidosaurs, crocodiles, pterosaurs, and mammals (Rauhut and Puerta 2001; Rauhut *et al.* 2001, 2002; Rauhut, unpublished data). Dinosaurs are so far represented only by saurischians. Two taxa of basal sauropods were described by Bonaparte (1979, 1986) as *Volkheimeria chubutensis* and *Patagosaurus fariasi*. The material referred to *Patagosaurus* includes at least one further, undescribed, taxon of sauropod (Rauhut 2002a, b, 2003a). Theropods include *Piatnitzkysaurus floresi* and the new taxon described here. Abundant fishes and the sauropod dinosaur *Tehuelchesaurus*, which were thought to be from this formation (Cione and Pereira 1987; Rich *et al.* 1999), come from a different sedimentary unit of Kimmeridgian–Tithonian age (pers. obs. and Khoukarsky, pers. comm. 2002).

The material described here comes from a breccia within a series of lacustrine marls, limestones and tuffites with frequently intercalated conglomerates and breccias in the Las Chacritas canyon (Text-fig. 1). The breccia forms a lenticular body with poorly sorted and poorly to moderately rounded clasts up to 15 cm in diameter. Clast size rapidly decreases within 10 m of the eastern border of the lens. In its central part, the lens has a thickness up to 60 cm. Bones occur as disarticulated and usually broken elements, with most fractures being straight and at approximately right angles to the surface of the bone, indicating that they were post-burial. The deposit thus represents a gravity flow with the dinosaur remains being redeposited after initial burial and prefossilization. However, only a few individuals seem to be represented by the material. Apart from the theropod remains described here, bones of a large sauropod (probably *Patagosaurus*) and fragmentary remains of a much larger theropod were found.

MATERIAL AND METHODS

The new taxon is represented by a fragmentary postcranial skeleton (Text-fig. 2), including elements of the vertebral column, pelvic girdle, hindlimbs, and two teeth. Although found disarticulated, all the material is thought to represent a single individual for the following reasons. (1) All of the elements are of matching size and, in the case of the vertebrae and femora, matching morphology, and no element is duplicated. (2) All elements are of matching preservation. Specifically, several elements of the vertebral column show preburial erosion on the right side, indicating that they belong to a single skeleton that was exposed for some time prior to redeposition. (3) Matching size, morphology and preservation is also found in the remains of the sauropod and larger theropod from the locality, indicating that only a few individuals are represented, each fragmented during redeposition.

The teeth have been referred to the new taxon because of their matching size and the fact that they preserve parts of the root and were therefore not derived from scavengers. Thus, all the material probably represents a single individual. However, given the fact that the material was derived from a bonebed, a single diagnostic element is designated as the holotype and the rest of the elements are treated as referred specimens. This is done to prevent taxonomic confusion in case any of these elements should later prove to represent a different animal.

In the anatomical description of the vertebrae, the standardized anatomical nomenclatures of Wilson (1999) for vertebral laminae and of Makovicky (1997) for lateral vertebral recesses were used. The systematic position of the new taxon is discussed in the light of proposed synapomorphies within theropod phylogeny based on recent



TEXT-FIG. 2. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina; outline drawing, showing preserved elements. Scale bar represents 50 cm.

published cladistic analyses (Holtz 2000; Carrano *et al.* 2002; Rauhut 2003b), because a detailed phylogenetic analysis of basal theropods is beyond the scope of this paper.

Institutional abbreviations. MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; OUM, Oxford University Museum, Oxford, England; PVL, Paleontología de Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina; QG, National Museum of Natural History, Harare, Zimbabwe; UCMP, University of California, Museum of Paleontology, Berkeley, USA; UMNH, Utah Museum of Natural History, Salt Lake City, USA.

SYSTEMATIC PALAEOONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

Genus *CONDORRAPTOR* gen. nov.

Derivation of name. Condor, for the village of Cerro Cóndor, in the vicinity of which the holotype was found, and *raptor*, Latin for ‘robber’ or ‘snatcher’.

Type and only known species. *Condorraptor currumili* sp. nov.

Diagnosis. As for the only known species, *C. currumili*.

Condorraptor currumili gen. et sp. nov.

Text-figures 2–14

Derivation of name. In honour of Hipólito Currumil, the landowner and discoverer of the locality.

Holotype. MPEF-PV 1672, an incomplete left tibia.

Hypodigm. MPEF-PV 1694–1695, teeth; MPEF-PV 1673–1675, cervical vertebrae; MPEF-PV 1676–1680, 1697, 1700, 1705, dorsal vertebrae and vertebral fragments; MPEF-PV 1681, 1701, sacral vertebrae; MPEF-PV 1682–1683, 1702, caudal vertebrae; MPEF-PV 1684–1685, 1703, rib fragments and chevron; MPEF-PV 1686–1689, 1696, 1704, partial ilium, pubes and ischium; MPEF-PV 1690–1693, partial femora, metatarsal IV and pedal ungual; all from the same locality and most probably from the same individual as the holotype (see above).

Locality and horizon. Las Chacritas locality, 2.3 km west of Cerro Cóndor. The dinosaur-bearing layer is a breccia within a series of lacustrine clays, tuffs and limestones of the Cañadón Asfalto Formation; Callovian.

Diagnosis. *Condorraptor currumili* gen. et sp. nov. is characterized by the following autapomorphic characters: posterior incision between fibular condyle and medial part of proximal tibia absent; and large, shallow depression laterally on the base of the cnemial crest. The following apomorphic characters are based on the referred material: pleurocoel in anterior cervical vertebrae placed behind the posteroventral corner of the parapophyses; large nutrient foramina on the lateral side of the ischial peduncle of the ilium; metatarsal IV with a distinct step dorsally between shaft and distal articular facet.

Remarks. The tibia is selected as the holotype because it shows several autapomorphic characters. The presence of a posterior incision between the medial part and the fibular condyle is a neotheropodan synapomorphy (Rauhut 2003b), which, among non-avian theropods, is only reversed in very few advanced maniraptorans, such as *Avimimus* (Rauhut 2003b). Thus, the absence of this incision in *Condorraptor* clearly represents an apomorphic reversal. A depression on the lateral base of the cnemial crest has not been described or observed in any other theropod dinosaur.

Likewise, the diagnostic characters found in the referred material also represent autapomorphies of the new taxon. The pleurocoel in anterior cervical vertebrae is usually placed dorsally or posterodorsal to the parapophysis, and not ventrodorsally, and a large nutrient foramen on the ischial peduncle of the ilium and a distinct step between the shaft and distal articular facet of metatarsal IV has not been described or observed in any other theropod.

Description

Teeth. The two teeth referred to *Condorraptor* are lateral maxillary or dentary teeth (MPEF-PV 1694 and 1695; Text-fig. 3). As is usual in theropod teeth, the crown is labiolingually compressed, strongly recurved and exhibits serrated carinae. MPEF-PV 1694 is slightly more robust than MPEF-PV 1695 and has the distal carina slightly displaced labially, indicating that it is from a more mesial tooth position. Whereas the distal carina extends all the way to the root, the mesial carina terminates in the apical half of the crown. The denticles are best preserved in MPEF-PV 1695, with only a few worn denticles present on the distal carina in MPEF-PV 1694. They are chisel-shaped and extend perpendicular to the long axis of the carina. The mesial denticles are lower, but not smaller than the distal ones; there are approximately three denticles per millimetre. No basally pointing grooves, blood pits or enamel wrinkles are present at the bases of the denticles.

Both teeth have part of the root preserved, which is at least as long or longer than the crown and of subequal width to the base of the latter. No incision between crown and root is present. For measurements of the teeth, see Table 1.

Cervical vertebrae. Three cervical vertebrae of *Condorraptor* are preserved. In the most anterior of these vertebrae (?fourth; MPEF-PV 1673), the articular surfaces of the centrum are



TEXT-FIG. 3. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Teeth. A, MPEF-PV 1695. B, MPEF-PV 1694. Both in lingual view; thin lines indicate the approximate crown–root junction. Scale bar represents 30 mm.

strongly offset from one another (Text-fig. 4A–D). Thus, the anterior surface is positioned considerably higher than the posterior one and faces very slightly ventrally in relation to the latter. The centrum is amphi-platycoelous, with a flat anterior articular surface and a concave posterior one. The anterior articular facet is broadly oval, almost rectangular and very slightly broader than high (Text-fig. 4B). The posterior articular facet is higher than broad, oval and with a broad indentation dorsally for the neural canal (Text-fig. 4C). Ventrally, a stout keel is developed in the anterior third of the centrum. This keel continues posteriorly as a slight ventral ridge. A small ridge runs on either side from the anterior end of the keel anterolaterally towards the ventral side of the parapophyses. The latter is situated antero-ventrally on the lateral side of the centrum (Text-fig. 4D).

The parapophyses are round to oval in shape and the articulation with the capitulum is distinctly concave. A well-developed pleurocoel is situated behind the posteroventral edge of the parapophysis. The pleurocoel on the left is more than twice the size of that on the right and obviously led into large internal chambers, which are visible through the completely prepared left pleurocoel.

The neural arch encloses a large neural canal, which is broadly subrectangular anteriorly, but an elongate oval posteriorly. The diapophysis is short and directed ventrolaterally. It is supported ventrally by a stout posterior centrodiapophyseal lamina and a very short and broad anterior centrodiapophyseal lamina, which is hidden in lateral view by the prezygodiapophyseal lamina. The latter forms the anterior continuation of the posterior centrodiapophyseal lamina and is slender, forming a sharp edge latero-ventrally. Anteriorly, it connects to the ventral side of the prezygapophysis. The postzygodiapophyseal lamina is stout, but low, and meets the diapophysis on its dorsal side. Together with the short and broad centroprezygapophyseal lamina, these diapophyseal laminae define the lateral fossae of the arch, which are better developed on the left side than on the right. The infraprezygapophyseal fossa is the smallest in area but deepest of the three fossae. The biggest fossa, the infrapostzygapophyseal fossa, is very shallow.

The prezygapophyses are long processes that considerably overhang the centrum anteriorly. The articular facets are large, oval in outline and widely spaced, being situated entirely lateral to the neural canal. The postzygapophyses are not preserved. Anteriorly, two short spinoprezygapophyseal lamina define a deep groove on the anterior surface of the broken neural spine at its base. Laterally within this groove, two large foramina lead into the interior of the neural arch. Posteriorly, a broad, deep depression is present in the base of the neural spine. On the left side, a further deep, cone-shaped recess invades the postzygapophysis lateral to this depression; this recess seems to be absent, or at least much less developed, on the damaged right side.

A posterior middle cervical vertebra (?seventh; MPEF-PV 1674) also has an amphi-platycoelous centrum, but is more elongate and does not show as strong an offset of the articular surfaces as the more anterior element (Text-fig. 4E–F). The centrum is flattened ventrally, without a keel, and is noticeably transversely concave in its anterior part between the broken parapophyses (Text-fig. 4F). As the parapophyses are missing, it is impossible to say whether the anterior transverse ridges

TABLE 1. Measurements of teeth and vertebrae of *Condorraptor currumili* gen. et sp. nov. in millimetres. Abbreviations: BW, basal width; CL, centrum length; CHA, centrum height anterior; CHP, centrum height posterior; CWA, centrum width anterior; CWP, centrum width posterior; FABL, fore-aft basal length; NAL, length of neural arch; TCH, tooth crown height; TH, total height; ¹ articular surface only, excluding the parapophyses in anterior presacrals; ² dorsally; ³ ventrally; ⁴ articular surface only; ⁵ articular surface plus hypapophysis.

| Teeth | FABL | | BW | | TCH | |
|--------------|------|--|-----|--|-------|--|
| MPEF-PV 1694 | 11 | | 7 | | – | |
| MPEF-PV 1695 | 10.5 | | 6.5 | | c. 26 | |

