The European Early Cretaceous cryptodiran turtle *Chitracephalus dumonii* and the diversity of a poorly known lineage of turtles

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Chitracephalus dumonii was named based on some of the most complete turtle remains from the Lower Cretaceous of Europe, and yet the taxon has barely been mentioned since. Indeed, new specimens were erroneously attributed to a new taxon, "*Salasemys pulcherrima*". The synonymy is recognized here, and this extends the geographical range of this turtle and provides examples of individuals at different stages of ontogenetic development. The peculiar structure of its shell, and its ontogenetic development, are unique to this taxon. The systematic position of *C. dumonii* was previously unclear, usually being referred to Testudinata incertae sedis. Here, it is placed in a cladistic analysis, which shows that *C. dumonii,* and the recently described *Hoyasemys jimenezi* form part of a Lower Cretaceous European clade of Cryptodira that includes "macrobaenid", "sinemydid", and panchelonioidean turtles.

Key words: Testudines, Eucryptodira, Cryptodira, *Chitracephalus dumonii*, "*Salasemys pulcherrima*", Cretaceous, Belgium, Spain.

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Introduction

In 1885, Louis Dollo published a paper about the Lower Cretaceous turtles from the famous mines of Bernissart (Hainaut, Belgium). In this work he described two new taxa, *Peltochelys duchastelii* and *Chitracephalus dumonii*. Dollo (1885) attributed several shells to *P. duchastelii*, of which only the holotype is currently considered to be a potential representative of the trionychian stem lineage (Meylan 1988; Joyce 2007), whereas the other specimens are thought to be indeterminate juveniles (Pérez-García 2011). *C. dumonii* was represented by a single individual, which retained most of its skeletal elements. Dollo (1885) attributed *C. dumonii* to "Thalassemydes" and therefore considered it to be the only taxon of this group with a post-Jurassic distribution.

Dollo (1885) considered his work to be a preliminary note and stated his intention to publish a further paper with a more accurate analysis of the turtles from Bernissart. He included only photographs of the type specimen of *C. dumonii*, but no interpretive drawings showing the boundaries between the bones of the skull or shell or the morphology of the vertebrae. However, Dollo never published any more on these turtles. Until now no additional material has been assigned to *C. dumonii*, its morphology has not been reviewed, and it has never been placed in a phylogenetic hypothesis. For this reason, *C. dumonii* has often been identified as Testudinata incertae sedis (e.g., Gaffney 1979; Carroll 1988; Lapparent de Broin 2001). Although *C. dumonii* has been identified as a representative of an unspecified node of Pleurodira (Casier 1978; Martínez Marmaneu and Sanfeliú Montolio 1978), specifically as a representative of Chelidae (Nopcsa 1934), or grouped with the enigmatic *Apertotemporalis baharijensis* (taxon identified as Bothremydidae incertae sedis by Lapparent de Broin 2000, and as a nomen dubium by Gaffney et al. 2006) in Apertotemporalidae (Kuhn 1964; Mlynarski 1976), others authors have considered it to be a member of Eucryptodira (Hirayama et al. 2000; Pérez-García et al. 2010b). Unfortunately, no morphological observations were provided that would support these assignments.

The record of Lower Cretaceous European continental turtles is relatively limited and complete turtle skeletons are rare (Pérez-García et al. 2012). However, the study of these skeletons may significantly increase knowledge about European Mesozoic turtles, which are generally known by cranial material or partial shells, and which therefore, have suffered from parataxonomic conflicts (e.g., Joyce 2000).

The purpose of this study is to provide for the first time a detailed description of the type material of *C. dumonii*. The geographical range of this taxon is expanded (Fig. 1) through the referral of the little known Spanish taxon "*Salasemys pulcherrima*". The identification of several specimens attributed to *C. dumonii* allows the recognition of structural and

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Fig. 1. Geographical location of the areas where *Chitracephalus dumonii* has been identified: The type locality, Bernissart (Hainaut, Belgium), and the Spanish localities of Tenadas del Jabalí (Burgos) and Torremuña (La Rioja).

ornamental patterns not shared with any other taxon, as well as ontogenetic variation.

