

appearance of the cuticle from Enspel is similar to that of modern beetles (Fig. 1B), although the organic matrix surrounding the fibers has partially degraded. The preservation of chitin in the beetles and not in the flies may reflect the greater thickness and degree of cross-linking in the cuticle of the former. This study demonstrates that the primary control on the preservation of these biomolecules in ancient rocks is not time but the nature of the depositional environment and the inhibition of diagenetic alteration. In the case of Enspel, the combination of high productivity (evidenced by the abundance of diatoms in the matrix) and strongly reducing bottom conditions (23) played a key role in the enhanced preservation of the chitin-protein complex.

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- J. Carter and A. Gledhill (mass spectrometry facilities), S. Kearns (SEM), S. Powell (photography), and I. Duncan (modern insects) provided essential support, and we benefited from discussions with P. van Bergen and H. Poinar. M. Poschmann assisted with the collection of the samples. S. Wedmann identified the fossil insects. Supported by the Natural Environmental Research Council (NERC) grant GST/02/1027 to D.E.G.B. and R.P.E.; NERC also supported mass spectrometry facilities (grants GR3/2951 and GR3/3758). Collaboration between D.E.G.B. and M.W. was funded by the British-German Academic Research Collaboration program.

21 February 1997; accepted 16 April 1997

## A Nestling Bird from the Lower Cretaceous of Spain: Implications for Avian Skull and Neck Evolution

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A feathered skeleton of a Lower Cretaceous enantiornithine bird from Spain indicates that the modified diapsid skull of modern birds did not evolve until late in their evolution: Basal birds retained an essentially primitive diapsid design. The fossil provides data clarifying long-standing debates on the cranial morphology of the basalmost bird, *Archaeopteryx*. It also reemphasizes the notion that the early morphological transformations of birds were focused on the flight apparatus. This fossil was a nestling and suggests that early postnatal developments in the Cretaceous enantiornithine birds and those in their extant counterparts are comparable.

In recent years, a profusion of Mesozoic avians has greatly augmented existing knowledge on the early phases of bird evolution. These findings document an enormous diversity of basal birds and provide the foundations for a more accurate reconstruction of the morphological changes leading to the modern avian design (1–3). However, these important data have not advanced our understanding of early transformations of the avian skull and neck much beyond what was learned from the first complete skull of *Archaeopteryx* unearthed over 100 years ago.

Here we describe a fossil bird from the Lower Cretaceous La Pedrera Konservat-

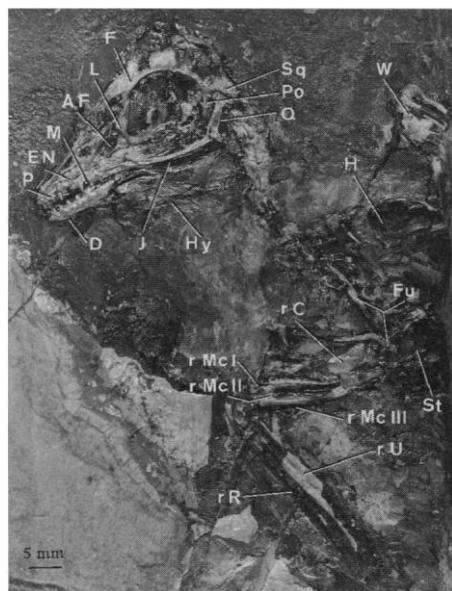
Lagerstätte, a renowned locality of the La Pedrera de Rúbies Lithographic Limestones Formation in the Spanish Serra de El Montsec (south-central Pyrenees, in the province of Lleida) (4). Its skull (5) (Figs. 1 and 2) is slightly crushed: the right side is elevated and displaced forward (Fig. 3). The first 12 presacral vertebrae are preserved, along with parts of both wings and shoulders, part of the sternum, and some incomplete feathers. Large clusters of tiny foramina interrupt the periosteal bone of the cervical vertebrae, humerus, ulna, and the articular region of the mandible, a pattern of ossification found in neonates of modern birds (Fig. 4). The incomplete ossification of the periosteal bone and the relative proportions of (i) the orbit and the rostrum and (ii) the skull and the postcranium strongly suggest that the bird was immature, most likely a nestling (6).

