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A long-necked pterosaur (Pterodactyloidea, Azhdarchidae) from the Upper Cretaceous of Valencia, Spain

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Abstract

Fragmentary remains, including cervical vertebrae and limb bones, of a large pterosaur from the Upper Cretaceous of Tous, province of Valencia (Spain), are described. The material was recovered from lacustrine beds in the upper part of the Calizas y Margas de Sierra Perenchiza Formation, which is probably Maastrichtian in age. Six fragments of vertebrae allow a reconstruction of the anatomy of the mid-series cervicals of the animal. The general morphology of the cervical vertebrae is closely similar to that of the long-necked Azhdarchidae. Compared to other azhdarchids, the Valencia pterosaur shows minor differences from the genera *Azhdarcho* and *Quetzalcoatlus*, and is here provisionally referred to as Azhdarchidae indet. A wingspan of about 5.5 m is calculated by comparison with other known azhdarchids. This is the second azhdarchid pterosaur described from the Iberian peninsula. It confirms the wide distribution of this group of large pterosaurs at the end of the Cretaceous.

Abbreviations: MCNA: Museo de Ciencias naturales de Alava, Alava (Spain); MGUV: Museo del Departamento de Geología, Universidad de Valencia, Valencia (Spain); MPV: Museo Paleontológico Municipal de Valencia, Valencia (Spain); TMM: Texas Memorial Museum, Austin, Texas (USA)

Introduction

Pterosaurs are well known from Early Cretaceous (Wealden, Cambridge Greensand) and early Late Cretaceous (Chalk) formations of England and elsewhere in Europe (Wellnhofer 1991). Until recently, our knowledge of latest Cretaceous pterosaurs of Europe was based on only a few specimens from central and eastern regions (Wellnhofer 1978, 1991; see also Bakhurina & Unwin 1995, and references therein).

This situation has changed during recent years with the discovery of new pterosaur material at several localities in southwest Europe, i.e., the Iberian peninsula (Astibia et al. 1990, Buffetaut in press) and southern France (Buffetaut et al. 1996, 1997). In the present contribution, we report on some azhdarchid pterosaur remains from the uppermost Cretaceous of the province of Valencia, eastern Iberian peninsula. The new material represents the second Iberian record of flying reptiles at the very end of the Cretaceous.

Latest Cretaceous European pterosaurs

The first description of pterosaur bones from the very latest Cretaceous deposits of Europe was Seeley's (1881) report on *Ornithocheirus bunzeli* Seeley from the Campanian Gosau Formation of Muthmannsdorf, Austria. Previously, Bunzel (1871) had figured one of

the bones, but had referred it erroneously to a lizard. Wellnhofer (1980) revised the Gosau material and described a lower-jaw fragment as *O. bunzeli*, and several wing phalanges and a humerus as *Ornithocheirus* sp. More recently, the humerus has been reinterpreted as that of a possible member of the family Nyctosauridae (sensu Bennett 1989) by Jianu et al. (1997).

In Transylvania, pterosaur remains from the Maastrichtian Sânpetru Formation of the Hateg Basin have been known for nearly a century. Nopcsa (1914) listed the occurrence of isolated teeth, vertebrae (including a notarium) and hollow bone fragments, which he interpreted as closely related to *Ornithodesmus* (Nopcsa 1923). *Ornithodesmus cluniculus*, the type species, is now regarded as a maniraptoran theropod, and the other known species, *'O.' latidens*, should be transferred to a new genus (Howse & Milner 1993). Nopcsa's material was never figured and was considered lost until recently, when Coralia-Maria Jianu and David B. Weishampel rediscovered part of it at the Magyar Allami Földtani Intézet (Budapest). The Sânpetru site has yielded new pterosaur remains in recent years, including two notaria as well as limb bones. Jianu et al. (1997) provisionally referred this material to the Pteranodontidae (sensu Bennett 1989).

The first pterosaur material found on the Russian platform was a single incomplete cervical vertebra from the marine Phosphatic Greensand (Coniacian?–Santonian, or possibly Early Campanian) of the Penza District (province of Saratov, Volga region). The specimen, now lost, was named *Ornithostoma orientalis* by Bogolubov (1914) but was later regarded as a new azhdarchid genus, *Bogolubovia* (Nessov & Yarkov 1989). In a recent revision, Bakhurina & Unwin (1995) considered this taxon to be a *nomen dubium* and tentatively assigned the vertebra to the Azhdarchidae.

In Portugal, De Lapparent & Zbyszsewki (1957) mentioned – but did not figure – four caudal vertebrae from the Upper Campanian-Maastrichtian of Viso (formerly Vizo), in the province of Beira Litoral. These vertebrae were believed to be of a long-tailed 'rhamphorhynchoid' pterosaur (De Lapparent & Zbyszsewki 1957). Antunes & Pais (1978) listed the Viso vertebrae as indeterminate pterosaurian, pointing out that they had previously been identified by Sauvage (1898) as ?bird. Recently, Galton (1994, 1996) referred two of the caudal vertebrae from Viso to a coelurosaurian theropod as Maniraptora *incertae sedis*, while the other 'vertebrae' were reinterpreted as indeterminate distal caudal vertebrae and a fragmentary long bone. Thus, no pterosaurian material is currently known from the Upper Cretaceous of Portugal.

Astibia et al. (1990) reported the occurrence of pterosaur remains in the Laño quarry, northern Iberian Peninsula. Laño is the most productive pterosaur locality in the Upper Cretaceous of Europe to date. The material consists of a jaw fragment, several elements of the vertebral column and limb bones of a large, but not gigantic, azhdarchid pterosaur. Buffetaut (1999) points out that the Laño pterosaur shows a strong resemblance to the genus *Azhdarcho*, an azhdarchid from the Turonian–Coniacian of Uzbekistan (Nessov 1984, 1997, Archibald et al. 1998).

Other pterosaur material from the Ibero-Occitan region has been found recently in southern France. The first pterosaur material found in the Upper Cretaceous of Languedoc consists of an indeterminate bone fragment from the Maastrichtian of Fontjoncouse, Aude (Buffetaut et al. 1996). In addition, Buffetaut et al. (1997) described a very large *Quetzalcoatlus*-like vertebra from the Maastrichtian of Mérigon (Ariège), in the foothills of the Pyrenees, and referred it to the Azhdarchidae.