Institutional abbreviations.—ICIPLR, Igea, Centro de Interpretación Paleontológico de La Rioja, La Rioja, Spain; IRSNB, Institut Royal des Sciences Naturelles, Brussels, Belgium; MDS, Museo de Dinosaurios de Salas de los Infantes, Burgos, Spain.

Phylogenetic analysis

I present the phylogenetic analysis first, in order to establish the systematic position of *Chitracephalus dumonii*. Considering that this taxon is an unequivocal pancryptodire (sensu Joyce et al. 2004) (see Discussion), I used the reduced version of the data matrix of Joyce (2007) proposed in Pérez-García et al. (2012). *C. dumonii* was scored for 49 of 136 characters (see Appendix 1), based on the holotype (IRSNB R11 and IRSNB R12) and the two Spanish specimens (MDS-JTS.V.1–40 and ICIPLR-1). As in Pérez-García et al. (2012), the phylogenetic analysis was conducted using the program TNT v. 1.0 (Goloboff et al. 2008) with *Proganochelys quenstedti* as the outgroup. All characters were considered unordered and equally weighted. The phylogenetic analysis resulted in 73 most parsimonious trees (MPTs) of 298 steps (consistency index (CI) = 0.567, retention index (RI) = 0.872). The majority rule tree (Fig. 2) shows a composition of the node Cryptodira different from that obtained by Joyce (2007) and by Pérez-García et al. (2012). Moreover, a polytomy is observed at the base of Pancryptodira, which includes *Dorsetochelys delairi*, Paracryptodira, and Eucryptodira. In the preferred phylogenetic hypothesis of Joyce (2007), Eucryptodira was hypothesized to be the sister taxon of *D. delairi* + Paracryptodira. In the cladogram obtained in Pérez-García et al. (2012), Paracryptodira and Eucryptodira were placed as sisters to the exclusion of *D. delairi*. *Dorsetochelys delairi* is only represented by a crushed skull and its phylogenetic position within Pancryptodira remains uncertain. It has been suggested that this skull may belong with the shell taxa "*Glyptops*" *typocardium* (Milner 2004) or *Hylaeochelys belli* (Hirayama et al. 2000) and that *D. delairi* may therefore be a paracryptodire or eucryptodire, respectively. Neither of these synonymies has been substantiated.

Chitracephalus dumonii is placed within the crown group Cryptodira, in a node that groups *Hoyasemys jimenezi* and the members of "Sinemydidae", "Macrobaenidae" (except *Kirgizemys hoburensis*), and Panchelonioidea (Fig. 2, node F).

The node that groups all turtles more derived than *Xinjiangchelys latimarginalis* (Fig. 2, node D), is diagnosed by: epiplastra elongate in shape, with long posteromedial contact with the hyoplastra (character 83 in Joyce 2007); extragular scutes absent (character 92); posterior cervicals with strongly developed ventral keels (character 103); and presence of cervical central articulations (character 105). Cryptodira (Fig. 2, node E) is diagnosed by the absence of a parietal–squamosal contact due to the extensive development of an upper temporal emargination (character 11).