The toothed skull is similar to that of *Archaeopteryx* (7–9). It is subtriangular, with a large circular orbit and a vaulted braincase (Fig. 3). The snout is roughly half the total length of the skull. The external nares are subelliptical and slightly larger than the triangular antorbital fossa.

As in *Archaeopteryx* (7–9) and in the

Lower Cretaceous enantiornithine *Cathayornis* (10), the premaxilla is restricted to the rostral end and bears four teeth. Its nasal process is relatively short, ending slightly rostral to the caudal margin of the external nares, a condition also shared by these basal birds. The maxilla comprises most of the rostrum and holds at least five teeth (Fig. 3). Maxillary teeth were retained by several early avians (7–11) but were independently lost in the Lower Cretaceous *Confuciusornis* (12) and in the Upper Cretaceous enantiornithine *Gobipteryx* (13, 14). As in all birds, including *Archaeopteryx* (15, 16), the rod-like jugal bar lacks a dorsal, postorbital process. The jugal bar is caudally forked (Fig. 3) and has a short caudal process and a long dorsocaudal process that articulates with the quadrate, another feature in common with *Archaeopteryx*. The quadrate has an ample orbital process similar to that of *Archaeopteryx*, other basal birds (17, 18), and nonavian theropods (19, 20). Its distal articulation retains the two ancestral, transversely oriented condyles, instead of the derived three-condylar articulation of modern birds.

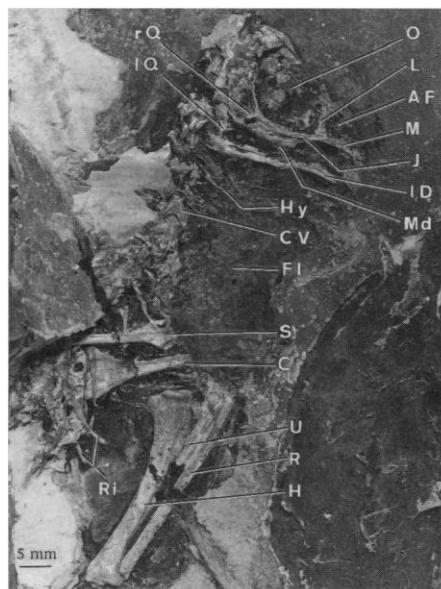
The bird also has a postorbital bone (Fig. 3), which articulates rostradorsally to the frontal and caudally to the squamosal. This bone bears a ventral, splint-like jugal process



**Fig. 1.** Slab of the Lower Cretaceous bird from El Montsec (specimen LP-4450-IEI; Institut d'Estudis Il·lerdencs, Lleida, Spain). The skull is in left lateral view, whereas the postcranial elements are in ventral view. Abbreviations: AF, antorbital fenestra; D, dentary; EN, external nares; F, frontal; Fu, furcula; H, humerus; Hy, hyoids; J, jugal; L, lachrymal; M, maxilla; P, premaxilla; Po, postorbital; Q, quadrate; rC, right coracoid; rMcI, right first metacarpal; rMcII, right second metacarpal; rMcIII, right third metacarpal; rR, right radius; rU, right ulna; Sq, squamosal; St, sternum; and W, wrist.

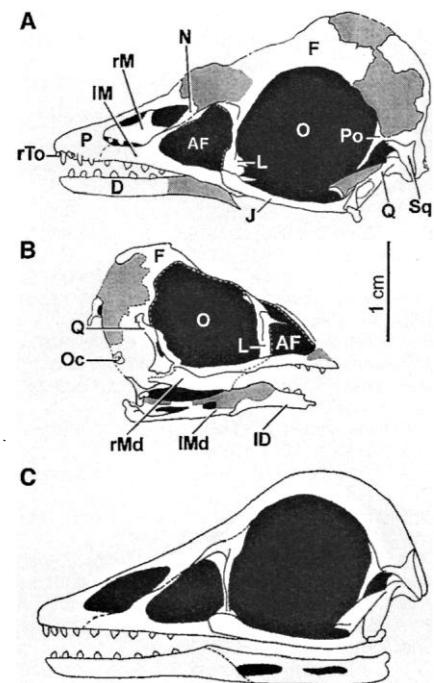
that does not contact the jugal bar and only partially separates the orbit from the infratemporal fenestra. The postorbital bone is absent in modern birds but is present in nonavian theropods (19). Workers have argued about this bone's presence in *Archaeopteryx* (7–9, 15, 16), but the presence of a postorbital in the new fossil casts doubt on interpretations that it is absent in *Archaeopteryx*.