Additional data are needed for a more detailed picture of latest Cretaceous pterosaurs of Europe. The material available to date, relatively incomplete as it is, does suggest the presence in Europe of representatives of several families of pterodactyloids (Table 1). In central Europe, ornithocheirids such as *Ornithocheirus* and a possible nyctosaurid are present in the Lower Campanian of Austria (Wellnhofer 1980, Jianu et al. 1997), and a basal pteranodontid has been reported from the Maastrichtian of Transylvania (Jianu et al. 1997). According to these authors, this family is also represented in the Turonian of Bohemia, e.g. *Ornithocheirus hlavatschi* of Fritsch (1881). The assignment of these fragmentary remains to either Ornithocheiridae, Nyctosauridae or Pteranodontidae is controversial, however, and additional material is needed to determine whether these families of pterosaurs are really represented in the Upper Cretaceous of Europe (D. Unwin, pers. comm.). On the contrary, azhdarchids are best represented in – and have been recorded from – several Campanian-Maastrichtian localities in southern France and the Iberian Peninsula (Astibia et al. 1990, Buffetaut et al. 1997, Buffetaut 1999); they include the new material from the province of Valencia described in the present contribution. In eastern Europe, azhdarchids are known from

Table 1. List of Late Cretaceous pterosaurs of Europe.

Taxon	Material	Age	Locality	Depositional environment	Reference
F. Azhdarchidae					
Azhdarchidae indet.	jaw fragment, vertebrae, and limb bones	Late Campanian (or Early Maastrichtian)	Laño, Treviño County, Iberian Peninsula	Fluviatile	Astibia et al. 1990 Buffetaut (in press)
Azhdarchidae indet.	vertebrae, limb bone fragments	Maastrichtian	Tous, Valencia Prov., Iberian Peninsula	Lacustrine or palustrine	This issue
?Azhdarchidae indet.	cervical vertebra	Maastrichtian	Mérigon, Ariege Dept., Gascogne	Freshwater to brackish	Buffetaut et al. 1997
?Azhdarchidae indet.	cervical vertebra	?Coniacian-Campanian	Malaya Serdova, Penza District, Russia	Marine	Bakhurina & Unwin 1995
F. ?Ornithocheiridae					
Ornithoceirus bunzeli	jaw fragment	Early Campanian	Muthmannsdorf, Austria	Estuarine	Wellnhofer 1980
Ornithocheirus sp.	wing phalanges	Early Campanian	Muthmannsdorf, Austria	Estuarine	Wellnhofer 1980
F. ?Nyctosauridae					
cf. Nyctosauridae indet.	humerus	Early Campanian	Muthmannsdorf, Austria	Estuarine	Jianu et al. 1997
F. Pteranodontidae					
Pteranodontidae indet.	notaria, humerus, femur	Maastrichtian	Sânpetru, Transylvania	Fluviatile	Jianu et al. 1997
Family indet.					
Pterosauria indet.	bone fragment	Maastrichtian	Fontjoncouse, Aude Languedoc	Fluviatile	Buffetaut et al. 1996
?Pterosauria indet.	bone fragments	Campanian	Lysaya Gora, Volgograd District, Russia	Marine	Bukhurina & Unwin 1995

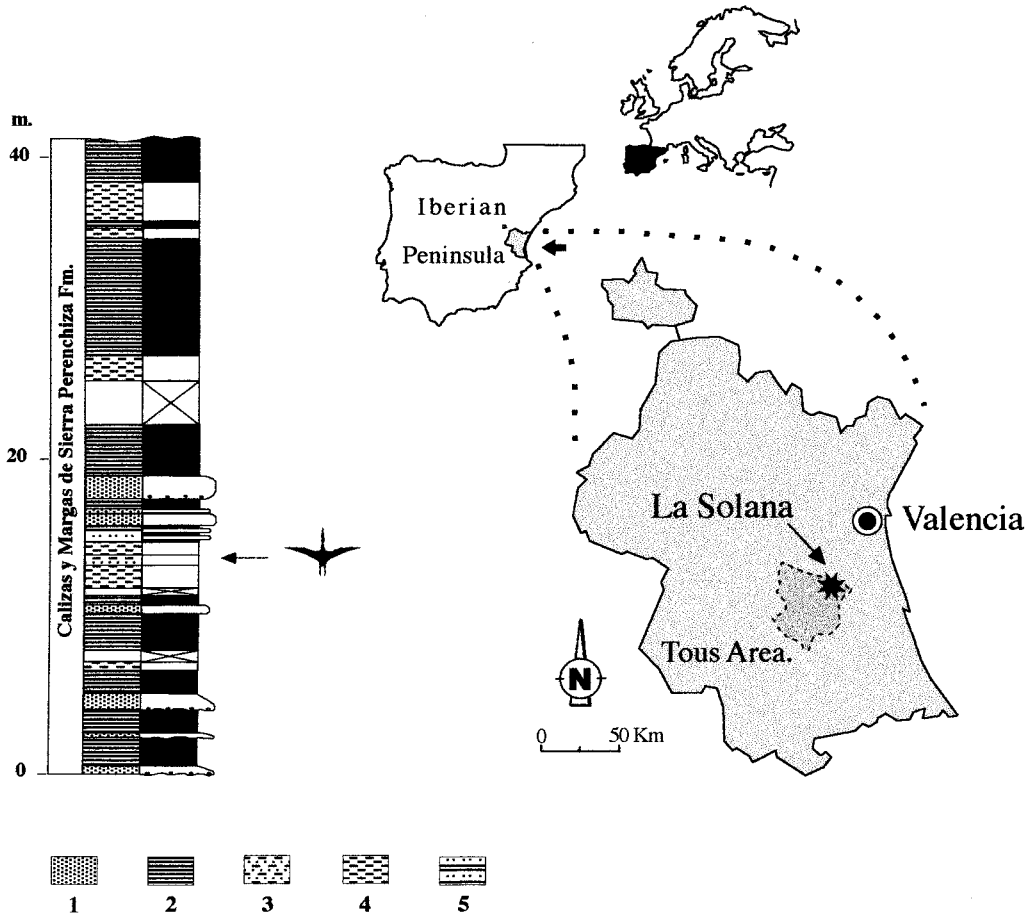

Figure 1. Map showing the locality of La Solana (Tous area, eastern Spain), and the stratigraphic provenance of the pterosaurian material collected. 1 = sandstones; 2 = shales; 3 = silty marls; 4 = marls; 5 = interbedded marls and shales.

the Coniacian-Campanian of the Russian platform (Bogolubov 1914, Bakhurina & Unwin 1995).