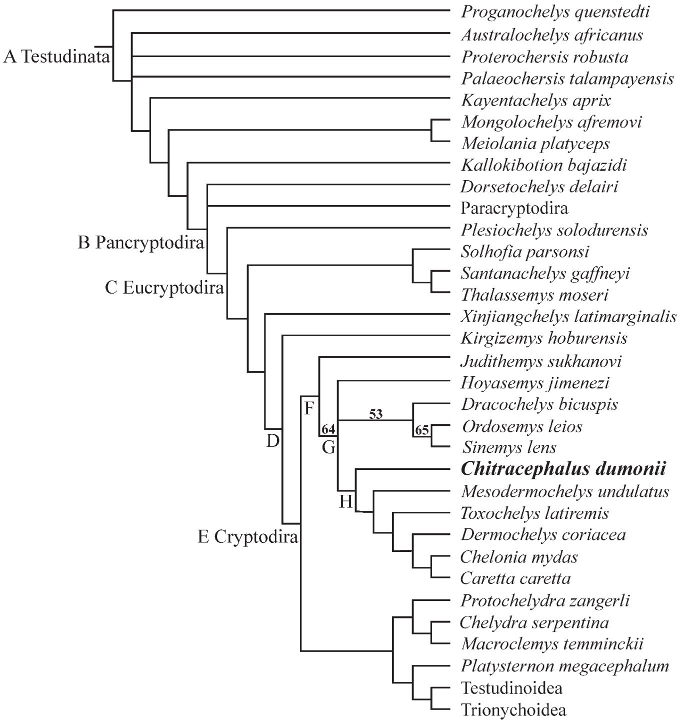

Fig. 2. Majority rule tree from the 73 most parsimonious trees produced by the cladistic analysis of *Chitracephalus dumonii* using the modified data set of Joyce (2007) proposed in Pérez-García et al. (2012). Retention index (RI) = 0.872 and consistency index (CI) = 0.567. Values refer to percentages under 100% obtained in the majority rule analysis; those with values below 50% are collapsed. Letters refer to the nodes mentioned in the text.

In Pérez-García et al. (2012), *Hoyasemys jimenezi*, *Judithemys sukhanovi*, *Dracochelys bicuspis*, *Sinemys lens*, and *Ordosemys leios* formed an unnamed clade in 65% of trees. This group was diagnosed by the absence or underdevelopment of chevrons (character 117). In this analysis, that node is obtained in all trees (Fig. 2, node F), and so is diagnosed by the same synapomorphy. This node includes *C. dumonii*, but also *Mesodermochelys undulatus*, *Toxochelys latiremis*, *Dermochelys coriacea*, *Chelonia mydas*, and *Caretta caretta*. (*Chitracephalus dumonii* + (*Mesodermochelys undulatus* + (*Toxochelys latiremis* + (*Dermochelys coriacea* + (*Chelonia mydas* + *Caretta caretta*))))) is obtained as a polytomy with (*Dracochelys bicuspis* + (*Ordosemys leios* + *Sinemys lens*)), and with *Hoyasemys jimenezi* (Fig. 2, node G). The node (*Chitracephalus dumonii* + (*Mesodermochelys undulatus* + (*Toxochelys latiremis* + (*Dermochelys coriacea* + (*Chelonia mydas* + *Caretta caretta*))))) (Fig. 2, node H) is diagnosed by the presence of a xiphiplastral fontanelle, which involves the reduction of the xiphiplastra in narrow struts that frame it (character 88). (*Mesodermochelys undulatus* + (*Toxochelys latiremis* + (*Dermochelys coriacea* + (*Chelonia mydas* + *Caretta caretta*))) differ from *C. dumonii* in the presence of well developed costal fontanelles (character 69). Chelonioidea in not obtained here as a monophyletic group because *Toxochelys latiremis* is situated between its representatives. *C. dumonii* has two autapomorphies in this cladistic analysis: absence of quadratojugal, due to the presence of a deep temporal emargination (character 16); and presence of extragular scutes (character 92). Among the taxa of node F, quadratojugals are also absent in *Sinemys lens* and *S. gamera*, but this is associated with a lack of ossification of the temporal bar and not a result of the deep temporal emargination (Joyce 2007). The primitive presence of extragular scutes is shared with some representatives of Eucryptodira less derived than *Kirgizemys hoburensis*, such as *Plesiochelys solodurensis* and *Xinjiangchelys latimarginalis*.

