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rotating and will be rafted away from the EPR axis. There is some evidence that this has happened in the past. A newly discovered trough, which we call the 'extinct rift', located north and east of the IR (Fig. 3a) may represent the northern boundary of such an extinct microplate.

Our new view of the Galapagos triple junction is that of two adjacent counter-rotating microplates distributing the strain around this triple junction. A kinematic solution shows that edge-driven microplate mechanisms can explain the motions of this dual microplate system. If this model is correct, we speculate that it may be applicable to other triple junctions[17,18,20]. In the specific case of the Galapagos triple junction, we suggest that the dual microplate system acts to control the location and configuration of the Hess Deep rift and the stability of the Galapagos triple junction. □

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New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia

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Most of what is known about the evolution of deinonychosaurs (that is, the group of theropods most closely related to birds) is based on discoveries from North America and Asia[1]. Except for *Unenlagia comahuensis*[2,3] and some fragmentary remains from northern Africa[4], no other evidence was available on deinony-chosaurian diversity in Gondwana. Here we report a new, Late Cretaceous member of the clade, *Neuquenraptor argentinus* gen. et sp. nov., representing uncontroversial evidence of a deinonychosaurian theropod in the Southern Hemisphere. The new discovery demonstrates that Cretaceous theropod faunas from the southern continents shared greater similarity with those of the northern landmasses than previously thought. Available evidence suggests that deinonychosaurians were probably distributed worldwide at least by the beginning of the Cretaceous period. The phylogenetic position of the new deinonychosaur, as well as other Patagonian coelurosaurian theropods, is compatible with a vicariance model of diversification for some groups of Gondwanan and Laurasian dinosaurs.

Theropoda Marsh, 1881
Coelurosauria Huene, 1920
Maniraptora Gauthier, 1986
Deinonychosauria Colbert and Russell, 1969
Dromaeosauridae Matthew & Brown, 1922
Neuquenraptor argentinus gen. et sp. nov.

Etymology. *Neuquén*, a province of northwest Patagonia, and *raptor*, meaning robber in Greek; *argentinus*, in reference to Argentina.

Holotype. MCF PVPH 77 (Museo Carmen Funes, Plaza Huincul, Neuquén Province, Argentina) consists of fragments of cervical vertebra, dorsal ribs, haemal arches, left proximal radius, right femur and distal tibia, proximal tarsals, and most of the foot of the left hindlimb. It was discovered serendipitously by P. F. Puerta and F.E.N. in 1996 while digging up the rib cage of a titanosaurid sauropod.

Locality and horizon. Upper Cretaceous (Coniacian[5]), Portezuelo Formation, Sierra del Portezuelo, Neuquén Province, Argentina. Other theropods recorded in this unit are *Unenlagia*[2,3], *Patagony-kus*[6], *Megaraptor*[7] and an undescribed neornithine coracoid.

Diagnosis. A probable dromaeosaurid with the following combination of characters: metatarsal II with lateral expansion over the caudal surface of metatarsal III (autapomorphic); metatarsal III proximally pinched; extensor sulcus on proximal half of metatarsus; distal end of metatarsal III is incipiently ginglymoid (to a lesser degree than other dromaeosaurids); pedal digit II with phalanges 1 and 2 sub-equal in length, and bearing a trenchant ungual phalanx.

The holotype specimen of *Neuquenraptor argentinus* (Fig. 1) is approximately 2 m long. The radius is long and gracile, with a triangular-shaped proximal articular surface, closely resembling that of *Saurornitholestes langstoni* (Museum of the Rockies, MOR 660). The femur is proportionally short and robust, similar to *Deinonychus* and *Saurornitholestes*, but different compared with

the longer and slender femur of *Unenlagia comahuensis*, thus demonstrating that MCF PVPH 77 is not a juvenile specimen of *U. comahuensis*. The fibula of *Neuquenraptor* is distally splint-like, and the calcaneum is lateromedially compressed. The preserved portion of the astragalar ascending process indicates

Figure 1 *Neuquenraptor argentinus*, MCF PVPH 77, holotype. **a**, Proximal end of left radius in lateral view. **b**, **c**, Right femur in cranial (**b**) and lateral (**c**) views. **d**, Left tibia (t), fibula (fi), astragalus (as) and calcaneum (ca) in cranial view. **e**, Left foot in cranial view. **f**, Metatarsal IV (mt IV) and III (mt III) in lateral view. **g**, Metatarsals II–IV in caudal view. **h**, Pedal digit II in medial view. dg I–IV, digits I–IV; fmt IV, posterolateral flange on metatarsal IV; le, lateral expansion of metatarsal II over caudal surface of metatarsal III.

that it was proximodistally high, as usual among derived coelurosaurs.