Geological and palaeontological context of the specimen described

The locality of the new pterosaur, La Solana, is located in the Tous area, 11 km east of the city of Valencia, in the province of Valencia (eastern Iberian Peninsula, Figure 1). The material was recovered from the upper beds of the Calizas y Margas de Sierra Perenchiza Formation, which probably is Maastrichtian in age (Gutiérrez et al. 1984). These deposits represent a lacustrine sussession, composed of dark red and grey clays and silts with interbedded beds of silty marls, which are overlain by Palaeogene fluvial sandstones. In addition to pterosaur remains, the La Solana locality vertebrate assemblage includes bones and teeth of fishes, frogs, turtles, crocodiles and dinosaurs (Company et al. 1997, 1998).

The pterosaur remains were found scattered at the site. The material consists of disarticulated fragmentary cervical vertebrae and miscellaneous limb fragments. No cranial material is known and none of the bones is complete. The variable size of the vertebral specimens indicates the occurrence of several individuals of large pterodactyloid pterosaurs (see Table 2). All specimens have internal cavities filled by a calcareous matrix, and many of them have become encrusted by calcareous and haematitic material. This external and internal covering preserved the bones from both diagenetic compaction and weathering, so that the specimens are well preserved and have main-

Table 2. Measurements (in mm) of the cervical vertebrae of the Tous pterosaur.

Specimen	M1	M2	M3	M4	M5	M6	M7
MGUV 2271	91	–	30	64	68**	12	9
MPV TT48	73	43*	–	–	–	9	6

M1 = Length as preserved.
M2 = Maximum width of the centrum.
M3 = Maximum width of the centrum.
M4 = Maximum distance across the postzygapophyses.
M5 = Maximum distance across the postexapophyses.
M6 = Maximum diameter of the neural foramen.
M7 = Maximum diameter of the pneumatic foramina.
* Width as preserved. ** Reconstructed specimen measurement.

tained their original three-dimensional character. Only the outer layer of compact bone is somewhat cracked and slightly crushed or distorted.

The calcareous crust was removed using a 5% solution of formic acid buffered with calcium phosphate (Rutzky et al. 1994). The Waller method (Blum et al. 1989) was applied to remove the ferruginous concretions.

Systematic palaeontology

Order Pterosauria Kaup 1834
Suborder Pterodactyloidea Plieninger 1901
Family Azhdarchidae Nessov 1984 (emend. Padian 1986)
Genus and species indeterminate (Plates 1–2; Figures 2–7, Table 2)

Material

The material listed below is housed and catalogued in the mgUV and MPV vertebrate collections as follows:
MGUV 2194: right postexapophysis of a cervical vertebra;
MGUV 2195: fragmentary limb bone;
MGUV 2239: fragmentary limb bone;
MGUV 2271: posterior end of a mid-series cervical vertebra;
MGUV 3207: partially preserved anterior end of a mid-series cervical vertebra;
MGUV 3209: right prezygapophysis of a cervical vertebra;
MGUV 3210: left postexapophysis of a cervical vertebra;
MPV TT48: anterior end of a mid-series cervical vertebra;
MPV TT49: fragmentary limb bone (probably a wing phalanx).

Description of the material

Cervical vertebrae – At least six fragmentary cervical vertebrae are known, inclusive of portions of the centra and neural arches.

MPV TT48 (Figure 2A–D; Plate 1: A–D) comprises the anterior end of an elongate mid-series cervical vertebra. The total length of the specimen as preserved is 73 mm. The anterior articular region is partially missing and only the base of the right prezygapophysis is preserved. The cervical shows a slight lateral distortion, so that the neural spine and ventral hypapophysis are not placed in the same vertical plane, but otherwise the specimen is uncrushed. The lateral sides are eroded, and the internal delicate trabecular tissue is visible.

MGUV 3207 (Plate 1: E–F) is a second anterior fragment of a mid-cervical with both prezygapophyses.

MGUV 2271 (Figure 3A–C; Plate 2: A–F) is the posterior end of a mid-series cervical vertebra, most probably the sixth (W. Langston, pers. comm.). Only the posterior 91 mm are preserved. The end of the left postexapophysis is broken off. This specimen is uncrushed and is relatively well preserved for a pterosaur. Cortical bone thickness ranges from 2.3 mm in the lateral walls of the centrum to 0.5 mm on the condylar region and less than 0.2 mm on the extremely thin walls of the pneumatic foramina and the neural canal.

MGUV 2194, 3209 and 3210 are fragmentary apophyseal elements of cervical vertebrae (Figure 4A–C; Plate 1: G–K).

As reconstructed, the mid-series cervical is strongly procoelous. The body of the vertebra is long, waisted anteroposteriorly and flattened dorsoventrally, with both articular ends wider than high. The centrum gradually increases in width from the base of the posterior apophyses to the anterior end (Figure 5), where the cross-section of the vertebra displays a rhomboidal shape.

The anterior cotyle (**anc**) is heart-shaped, dorsoventrally compressed, with the dorsal margin concave and the ventral one clearly convex. There is a well-marked hypapophysis (**hyp**) on the anterior end of the ventral margin of the centrum. The height of this structure diminishes progressively towards the mid-length of the vertebra. No longitudinal sulci are