Systematic palaeontology

Testudines Batsch, 1977

Pancryptodira Joyce, Parham, and Gauthier, 2004

Cryptodira Cope, 1868 sensu Joyce et al. (2004)

Genus *Chitracephalus* Dollo, 1885

2003 *Salasemys*; Fuentes Vidarte, Meijide Calvo, and Meijide Fuentes 2003.

Type species: *Chitracephalus dumonii* Dollo, 1885; Bernissart, Belgium, Barremian–Aptian. Monotypic.

Diagnosis.—The same as for the species; see below.

Stratigraphic and geographic range.—Lower Cretaceous of Western Europe (Dollo 1885; Martín-Closas and Alonso Millán 1998; Fuentes Vidarte et al. 2003; Dejax et al. 2007; Schnyder et al. 2009; Pérez-García et al. 2010a).

Chitracephalus dumonii Dollo, 1885

Figs. 3–7.

2003 *Salasemys pulcherrima*; Fuentes Vidarte, Meijide Calvo, and Meijide Fuentes 2003: 115, 117, pls 1, 2.

Holotype: IRSNB R11 and IRSNB R12, an almost complete skeleton (Figs. 3, 4).

Type locality: Sainte Barbe pit, Bernissart (Hainaut, Belgium) (Fig. 1).

Type horizon: Sainte-Barbe Clays Formation, Mons Basin. Barremian–Aptian (Dejax et al. 2007; Schnyder et al. 2009).

Referred material.—MDS-JTS.V.1–40, a partial skeleton from the Hauterivian–Barremian of Tenadas del Jabalí (Salas de los Infantes, Burgos, Spain) (Fig. 1), the holotype of "*Salasemys pulcherrima*". Pinilla de los Moros Formation, Urbion Group (Martín-Closas and Alonso Millán 1998; Fuentes Vidarte et al. 2003) (Figs. 5, 6). ICIPLR-1, several fragments of plates of a partial carapace from the Barremian–Aptian of Torremuña (La Rioja, Spain) (Fig. 1). Enciso Group (Martín-Closas and Alonso Millán 1998; Pérez-García et al. 2010a) (Fig. 7).

Emended diagnosis.—Cryptodiran turtle with the following autapomorphies: skull very elongate and depressed, with large orbits in antero-dorsal position; temporal area characterized by a very elongated emargination that connects the upper and lower temporal areas; complex ornamentation pattern of the carapace, symmetrical around the axial plane, consisting of numerous bony rods, that converge upon one other, dividing the carapace in thin sub-triangular and subrhombic polygons; conical and very narrow anterior area of the hyoplastra, lacking of sutured contact with the epiplastra and the entoplastron. Differing from other representatives of Cryptodira in the following character combination: shell longer than wide, rectangular in shape; low shell; deep notch in the nuchal region; mediolaterally expanded posterior peripherals; short first dorsal rib; ligamentous connection between carapace and plastron; absence of costal-peripheral and bridge fontanelles; presence of central plastral fontanelle; presence of a large xiphiplastral fontanelle; epiplastra very elongate; absence of anal notch; presence of extragular scutes.

Description

Holotype of *Chitracephalus dumonii*.—The holotype of *Chitracephalus dumonii* is a relatively complete skeleton. The posterior two thirds of the shell and the axial and appendicular elements located in this region were split between two slabs. In one of them, IRSNB R12, the ventral view of much of the plastron is preserved (Fig. 4A). The preserved bones include most of the right hyoplastron and a small fragment of the posterior area of the left one, the hypoplastra and the xiphiplastra. The entoplastron and the epiplastra of this specimen are not known. These plates might be present, but the anterior area of the plastron has not been prepared. In addition, the ventral view of the costal and peripheral plates, some dorsal and caudal vertebrae, some elements of the pelvis and the hindlimbs can be observed in this slab. IRSNB R11 consists of several elements. One of them is the counter slab (Fig. 3A), which preserves the dorsal view of the above listed elements, including the dorsal view of the anterior region of the hindlimbs and caudal vertebrae. The other elements are: a block that shows the dorsal view of the anterior region of the carapace, a partial and a complete cervical vertebra and the forelimbs (Fig. 3A, B); the skull with the atlas, extracted from the matrix (Fig. 3C, D); and the second to fifth articulated cervical vertebrae, also extracted from the matrix (Fig. 4C–E).