Equally interesting is the presence of a tetroradiated squamosal that, in contrast to modern birds, is not incorporated into the braincase (Fig. 3). Its rostrrolateral process terminates in a bifurcated facet for articulation with the postorbital. A short, ventromedial projection tapers distally. Caudomedial and caudal processes about the parietal and paroccipital process, respectively. A long-standing controversy involves the squamosal of *Archaeopteryx*: Different bones of the skull of the Eichstätt specimen have been regarded as the squamosal, and some authors have argued that this bone may have been totally reduced (9). A recent study of the skull of the seventh *Archaeopteryx* specimen suggested that the squamosal was present and not incorporated into the braincase (16, 21). The morphology of the squamosal of the new bird from El Montsec, which is remarkably similar to the squamosal bone in the seventh *Archaeopteryx* specimen, supports the latter interpretation.



**Fig. 2.** Counterslab of the Lower Cretaceous bird from El Montsec (specimen LP-4450-IEI; Institut d'Estudis Il·lerdencs, Lleida, Spain). The skull is in right lateral view, whereas the postcranial elements are in dorsal view. Abbreviations: AF, antorbital fenestra; C, coracoid; CV, cervical vertebrae; FI, feathers; H, humerus; Hy, hyoids; J, jugal; L, lachrymal; ID, left dentary; IQ, left quadrate; M, maxilla; Md, mandible; O, orbit; R, radius; Ri, ribs; rQ, right quadrate; S, scapula; and U, ulna.

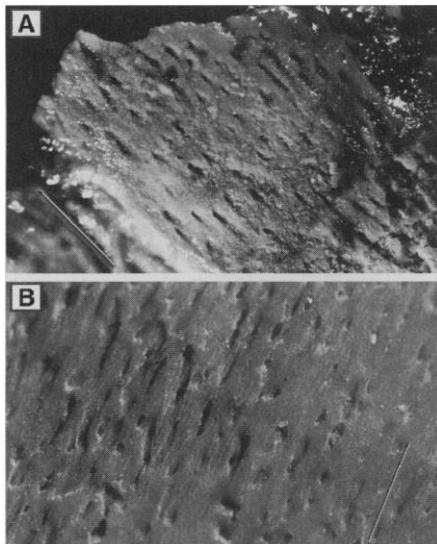
The dentary of the nestling has eight teeth. As opposed to *Archaeopteryx* (16), its medial surface does not show any evidence of interdental plates. In medial view, the postdentary portion of the jaw shows two large, elongated fenestrae (Fig. 3). The angular forms most of the ventral border of the rostral mandibular fenestra. This bone also contributes to the rostroventral corner of the caudal mandibular fenestra, which is otherwise surrounded by the surangular (Fig. 3). Two mandibular fenestrae of similar structure are known in a variety of nonavian theropods (19). This condition is highly variable among modern birds, which may show one, two, or no fenestrae (22). But modern birds differ from nonavian theropods in that the dentary lining presents most of the ventral margin of the rostral mandibular fenestra both laterally and medially. In *Archaeopteryx*, data from both the Eichstätt and Solenhofer Aktien-Verein specimens suggest



**Fig. 3.** Skull of the bird from the Lower Cretaceous of El Montsec: (A) left lateral view (slab), (B) right lateral view (counterslab), and (C) reconstruction of the skull in left lateral view. Regardless of the fact that there are some teeth in early stages of eruption, the dental series is homodont. A straight base is separated by a weak constriction from a triangular crown. The tip of the crowns are occlusally oriented, a condition different from the more caudally oriented apex of the dentary teeth of *Archaeopteryx* (23). The teeth are devoid of carinae, lacking any kind of ornamentation. Abbreviations: AF, antorbital fenestra; D, dentary; F, frontal; J, jugal; L, lachrymal; ID, left dentary; IM, left maxilla; IMd, left mandible; N, nasal; O, orbit; Oc, occipital condyle; P, premaxilla; Po, postorbital; Q, quadrate; rM, right maxilla; rMd, right mandible; rQ, right quadrate; and rTo, right tooth.