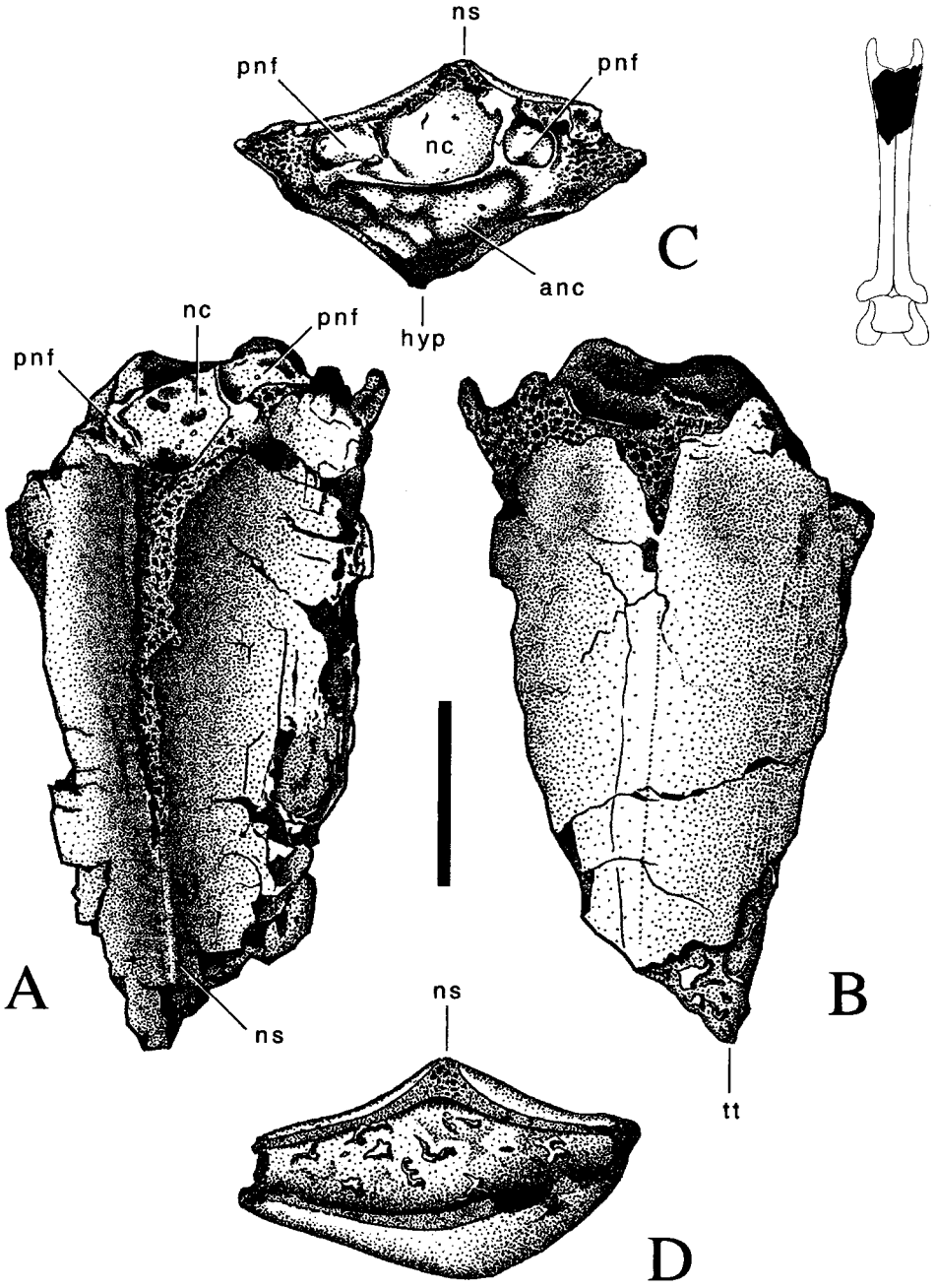

Figure 2. Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). Scale bar equals 20 mm. Anterior end of cervical vertebra (MPV TT48) in dorsal (A), ventral (B), anterior (C), and posterior (D) views. Inset shows position of fragment in the complete element. anc = anterior cotyle; hyp = hypapophysis; nc = neural canal; ns = neural spine; pnf = pneumatic foramen; tt = trabecular tissue.

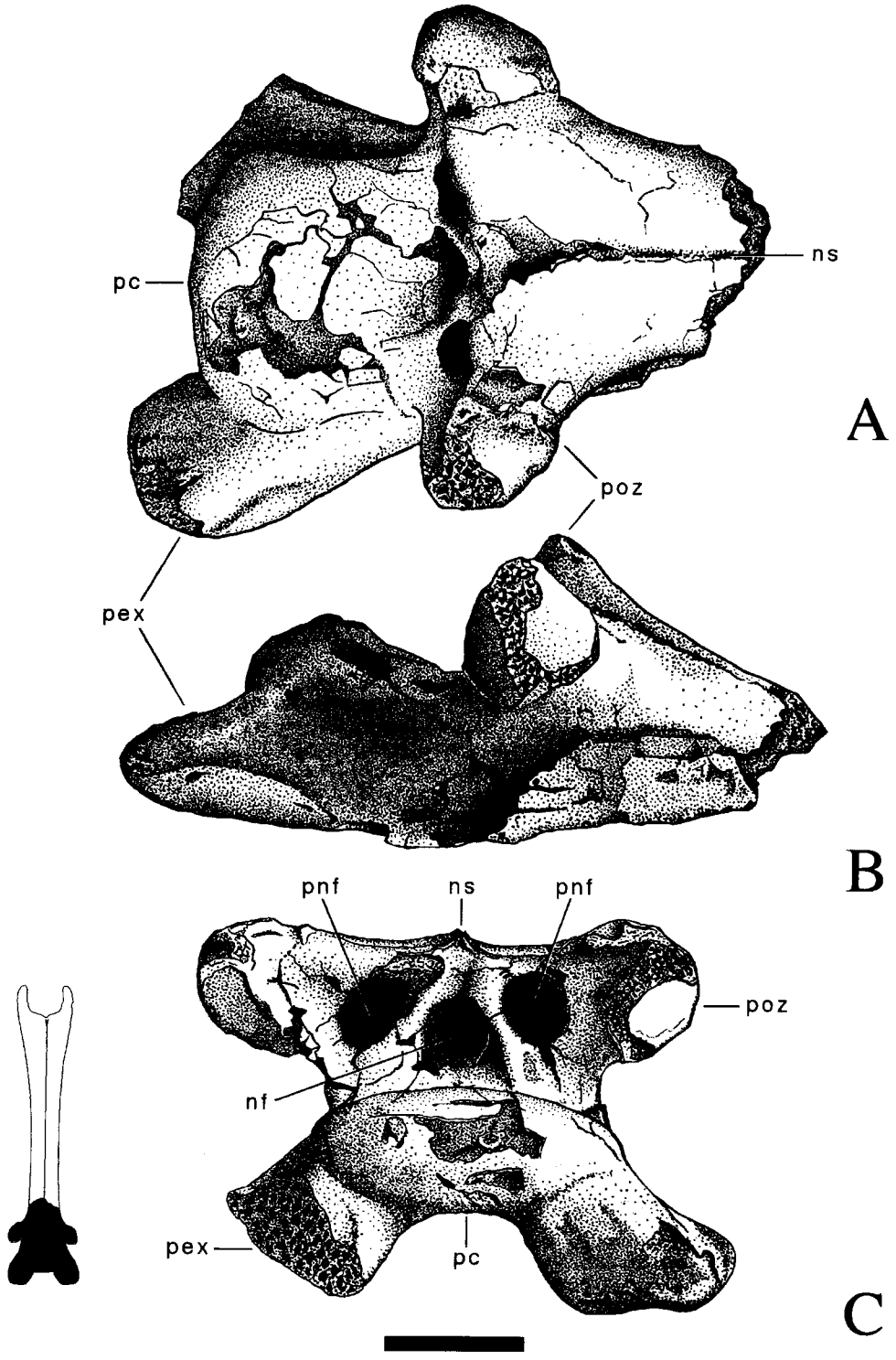

Figure 3. Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). Scale bar equals 20 mm. Sixth cervical vertebra (MGUV 2271) in dorsal (A), right lateral (B), and posterior (C) views. Inset shows position of fragment in the complete element. nf = neural foramen; ns = neural spine; pnf = pneumatic foramen; pc = posterior condyle; pex = postexapophysis; poz = postzygapophysis.