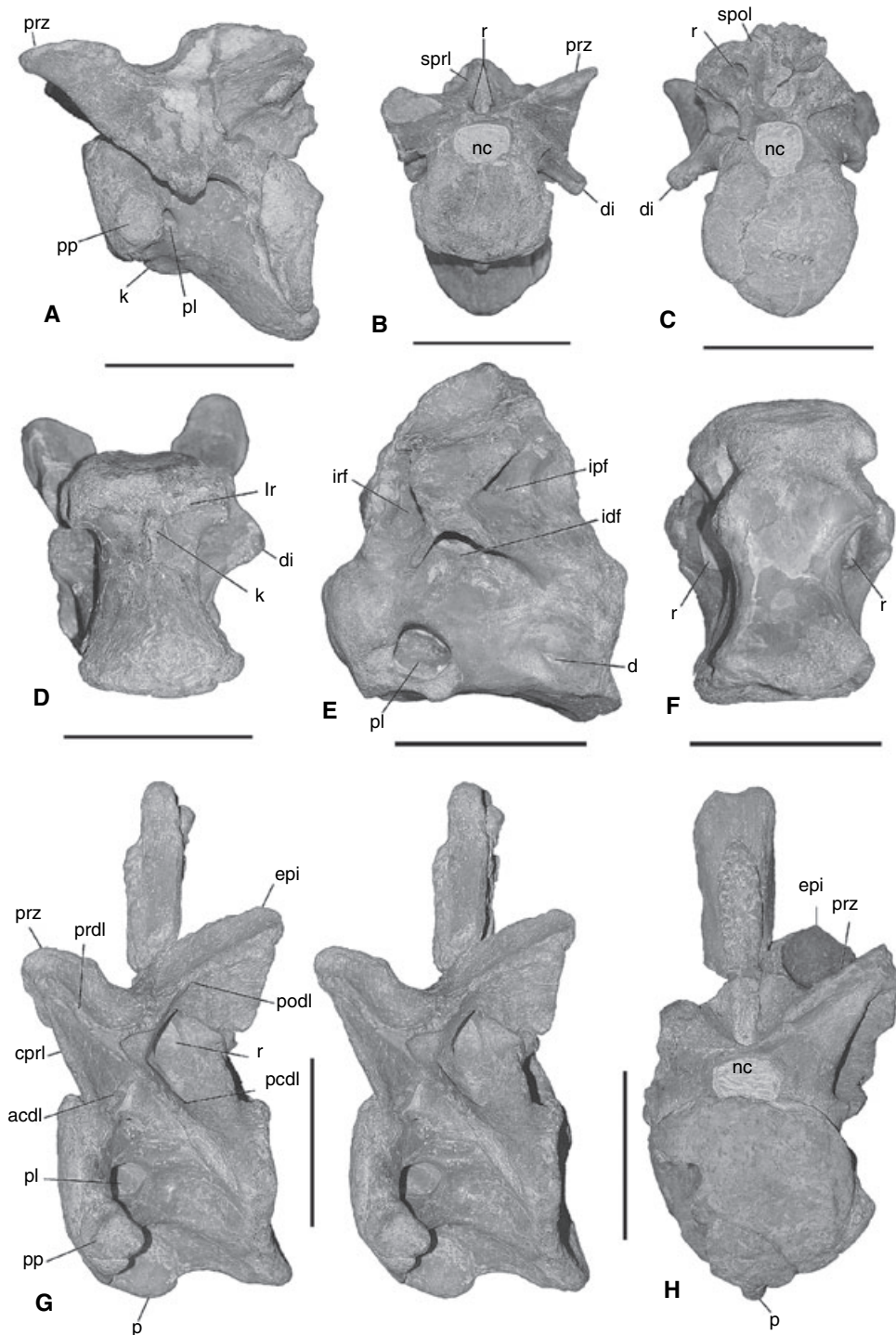
| Vertebrae | CL | CWA ¹ | CWP | CHA | CHP | NAL | TH |
|----------------|-----------------------------------|------------------|-------|-----------------------------------|-------|-------|-----|
| MPEF-PV 1673 | 62 ² ; 57 ³ | 35 | 41 | 33 | 41 | 80(+) | – |
| MPEF-PV 1674 | 77 ² ; 70 ³ | 38 | 46(+) | c. 33 | 40(+) | – | – |
| MPEF-PV 1675 | 59 | 57 | 63 | 54 ⁴ ; 61 ⁵ | 53 | 71 | 149 |
| MPEF-PV 1676 | 61 | 56 | 51(+) | 54 ⁴ ; 61 ⁵ | 53 | – | – |
| MPEF-PV 1697 | 57.5 | 53 | 53 | 57 | 58 | – | – |
| MPEF-PV 1705 | 65 | – | – | – | – | – | – |
| MPEF-PV 1677 | c. 70 | – | – | – | – | – | – |
| MPEF-PV 1678 | c. 68 | – | – | – | – | – | – |
| MPEF-PV 1700 | 76 | 77 | 74(+) | 77 | 81 | 99 | – |
| MPEF-PV 1680 | 80 | 86 | 84 | 81 | 81 | c. 94 | – |
| MPEF-PV 1701 | 69 | 72 | 54 | 73 | 61 | 77 | – |
| MPEF-PV 1681-1 | 75 | – | – | 62 | – | – | – |
| MPEF-PV 1681-2 | 75 | – | – | – | – | – | – |
| MPEF-PV 1681-3 | 72 | – | 58 | – | 62 | – | – |
| MPEF-PV 1702 | 56 | 61 | 59 | 73 | 67 | – | – |
| MPEF-PV 1682 | 77 | 66 | 65 | 68 | 63 | – | 198 |
| MPEF-PV 1683 | 67 | 24 | 26 | 22(+) | 24 | – | – |

running to the underside of the parapophyses were present. A very large pleurocoel is present at the posterodorsal corner of the parapophysis. It leads into large chambers within the vertebra, which are separated from each other by a median septum. A small, elongate posteroventral depression is present on the lateral side of the centrum; on the right, a small foramen is placed in the anteriormost corner of this depression.

The neural arch is approximately as high as the centrum. The neural canal is large. It forms an inverted triangle in anterior outline, but is rectangular posteriorly. The centrodiapophyseal laminae are well developed, with the posterior laminae being stouter, longer and more inclined than the anterior one. The infraprezygapophyseal fossa and infradiapophyseal fossa are especially well developed and extend deep into the lateral side of the neural arch mediodorsally. The infrapostzygapophyseal fossa is large and triangular, and is shallower than the other two fossae. In the left infradiapophyseal fossa there is a large dorsomedial opening that might lead into internal cavities above the neural canal; this area is covered by matrix on the right side, but a similar opening may be present in the infrapostzygapophyseal fossa. Pre- and postzygapophyses are missing; their respective diapophyseal laminae are similar to those described for the more anterior vertebra in their development and orientation. A low, broad, almost vertical ridge is present in the posterior part of the infrapostzygapophyseal fossa, obviously supporting the base of the postzygapophysis.

Anteriorly, a small, conical recess is present on both sides of the neural arch, dorsolateral to the large neural canal and below the prezygapophysis. Posteriorly, a similar deep, conical recess is present on the left side, but absent on the right, as in the anterior vertebra. Well-developed recesses are also present in the anterior and posterior bases of the broken neural spine. The anterior recess is subequal in width to the posterior one.

The remaining cervical vertebra (MPEF-PV 1675) represents the last element in the cervical series (tenth; Text-fig. 4G–H). As in the more anterior cervicals, the centrum is amphi-platycoelous, but the articular surfaces are only very slightly offset from each other. The centrum is much more markedly constricted between the articular ends than in the more anterior cervicals and has a sharp ventral keel, which deepens anteriorly and extends ventrally to form a well-developed, rounded process (Text-fig. 4G). A stout ridge, extending from the anteroventrally placed parapophyses posteriorly, separates the ventral and lateral sides of the centrum. A large pleurocoel is placed anteriorly above the ridge and above the posterodorsal edge of the parapophysis. It leads into several large, subdivided internal chambers. Posterior to the pleurocoel, the lateral side exhibits a shallow depression, which is smaller on the right than on the left. The neurocentral suture is partially visible in this vertebra. It runs dorsal to the pleurocoel at its midpoint, but extends slightly downwards anteriorly and posteriorly, so that the centrodiapophyseal laminae are formed entirely from the neural arch.



TEXT-FIG. 4. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Cervical vertebrae. A–D, anterior cervical vertebra, MPEF-PV 1673, in left lateral (A), anterior (B), posterior (C) and ventral (D) views. E–F, mid-cervical vertebra, MPEF-PV 1674, in left lateral (E) and ventral (F) views. G–H, last cervical vertebra, MPEF-PV 1675, in left lateral (G, stereopair) and anterior (H) views. acdl, anterior centrodiapophyseal lamina; cprl, centroprezygapophyseal lamina; d, depression; di, diapophysis; epi, epipophysis; idf, infradiapophyseal fossa; ipf, infrapostzygapophyseal fossa; irf, infraprezygapophyseal fossa; k, ventral keel; lr, lateral ridge; nc, neural canal; p, anteroventral process; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; pp, parapophysis; prdl, prezygapodiapophyseal lamina; prz, prezygapophysis; r, recess; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Scale bars represent 50 mm.

The neural arch is tall and exhibits well-developed laminae. Both anterior and posterior centrodiaepophyseal lamina are long and slender. The anterior centrodiaepophyseal lamina connects to the anteroventral surface of the posterior centrodiaepophyseal lamina a short distance below the broken transverse process. The posterior centrodiaepophyseal lamina is broadened in its ventral part and a shallow longitudinal sulcus is found in this area on the left side. A very well-developed, thin and more laterally than anteriorly directed centroprezygapophyseal lamina is present. The prezygapophyses overhang the centrum anteriorly only slightly; they are large, considerably broader than long and widen laterally. Their inclination is similar to that of the prezygapophyses of the anterior cervical vertebra. The prezygodiapophyseal lamina is short but stout and, as in the anterior cervical, forms the anterodorsal elongation of the posterior centroprezygapophyseal lamina. The postzygodiapophyseal lamina is less steeply inclined than in the more anterior cervicals; together with the posterior centrodiaepophyseal lamina it defines a very large, triangular infrapostzygapophyseal fossa, in the deepest part of which a smaller, deep recess extends to the base of the neural spine. The infradiapophyseal fossa and infraprezygapophyseal fossa are smaller, but remain well developed and deep. The left infraprezygapophyseal fossa has a further large pocket extending into its deepest part; this pocket seems to be absent on the right side.

The postzygapophyses are very broad transversely, but rather short anteroposteriorly. On the dorsal surface of the postzygapophysis, a large epipophysis is developed as a high ridge that bends laterally in its distalmost extremity. Between the postzygapophyses, a small recess is present at the base of the neural spine. The neural spine is anteroposteriorly short and approximately as high as the centrum. It gradually expands dorsally and shows a very slight bifurcation at its tip. Well-developed spinopostzygapophyseal lamina were obviously present, but are largely broken off. Anteriorly and posteriorly, between the spinopostzygapophyseal lamina, well-developed rugosities for the attachment of the spinal ligaments are present; the posterior rugosity extends further dorsally than the anterior one.

Dorsal vertebrae. A total of seven dorsal vertebrae are preserved, all of them missing at least part of their neural arch.

Only the centrum of the first dorsal vertebra is preserved (MPEF-PV 1676; Text-fig. 5A–B). It is generally very similar to that of the last cervical vertebra, but differs in that the parapophyses are placed slightly higher on the centrum, and the anteroventral process is less pronounced and restricted to the anteriormost end of the centrum. Furthermore, the centrum is slightly shorter dorsally than ventrally, thus contributing to the upward curve of the vertebral column at the base of the neck. Owing to the dorsal displacement of the parapophyses, the anterior centrodiaepophyseal lamina has its stout ventral base on the dorsal rim of the latter.

The next vertebra, probably the second dorsal (MPEF-PV 1697), still exhibits a very well-developed, deep ventral keel, but no anteroventral process (Text-fig. 5C–E). Unlike the last cervical and first dorsal, the keel is not offset from the lateral side of the vertebra by ridges extending from the parapophyses, but

gradually merges into the sides. The parapophyses are placed dorsally at the anterior end of the centrum, just below the neural arch. A pleurocoel is present on either side in the posterior rim of the parapophysis and extends anteriorly into the latter (Text-fig. 5D).