Metatarsal II is transversely wider than metatarsal IV (contrasting with troodontids in which metatarsal IV is robust[8]), and ends distally in a well-developed ginglymoid articulation, a condition present in Dromaeosauridae and the basal birds *Rahonavis* and probably *Jeholornis* (X. Xu, personal communication). Metatarsal III is craniocaudally compressed, in contrast with the more robust metatarsals II and IV, which are deeper anteroposteriorly than they are mediolaterally wide. The proximal end of metatarsal III appears to be visible both cranially and caudally, as is the case with other basal deinonychosaurs. The distal end of metatarsal III expands over the cranial surfaces of metatarsals II and IV, and inversely, it is caudally hidden by lateral and medial projections of metatarsals II and IV, respectively (Fig. 1e, g). This peculiar metatarsal articulation corresponds with the arctometatarsalian condition[9], characteristically occurring among troodontids, ornithomimids, caenagnathids, tyrannosaurids, and the dromaeosaurids *Sinornithosaurus*[10] and *Microraptor*[8,11,12]. Metatarsal IV of *Neuquenraptor* has a prominent and sharp longitudinal ridge posteriorly directed along its posterolateral margin (similar to the crista plantaris lateralis of living birds[13]), a feature absent in other paravians (that is, the clade containing deinonychosaurians and birds[14]), with the exception of the troodontids *Sinornithoides youngi* (Institute of Vertebrate Paleontology and Paleoanthropology, IVPP V9612) and *Sinovenator changii*[8,15], and the basal dromaeosaurids *Microraptor zhaoianus*[8,11,12] and possibly *Sinornithosaurus millenii* (IVPP V12811). This is in conflict with former interpretations[11], according to which, in the dromaeosaurids *M. zhaoianus* and *S. millenii*, such a posterolateral ridge of metatarsal IV was interpreted as extending medially along the posteromedial edge.

An extensor sulcus exists on the cranial surface of metatarsal III, a feature also present in troodontids (for example, *Sinovenator* and *Tochisaurus*) and basal dromaeosaurids (for example, *Sinornithosaurus millenii* IVPP V12811, *Graciliraptor*[8] and probably *Microraptor*). This extensor sulcus is absent in most theropods, including derived dromaeosaurids (for example, *Velociraptor*, *Deinonychus*, *Hulsanpes*).

Pedal digit II exhibits distinctive deinonychosaurian features (also present in the basal bird *Rahonavis*, but not in other avialans). For example, phalanges 1 and 2 have expanded distal ginglymoidal joints, and phalanx 2 bears a strong proximoventral process for extensive dorsoventral excursions. The ungual phalanx of digit II is enlarged, strongly curved, and with a sharp cutting edge. This ungual phalanx is grooved on both sides, with the lateral groove occupying a more dorsal position than the medial one—as usual among dromaeosaurids but differing from most troodontids in which the ungual phalanx is symmetrical[8]. The unguals of digits III and IV are deep, flat-bottomed, with deep collateral grooves, and with developed flexor tubercles, as in other paravians.