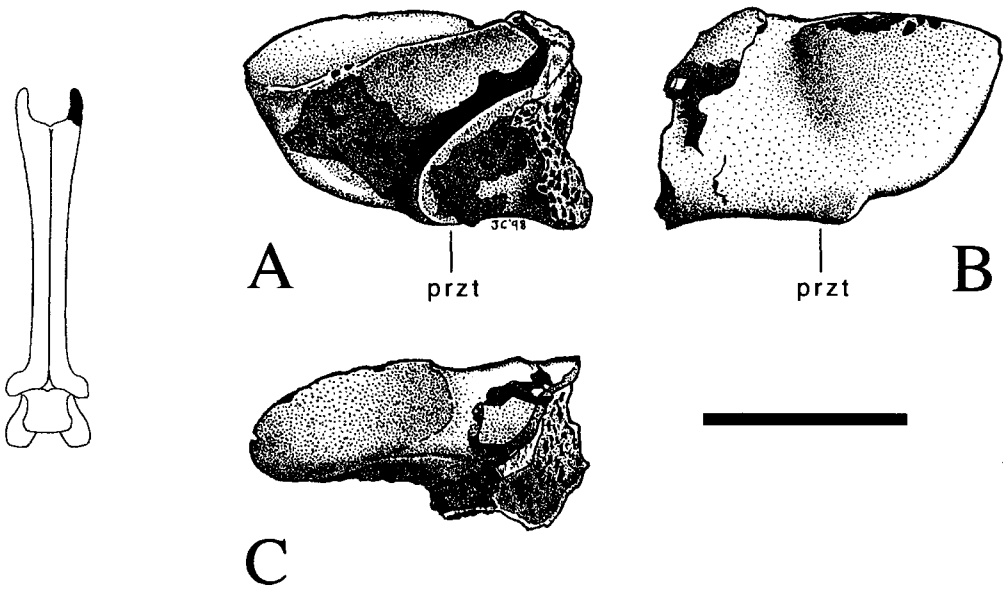

Figure 4. Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). Scale bar equals 20 mm. Right prezygapophysis (MGUV 3209) in medial (A), lateral (B) and dorsal (C) views. Inset shows position of fragment in the complete element. przt = pregapophysial tubercle.

observed in the specimens. The articular surface of the posterior condyle (**pc**) is flat oval in shape. The dorsal face of the centrum anterior to the condyle is flat, whereas its ventral surface is clearly concave, owing to the large size of the exapophyses.

The neural arch is low, but becomes somewhat higher at the anterior and posterior ends. As in other known azhdarchids, the neural spine (**nsp**) consists of a low longitudinal mid-line ridge on the dorsal side of the neural arch. Its wide anterior and posterior broken base (preserved as eroded surfaces) suggests that this structure was more prominent towards either end of the neural arch, and tended to fade away towards the middle part of the vertebra (see Howse 1986). Anteriorly, the flanks of the neural arch adjacent to the neural spine are flat or shallowly concave.

The anterio-lateral margins of the neural arch are projected into two elongate prezygapophysial processes (**prz**). They terminate in elliptical articular surfaces that are dorsomedially oriented. The prezygapophyses bear a flat ventromedial tubercle (**przt**), close to the lateral border of the cotylar region (Figure 4). As in other long-necked Late Cretaceous pterosaurs, the prezygapophyses are nearly parallel, or diverge sligtly anteriorly.

The posterior region of the vertebra displays two pairs of well-developed apophysial processes. The postexapophyses (**pex**) are posterolaterally directed and emerge from the ventrolateral margins of the posterior condyle. They diverge, with an angle between their medial edges of about 50°. A postzygapophysial process **(poz)** arises from either side of the dorsal margin of the neural arch. These processes are widely divergent and terminate in oval articular facets, which faces backwards, somewhat outwards and slightly downwards. The posterior articular condyle and the postexapophyses extend posteriorly far beyond the maximum extension of the postzygapophysial processes.

The anterior and posterior ends of the neural arch bear three large foramina (Figures 2A, C, 3C; Plate 1: A; Plate 2: A). The biggest and central foramen (see measurements in Table 2) is the opening of the neural canal (**nc**). The lateral foramina are smaller and almost circular in shape. They are interpreted as pneumatic foramina (**pnf**).

The exposed surfaces of the broken proximal and distal ends of the vertebrae show the internal structure of the neural arch. The interior of this vaulted structure is filled by carbonate matrix. There is no evidence of either the bony tube (tuba vertebralis, sensu Martill et al. 1998) that enclosed the medulla or the extension of the pneumatic foramina. Only a little dense trabeculae tissue (**tt**) is visible.

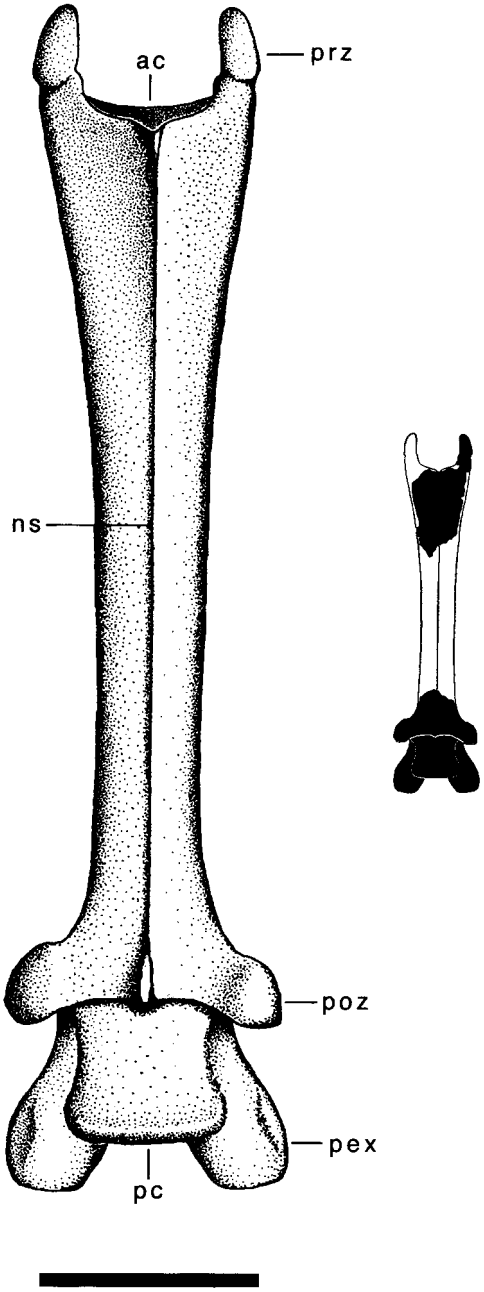

Figure 5. Speculative reconstruction of a mid-cervical vertebra of an indeterminate azhdarchid pterosaur from the Upper Cretaceous of La Solana (Tous area, Spain) in dorsal view, based on specimens collected and on other known azhdarchids (TMM 41544.15, MCNA 8563). Scale bar equals 50 mm. Inset shows position of fragments in the complete element. For abbreviations: see Figures 2 and 3; prz = prezygapophysis.