As in other specimens from Bernissart, for example in juvenile specimens identified as indeterminate turtles (see Pérez-García 2011), the external surface of the bones is partly altered. For this reason, it is not possible to determine if the outer surface of the shell was smooth or ornamented. For the same reason, it is not possible to identify the sutures between some of the carapace plates or some of the skull bones, the boundaries between scutes, all the caudal vertebrae, and some elements of the limbs. After the primary description by Dollo (1885), some elements were damaged or lost, in particular all elements anterior to the postorbital and the second pair of branchial horns (see Dollo 1885: pl. 1: 1–4).

Skull, lower jaw, and hyoid apparatus.—The skull fragment includes the posterior three-quarters of its length, from the posterior edge of the orbits to the occipital condyle (Fig. 3C, D). The medial and posterior rami of both branches of the mandible, the hyoid complex, and the atlas remain in articulation with this portion of the cranium.

The skull is elongated and depressed. The orbits are large and are situated in a relatively dorsal and anterior position of the skull (Dollo 1885: pl. 1: 1–4). Preservation does not allow many of the sutures to be recognized, such as the limits of the prootic, opistootic, basioccipital, basisphenoid, or pterygoid. Because of its poor preservation, it has been argued (Gaffney 1979) that the study of the skull will not allow determination the relationships of this taxon, even to the level of Panpleurodira or Pancryptodira. The temporal area is characterized by confluent upper and lower temporal emarginations, a character highlighted by Meylan (1987). Therefore, a contact between the parietal and squamosal was likely absent, and this taxon probably lacks a quadratojugal. The frontals contribute to the posteromedial rim of the orbits. From that point, the lateral margins of the frontal diverge to the posterior end. The postorbitals contribute to the orbits and are broadly exposed on the dorsal skull roof. The parietals are long and narrow. The supraoccipital has a small exposure on the dorsal skull roof and barely penetrates between the parietals.

Both mandibular rami are preserved in articulation with the skull. These elements are dorsoventrally low. Preservation does not allow any sutures to be identified.

The hyoid apparatus is represented by two pairs of branchial horns. The anterior one consists of two ossified rods extending from the middle of the palate to the posterolateral corner of the skull. A high percentage of these elements have been lost after the original description (Dollo 1885: pl. 1: 1, 2). The corpus hyoidei can be identified, but its boundaries are not clear.

Vertebral column. — Some cervical, dorsal and caudal vertebrae can be recognized in the holotype. However, the preservation varies in different areas of the vertebral column.

The best-preserved vertebrae are the cervicals. The first five vertebrae and two vertebrae of indeterminate position, corresponding to the posterior part of the cervical series, are identified. The atlas is attached to the skull, and its anterior region is hidden (Fig. 3C, D). The axis and third to fifth cervicals remain in articulation with one another (Fig. 4C–E) and have been extracted from the sediment. A disarticulated cervical vertebra is preserved in front of the nuchal plate (Fig. 3A). A final cervical is preserved ventral to the nuchal.

The vertebral centra are elongated and laterally compressed. The neural arches are poorly developed. There are well developed ventral keels from the axis to the posterior cervicals, and these are more strongly developed in the posterior vertebrae. On each vertebra, the keels are better developed caudally. The postzygapophyses are longer than the prezygapophyses. The prezygapophyses are more transversely expanded toward the posterior section of the preserved cervical series. The transverse processes are situated slightly anterior from the centre of the length of the vertebrae.

Through the plastral fontanelles three dorsal vertebrae can be seen, slightly displaced with respect to their position in life (Fig. 4A). Two are in articulation. These vertebrae are platycoelous.