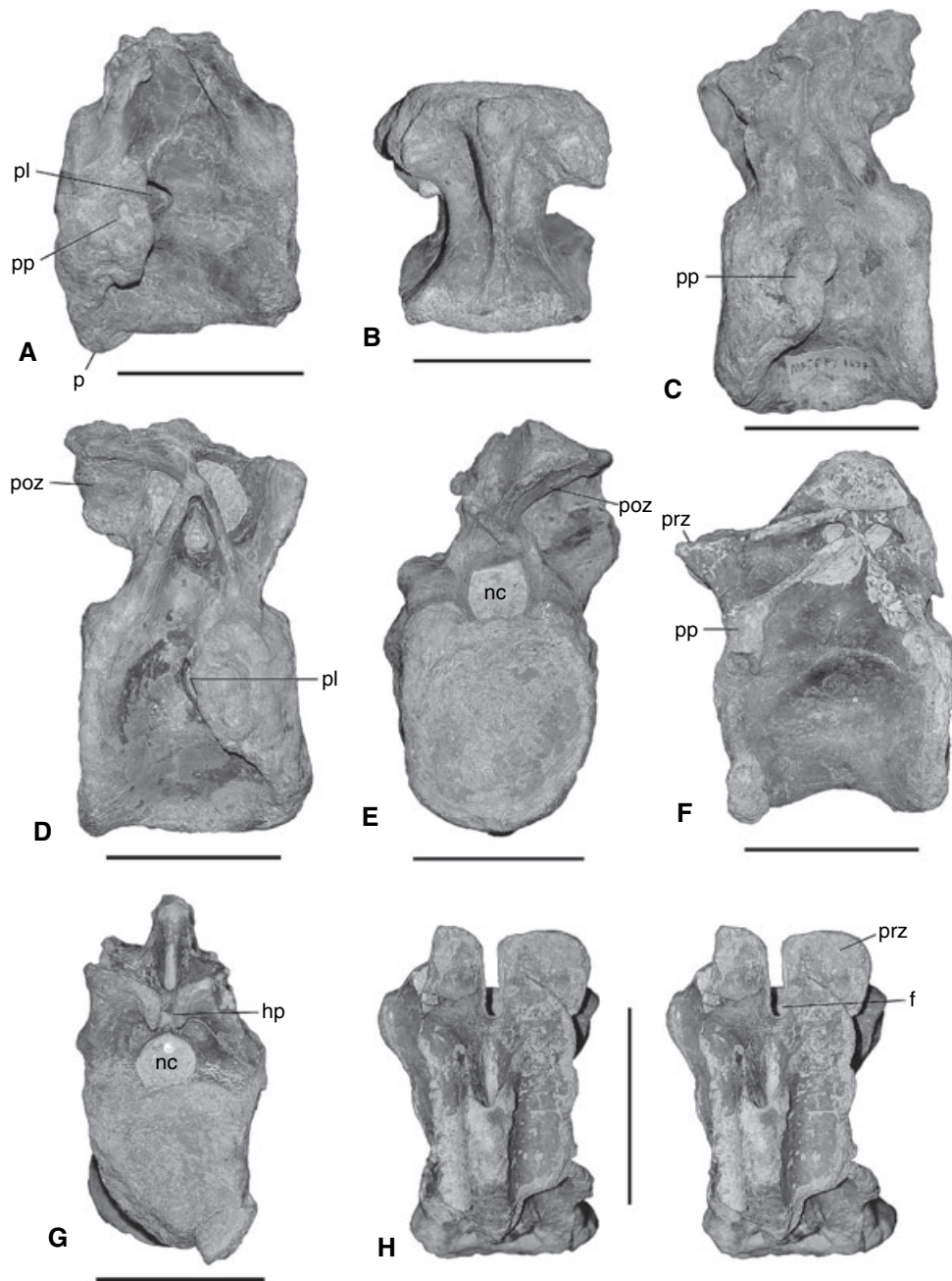
On the neural arch, both the posterior and the anterior centrodiaepophyseal lamina are well developed and form an almost even-sided triangle, with the posterior lamina being slightly more robust than the anterior lamina. Anteriorly, a strongly developed, mainly laterally directed and slightly anterodorsally inclined centroprezygapophyseal lamina is present. Whereas this lamina is robust in its lateral part, it becomes very thin medially. There might be an opening between the infraprezygapophyseal fossa and the anterior depression above the neural canal, although, given the extreme thinness of the lamina in this part, it cannot be ascertained whether this is an artefact of preservation. All three lateral fossae are well developed and the infrapostzygapophyseal fossa exhibits an expansion in its anteromedial part. The infrapostzygapophyseal fossa is bordered posterovertrally by a small, mainly laterally directed centropostzygapophyseal lamina.

The prezygapophyses, transverse processes and neural spine are missing, and only the right postzygapophysis is preserved. It is oval in shape and considerably broader transversely than long anteroposteriorly. Both the medial and the lateral side are flexed somewhat ventrally, making the articular surface transversely concave (Text-fig. 5E). On the dorsal surface of the postzygapophysis, the epipophysis is developed as a stout, high ridge extending from the base of the neural spine posterolaterally. The epipophysis slightly overhangs the postzygapophysis, and in posterior view, the ridge flexes laterally in its posteriormost part and unites laterally with the lateral rim of the zygapophysis. A broad and short hyposphene seems to have been present between the postzygapophyses.

Only the broken base of the neural spine is preserved. The spine was anteroposteriorly short and transversely almost as broad as long, and has well-developed median excavations in its base anteriorly and posteriorly.

A third anterior dorsal (MPEF-PV 1705) preserves the damaged centrum and part of the neural arch (Text-fig. 5F–H). The centrum is platycoelous, slender and exhibits a weak, but sharp ventral keel. The parapophysis is situated just dorsal to the neurocentral suture and no pleurocoel is present. The transverse processes are supported ventrally by a very robust, only slightly anterodorsally inclined posterior centrodiaepophyseal lamina and a thin, strongly posterodorsally inclined parapodiapophyseal lamina that originates from the posterodorsal corner of the parapophysis. The three lateral fossae are well developed, with the infrapostzygapophyseal fossa exhibiting a medial expansion on the right side at least. Anteriorly, a robust, anterolaterally directed centroprezygapophyseal lamina supports the prezygapophysis from below. It borders a small, round depression on the anterior side of the neural arch just below the prezygapophyses.

The prezygapophysis is almost quadrangular in outline and has a well-developed, ventrally expanded hypantrum medially (Text-fig. 5G–H). The gap between the prezygapophyses slightly widens posteriorly in front of the neural spine to form a



TEXT-FIG. 5. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Anterior dorsal vertebrae. A–B, first dorsal vertebra, MPEF-PV 1676, in left lateral (A) and ventral (B) views. C–E, second(?) dorsal vertebra, MPEF-PV 1697, in left lateral (C), right lateral (D) and posterior (E) views. F–H, anterior dorsal vertebra, MPEF-PV 1705, in left lateral (F), anterior (G) and dorsal (H, stereopair) views. Abbreviations as in Text-figure 4 and: f, ‘foramen’ opening onto the neural canal posterior to the hypantrum; hp, hypantrum; poz, postzygapophysis. Scale bars represent 50 mm.

rounded dorsal foramen opening in the neural canal (Text-fig. 5H). The presence of this rounded foramen might be another autapomorphy of the new taxon, although the lack of detailed descriptions or dorsal views of theropod dorsal vertebrae make it difficult to confirm this.

The postzygapophyses are not preserved, nor is the neural spine. At the base of the broken postzygapophyses, the poster-

ior rim of a lateral facet on the lateral side of the neural arch is preserved and offset from the more anterior part of the lateral side of the neural arch by a well-developed step. The base of the neural spine lies on the posterior half of the centrum and exhibits stout spinoprezygapophyseal lamina anteriorly, with a well-developed, very deep longitudinal groove between them.



TEXT-FIG. 6. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Mid-dorsal vertebrae. A, MPEF-PV 1677, left lateral view. B, MPEF-PV 1678, left(?) lateral view. C–D, left transverse process and postzygapophysis MPEF-PV 1679 in posterior (C) and dorsal (D) views. Abbreviations as in Text-figure 4 and: pn, pneumatic cavity in the interior of the centrum. Scale bars represent 50 mm.

Apart from these anterior dorsal vertebrae, an isolated left transverse process, including the postzygapophysis, is also preserved (MPEF-PV 1679; Text-fig. 6C–D). The transverse process consists of a thin horizontal lamina that is supported ventrally by a robust ridge (most probably the prolongation of the posterior centrodiapophyseal lamina), which is placed slightly posterior to the middle of the process. Distally, this ridge expands and merges with the horizontal lamina to form a slightly ventrally facing, triangular articular facet for the tuberculum of the rib. The postzygapophysis is broadly rectangular in shape, but relatively less broad transversely than in the last cervical or the probable second dorsal. As in the latter, both the medial and the lateral edges of the articular facet of the postzygapophysis are slightly flexed ventrally (Text-fig. 6C). A well-developed epiphysis is present, but it is lower than in the second dorsal and does not overhang the postzygapophysis posteriorly (Text-fig. 6C–D). In its posteriormost part, the ridge forming the epiphysis also flexes laterally.

Two mid-dorsal vertebrae (MPEF-PV 1677 and 1678) are represented mainly by their damaged centra (Text-fig. 6A–B). MPEF-PV 1677 has a slender, ventrally rounded centrum. A pleurocoel is absent, but there seems to be an internal cavity ventrally, as indicated by a matrix infill in the broken anteroventral part of the centrum (Text-fig. 6A). The parapophysis is not preserved and thus was most probably placed entirely on the neural arch. The broken base of a robust, anterodorsally inclined posterior centrodiapophyseal lamina is present, as is the trace of an anteriorly placed, almost vertical lamina. This lamina might represent the anterior centroparapophyseal lamina, because it is placed too far anteriorly and not inclined enough to represent the anterior centrodiapophyseal lamina. Thus, as is usual in the mid-dorsal vertebrae, no true anterior centrodiapophyseal lamina is present.

The second mid-dorsal is represented by the ventral half of a slightly more massive, ventrally rounded centrum that exhibits a pronounced constriction between the articular facets (Text-fig. 6B).

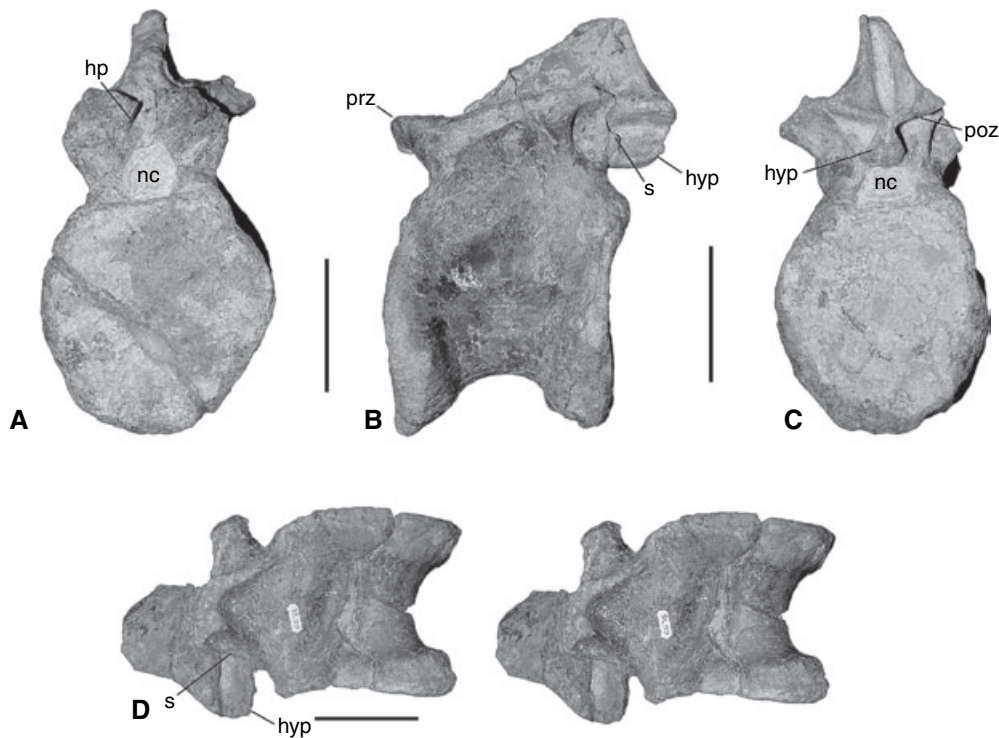
The remaining two dorsal vertebrae are posterior dorsals, though probably not the last elements in the dorsal vertebral column (MPEF-PV 1680 and 1700). They have massive, broadly rounded, platycoelous centra that are strongly constricted

between the articular surfaces (Text-fig. 7). Pleurocoels are absent, but a well-developed, though superficial, pleurocentral depression is present in the dorsal part of the centra. A short, but very robust posterior centrodiapophyseal lamina, which originates from the lateral wall of the neural canal rather than from the dorsal rim of the centrum, supports the transverse process ventrally; the processes themselves are missing on both sides in both vertebrae. In MPEF-PV 1700, the more anterior element, the parapophysis, is placed at the anterior rim of the neural arch, just below the prezygapophysis (Text-fig. 7B). Thus, a short and steeply inclined anterior centroparapophyseal lamina and a much more horizontal paradiapophyseal lamina are present in this vertebra. The latter merges rapidly posteriorly with the very short and poorly developed prezygodiapophyseal lamina. In MPEF-PV 1680, no parapophysis is present on the neural arch, and a stout, posterodorsally inclined anterior centrodiapophyseal lamina is found (Text-fig. 7D). As in the anterior vertebra, the prezygodiapophyseal lamina is short and low, but slightly better defined as the angle between it and the anterior centrodiapophyseal lamina is greater.

