

simple surface titrations, the need for long and tedious dissolution experiments is reduced to finding the rate constant and exponent for the surface species, rather than empirically determining the dissolution rate throughout the full range of solution compositions. However, we must caution that much more dissolution kinetic work must still be done to verify the cases where first-order dependence is valid, and we need to explore the surface chemistry of silicates much more thoroughly. Nonetheless, understanding the surface chemistry of dissolution promises to unify the rate data and dissolution mechanisms of a wide range of silicates.

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Fig. 1 Isolated feather from the Neocomian outcrop of Las Hoyas (Cuenca, Spain).

## Unusual Early Cretaceous birds from Spain

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The Neocomian Spanish outcrops of Montsec (province of Lérida) and the new one of Las Hoyas (province of Cuenca) have yielded several avian remains in the last few years. Several isolated feathers have been reported from Montsec, and a specimen of some feathered wing bones has recently been found. Las Hoyas has yielded an isolated feather and a nearly articulated small fossil bird that lacks the skull. This new specimen, reported here, presents a combination of derived (strut-like coracoids, pygostyle) and primitive (pelvic girdle, sacrum, hind limb) character states. If one considers *Archaeopteryx*, Ornithurae and the new Spanish fossil bird, it seems clear that the latter taxon is the sister group of Ornithurae (extant birds and all other fossil birds that are closer to recent forms than is *Archaeopteryx*).

Three years ago a new Early Cretaceous outcrop was found in the province of Cuenca, east-central Spain. It was called 'Las Hoyas' ('The Dales'), and it is probably equivalent to the formation 'Calizas de la Huérguina'<sup>1</sup>, Neocomian (probably

Hauterivian-Early Barremian) in age (some 130-120 Myr BP). The lithology is made of lithographic limestones from a lacustrine environment. Floral and faunal remains are relatively abundant, arthropods (insects and crustaceans) especially so. The vertebrate fauna is made up mainly of fishes along with an urodela, an anuran, a chelonian and a little lizard. The faunal and floral assemblage from Las Hoyas seems, as a whole, very similar to that of the classic Neocomian outcrops of Montsec.

Both Neocomian Spanish outcrops, Montsec and Las Hoyas, have yielded several avian specimens in the last few years. Several feathers from the first one have been described<sup>2</sup>. Some remains of feathered bones have recently been found from the Montsec. They are scattered in a lithographic limestone matrix. Both humeri, ulnae and radii can be seen, as well as a partially exposed furcula (wish-bone) with an acute hypocleidium. In *Archaeopteryx*, feathers have been preserved as impressions or even casts<sup>3</sup>. Unlike *Archaeopteryx*, the feathers of the Montsec specimen are dark carbon films.

To date Las Hoyas has yielded an isolated feather (Fig. 1) and an almost complete little fossil bird which was found by a local collector, Mr Armando Diaz Romeral who kindly loaned it to us for study. The specimen (number LH022R, Figs 2 and 3) is now housed in the Unidad de Paleontología of the Universidad Autónoma de Madrid. This Early Cretaceous Spanish bird is small (femur length 15 mm) and is exposed in a limestone slab mainly in lateral (left) view. The fossil is nearly articulated, but it lacks the skull and some cervical vertebrae, as well as the carpus and manus.

A striking characteristic of this Early Cretaceous bird is its combination of primitive (pelvic girdle, sacrum and hind limbs) and derived (coracoids and pygostyle) character states. These features allow it to be placed in an intermediate phylogenetic position between *Archaeopteryx* and later birds. The number of dorsal vertebrae is 11. This figure is intermediate between that of *Archaeopteryx* (13-14 segments<sup>4</sup>) and the greatly reduced



**Fig. 2** The new Mesozoic bird (LH022R) from the Neocomian outcrop of Las Hoyas (Cuenca, Spain).

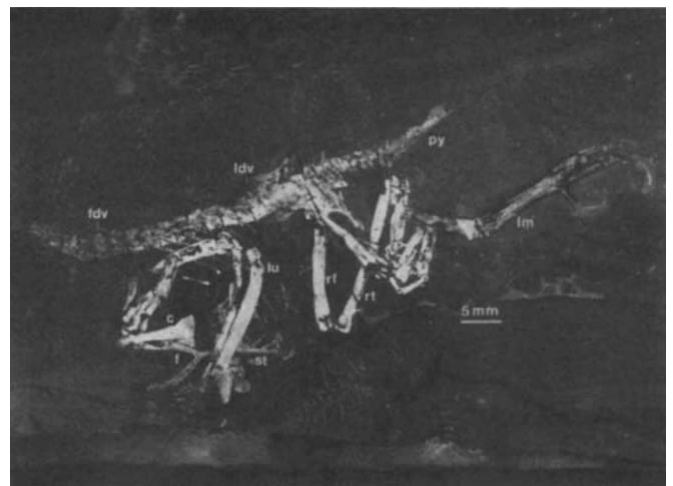
number in extant birds (4–6 segments<sup>5</sup>). The number of sacral vertebrae is probably five, which is symplesiomorphic with *Archaeopteryx* and all dinosaurs<sup>6</sup>. One of the most notable features of this small Spanish fossil bird is the appearance of a conspicuous pygostyle. This structure fuses a relatively large number of caudal vertebrae, probably 10–15, and seems larger than that of modern birds. Between the pygostyle and the sacrum are a series of eight free caudal vertebrae. The presence of a pygostyle, even in such an unusual form, appears to be a synapomorphy of this fossil bird with the Ornithurae (*sensu* Gauthier<sup>6</sup> and Cracraft<sup>7</sup>). There is no evidence of gastralia, an apomorphic character state in relation with *Archaeopteryx* and theropod dinosaurs.