Caudal vertebrae can be recognized in both slabs (Figs. 3A, 4A). However, their preservation does not allow any comments on morphology or limits.

Shell.—The shell of the holotype of *C. dumonii* is slightly deformed (Figs. 3A, 4A). It is as broad as long and characterized by its lack of ossification.

Owing to poor preservation, the boundaries between the neural, costal, and peripheral plates cannot be recognized (Fig. 3A). A large percentage of the surface of the carapace consists of fontanelles. In the area of the neural and costal plates, only the bony bars that generate a complex ornamental pattern, and the middle and distal regions of the ribs are ossified. The distribution of the bars is independent of the plates and shows bilateral symmetry. Between the fourth and fifth dorsal ribs, ten of these bars converge, forming a star. The possibility that the two bars perpendicular to the axial plane could correspond to the proximal region of the fifth pair of ribs cannot be excluded. Laterally, in some places three bars converge.

The nuchal plate is ossified. Medially, this plate is crossed by a bar that converges with the front end of the carapace. The outer margin of the anterior region of the peripheral series has positive relief, and this creates another place where three bars converge. The nuchal area has a deep notch, not limited to this plate.

The peripheral plates are poorly ossified (Figs. 3A, 4A). There are large fontanelles between these plates and the ribs. Some plates of the plastron, elements of the vertebral col-