Character analysis (Fig. 2) depicts *Neuquenraptor* as being located basally within Deinonychosauria[14,16]. This position is supported by the combination of an arctometatarsalian condition with a posterolateral flange on the caudal surface of metatarsal IV; a trenchant claw on the second pedal digit; and a distal end of metatarsal III that is incipiently ginglymoid. Some outstanding synapomorphies of all known troodontids (for example, asymmetrical foot with slender metatarsal II and robust metatarsal IV) or of derived troodontids (for example, tongue-like distal articular surface on metatarsal III) are absent in the new Patagonian form. In contrast, the Patagonian form exhibits a combination of pedal features (for example, metatarsal II with ginglymoidal distal end; phalanges II.1 and II.2 sub-equal in length; phalanx II.2 strongly constricted dorsoventrally at mid-shaft; and ungual of pedal digit II strongly compressed laterally and with collateral grooves asymmetrically arranged)[4,8,17] that occur (albeit not exclusively; X. Xu, personal communication)
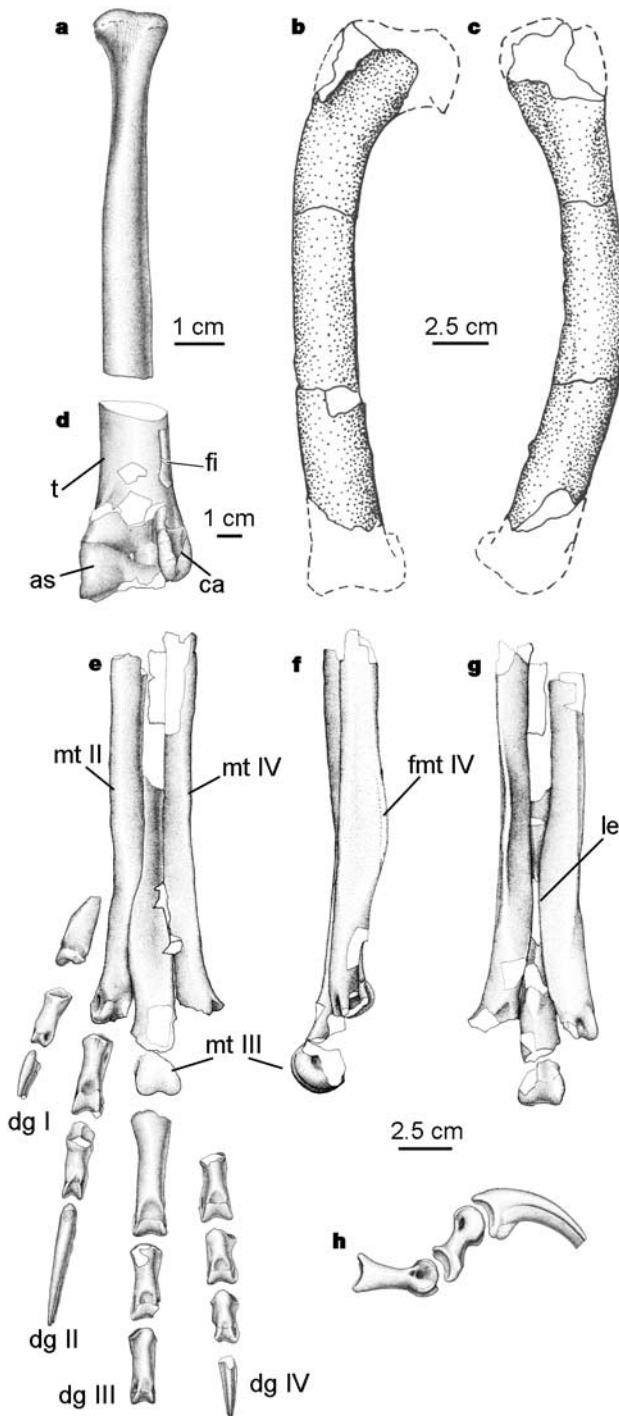
in Dromaeosauridae, thus suggesting that *Neuquenraptor* may represent a member of this clade of deinonychosaurs (see Supplementary Information).