Posteriorly, no postzygapodiapophyseal lamina is present on either of the vertebrae, but there is a notch between the laterally expanded articular surfaces of the postzygapophyses and the bases of the transverse processes.

The prezygapophyses are small, short processes that overhang the centrum only marginally anteriorly. The articular surfaces are slightly longer than broad and inclined at an angle of approximately 20 degrees. The prezygapophyses are very narrowly spaced and enclose a well-developed hypantrum, whose small, elongate articular facets stand at an angle of slightly more than 90 degrees to the articular surfaces of the zygapophyses (Text-fig. 7A). As in the more anterior vertebra, the gap between the prezygapophyses widens posteriorly to form a nearly round fenestra into the neural canal just in front of the base of the neural spine.

The postzygapophyses are roughly triangular in outline and taper laterally. Their inclination corresponds to that of the prezygapophyses, and a well-developed hyposphene is present (Text-fig. 7C). It gradually expands ventrally and is thus triangular in posterior outline. A slight median ventral ridge seems to



TEXT-FIG. 7. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Posterior dorsal vertebrae. A–C, MPEF-PV 1700 in anterior (A), left lateral (B) and posterior (C) views. D, MPEF-PV 1680, right lateral view (stereopair). Abbreviations as in Text-figures 4–5 and: hyp, hyposphene; s, step-like ridge, bordering the hypantrum facet anteriorly. Scale bars represent 50 mm.

be present below this expansion in MPEF-PV 1700, and a vertical groove is present on the posterior surface of the hyposphene in MPEF-PV 1680; this area is damaged in the former vertebra. The articular surface of the hyposphene is bordered anteriorly by a short, but robust, step-like ridge that runs from the dorsal margin of the neural canal anterodorsally to the posterior base of the transverse process.

Well-developed spinopostzygapophyseal lamina expand from the dorsal surface of the postzygapophyses onto the neural spine and form the posterolateral borders of the latter. Between these laminae, a deep depression is present on the posterior base of the neural spine. The spine is damaged in both vertebrae; it was obviously higher than long and placed over the posterior half of the centrum. Anteriorly, there is a slight depression at the base of the spine, but the spinoprezygapophyseal laminae are only poorly developed.

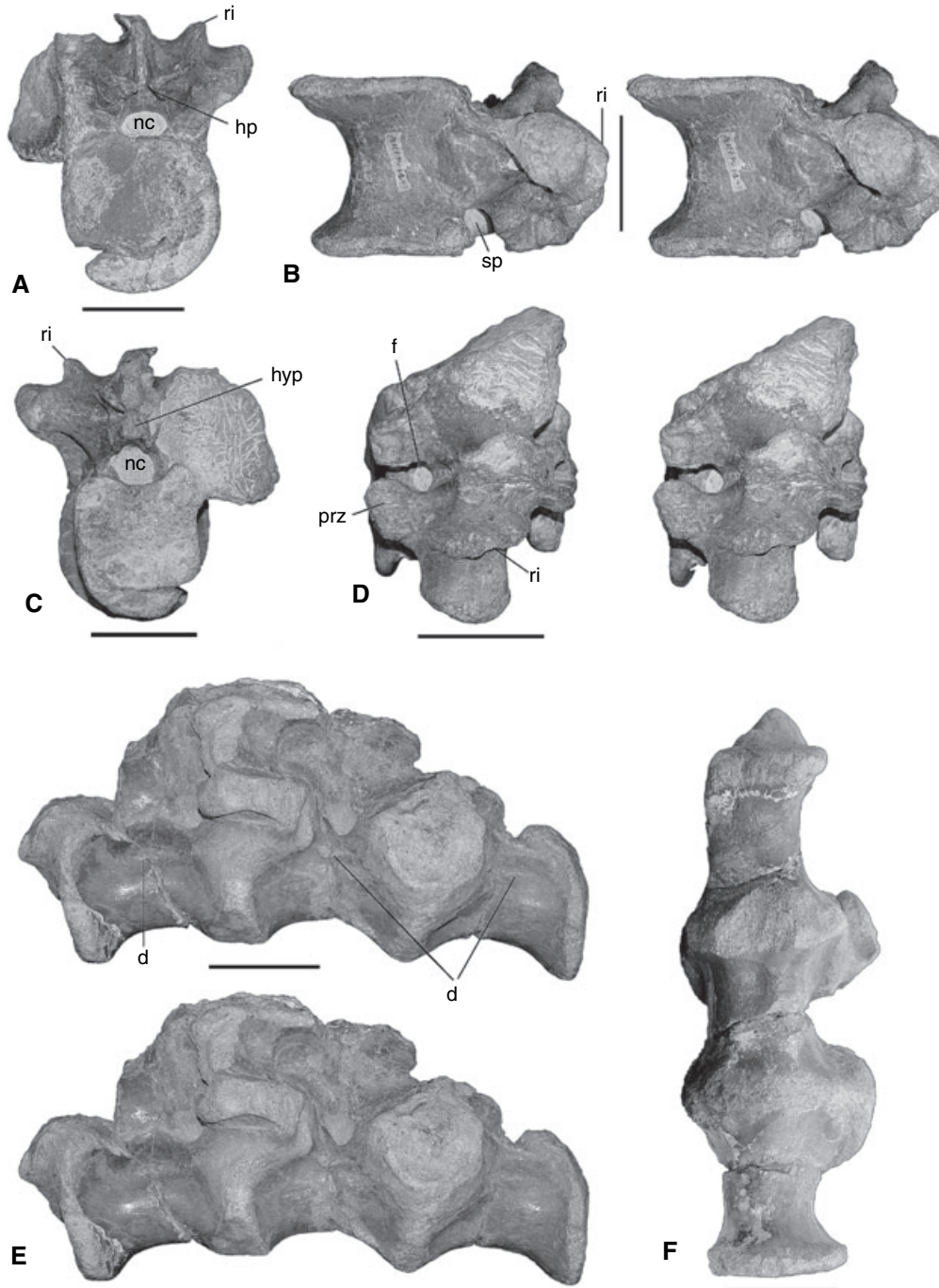
Sacral vertebrae. Four sacral vertebrae are preserved: an isolated first vertebra, and fused second to fourth vertebrae. Given the morphology of the vertebrae, and comparisons with other theropods, the total number of sacral vertebrae was at least five. That only three of these vertebrae are fused indicates that this individual represents a juvenile or subadult.

The centrum of the first sacral vertebra (MPEF-PV 1701) is generally similar to that of the posterior dorsals (Text-fig. 8A–D). It is broadly rounded ventrally, strongly constricted between the articular ends, and exhibits only a weakly developed pleuro-

central depression. A small, rounded lateral facet is present on the posterodorsal rim of the lateral side of the centrum, where the rib of the second sacral slightly overlapped the centrum of the first (Text-fig. 8B). The posterior articular surface is notably smaller than the anterior one.

The neural arch has a short and very massive transverse process that is placed on the anterior half of the centrum, and buttressed below by a very strongly developed anterior centrodiapophyseal lamina and a much weaker posterior centrodiapophyseal lamina. As in the posterior dorsals, the latter does not extend all the way to the centrum, but originates from the lateral wall of the neural canal. The infradiapophyseal fossa is small but deep, and elongated-oval in shape (Text-fig. 8A–B). The prezygodiapophyseal lamina is very short but massive, and the infraprezygapophyseal fossa is small, triangular and superficial. On the dorsal surface of the transverse process, a high, slightly dorsolaterally inclined ridge is present between the posterolateral corner of the prezygapophysis and the anterolateral edge of the postzygapophysis (Text-fig. 8A–B, D), thus obliterating the postzygodiapophyseal lamina. The infrapostzygapophyseal fossa is large, but only moderately deep.

The prezygapophyses are generally similar to those of the posterior dorsals, but slightly broader than long. Their lateral border flexes slightly dorsally, so that the articular surface is very slightly concave transversely. A well-developed hypantrum is present. As in the dorsal vertebrae, a pronounced round dorsal fenestra is present on the midline behind the hypantrum, just in



TEXT-FIG. 8. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Sacral vertebrae. A–D, sacral 1, MPEF-PV 1701, in anterior (A), left lateral (B, stereopair), posterior (C) and dorsal (D, stereopairs; anterior is to the left) views. E–F, fused sacra 2–4, MPEF-PV 1681, in left lateral (E, stereopair) and ventral (F, anterior is to the top) views. Abbreviations as in Text-figures 4–7 and: ri, dorsal ridge on the transverse process; sp, opening for the exit of the spinal nerve. Scale bars represent 50 mm.

front of the base of the neural spine (Text-fig. 8D). The postzygapophyses are identical in shape to those of the posterior dorsals, but relatively smaller (Text-fig. 8C). A robust hypophyseal process is present, with a well-developed oblique ridge bordering the articular surface of the hypantrum anteroventrally, as in the poster-

ior dorsals. Below the hypophyseal process, a large, rounded notch, the intervertebral foramen, is present in the posterior lateral wall of the neural canal for the exit of a spinal nerve.

The neural spine is broken. It was anteroposteriorly short, with a nearly vertical anterior border, weakly developed

spinoprezygapophyseal lamina and only moderately developed spinopostzygapophyseal lamina.

The vertebral centra and parts of the fused neural arches of the second and third sacral are preserved from the fused second to fourth sacral unit (MPEF-PV 1681). These three fused sacrals form a slightly arched structure (Text-fig. 8E–F). The bodies of the centra, especially those of the second and third sacrals, are massive and considerably broader than that of the first. The anterior articular surface of the second sacral and the posterior articular surface of the fourth are flat. The borders between these three vertebrae are marked by well-developed swellings, but no junction between them is visible. The ventral surfaces of the second and third sacrals are flattened, with a very shallow groove being present in the anterior half of the third (Text-fig. 8F). The fourth sacral again has a ventrally broadly rounded centrum. Laterally, small but deep and well-defined pleurocentral depressions are present on the dorsal halves of the centra (Text-fig. 8E). The depression is largest on the second sacral and smallest, but more sharply defined, on the third. On the second sacral, the attachment of the rib seems to extend onto the anterodorsal end of the centrum, although this region is too strongly damaged to determine its detailed structure. The transverse process and its laminae were restricted to the anterior half of the neural arch, as no laminae are present on the preserved posterior part. The neural arch of this vertebra is fused to that of the third sacral without any visible suture. As in the first sacral, and also the third and fourth, a large, round opening is present in the neural arch posteriorly. From this opening, a broad groove runs posterolaterally and very slightly ventrally over the anteroventral part of the attachment of the third sacral rib. The latter attachment is very massive and is partially formed by the posterodorsal part of the second sacral centrum, although most of this attachment occupies the anterodorsal part of the centrum and the anterior half of the neural arch of the third sacral vertebra. The attachment consists of a broad, ventral horizontal part and an anteriorly placed, slightly more slender vertical part that led to the broken transverse process. Above the horizontal part, and behind the vertical part, a small, slightly diverging, robust lamina is present. Behind this lamina, a large depression is found on the lateral side of the neural arch; it leads posteroventrally to the opening for the spinal nerve. Above this opening, a slight lateral swelling is present on the neural arch.

The attachment for the fourth sacral rib is very massive and almost round in outline. It is formed in approximately equal parts by the posterior third of the third sacral vertebra, and the anterior quarter of the fourth and extends below the mid-height of the centrum.

Caudal vertebrae. Three caudal vertebrae are known: an anterior caudal, an anterior mid-caudal and a distal caudal.