More 'evolutionary novelties' can be seen in the pectoral region. The coracoid is typically avian, strut-like, with a conspicuous head and an expanded distal end for the connection with the sternum. The furcula has a developed styloideus furcular process (hypocleidium) seen in anterior view that seems very similar to that of the feathered Montsec remains reported above.

The pelvic girdle is poorly preserved. The ilium is probably primitive, similar to that of *Archaeopteryx* and the coelurosaurian dinosaurs. The pre-acetabular portion seems to be relatively deep, and its surface greater than that of the post-acetabular region. The acetabulum is relatively small, similar to that of *Archaeopteryx*. The pubis is missing. The ischium lacks the peculiar outline of that of *Archaeopteryx*<sup>8</sup>, being more primitive than that of the Bavarian Jurassic bird. The pelvic elements are unfused<sup>7</sup>, a plesiomorphic character state shared with *Archaeopteryx*. The features of the hind limb are primitive too. The astragalus (which has a conspicuous theropodan ascending process) and calcaneum are free, not fused to the tibia. The free distal tarsals cap the proximal area of metatarsals, which are also unfused. Some synapomorphies of Carinatae, like the strut-like coracoid, can be found in a bird even more primitive than the Ornithurae. The Spanish Early Cretaceous bird lacks several of the synapomorphies proposed by Cracraft<sup>7</sup> for the Ornithurae, like a complete fused tarsometatarsus or ossified uncinata processes.

The new fossil reported here represents a previously unknown level in the organization of birds, intermediate between *Archaeopteryx* and later birds. Considering this Early Cretaceous bird, *Archaeopteryx* and the Ornithurae, based on the character

states mentioned above, it seems clear that this new taxon is the sister group of the Ornithurae. The main synapomorphies which define this clade are the appearance of a pygostyle and the strut-like coracoids. The new fossil suggests that the early evolution of birds was firmly and rapidly influenced by the requirements of flight. So, the avian condition of scapular girdle and wing skeleton contrast with the conservative level of pelvic girdle, sacrum and hind limb. Even the appearance of a pygostyle precedes other typical avian features such as the fusion of the proximal tarsals to the tibia or the co-ossification of the metatarsals. The fossil also suggests a relatively rapid change in morphology from that of *Archaeopteryx* to that of Early Cretaceous birds, as was suggested by Kurochkin<sup>9</sup>, based on *Ambiortus*. It represents the only Spanish fossil material actually related to mesozoic birds. Some isolated feathers from the Montsec have been denominated *Ilerdopteryx*<sup>2</sup>. In 1902



**Fig. 3** Ultraviolet-induced fluorescence photograph of the new Spanish Neocomian bird (Las Hoyas, province of Cuenca). c, coracoid; f, furcula; fdv, first dorsal vertebra; ldv, last dorsal vertebra; lm, left metatarsals; lu, left ulna; py, pygostyle; rf, right femur; rt, right tibia; st, sternum.

Vidal<sup>10</sup> reported a bird from Montsec lost by a workman. *Cose-saurus*<sup>11,12</sup> is probably related to the prolacertid lepidosaurs<sup>13</sup>, and *Priscavolucris*<sup>14</sup> was based on very doubtful remains.

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## Polarization-opponent interneurons in the insect visual system