that this taxon does not have lateral mandibular fenestrae (23, 24). The new fossil, however, indicates that the same two fenestrae typical of some nonavian theropods were present in certain basal birds and that, unlike in modern birds, the rostral mandibular fenestra was not primitively lined by caudal projections of the dentary.

The neck of the El Montsec nestling is composed of nine vertebrae (Figs. 1 and 2), comparable to *Archaeopteryx* and many nonavian theropods (19, 25). However, in contrast to these taxa, the cranial articular surfaces of the bird's cervicals are heterocoelous, and the caudal surfaces do not appear to be heterocoelous. This primitive stage of heterocoely, with saddle-shaped cranial articular surfaces and slightly concave caudal surfaces, is similar to that of certain enantiornithine cervical vertebrae from Argentina (26). The axis bears enormous epiphyses that project caudally, far beyond the postzygapophysial facets. In the subsequent vertebrae, they gradually decrease in size, although they are still prominent in the fifth cervical vertebra. This condition is unlike the much smaller epi-



**Fig. 4.** Pattern of foramina (A) in the surface of the humerus of the El Montsec bird and (B) in a nestling of the extant species *Ciconia ciconia*, the white stork. The pattern of foramina present in several bones of the El Montsec fossil was compared to a pattern of grooves and foramina of the periosteal bone of several extant bird neonates (40). With increasing age, initial grooves carving the periosteal bone decrease in size, turn into isolated foramina, and finally disappear. In extant neonates, this entire process is completed within the first few weeks after hatching (finishing sooner or later according to species size, later if the adult is larger). The foramina present in the El Montsec bird are comparable to those composing the final stage of obliteration of the longitudinal grooves that occur on the periosteal bone of the earliest neonates. The arrow indicates the humeral head.

pophyses of modern birds, but is strikingly like that of *Deinonychus* (27). In the latter taxon, however, these prominent epiphyses are present throughout the neck. Problems with preservation prevent verification of this character in *Archaeopteryx*, but the El Montsec nestling appears to be intermediate between modern birds and dromaeosaurid theropods.

Despite the cranial similarities to *Archaeopteryx*, the morphology of the thoracic girdle and wing of the bird is comparable to that of the more advanced ornithothoracine birds—in particular, the Enantiornithes (14, 28)—and suggests improved flying ability with respect to *Archaeopteryx*. As in modern flyers, the coracoid is strut-like (Figs. 1 and 2), and it has the large, triangular dorsal fossa of enantiornithines. The furcula has an interclavicular angle of 60° (Fig. 1), in contrast to the boomerang-like furcula of *Archaeopteryx*, *Confuciusornis*, and nonavian theropods (for example, *Oviraptor*), and it has a well-developed hypocleidium as well. Moreover, the proportions among wing elements are typical of those of modern flying birds (also shared by the remaining enantiornithines) and are unlike those of *Archaeopteryx*, *Confuciusornis*, and nonavian theropods: The radius and ulna are slightly longer than the humerus, the mid-shaft width of the radius is roughly two-thirds the width of the ulna, and the length of the hand is shorter (~80%) than that of the ulna (Figs. 1 and 2).

The limited data on immature Mesozoic birds forces comparison between the fossil nestling and adults rather than with semaphoronts of other species. A cladistic analysis performed on the new fossil and other basal birds clusters the new taxon within the ornithothoracine Enantiornithes (29). Cranial similarities shared by the bird and *Archaeopteryx* (including general subtriangular shape, proportions between nares and antorbital fossa, and squamosals not incorporated into the braincase) are primitive and also exist in nonavian theropods (19). A set of primitive similarities has stimulated the notion that *Archaeopteryx* and the Enantiornithes form a monophyletic group (30), the “Sauriurae.” This taxon, however, is certainly paraphyletic, a conclusion supported by the large number of synapomorphies common to the Enantiornithes and the Ornithurae but absent in *Archaeopteryx* (18, 31). The fossil further supports the paraphyletic status of “Sauriurae,” even though it retains several plesiomorphic characteristics, primarily in the skull.