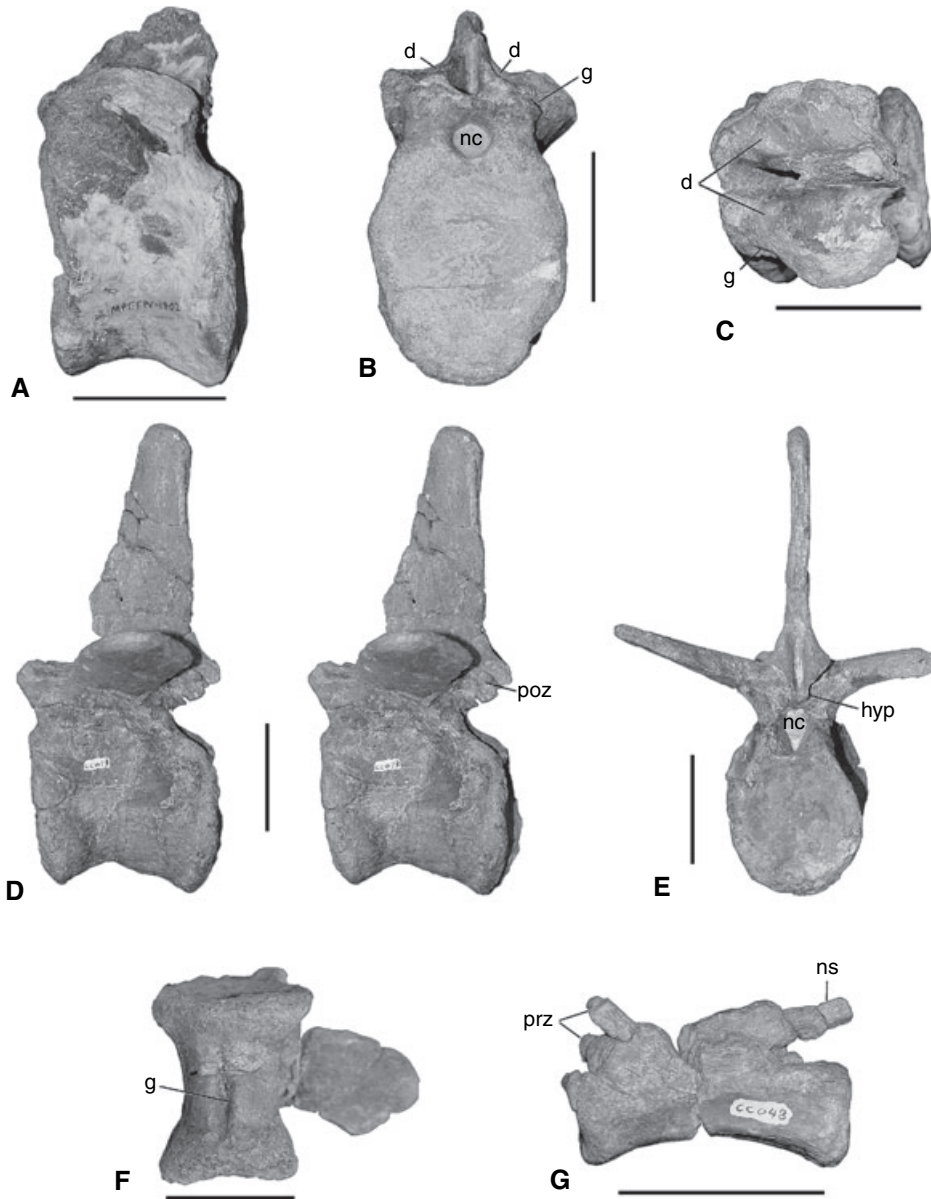
The anterior caudal vertebra (MPEF-PV 1702) has a relatively short and high centrum (Text-fig. 9A–C), more so than the posterior dorsals or the anterior mid-caudal. The articular ends are oval in outline and slightly offset from each other, with the anterior end being situated slightly higher than the posterior one. As in most theropods, the anterior articular surface of this vertebra is slightly more concave than the posterior one. The ventral surface of the centrum is set off from the lateral sides by rounded,

but notable edges. No ventral groove is present and true chevron facets are absent, although the ventralmost part of the posterior articular surface flexes slightly anteroventrally. A small, oval depression is found on the posterodorsal side of the centrum.

The neural arch is dominated by the massive bases of the broken transverse processes. Not even rudimentary centrodiapophyseal laminae are present, and the transverse processes, which were dorsolaterally and slightly posteriorly directed, are broadly oval in cross-section at their bases. On both sides, a well-developed, narrow horizontal groove is found just anterior to and extending onto the anterior base of the transverse process (Text-fig. 9B–C). Two small foramina are situated in this groove on the right side, and at least one small foramen is present in the less well-preserved left side. Pre- and postzygapophyses are missing. Robust, but low spinoprezygapophyseal laminae are present anterior to the neural spine. They enclose a very deep recess anterior to the spine, which in its deepest part exhibits a large foramen on either side that might lead into cavities within the neural arch (Text-fig. 9B). Small, shallow, triangular depressions are present on the dorsal surface of the neural arch between the spinoprezygapophyseal lamina and the bases of the transverse processes (Text-fig. 9C). Larger, oval depressions are also present on the posterior surface of the neural arch, just dorsolateral to the neural canal. The latter is notably smaller than in the posterior dorsals, with a round outline anteriorly, and a triangular shape posteriorly. The neural spine is missing.

The anterior mid-caudal (MPEF-PV 1682) is one of the most complete axial elements found (Text-fig. 9D–F), as it includes almost complete transverse processes and a complete neural spine; only the prezygapophyses are missing. The centrum is more elongate than in the anterior caudal, but shows a similar offset of the articular surfaces, and a more strongly concave anterior than posterior articular surface. Chevron facets are present posteriorly, but poorly developed. A narrow but deep ventral groove is present on the ventral surface (Text-fig. 9F). Very shallow pleurocentral depressions are present on the dorsal part of the lateral side of the centrum.

On the neural arch, the transverse processes are prominent and extend over most of its length, but they are less massive than in the more anterior vertebra. The transverse processes are mainly laterally and only slightly dorsally and posteriorly directed. They are shorter than the centrum and expand slightly distally. As in the more anterior vertebra, centrodiapophyseal laminae are not present, although a slight swelling is developed in the course of the posterior centrodiapophyseal lamina. Between the base of the transverse process and the weakly developed spinoprezygapophyseal lamina, a small, triangular depression is present on the anterolateral dorsal surface of the neural arch, very similar to the situation in MPEF-PV 1702. A further, very shallow depression is found on the dorsal side of the base of the transverse process and is confluent with a slight depression on the lateral side of the base of the neural spine, which is bordered posterodorsally by a slightly elevated, curved ridge. A deep, elongate recess is present anteriorly between the spinoprezygapophyseal lamina at the base of the neural spine, but does not extend dorsally onto the anterior side of the spine further than its lowermost fifth. The postzygapophyses are placed below the posterior base of the neural spine. They are relatively small,



TEXT-FIG. 9. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Caudal vertebrae. A–C, anterior caudal vertebra, MPEF-PV 1702, in left lateral (A), anterior (B) and dorsal (C) views. D–F, mid-caudal vertebra, MPEF-PV 1682, in left lateral (D, stereopair), posterior (E) and ventral (F; anterior is to the top) views. G, posterior caudal vertebra, MPEF-PV 1683, in left lateral view. Abbreviations as in Text-figures 4–8 and: g, groove; ns, neural spine. In G, prz indicates the broken attachment of the prezygapophysis. Scale bars represent 50 mm.

approximately as broad as long and are steeply inclined at an angle of more than 50 degrees. Medioventrally to the postzygapophyses, a small, slender hyposphene is present (Text-fig. 9E). A deep recess is found between the postzygapophyses, but does not extend far onto the neural spine, so that the spinopostzygapophyseal laminae are short. The neural canal is round in outline anteriorly and triangular posteriorly, as in the more anterior caudal.

The neural spine is high and vertical, not posteriorly inclined as in most theropods. It seems to expand slightly anteroposte-

riorly in its lowermost quarter and then tapers gradually towards the tip. Only posteriorly is a weak, dorsally placed medial ridge developed for the attachment of the interspinal ligaments.

The final vertebra preserved (MPEF-PV 1683) is a posterior caudal (Text-fig. 9G). The centrum is low, elongate and approximately hexagonal in cross-section. Thus, a well-developed ridge is present along the side of the centrum, just dorsal to the mid-height, and the ventral surface is offset from the sides by pronounced edges. A very shallow longitudinal groove is present

ventrally. As in the more anterior vertebrae, the posterior articular surface is offset ventrally from the anterior facet. Chevron facets are weakly developed. The neural arch is low and extends over almost the whole length of the centrum. The prezygapophyses are broken off, but their high, broad attachments indicate that they were considerably elongated, as in most theropods. The attachments are well separated and diverge slightly, so that a small, triangular, anteriorly opening flat area is present on the anterior roof of the neural arch. The neural spine is slender, elongate and inclined posteriorly at an angle of approximately 60 degrees, overhanging the centrum posteriorly. A weak longitudinal groove is developed in its dorsal surface. On the lateral side of the posterior half of the neural arch, a slight, anteriorly narrowing depression is present, probably indicating the overlap of the prezygapophyses of the following vertebra.

For measurements of all vertebrae, see Table 1.

Dorsal ribs and chevrons. Only fragments of two dorsal ribs (MPEF-PV 1684 and 1685) and a partial chevron (MPEF-PV 1703) are preserved. The rib fragments consist of parts of the proximal shaft (Text-fig. 10A) and are rather uninformative. The proximal shaft is L-shaped in cross-section, with a plate-like, posteriorly tapering lateral part and a more massive, medially rounded medial part. No internal cavities are present in the ribs.

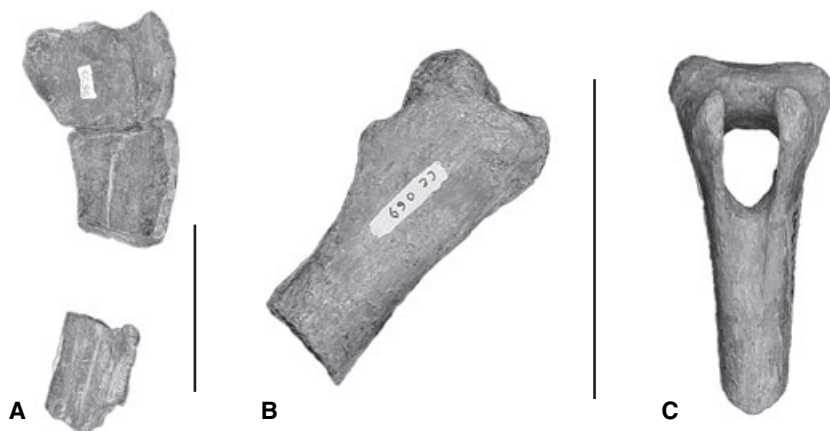
The chevron (Text-fig. 10B–C) is probably derived from the mid-caudal series. Proximally, it has a well-developed, anteroposteriorly short but broad articular surface. This surface has anterodorsal and posterodorsal facets and is strongly concave transversely, forming a bridge over the relatively large, oval haemal canal. The two proximal branches of the body of the chevron overhang the proximal articular surface and thus give the impression of well-developed anterior and posterior processes proximally, with the anterior being slightly bigger than the posterior. The two branches unite below the haemal canal and form a slender and rather massive chevron shaft, which is inclined posteroventrally at an angle of approximately 45 degrees relative to the long axis of the vertebral column. Both anteriorly and posteriorly, a shallow groove runs distally from the haemal canal, but seems to persist further on the posterior surface. The distal end of the chevron is broken, so it is not possible to determine whether it was expanded.

Pelvic girdle. Some fragments of the ilium, the proximal part of the right pubis, a fragment of the shaft of the left pubis and a partial left ischium are preserved.