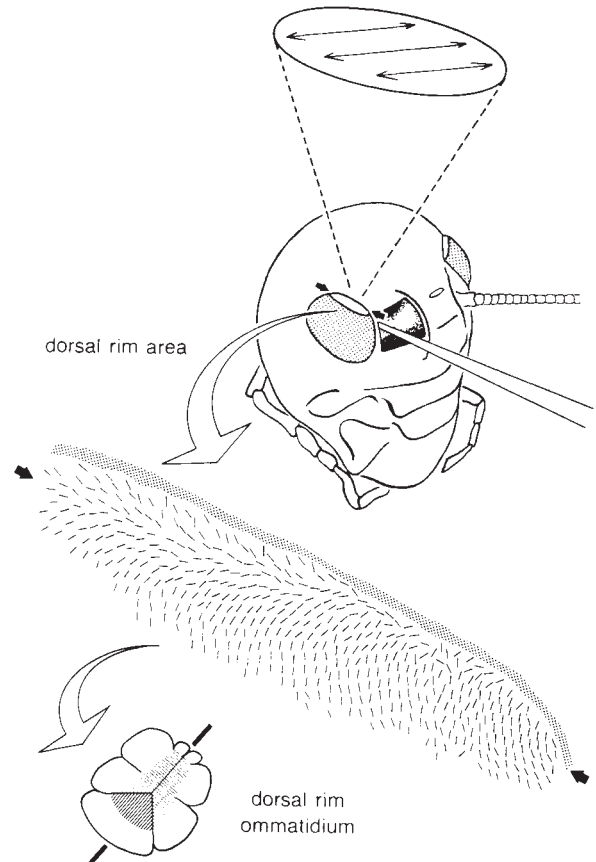
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Recent behavioural experiments dealing with the mechanism of polarized skylight navigation in bees indicated that processing of *e*-vector information in the visual system involves antagonistic interaction between polarization-sensitive photoreceptors<sup>1,2</sup>. Here we report electrophysiological recordings from polarization-opponent interneurons in the optic lobe of crickets. These neurons receive antagonistic input from polarization sensitive photoreceptors with orthogonally arranged analyser orientations. Although polarization-sensitive interneurons have previously been reported from the visual system of crabs<sup>3</sup> and goldfish<sup>4,5</sup>, this is the first demonstration of polarization-opponent units.

In both bees and crickets polarization vision is mediated by a small group of specialized ommatidia situated at the dorsal rim of the compound eye<sup>6,7</sup>. Each of these ommatidia contains two sets of homochromatic, strongly polarization-sensitive photoreceptors with orthogonally arranged analyser directions<sup>8-11</sup>, as indicated by the orthogonal orientation of the microvilli (Fig. 1). The receptors have greatly enlarged visual fields due to optical specializations (bees, corneal pore canals; crickets, no retinal screening pigment)<sup>8,10-12</sup>. These common features suggest that bees and crickets use similar mechanisms in *e*-vector detection and orientation.

This study was aimed towards an understanding of the physiology of polarization-sensitive interneurons within the optic lobe (medulla) of field crickets. The dorsal rim area was stimulated with flashes of polarized light with different *e*-vector directions or with a continuously rotating *e*-vector. The huge and strongly overlapping visual fields have the advantage that all dorsal rim ommatidia can be stimulated simultaneously by a single stimulus positioned approximately in the optical center



**Fig. 1** Sketch of cricket head shows position of the specialized dorsal rim area of the eye (thick black arrows) and demonstrates method of stimulation and recording. In the expanded view of the dorsal rim area the orientations of transverse axes of the rhabdoms are indicated by bars. Note fan-shaped arrangement. Enlarged cross section of a dorsal rim ommatidium demonstrates the presence of two orthogonal microvillar directions within each rhabdom and defines the transverse axis of the rhabdom.

**Methods.** The dorsal rim area of field crickets, *Gryllus campestris*, was stimulated with polarized stimuli subtending visual angles of 1.5° or 50° and positioned 32° contralateral to the zenith (with respect to natural head position). For measuring the *e*-vector response (see Fig. 2 *a-e*) white light (Xenon arc) polarized with a HNPB polarizer (Polaroid) was used, giving 800 lux (1.5° stimulus) or 150 lux (50° stimulus) at the eye. Monochromatic light, as used for measuring spectral response and some of the intensity response functions, was produced with small-band interference filters (Schott). Intensity was adjusted with a quartz neutral-density wedge (Dyn Optics). Intra- and extracellular recordings from POL-neurons were obtained with KCl-filled glass micropipettes inserted into the medulla using standard electronic equipment and stored with an FM tape recorder. Response functions were determined off-line by counting the number of spikes during the last 800 ms of the 1,000-ms flashes with a window discriminator. *e*-vector response functions could also be obtained from experiments with continuously rotating *e*-vectors by counting spike numbers in 20° intervals. The  $\Phi_{\max}$  and  $\Phi_{\min}$  values were calculated by fitting second-order polynomials (parabolas) to the upper and lower arcs of the *e*-vector response functions. All *e*-vectors indicated in the paper refer to the long axis of the dorsal rim area of the right eye as specified in Fig. 4 (bottom).

of the dorsal rim area. Most neurons recorded responded strongly to changes of light intensity<sup>13</sup> but were polarization-insensitive. This was in marked contrast to a number of neurons whose spike activity could be controlled by the orientation of the polarizer but were indifferent to intensity variations. We shall term these units POL-neurons.

POL-neurons exhibit spontaneous spike activity in the dark