Appendicular skeleton – The appendicular material from Tous includes remains of three limb bones. These bones are somewhat crushed and distorted but, like the vertebrae, they are preserved without having been compressed. The specimens are fragmentary and lack the articular ends, so it is difficult to determine whether they represent metacarpal or phalangeal elements. In spite of the crushed condition, the bony walls show by their curvature that the original cross-section was slightly elliptical. The bones are hollow and their interior is filled with calcareous matrix (**cm**).

MGUV 2239 is a 65 mm long fragment of an indeterminate limb bone (Figures 6A–B; Plate 2: G–H). The cross-section of the shaft is elliptical and the thickness of the cortical bone (**cbn**) is approx. 2 mm.

MGUV 2195 is a second fragment, 22 mm long and similar in shape to MGUV 2239.

MPV TT49 is a slightly cone-shaped limb bone of about 67 mm in length. The outline of the shaft is oval (greatest diameter at the ?proximal end is 26 mm, greatest diameter at the ?distal end is 24 mm) and the wall thickness is 4.2 mm.

Discussion

The following discussion is based mainly on the cervical material, since the limb bones are too fragmentary to provide much useful information. Among pterosaurs, only the Late Jurassic–Early Cretaceous ctenochasmatoids and the Late Cretaceous (and probably Early Cretaceous; see Murry et al. 1991, Martill & Frey 1998, 1999) azhdarchids have long and slender mid-series cervical vertebrae, similar to those of the Valencia pterosaur. The overall morphology of the cervical (e.g., elongate centrum, low or vestigial neural spine and absence of preexapophyseal processes) resembles that of the family of Azhdarchidae (Nessov 1984, Howse 1986, Bennett 1989, Wellnhofer 1991, Frey & Martill 1996, Martill et al. 1998). Finally, the stratigraphic position of the fossil remains is consistent with the temporal distribution of this group of long-necked pterosaurs (Wellnhofer 1991). Consequently, we assign the cervical remains from Tous to the Azhdarchidae. In view of their association with the cervical vertebrae and their close agreement in size, the fragments of wing phalanges are also assigned to the Azdarchidae.

The Tous specimen shows major vertebral differences as compared with *Arambourgiania philadelphiae* from the Maastrichtian of Jordan (Frey &

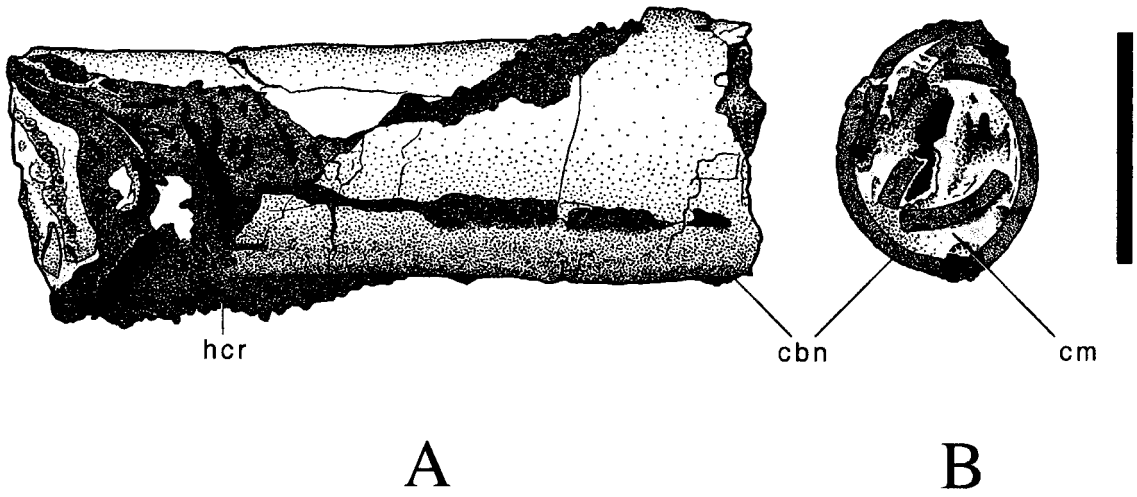

Figure 6. Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). Scale bar equals 20 mm. Limb bone fragment (MGUV 2239) in ?dorsal (A) and ?proximal (B) views. cbn = cortical bone; hcr = haematitic crust; cm = carbonate matrix.

Martill 1996, Martill et al. 1998). This species is based mainly on a very large and extremely elongate cervical vertebra, which differs from the Spanish pterosaur in having three low dorsal carinae on the neural arch (i.e., the neural spine and two lateral divergent carinae, anteriorly placed), posteroventrally oriented postexapophyses, high oval outline at the midpoint of the centrum, a heart-shaped articular cotyle that is higher than wide, a neural canal (tuba vertebralis of Martill et al. 1998) that has been ossified throughout its length, and an anterior opening of the neural canal smaller than the pneumatic foramina.

The vertebral material of the Tous pterosaur seems closer to those of the azhdarchids *Azhdarcho lancicollis* from the Turonian-Coniacian of Uzbekistan (Nessov 1984, 1997, Bakhurina & Unwin 1995) and *Quetzalcoatlus* sp. from the Maastrichtian of Texas (Lawson 1975, Langston 1981, Howse 1986). The overall form of the anterior cotyle and the shape and orientation of the zygapophyses preserved in *A. lancicollis* agree with those in the specimens described above. Nevertheless, the cervical vertebrae of *Azhdarcho* differ from those of the Tous pterosaur in the presence of a third pneumatic foramen placed above the neural canal (Nessov 1984, Bakhurina & Unwin 1995), in the existence of ridges lateral to the neural spine, and in having a higher neural arch in the anterior end of the vertebra. A preliminary comparison of the Valencia pterosaur with the cervical vertebrae of *Quetzalcoatlus* sp. (Langston in prep.) suggests minor differences. *Quetzalcoatlus* bears less well-developed postexapophyses which merge from a bulbous condyle. These features resemble those of the indeterminate azhdarchid pterosaur from the Upper 'Senonian' of Senegal (Monteillet et al. 1982).