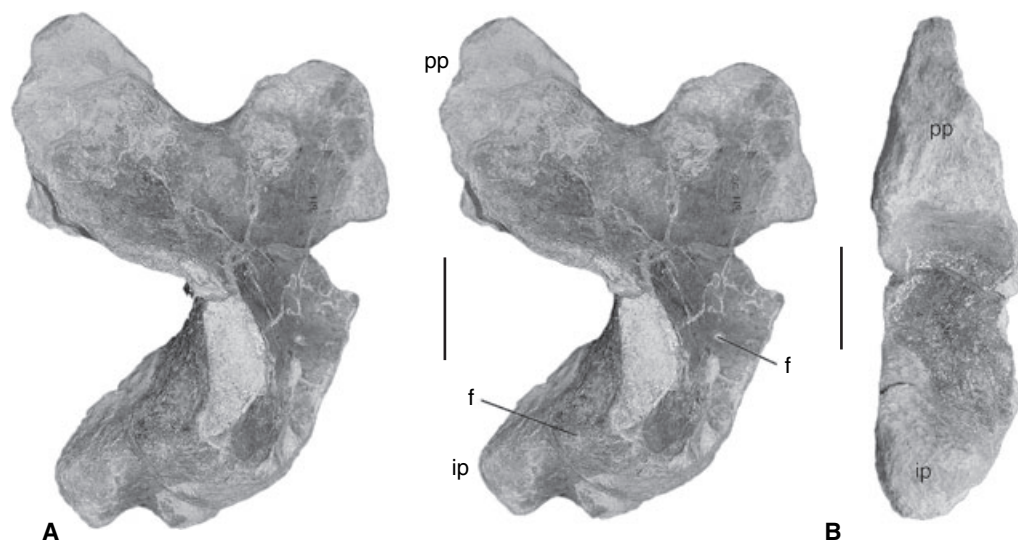
The most informative part of the ilium is the acetabular border of the left element (MPEF-PV 1687; Text-fig. 11). The acetabular width is approximately 110 mm. The pubic peduncle of the ilium is considerably longer anteroposteriorly (c. 96 mm) than the ischial peduncle (c. 38 mm) and is triangular in ventral outline (Text-fig. 11B), with the width of the acetabular border at the articular facet for the pubis being approximately three-fifths of the anteroposterior length of the peduncle. The ischial peduncle is broader transversely than long anteroposteriorly and terminates in a convex articular facet. A supraacetabular crest was present anterior and dorsal to the acetabulum, but is badly damaged. It terminates above the ischial peduncle and is not confluent with the lateral brevis shelf, as is the case in some basal theropods. Anteriorly, the broken base of the preacetabular process of the ilium is situated dorsal to the straight anterior margin of the pubic peduncle. A small nutrient foramen, which in most theropods is placed in the lateroventral base of this process, is present on the medioventral side. Another, larger foramen is present above the supraacetabular rim, situated approximately above acetabular mid-length, in the anterior side of what seems to have been a swelling on the lateral iliac blade above the acetabulum (Text-fig. 11A). A third, slightly smaller foramen is found on the posterolateral side of the dorsal part of the ischial peduncle. The attachment of the medial brevis shelf extends ventrally to approximately half the height of the ischial peduncle on the posterior side of the latter.

Two other fragments might represent parts of the ilium, although this cannot be ascertained with certainty. MPEF-PV 1686 may be a fragment of the preacetabular blade of the right ilium, and MPEF-PV 1704 may be part of the brevis shelf of the left ilium.

The right pubis (MPEF-PV 1696) is missing the distal half of the shaft and the pubic boot, but is otherwise well preserved (Text-fig. 12A–C). The pelvis was propubic, although the pubis seems to have been only very slightly anteriorly directed. The articular facet for the ilium is an elongate triangle in outline, wider posteriorly than anteriorly. It is offset from the very short acetabular rim of the pubis by an angle of only 10–15 degrees. The acetabular rim is approximately half as long as the facet for



TEXT-FIG. 10. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. A, proximal fragments of a right dorsal rib, MPEF-PV 1685, posterior view. B–C, proximal part of chevron, MPEF-PV 1703, in right lateral (B) and anterior (C) views. Scale bars represent 50 mm.



TEXT-FIG. 11. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Acetabular rim of left ilium, MPEF-PV 1687. A, lateral view (stereopair; anterior to the top). B, ventral view (anterior to the top). f, foramen; ip, ischial peduncle; pp, pubic peduncle. Scale bars represent 50 mm.

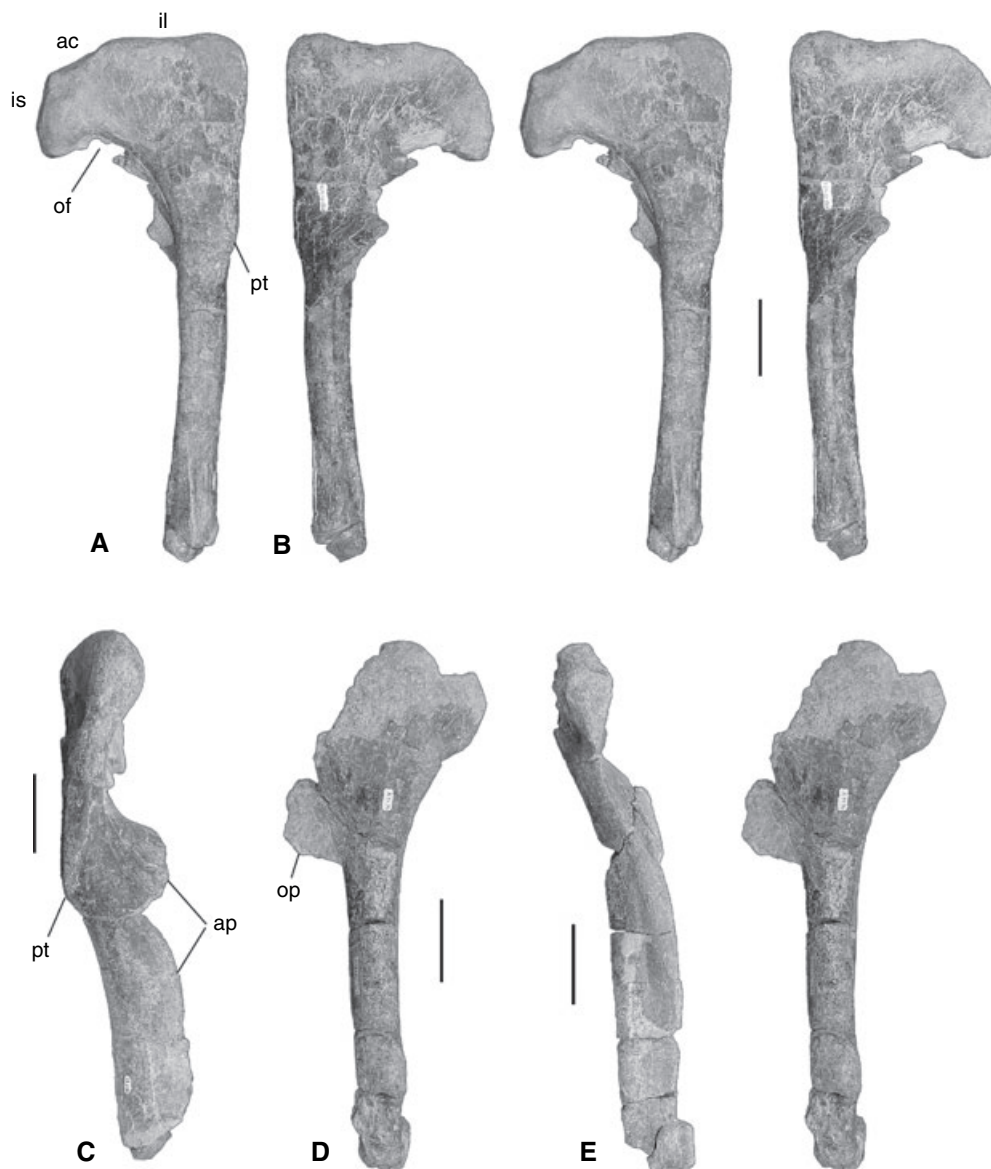
the ilium, but almost as wide as the widest part of the latter, and is very slightly laterally directed. The facet for the ischium is more notably offset from the acetabular rim. It is short and half oval in outline, with a flat medial side and a tapering ventral end. From the widest part of the iliac facet a broad, low swelling extends ventrally, becomes less notable and finally disappears just above the base of the pubic shaft (Text-fig. 12A). The subacetabular plate of the pubis is largely missing, but it was obviously lower than the height of the ischial articulation and pierced dorsally by a small, elongate oval obturator foramen that was completely enclosed by bone. This foramen opens mainly dorsally and is thus almost hidden in lateral view by the overhanging rim of the ischial peduncle (Text-fig. 12A). A few centimetres below the obturator foramen a well-developed flange extends medially from the posteromedial corner of the pubic shaft to form the contact for the other pubis (Text-fig. 12B). Thus, there is not enough space for a ventral expansion of the subacetabular plate that would accommodate a pubic fenestra below the obturator foramen. From its origin at the posteromedial edge of the proximal pubic shaft, the pubic apron rapidly shifts onto the anteromedial edge and extends ventrally along this edge to the distal break (Text-fig. 12B). Thus, whereas the apron is confluent with the anterior surface of the pubic shaft, the posterior side of the latter stands out beyond the apron posteriorly. On the proximal part of the pubic shaft, the pubic tubercle is well developed and extends far distally beyond the subacetabular plate. The tubercle tapers distally, and below its distal end the shaft flexes strongly medially (Text-fig. 12C). A proximal extension of the tubercle, as is present in tyrannosaurs, for example (Hutchinson 2001a), is absent.

The broken fragment of the left pubis reveals the cross-section of the pubis just distal to the pubic tubercle. The cross-section is oval, with an anteromedial lip for the pubic apron. Further distally, the cross-section of the pubic shaft is triangular, with a similar anteromedial lip.

The left ischium (MPEF-PV 1689) is rather poorly preserved and is missing most of the articular processes and the distal end (Text-fig. 12D–E). The proximal end is transversely flattened and notably convex anteroposteriorly. A small, laterally depressed flange is present posteriorly near its proximal end. The shaft is flexed medially until the beginning of the facet for the medial articulation between the two ischia, which is placed some 120 mm below the proximal end. This articular surface is marked by several well-developed longitudinal ridges and grooves. In this part, the shaft is broader transversely than long antero-posteriorly and approximately triangular to half oval in cross-section, with a flattened medial side. The anterior side of the shaft is transversely convex, and a slight longitudinal depression is found on its posterior side. Although the obturator process is partially broken, it was obviously rather large and it seems that it had a small incision at its distal end between the process and the ischial shaft, as in many basal theropods. It cannot be determined whether the obturator process was offset from the pubic peduncle.

Hindlimb. Both femora, the proximal end of the left tibia, a left metatarsal IV and a partial pedal ungual are preserved.

The femora (MPEF-PV 1690, 1691) are rather poorly preserved and both lack the proximal end (Text-fig. 13A–H). The shaft is moderately curved in lateral view (Text-fig. 13E). The better preserved left femur shows the base of the lesser trochanter at its proximal break on the anterolateral side. The base is strongly developed and extends anteroproximally, indicating that the lesser trochanter was prominent and probably wing-like. Unfortunately, not enough of the proximal end is preserved to deduce the orientation of the femoral head. The fourth trochanter is placed on the posteromedial edge of the bone, just below the base of the lesser trochanter. It is developed as a low, but stout ridge, with a slight depression on its medial side (Text-fig. 13E–F). Posteriorly, a small, low ridge extends proximolaterally.