Neuquenraptor occupies a basal position in the Dromaeosauridae, because it lacks derived features (for example, shaft of metatarsal IV mediolaterally wide and craniocaudally flat, metatarsal III proximally broad) present in Laurasian members of this group[1,17,18]. In other words, *Neuquenraptor* does not belong to the derived dromaeosaurid sub-clade that radiated in Laurasia, which includes *Deinonychus*, *Velociraptor*, *Dromaeosaurus*, *Adasaurus* and *Utahraptor*, among others[1,19], a splitting that minimally occurred during Barremian times (Fig. 2).
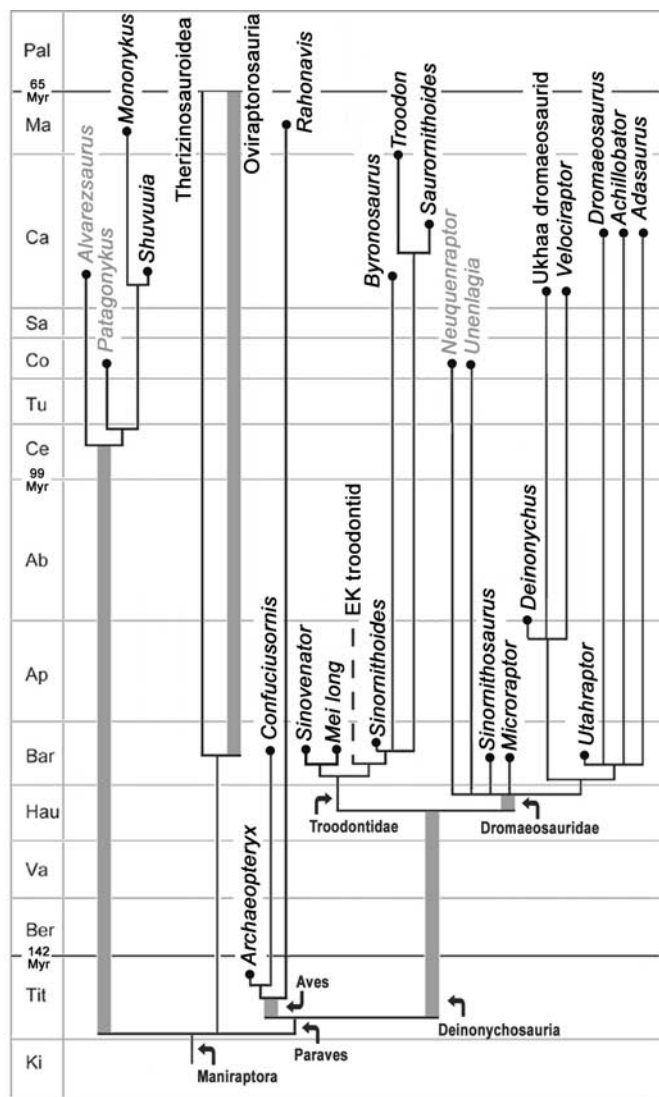

Figure 2 Reduced strict consensus depicting the phylogenetic relationships of *Neuquenraptor argentinus* within Maniraptora. Despite the large number of missing entries for *Neuquenraptor*, this taxon is unambiguously included within Dromaeosauridae based on the presence of synapomorphies of several inter-nested clades[1,20,30]. The proposed phylogenetic tree plotted against geological time indicates that the origination of most maniraptoran lineages must have occurred no later that the Late Jurassic period. South American maniraptorans are indicated in grey font. Thick grey lines represent maniraptoran lineages with South American representatives. See Supplementary Information for further phylogenetic data. Myr, million years. Pal, Palaeocene; Ma, Maastrichtian; Ca, Campanian; Sa, Santonian; Co, Coniacian; Tu, Turonian; Ce, Cenomanian; Ab, Albian; Ap, Aptian; Bar, Barremian; Hau, Hauterivian; Va, Valanginian; Ber, Berriasian; Tit, Tithonian; Ki, Kimmeridgian.

As prompted elsewhere[1,20], homoplasy is a common problem in coelurosaurian phylogeny. In this regard, the arctometatarsalian metatarsus shows a complex evolutionary history, and the basal position of *Neuquenraptor* provides useful information to test the monophyly of arctometatarsalian theropods. Our analysis is consistent with recent interpretations[1,15] that evolutionary transitions between the arctometatarsal and non-arctometatarsal foot occurred multiple times both in basal Coelurosauria (for example, Tyrannosauridae, Ornithomimidae) and maniraptorans (for example, alvarezsaurids, some oviraptorosaurs, derived troodontids and basal dromaeosaurids). The arctometatarsalian condition thus constitutes one of the homoplastic features most frequently evolved between Coelurosauria.

The discovery of *Neuquenraptor* increases the knowledge on the Gondwanan deinonychosaurs, which include the Patagonian *Unenlagia comahuensis*[2] and fragmentary elements from the Cenomanian of Northern Africa (Wadi Milk Formation, Sudan)[4]. The presence of these taxa in the Cretaceous period of South America and Africa dismisses the previous hypothesis[21] claiming that deinonychosaurians were endemic from Laurasia. Moreover, the Gondwanan record of non-avian maniraptorans is also formed by presumed oviraptorosaurs[22], alvarezsaurids (*Patagonykus, Alvarezsaurus*)[23,24] and bizarre representatives of large size[25,26]. This information strongly supports the hypothesis that an important adaptive radiation of maniraptoran theropods took place in the southern continents during the Cretaceous period.