This fossil also challenges recent claims regarding the basal ornithothoracine *Iberomesornis* (32), from the Lower Cretaceous of Spain, as an immature enantiornithine (3). The presence of enantiornithine syna-

pomorphies in the nestling, as well as in embryos considered to be of the enantiornithine *Gobipteryx* (33), indicates an early ontogenetic differentiation for these characters. Thus, the absence of enantiornithine synapomorphies in *Iberomesornis* cannot be explained by its alleged early ontogenetic age.

Fossils of Mesozoic birds in early ontogenetic stages are rare. Previous reports include only several embryos of the enantiornithine *Gobipteryx* (33) and an immature specimen of the ornithurine *Baptornis* (34) from the Upper Cretaceous of Mongolia and North America, respectively. This new Lower Cretaceous bird provides the oldest record of a fossilized avian nestling. The striking similarity of the pattern of ossification of the nestling to that of neonates of modern birds (Fig. 4) calls for comparisons between their postnatal ontogenetic development. This fossil suggests that early stages of enantiornithine postnatal growth may be comparable to those of modern birds. This idea is particularly interesting, insofar as the discovery of growth rings interrupting the bone deposition of adult enantiornithines (35) hints at a growth pattern that is unlike that of modern birds.

The primitive set of attributes of the skull of the nestling suggests that, despite certain specializations such as the independent loss of teeth in several lineages, early avians retained an essentially primitive diapsid cranial architecture: a complete supra-temporal fenestra and an only incipiently opened infratemporal fenestra. The finding also clarifies the controversial cranial morphology of *Archaeopteryx*, supporting a comparable diapsid morphology for the Urvögel. Furthermore, by documenting an intermediate morphology of the neck and skull (for example, epiphysal development and organization of the temporal region) between nonavian theropods and modern birds, the new early bird from El Montsec provides additional data solidifying the notion that modern birds are short-tailed, feathered descendants of theropod dinosaurs.