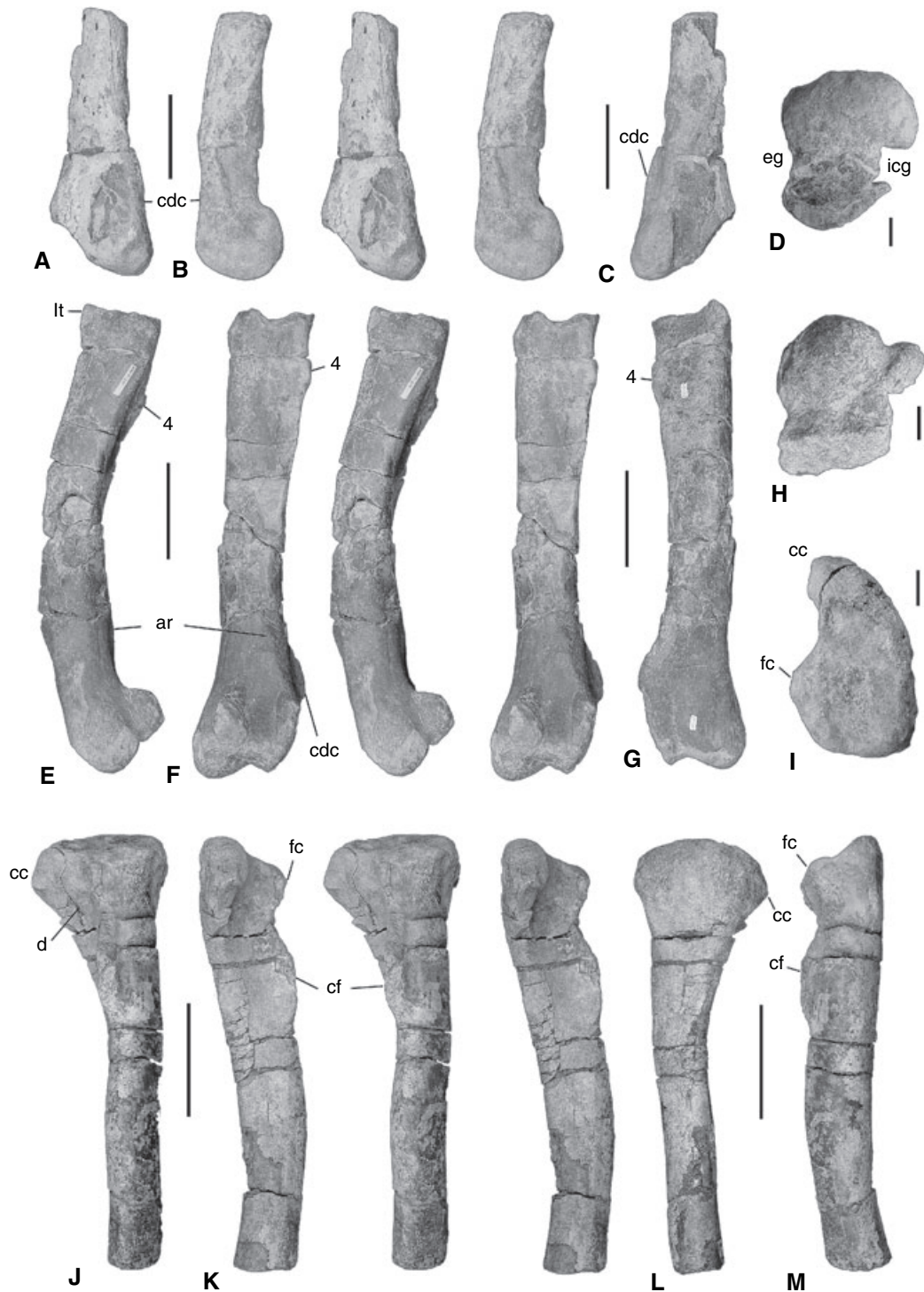


TEXT-FIG. 12. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Pelvic elements. A–C, right pubis, MPEF-PV 1696, in lateral (A, stereopair), medial (B, stereopair) and anterior (C) views. D–E, left ischium, MPEF-PV 1689, in lateral (D, stereopair) and posterior (E) views. ac, acetabular rim; ap, pubic apron; il, iliac peduncle; is, ischial peduncle; of, obturator foramen; op, obturator process; pt, pubic tubercle. Scale bars represent 50 mm.

ally from approximately the mid-height of this trochanter. Below the fourth trochanter, the femoral shaft is triangular in cross-section, with a pronounced anterolateral edge and a flattened posterior side. Just above the distal condyles, the adductor ridge (Hutchinson 2001b) is developed on the posterior side as a broadly rounded, low and slightly rugose ridge that extends from the distal posteromedial edge proximolaterally (Text-fig. 13F) and bifurcates proximally in the right femur. The distal condyles are strongly developed and well rounded distally. The medial condyle is more massive than the lateral and is confluent with the distal articular surface. In contrast, the slender lateral condyle is slightly set off from both the lateral border of the femur and the distal articular surface. A small laterodistal groove

is present between the condyle and the almost ball-shaped articular surface (Text-fig. 13H). Anteriorly, the extensor groove is only weakly developed and a large depression is present on the anteromedial side of the distal end (Text-fig. 13A). This depression is bound medially by a stout ridge, which widens distally in medial view and finally expands onto the medial side of the medial distal condyle (Text-fig. 13B). As is usual in theropods, the femur is hollow, but is comparatively thick-walled.

The holotype tibia is missing the distal end (Text-fig. 13I–M). The bone has a pronounced S-curve in anterior view, with the shaft first flexing outwards from the proximal end and then, more distally, inwards again (Text-fig. 13K). The lateral side of the proximal articular surface is distinctly lower than the medial



TEXT-FIG. 13. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Hindlimb elements. A–D, distal end of right femur, MPEF-PV 1691, in anterior (A, stereopair), medial (B, stereopair), posterior (C) and distal (D) views. E–H, left femur, MPEF-PV 1690, in lateral (E, stereopair), posterior (F, stereopair), anterior (G) and distal (H) views. I–M, left tibia, MPEF-PV 1672, holotype, in proximal (I), lateral (J, stereopair), anterior (K, stereopair), medial (L), and posterior (M) views. 4, fourth trochanter; ar, adductor ridge; cc, cnemial crest; cdc, craniomedial distal crest; cf, fibular crest; d, depression; eg, extensor groove; fc, fibular condyle; icg, intercondylar groove. Scale bars represent 100 mm (A–C, E–G, J–M) and 20 mm (D, H–I).

side, so that the latter forms a broad, raised medial ridge. A slight ridge is also present on the lateral side of the fibular condyle, so that the central part of the articular surface forms a marked depression. The cnemial crest is only moderately developed and rounded anteriorly (Text-fig. 13J, L), rather than the rectangular and proximally directed structure seen in most basal tetanurans. A low, triangular ridge is found proximally near the anterior end of the crest on its lateral side. Below this ridge, a marked depression is present on the lateral side of the distal base of the cnemial crest. The fibular condyle is roughly rectangular and not separated posteriorly from the medial part of the proximal end by a deep notch (Text-fig. 13I), unlike the situation in the vast majority of theropods. The lateral ridge for the attachment of the fibula is placed proximally, but clearly offset from the proximal end. It is developed as a stout semi-oval ridge that is slightly inclined anteriorly. Posterior to the distal end of this ridge, a large foramen is found on the lateral side of the bone. Below the ridge, the shaft of the tibia is semicircular to weakly triangular in outline, with a flattened anterior side. More distally, the cross-section of the shaft becomes broadly oval. As with the femur, the tibia is hollow, but rather thick-walled.

The left metatarsal IV (MPEF-PV 1692) is completely preserved (Text-fig. 14A–F) and 242 mm long. The bone is slender and slightly flexed laterally, so that the distal articular end diverges laterally from the proximal. The outline of the proximal articular surface is subquadrangular with rounded edges and a long, tongue-like posteromedial process that is first more medially directed and then flexes strongly posteriorly in its medial part. The anterior part of the articular surface is markedly depressed below the posterior and lateral rims (Text-fig. 14E).

Anterolaterally, the proximal articular surface overhangs the shaft of the bone, whereas medially a slightly anteriorly directed, transverse concave facet for the contact with metatarsal III is present. The posterior side is approximately flat proximally, with

a small ridge developed on the posterolateral edge of the bone. This ridge borders a short, weakly developed groove that extends from the posterolateral corner of the proximal end mediolaterally. Medially, the lip of the posteromedial process of the articular surface stands out posteriorly. Below the proximal articular end, the cross-section of the metatarsal shaft is suboval, with a flattened posterior side, and slightly deeper than broad. Just below the mid-length of the bone, an elongate semilunate muscle attachment is present on the posterolateral side of the shaft. This attachment is well defined and its medial border forms a raised ridge on the posterior side distally.

The distal articular end is strongly expanded anteroposteriorly but less so transversely. The articular facet is well rounded and extends over an angle of almost 180 degrees. It is also slightly convex transversely and is subdivided posteriorly into two small flanges. The smaller lateral flange expands posterolaterally and thus forms a posterolateral lip of the articular end. A small, shallow, collateral ligament pit is present medially, and a shallow groove extends from this pit to approximately the proximal end of the articular facet. Laterally, no ligament pit is developed, but a small swelling is found just above the posteroventral extension of the articular surface. Dorsally and dorsolaterally, the articular facet is strongly offset from the shaft of the metatarsal by a pronounced step (Text-fig. 14A, C).

Only the proximal part of a single pedal ungual is preserved (MPEF-PV 1693; Text-fig. 14G). It has a broad and almost symmetrical proximal articular surface, which is subdivided by a low median ridge. On the ventral side, the flexor tubercle is robust, but not very strongly expanded ventrally. The claw grooves on the sides of the ungual are slightly asymmetrical, with the left groove being placed slightly higher than the right, and do not bifurcate proximally, as in some theropods. At the distal break, the ungual is triangular in cross-section, with a wide ventral surface.



TEXT-FIG. 14. *Condorraptor currumili* gen. et sp. nov., Cañadón Asfalto Formation, Chubut, Argentina. Hindlimb elements. A–F, left metatarsal IV, MPEF-PV 1692, in lateral (A), anterior (B), medial (C), posterior (D), proximal (E, stereopair) and distal (F) views. G, pedal ungual, MPEF-PV 1693, lateral view. Scale bars represent 100 mm (A–D) and 20 mm (E–G).

DISCUSSION

The phylogenetic position of Condorraptor

Several characters of *Condorraptor* help to clarify its systematic position within recently published schemes of theropod phylogeny (Holtz 2000; Carrano *et al.* 2002; Rauhut 2003*b*). The new taxon can be shown to be a tetanuran theropod on the basis of the following characters:

1. One pair of pleurocoels in the cervical vertebrae (Rauhut 2003*b*: character 89). As discussed by Britt (1993), the presence of two pairs of pleurocoels in the cervical vertebrae seems to be the plesiomorphic character state within theropods, and the reduction of the posterior pleurocoels represents a synapomorphy of tetanurans. This hypothesis was confirmed by the phylogenetic analysis of Rauhut (2003*b*). In *Condorraptor*, only one pair of pleurocoels is present in the cervical and anterior dorsal vertebrae, situated posterior to the parapophyses. It might be noted that in some vertebrae, most notably the middle cervical MPEF-PV 1674, a rudimentary second, posteriorly placed pleurocoel seems to be present, further supporting the interpretation that the posterior pleurocoel was primitively present and is secondarily reduced in tetanurans.
2. Prezygapophyses of the anterior cervical vertebrae situated entirely lateral to the neural canal (Rauhut 2003*b*: character 99). As first noted by Makovicky (1995), the anterior cervical prezygapophyses are enlarged and situated lateral to the neural canal in tetanurans. This morphology is seen in the anterior cervical vertebra MPEF-PV 1673.
3. Presence of a pronounced ventral keel in the anterior dorsal vertebrae (Rauhut 2003*b*: character 108). Whereas the posterior cervical and anterior dorsal vertebrae are ventrally rounded or have only a very weakly developed keel in basal theropods, a high, sharp ventral keel is present in tetanurans. This keel is set off from the lateral sides of the vertebra by pronounced ridges that run posteriorly from the parapophyses. This morphology is seen in the last cervical and anterior dorsals of *Condorraptor*.
4. Supraacetabular crest of ilium shelf-like (Carrano *et al.* 2002: character 112). In most basal theropods, including coelophysids, *Dilophosaurus* and ceratosaurs, the supraacetabular crest is large and turns ventrally in its lateral part to overhang the acetabulum. In tetanurans, this crest is comparatively reduced and more shelf-like, without a lateral downturn. Although the lateral end of the supraacetabular crest is broken off in *Condorraptor*, the morphology

of the remaining parts is in accordance with the situation in tetanurans.

5. Iliac–ischial articulation smaller than iliac–pubic articulation (Holtz 2000: character 304). In basal theropods, the pubic peduncle of the ilium is subequal in size to the ischial peduncle, but it is significantly larger than the latter in tetanurans. This is also the case in the ilium of *Condorraptor*. The fact that the pubic peduncle in *Piatnitzkysaurus* (PVL 4073) is relatively shorter than that in the new taxon might therefore indicate that the former is a more basal representative of the Tetanurae (but see Holtz 2000).
6. Pubic peduncle of ilium more developed antero-posteriorly than mediolaterally (Holtz 2000: character 305). This character is linked with the previous one, because the increase in size of the pubic peduncle in tetanurans stems mainly from an antero-posterior enlargement. This character is also present in the ilium of *Condorraptor*.
7. Lateral ridge for contact with the fibula on the tibia offset from proximal end of the tibia (Rauhut 2003*b*: character 206). The presence of a lateral ridge on the tibia for the contact with the fibula is a theropod or neotheropod synapomorphy (Gauthier 1986; Rauhut 2003*b*). In basal theropods, this ridge is proximally placed and becomes gradually lower towards the proximal articular end of the bone. In tetanurans, this ridge is more distally placed and clearly offset from the proximal articular end, as is the case in the type tibia of *Condorraptor*.