Two alternative hypotheses (for example, vicariance and dispersal) may explain the presence of such a diversity of maniraptorans in Gondwana: either these lineages were descendants of Middle to Late Jurassic maniraptorans that attained a worldwide distribution, and that later produced vicariant taxa with the isolation of Gondwana from Laurasia; or that dispersal events of several maniraptoran lineages occurred later between northern and southern continents. Although dispersal of maniraptoran lineages can not be dismissed, vicariance constitutes the most parsimonious explanation for maniraptoran distribution[4,14]. First, the presence of *Archaeopteryx* in the Tithonian demonstrates that maniraptoran diversification was well underway at the end of the Jurassic period[1]. Second, the basal phylogenetic position of all known Patagonian maniraptorans (the deinonychosaurs *Neuquenraptor* and *Unenlagia*, and the alvarezsaurids *Alvarezsaurus* and *Patagonykus*) suggests a repeated cladistic pattern of area relationships compatible with a vicariance model[27,28]. In this context, *Neuquenraptor* may represent a Late Cretaceous survivor of basal dromaeosaurids, which were probably distributed worldwide by the Late Jurassic period. Similarly, a sub-clade of derived dromaeosaurids (comprising velociraptorines plus dromaeosaurines; Fig. 2) diversified separately in Laurasia during the Cretaceous period.

The documented diversity of derived coelurosaurians shows that their evolutionary history in the southern continents is more complex than originally thought. Furthermore, this leads us to reconsider the palaeobiogeographical history of Cretaceous theropod faunas recorded in the southern landmasses, traditionally interpreted as being markedly different compared with those of the northern continents[29]. On the basis of the new evidence, this difference still seems to apply to the large theropods (for example, abelisaurids, carcharodontosaurids, spinosaurids, tyrannosaurids), but distinctions are less important when theropods of small body size are compared (for example, deinonychosaurs, alvarezsaurids, oviraptorosaurs, basal avialans). Exceptions are gracile abelisauroid noasaurids, so far unrecorded in Laurasia. Further discoveries of Gondwanan coelurosaurs demonstrate that deinonychosaurs are among the most widely distributed clades of Cretaceous theropods. □

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Prokaryotic cells of the deep sub-seafloor biosphere identified as living bacteria

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Chemical analyses of the pore waters from hundreds of deep ocean sediment cores have over decades provided evidence for ongoing processes that require biological catalysis by prokaryotes[1–3]. This sub-seafloor activity of microorganisms may influence the surface Earth by changing the chemistry of the ocean and by triggering the emission of methane, with consequences for the marine carbon cycle and even the global climate[4–6]. Despite the fact that only about 1% of the total marine primary production of organic carbon is available for deep-sea microorganisms[7,8], sub-seafloor sediments harbour over half of all prokaryotic cells on Earth[7]. This estimation has been calculated from numerous microscopic cell counts in sediment cores of the Ocean Drilling Program[1,9]. Because these counts cannot differentiate between dead and alive cells, the population size of living microorganisms is unknown[10,11]. Here, using ribosomal RNA as a target for the technique known as catalysed reporter deposition-fluorescence in situ hybridization (CARD-FISH), we provide direct quantification of live cells as defined by the presence of ribosomes. We show that a large fraction of the sub-seafloor prokaryotes is alive, even in very old (16 million yr) and deep (>400 m) sediments. All detectable living cells belong to the Bacteria and have turnover times of 0.25–22 yr, comparable to surface sediments.

Direct evidence for the existence of a deep biosphere is provided by the following: (1) microscopic cell counts using unspecific fluorescent DNA (RNA) stains such as acridine orange; (2) sequences of high-molecular-weight prokaryotic DNA; (3) cultivation of diverse bacteria from subsurface sediments; and (4) bacterial activities measured with radiotracers[1]. Only a minute fraction of the enumerated cells were so far culturable and it has therefore remained unknown what fraction of cells is alive and active. The fluorochrome acridine orange, routinely applied in microscopic cell counting, binds unspecifically to DNA and RNA and thus does not provide information on the viability of the cells[10,11]. Potentially, a large part of the counted cells could be dormant or even dead and yet retain stainable DNA. RNA, in contrast, is much more labile and is readily degraded in cells that become inactive due to starvation. Cell death in pure cultures accelerates when less than half of the RNA remains[11]. Starved cells may still maintain an intact cell membrane and nucleic acids such as DNA or transfer RNA, but they rapidly loose their ribosomes[12]. The experience from pure culture studies is that cells with a significant ribosome content are living and metabolically active. We therefore used a highly sensitive molecular technique targeting specifically rRNA as an indicator of living cells in deeply buried marine sediments. The technique CARD-FISH was combined with quantitative, real-time polymerase chain reaction (Q-PCR) quantification of 16S ribosomal DNA genes, to determine what fraction of prokaryotic cells