The postzygapophyses, by contrast, are stouter in *Quetzalcoatlus* than in the Tous pterosaur and these processes are posteriorly directed in the Texas specimen. The ventral ridges of the centra observed in the cervicals of *Quetzalcoatlus* and *Azhdarcho* may correspond with the faint parallel striae present in MPV TT48.

The Laño quarry has yielded fragmentary pterosaur remains that have been described by Astibia et al. (1990). One of the most interesting specimens is a crushed but otherwise well-preserved mid-cervical vertebra (MCNA 8563), which is somewhat smaller than the Tous vertebrae. The Laño pterosaur has azhdarchid affinities (Buffetaut 1999) and may pertain to a taxon close to the Tous animal. Both are characterised by having stout postexapophyses larger than postzygapophyses – in contrast to *Quetzalcoatlus* – and weakly marked ventral crests.

The morphology of the cervical vertebrae of other azhdarchids such as *Montanazhdarcho minor* (see Padian et al. 1995) and *Zhejiangopterus linhaiensis* (see Cai & Wei 1994, Unwin & Lü 1997) is not well known, so that a comparison with the Tous material is impossible. As far as is known, *Montanazhdarcho* and *Zhejiangopterus* are smaller (2.5 and 3.5 m wingspan, respectively) than the Valencia pterosaur.

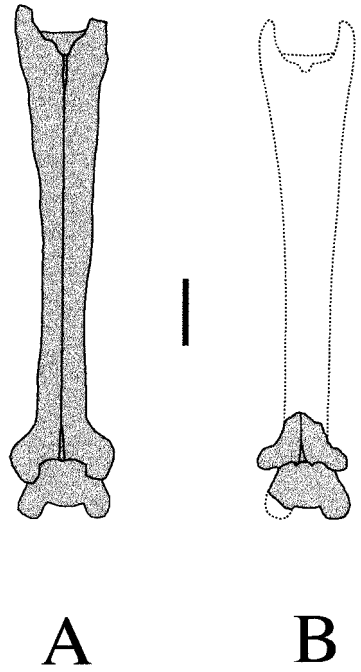

Figure 7. Comparative diagrams of mid-cervical vertebrae. Scale bar equals 50 mm. A: sixth cervical of *Quetzalcoatlus* sp. (TMM 42180-19). B: sixth cervical of the Tous pterosaur (MGUV 2271) in dorsal view.

All in all, the Tous pterosaur cervical vertebrae show minor differences from those of *Azhdarcho* and *Quetzalcoatlus*, and especially from that of the unnamed azhdarchid from Laño. The scanty nature of the remains makes it difficult to determine whether such differences represent ontogenetic, individual, sexual or intraspecific variation. Major differences are found in a comparison with *Arambourgiania*.

Estimated wingspan of the Tous pterosaur

It is difficult to estimate the total wingspan (wsp) of the Tous pterosaur because of the fragmentary nature of the material. The dimensions of the presumed sixth cervical (MGUV 2271) are very similar to those of the sixth cervical of *Quetzalcoatlus* sp. (TMM 42180-19) (Figure 7). Both specimens probably represent similar-sized pterosaurs, so that the wingspan of the Valencia animal could have been about 5.5 metres (see Langston 1981). Therefore, the pterosaur from La Solana represents a very large (wsp = 4–7.5 m) but not a giant form (wsp > 7.5 m) (Unwin 1987).

Conclusions

The pterosaur material from the Upper Cretaceous of Valencia is assigned to the Azhdarchidae mainly on the basis of the uniquely shared features of the cervical vertebrae. Even though the described pterosaur presents undoubted affinities with *Azhdarcho lancicollis*, *Quetzalcoatlus* sp. and especially with an unnamed form from the Laño quarry, the differences observed do not allow us to assign the Tous material to any known genus of this pterodactyloid family. Pending the discovery of new informative material, the specimens are here provisionally referred to as Azhdarchidae indet. The remains were found in terrestrial deposits, which supports the idea that these pterosaurs inhabited such environments. The estimated wing span of this pterosaur is close to 5 m.

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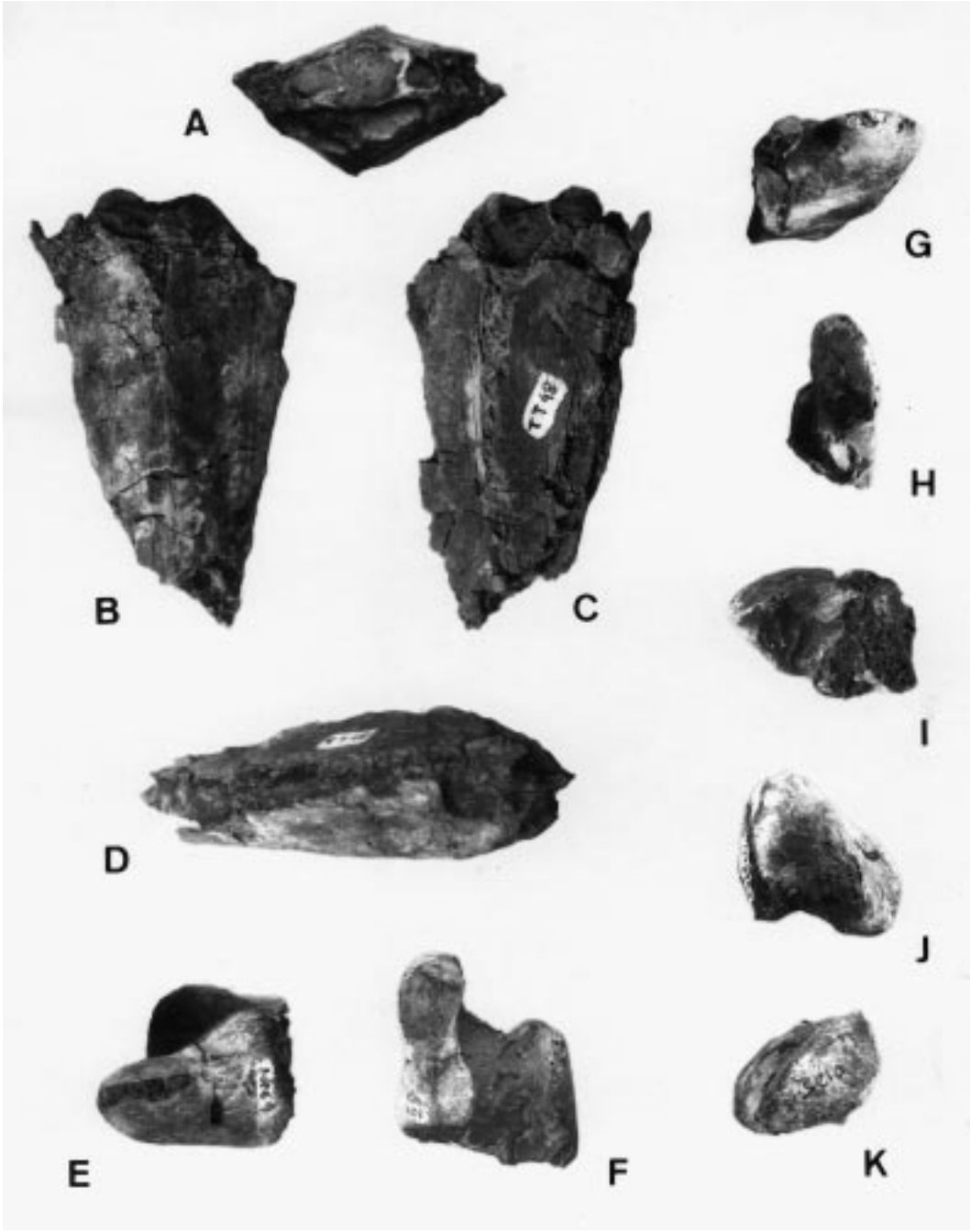