These characters thus indicate that *Condorraptor currumili* represents a tetanuran theropod. Within Tetanurae, the absence of any synapomorphies (see Holtz 2000; Rauhut 2003*b*) of more derived clades (Coelurosauria, Allosauroidae, Spinosauroidae) and the presence of several plesiomorphic characters (amphi-platycoelous cervical vertebrae; ventral keel in cervical vertebrae present; obturator foramen completely enclosed in bone) indicate that the new taxon is a basal representative of this clade, as might be expected for a Middle Jurassic tetanuran.

Comparison with other Jurassic theropods

Given the fragmentary nature of the material available of *Condorraptor*, a short discussion of the characters distinguishing it from the contemporaneous *Piatnitzkysaurus* from the same formation and other Jurassic theropods is warranted (apart from those listed in the diagnosis).

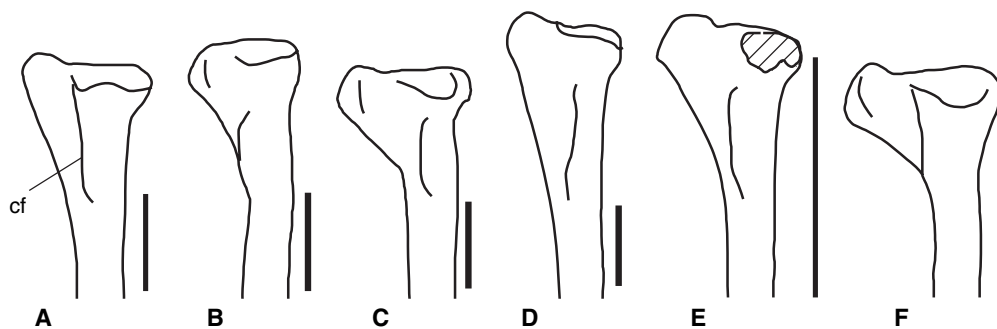
Although the vertebral and hindlimb anatomy of *Piatnitzkysaurus* and *Condorraptor* is similar in general terms, many differences are found when looking in detail. The

most significant of these differences are found in the sacral vertebrae and the tibia. Whereas the infraprezygopophyseal fossa is only shallow and superficial in the first sacral vertebra in *Condorraptor*, it is very deep and tunnel-like in *Piatnitzkysaurus* (PVL 4073, MACN CH 895). Furthermore, in the latter taxon, sacral vertebrae 2 and 3 are ventrally rounded, rather than flattened, and lack deep and well-defined lateral depressions. In the tibia of *Condorraptor*, the cnemial crest is significantly smaller, not anteroproximally directed, and rounded, rather than rectangular in lateral outline (Text-fig. 15). The fibular condyle extends to approximately the same level posteriorly as the medial part of the proximal side, rather than being restricted to the central part of the proximal end, and the tibia has a pronounced S-curve in anterior view, unlike the almost straight bone in *Piatnitzkysaurus*. Further differences from *Piatnitzkysaurus* might also be significant, but more studies of their individual variability within theropods are needed: lack of basally pointing grooves on the tooth enamel at the bases of the denticles; ventral keels in posterior cervicals and anterior dorsals relatively deeper and with more pronounced anteroventral process in the last cervical and first dorsal; angle between iliac peduncle and acetabular margin of pubis smaller and acetabular margin relatively longer; obturator foramen in pubis facing more ventrally than laterally; pubic tubercle considerably more strongly pronounced; considerably greater femoral curvature; metatarsal IV with depressed anteromedial part of the proximal articular surface.

Thus, *Condorraptor* clearly differs from *Piatnitzkysaurus*, and any similarities seen in their general anatomy are due to their similar position within theropod phylogeny and the general uniformity of basal tetanuran postcranial skeletons. Furthermore, considerable interspecific

variation in basal tetanurans seems to occur in the skull (see, e.g. Rauhut 2003b), and more complete remains of both taxa might demonstrate greater anatomical differences than those evident from existing material.

Comparisons with other Jurassic theropods are hampered by the fragmentary nature of *Condorraptor* and many other, especially Middle Jurassic, theropods. However, significant differences are found with basal theropods, including *Syntarsus*, *Dilophosaurus* and neoceratosaurs. In contrast to *Condorraptor*, all of these taxa have two pairs of pleurocoels in the cervical vertebrae and lack the well-developed, deep ventral keels in the posterior cervical and anterior dorsal vertebrae (Gilmore 1920; Janensch 1925; Raath 1969; Welles 1984; Madsen and Welles 2000). The posterior dorsals are relatively more elongate, the supraacetabular crest of the ilium is pendant, the pubis lacks the strongly pronounced pubic tubercle, the fibular crest on the tibia is confluent with the proximal end (Text-fig. 15A, F) and the proximal end of metatarsal IV lacks the posteromedial process. *Condorraptor* shares with basal theropods the slightly arched ventral margin of the sacrum, which was interpreted as a neoceratosaurian synapomorphy by Sereno (1999) and Carrano *et al.* (2002). However, this character is also present in the coelophysid *Syntarsus rhodesiensis* (QG 1; see Raath 1969) and the basal tetanurans *Piatnitzkysaurus* (PVL 4073, MACN CH 895) and ‘*Szechuanosaurus*’ *zigongensis* (Gao 1993), indicating that it might represent a plesiomorphic character within theropods. Likewise, Rowe and Gauthier (1990) noted the presence of a well-developed ventral groove in the caudal vertebrae as a possible ceratosaurian synapomorphy, but ventral grooves are present in the middle and distal caudals of many theropods, including most coelurosaurs. In *Condorraptor*, only the mid-caudal vertebra has a well-developed ventral



TEXT-FIG. 15. Comparison of the proximal ends of left theropod tibiae in lateral view. A, Early Jurassic basal theropod *Dilophosaurus* (based on UCMV V 4214). B, Middle Jurassic basal tetanuran *Condorraptor* gen. nov. C, Middle Jurassic basal tetanuran *Piatnitzkysaurus* (based on PVL 4073). D, Middle Jurassic basal tetanuran *Eustreptospondylus* (based on OUM J 13335). E, Middle Jurassic basal tetanuran *Gasosaurus* (redrawn from Dong and Tang 1985). F, Upper Jurassic ceratosaur *Ceratosaurus* (based on UMNH VP 5278). Drawn to the same shaft width and levelled at the distal end of the fibular crest. cf, fibular crest. Scale bars represent 10 cm.

groove, whereas the anterior caudal exhibits a flattened ventral surface that is offset from the lateral sides by rounded ridges, which is the morphology seen in many basal tetanurans (e.g. *Allosaurus*; Madsen 1976).

Condorraptor differs from most basal tetanurans in the shape and orientation of the cnemial crest of the tibia (Text-fig. 15), which is rectangular and anteroproximally directed in most taxa (e.g. *Allosaurus*, Madsen 1976; *Eustreptospondylus*, OUM J 13335; *Gasosaurus*, Dong and Tang 1985; a tibia referred to *Megalosaurus*, von Huene 1926; *Metriacanthosaurus*, von Huene 1926; *Piatnitzkysaurus*, PVL 4073; *Sinraptor*, Currie and Zhao 1993; *Torvosaurus*, Britt 1991), and the strongly pronounced pubic tubercle. Differences with carnosaurs (*sensu* Rauhut 2003b) further include the strongly opisthocoelous cervical vertebrae in the latter and the ventrally open obturator foramen in most forms. Apart from *Piatnitzkysaurus*, the taxa most similar to *Condorraptor* seem to be the Middle Jurassic theropods *Xuanhanosaurus* and '*Szechuanosaurus*' *zigongensis* from China, which also have amphi-platyan cervical and anterior dorsal vertebrae with well-developed ventral keels (Dong 1984; Gao 1993) and, in the case of '*S.*' *zigongensis*, a slightly arched sacrum and apparently very similar pubis and ischium (based on published drawings and photographs in Gao 1993). However, these similarities are plesiomorphic for tetanurans and thus reflect the similar phylogenetic position of these taxa at the base of Tetanurae (Rauhut 2003b), rather than indicating closer relationships with other tetanurans. *Xuanhanosaurus* differs from *Condorraptor* in the relatively larger pleurocoel and the lack of a depression on the posterolateral aspect of the anterior dorsal vertebra (IVPP V 6729; Dong 1984), but otherwise comparisons are hampered by the lack of overlapping material between the two taxa. '*Szechuanosaurus*' *zigongensis* differs from *Condorraptor* in many details, including the less deep ventral keel in the last cervical vertebra, the anteroposteriorly more elongate dorsal neural spines, and the straight, rather than S-shaped, tibia in anterior view (Gao 1993).

An interesting aspect of the vertebral morphology of *Condorraptor* is the anteroventral process of the ventral keel in the last cervical and first dorsal vertebra. Similar small anteroventral processes are present in these vertebrae in several basal tetanurans, including *Piatnitzkysaurus* (PVL 4073), *Sinraptor* (Currie and Zhao 1993), *Streptospondylus* (Allain 2001) and *Xuanhanosaurus* (Dong 1984). Furthermore, similar, or more pronounced anteroventral processes are present in many maniraptoran coelurosaurs, including dromaeosaurids (Ostrom 1969), troodontids (Rauhut 2003) and oviraptorosaurs (Sues 1997). These processes were considered homologous to the hypapophyses in bird vertebrae and interpreted as a maniraptoran synapomorphy by Gauthier (1986). However, their presence in several basal tetanurans indicates

that they define a more inclusive clade, but are highly variable between different taxa.

Evolutionary and biogeographic aspects

Although any interpretation of the evolutionary and biogeographic significance of this new taxon is hampered by the abysmal theropod fossil record from the Jurassic of the Southern Hemisphere, a few aspects are noteworthy. As a basal tetanuran, *Condorraptor* is an early representative of the theropod lineage that includes the vast majority of Cretaceous and all post-Cretaceous theropods.

The oldest certain representatives of the Tetanurae known currently are *Magnosaurus nethercombensis* and '*Megalosaurus*' *hesperis* from the Aalenian–Bajocian of England (Holtz 2000; Rauhut 2003b). Possible Early Jurassic representatives of this clade are the Antarctic genus *Cryolophosaurus* (Hammer and Hickerson 1994; Sereno *et al.* 1994, 1996) and the Chinese '*Dilophosaurus*' *sinensis* (Hu 1993; Lamanna *et al.* 1998), but more detailed descriptions and phylogenetic analyses of these taxa are needed to establish their tetanuran affinities. The alleged therizinosaur *Eshanosaurus* from the Lower Jurassic of China (Xu *et al.* 2001) might rather represent a prosauropod (Rauhut 2003b). Although it is possible that tetanuran origins reach back to the Early Jurassic or even the Late Triassic, this is not required by several recent phylogenetic analyses that consider the Ceratosauria *sensu* Gauthier (1986) to be a paraphyletic assemblage (Forster 1999; Carrano *et al.* 2002; Rauhut 2003b).

By the Bathonian, basal tetanurans are known from England (e.g. Buckland 1824; Phillips 1871; von Huene 1926; Walker 1964), France (e.g. Eudes-Deslongchamps 1838; Allain 2001, 2002; Allain and Chure 2002) and China (Dong 1984; Dong and Tang 1985; Gao 1993; Zhao and Currie 1993). Tetanuran diversification was already well underway at that time, as indicated by the presence of basal representatives of all major lineages, including the spinosauroid *Eustreptospondylus* and the coelurosaur *Proceratosaurus* from England, and the allosauroid *Monolophosaurus* from China (Sereno 1999; Holtz 2000; Rauhut 2003b). The presence of at least two basal tetanuran taxa in the upper Middle Jurassic of Argentina, *Piatnitzkysaurus* and *Condorraptor*, which apparently were not more closely related to each other than to Laurasian taxa, demonstrates that tetanuran diversification in the Middle Jurassic was global, and no faunal differentiation between the Northern and Southern Hemisphere is evident. Thus, it seems that *Piatnitzkysaurus* and *Condorraptor* are part of a global theropod fauna that was dominated by basal tetanurans during the late Middle Jurassic. However, more material, especially from the Southern Hemisphere, is needed to test this hypothesis.

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NOTE ADDED IN PROOF

Arcucci and Coria (2003) recently published an alleged basal tetanuran, *Zupaysaurus rougieri*, from the Upper Triassic of Argentina. However, this taxon exhibits a unique combination of characters, including several

coelophysoid synapomorphies, and might rather represent a member of the Coelophysoidea (Carrano and Sampson 2004). According to Carrano and Sampson (2004), the oldest known tetanuran might be a fragmentary hindlimb from the Liassic of England.