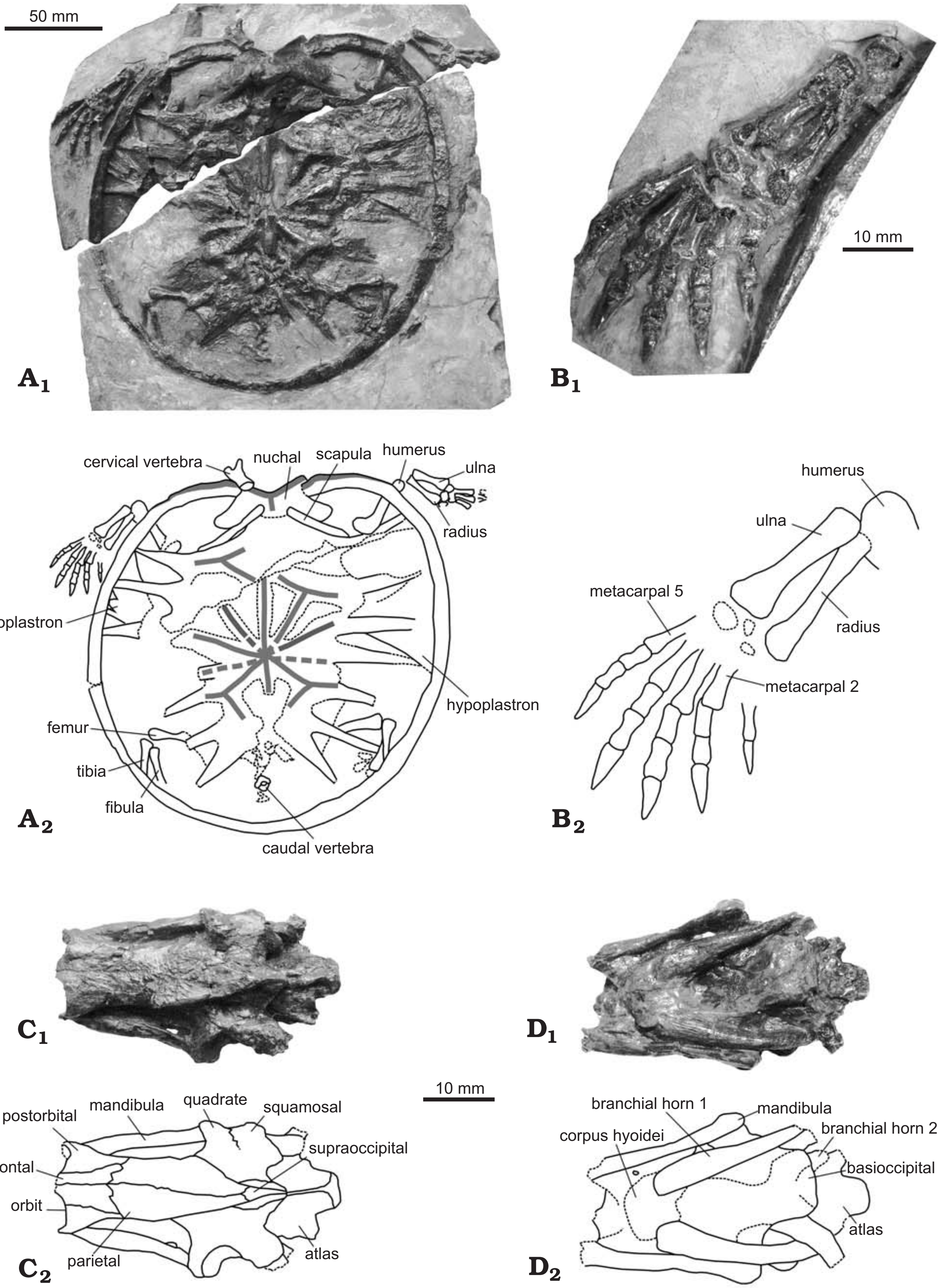

Fig. 3. Holotype of cryptodiran turtle *Chitracephalus dumonii* Dollo, 1885, from the Barremian–Aptian of Bernissart (Hainaut, Belgium). **A**, **B**. IRSNB R11. Carapace and appendicular skeleton in dorsal view (**A**), detail of the left forelimb (**B**). **C**, **D**. IRSNB R12. Skull in dorsal (**C**) and ventral (**D**) views. Photographs (A_1, B_1, C_1, D_1) and explanatory drawings (A_2, B_2, C_2, D_2).