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- the single, fragmentary specimen of *Noguerornis* (38), a basal bird of uncertain affinities.
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  6. The fossil displays characters unknown in any other enantiornithine bird. For example, the dorsal coracoid fossa approaches the humeral articular facet, and the ventral condyle of the humerus is strongly projected distally. Although these characters may be autapomorphies and thus justify the erection of a new taxon, the fact that the specimen is of an early ontogenetic age clouds the determination of these unique characters as true autapomorphies. Further studies or findings may prove that this specimen belongs to a species as yet unknown.
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  20. We regard the pterygoid flange of the quadrate of nonavian theropods as homologous to the orbital process of the avian quadrate.
  21. The presence of a bifurcated terminal facet in the rostral process of the squamosal of the seventh *Archaeopteryx* specimen, a condition virtually identical to that of the new fossil, also supports the presence of a postorbital in *Archaeopteryx*.
  22. J. J. Baumel and L. Witmer, in *Handbook of Avian Anatomy: Nomina Anatomica Avium*, J. J. Baumel, Ed. (Publ. 23, Nuttall Ornithology Club, ed. 2, 1993), pp. 45–132.
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  24. Except for a tiny foramen piercing the lateral surface of the surangular, the mandible of the Eichstätt specimen of *Archaeopteryx* appears to lack any other fenestra. Wellnhofer (23) showed that the jaw of the Solenhofer Aktien-Verein specimen has a well-developed medial fossa aditus, but this fossa does not appear to open laterally, corroborating the information available in the Eichstätt specimen. See also (9).
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  29. Skeletal characters of the bird were scored in the data matrix provided by Sanz, Chiappe, and Buscalioni (2). Several modifications to this matrix were introduced: (i) Dromaeosauridae was used as single outgroup; (ii) for simplicity, *Patagopteryx* was excluded from the analysis because it introduces no relevant information; (iii) *Concornis* was included within Enantiornithes; and (iv) in Enantiornithes, character states of characters 2 and 5 were rescored as "0" (primitive state), on the basis of new data [J. L. Sanz *et al.*, in preparation]. Eight additional characters were also added to the data matrix: (i) jugal-postorbital contact (present = 0, absent = 1); (ii) quadratojugal-squamosal contact (present = 0, absent = 1); (iii) squamosal incorporated to the braincase and lacking contact to the postorbital (absent = 0, present = 1); (iv) postorbital (present = 0, absent = 1); (v) caudal end of dentary forming most of the ventral margin of the caudal mandibular fenestra (absent = 0, present = 1); (vi) epiphyses [large, projecting caudally beyond the postzygapophysial facet throughout the cervical series (0); large, but restricted to the anterior portion of the cervical series (1), or small, not projecting beyond the postzygapophysial facet (2)]; (vii) dorsal fossa on the coracoid (absent = 0, present = 1); and (viii) metacarpal III longer than metacarpal II (absent = 0, present = 1). The parsimony analysis was conducted using the Hennig 86 software (39). This analysis resulted in a single, most parsimonious tree (length, 109 steps; CI, 0.86; RI, 0.87). The nodes of this cladogram are diagnosed by the following unambiguous synapomorphies: (i) Aves: contact between jugal and postorbital absent; contact between the quadratojugal and squamosal absent. (ii) Ornithothoraces: prominent ventral processes on cervicodorsal vertebrae; dorsal vertebral count less than 13 to 14 elements; presence of pygostyle; strutlike coracoid; scapula with sharp caudal end; humerus shorter than or nearly equivalent to ulna; shaft of radius considerably thinner than that of ulna (ratio of diameter of radius to that of ulna less than 0.70). (iii) Ornithurae: premaxillary teeth absent; orbital process of quadrate sharp and pointed; quadratojugal cotyle in lateral face of the mandibular process of quadrate; pneumatic articular; ossified uncinata processes; procoracoid process; sagittally curved scapular shaft; craniocaudally convex, spherical head of humerus; acetabulum small, ratio of acetabulum to ilium less than or equal to 0.11; iliac fossa for *M. cuppedicus* (equivalent to *M. iliofemoralis internus*); apices of pubis not in contact; shaft of pubis laterally compressed throughout its length; femur with a deep patellar groove; posterior trochanter of femur absent; cranial cnemial crest of tibiotarsus; extensor canal on tibiotarsus; distal tarsals and metatarsals fused completely to form a tarsometatarsus; metatarsal fusion starting distally; proximal end of metatarsal III plantarily