Plate I. Postcranial remains of Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). A–D: anterior end of mid-series cervical vertebra (MPV TT48) in anterior (A), ventral (B), dorsal (C) and right lateral (D) views, × 0.8. E–F: anterior end of mid-series cervical vertebra (MGUV 3207) in left lateral (E) and dorsal (F) views, × 0.85. G–I: right prezygapophysis (MGUV 3209) in right lateral (G), dorsal (H) and medial (I) views, × 0.85. J: right postexapophysis of cervical vertebra (MGUV 2194) in dorsal view, × 0.85. K: left postexapophysis of cervical vertebra (MGUV 3210) in dorsal view, × 0.85.

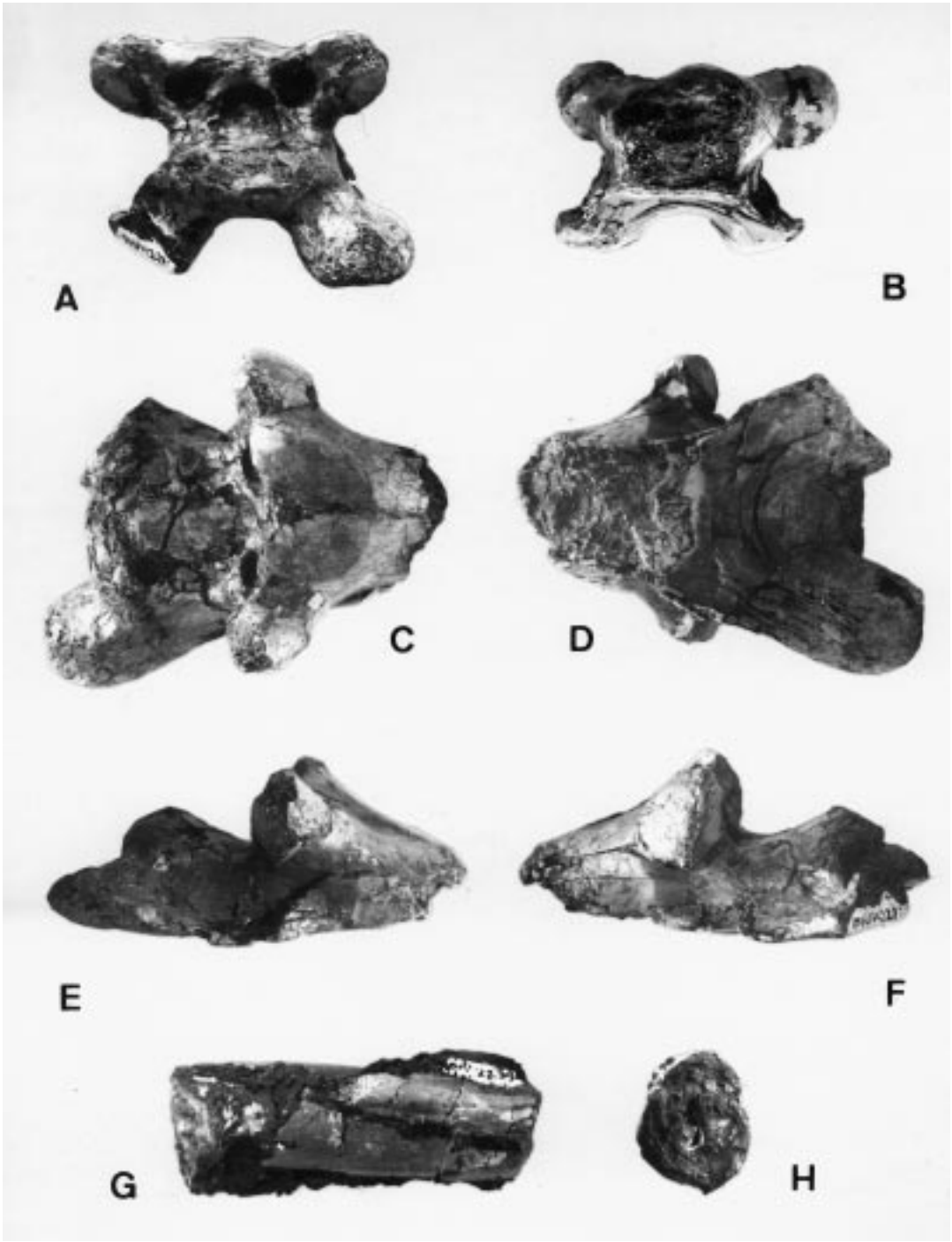

Plate II. Postcranial remains of Azhdarchidae indet. from the Upper Cretaceous of La Solana (Tous area, Spain). A–F: ?sixth cervical vertebra (MGUV 2271) in posterior (A), anterior (B), dorsal (C), ventral (D), right lateral (E), and left lateral (F) views, × 0.75. G–H: fragmentary limb bone (MGUV 2239) in ?dorsal (G) and ?proximal (H) views, × 0.85.