displaced with respect to metatarsal II and IV; intercondylar eminence of tarsometatarsus well developed; distal vascular foramen in metatarsus; squamosal incorporated to the braincase and lacking contact to the postorbital; absence of postorbital; small epiphyses, not projecting beyond the postzygapophysial facet. The new El Montsec bird is clustered with other enantiornithine birds by the following unambiguous synapomorphies: prominent bicapital crest of humerus, cranioventrally projected; convex lateral margin of the coracoid; supracoracoid nerve foramen of coracoid opening into an elongate furrow medially and separated from the medial margin by a thick bony bar; dorsal fossa on the coracoid; metacarpal III longer than metacarpal II.
  30. E. N. Kurochkin, *Russ. Acad. Sci. Paleontol. Inst.* (special issue) (1996); L. D. Martin, in *Perspectives in Ornithology*, A. H. Brush and G. A. Clark Jr., Eds. (Cambridge Univ. Press, Cambridge, 1983), pp. 291–338; in *L'Évolution des Oiseaux d'Après le Témoignage des Fossiles*, C. Mourer-Chauviré, Ed. (Doc. 99, Laboratoires de Géologie, Lyon, France, 1987), pp. 9–19.
  31. L. M. Chiappe, *Cour. Forsch. Senckenb.* **181**, 55 (1995); S. L. Olson, in *Avian Biology*, D. Farner, J. King, K. C. Parkes, Eds. (Academic Press, New York, 1985), vol. 8; A. Feduccia [*Science* **267**, 637 (1995)] used the paraphyletic "Sauriurae," although in his phylogenetic diagram he clearly specified that Enantiornithes are closer to modern birds than to *Archaeopteryx*.
  32. J. L. Sanz and J. F. Bonaparte, in *Papers in Avian Paleontology Honoring Pierce Brodkorb*, K. E. Campbell, Ed. (Sci. Ser. 36, Natural History Museum of Los Angeles County, Los Angeles, 1992), pp. 39–49.
  33. A. Elzanowski, *Palaeontol. Pol.* **42**, 147 (1981).
  34. L. D. Martin and O. Bonner, *Auk* **94**, 787 (1977).
  35. A. Chinsamy, L. M. Chiappe, P. Dodson, *Nature* **368**, 196 (1994); *Paleobiology* **21**, 561 (1995).
  36. The age of the La Pedrera de Rúbies Lithographic Limestones Formation is regarded as Upper Berriasi-Lower Valanginian on the basis of ostracods [P. Brenner, W. Geldmacher, R. Schroeder, *Neues Jahrb. Geol. Palaeontol. Monatsh.* **9**, 513 (1974)]. Nevertheless, it could be somewhat younger (Upper Hauterivian-Lower Barremian), on the basis of a work in progress on its charophytes [C. Martin-Closas and N. López-Morón, in (37), pp. 29–31].
  37. X. Martínez-Delcòs, Ed., *Montsec and Montal-Alover, Two Konservat-Lagerstätten (Catalonia, Spain), Field Trip Guide Book* (Institut d'Estudis Ilerdencs, Lleida, Spain, 1995).
  38. A. Lacasa-Ruiz, *Terra Nova (UK)* **1**, 45 (1989); A. Lacasa-Ruiz, *Estud. Geol. (Madrid)* **45**, 417 (1989). The new El Montsec bird is not considered cogenetic with *Noguerornis* on the basis of differences in the furcula and humerus, aside from the size (*Noguerornis* is an adult, being smaller than the nesting specimen). In addition to *N. gonzalezi*, *Ilerdopteryx viai* was based on an isolated feather [A. Lacasa, in *Les Calcaries Litogràfiques del Cretaci Inferior del Montsec, Deu Any de Campanyes Paleontològiques*, X. Martínez-Delcòs, Ed. (Institut d'Estudis Ilerdencs, Lleida, Spain, 1991), pp. 147–150]. We believe, however, that the holotype of *Ilerdopteryx viai* is not diagnostic for a specific status and regard this taxon as a *nomen dubium*.
  39. J. Farris, *Hennig 86 References: Documentation for Version 1.5* (privately published, 1988).
  40. Sixteen neonate specimens of the following taxa were examined: *Burhinus oecdinemus* (Charadriiformes, three specimens), *Ciconia ciconia* (Ciconiiformes, two specimens), *Columba palumbus* (Columbiformes, two specimens), *Clamator glandarius* (Cuculiformes, one specimen), *Alectoris rufa* (Galliformes, two specimens), *Picus viridis* (Piciformes, two specimens), *Pica pica* (Passeriformes, two specimens), and *Athene noctua* (Strigiformes, two specimens). These specimens belong to the skeletal collection of the Unidad de Arqueozoología from the Universidad Autónoma de Madrid. All examined specimens presented the pattern of foramina or grooves discussed in Fig. 4.
  41. We thank J. I. González, who found the specimen and kindly made it available for study; L. Witmer for comments on an early version of the manuscript; and S. Copeland, P. Dandonoli, and D. Treon for general editorial suggestions. Photographs used for Figs. 1 and 2 were taken by G. F. Kurtz and those for Fig. 4 by M. Bautista. This research was supported by the Institut d'Estudis Ilerdencs, the Junta de Comunidades de Castilla-La Mancha, DGIICYT (Promoción General del Conocimiento, PB93-0284), the European Union (Human Capital and Mobility Program, CHRXCT930164), and grants to L.M.C. from NSF (DEB-9407999), J. S. Guggenheim Foundation, The Dinosaur Society, and the Frank M. Chapman Memorial Fund (American Museum of Natural History).

5 February 1997; accepted 11 April 1997