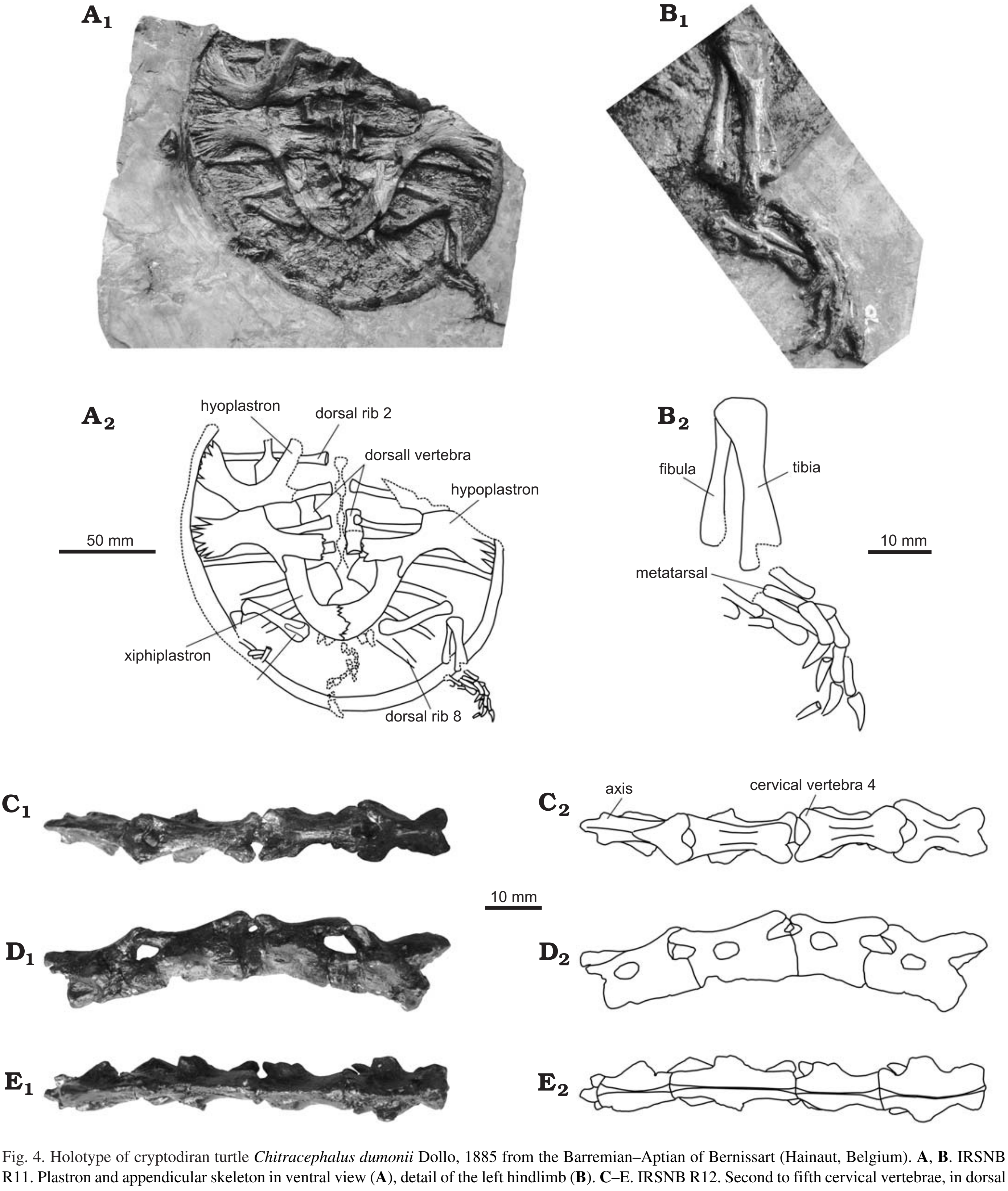

Fig. 4. Holotype of cryptodiran turtle *Chitracephalus dumonii* Dollo, 1885 from the Barremian–Aptian of Bernissart (Hainaut, Belgium). **A**, **B**. IRSNB R11. Plastron and appendicular skeleton in ventral view (**A**), detail of the left hindlimb (**B**). **C**–E. IRSNB R12. Second to fifth cervical vertebrae, in dorsal (**C**), left lateral (**D**), and ventral (**E**) views. Photographs (A_1, B_1, C_1, D_1, E_1) and explanatory drawings (A_2, B_2, C_2, D_2, E_2).

umn, and bones of the axial skeleton can be observed through these fenestrae. The poor ossification and poor preservation of the shell does not allow identification of grooves that demarcate the keratinous scutes, nor it is possible to know whether the surface of the peripherals was smooth or ornamented.

Much of the plastral surface is reduced through the presence of fontanelles (Fig. 4A). The medial regions of the hyoplastra are not preserved, so it is not known if these plates contact one another medially. A large, oval fontanelle that is much wider than long is situated in the center of the plastron. This fontanelle is located between the posterior region of the hyoplastra and the anterior half of the hypoplastra. Another large fontanelle is present that prevents the medial contact of the proximal and medial regions of the xiphiplastra. These two fontanelles are connected because there is no median contact between the hypoplastra. In addition, this specimen also has fontanelles in the bridge between the lateral regions of the hyoplastra, hypoplastra, and the bridge peripherals.

The bridge is ligamentous, as is apparent from fingered nature of the lateral region of the hyoplastra and hypoplastra. The medial edge of the hypoplastra, in the area where both plates are closer together, is also digitated. The xiphiplastra contact each other posteromedially, along a jagged suture.

Due to poor preservation, the length of the hyoplastra and the morphology of its anterior end are not known. The axillary and inguinal notches are wide. The hypoplastra is wider than long. This pair of plates has narrow and elongated posterior processes, which project onto the anteror-lateral region of the xiphiplastra. The xiphiplastra are narrow and elongated. *C. dumonii* lacks an anal notch and mesoplastra.

Appendicular skeleton.—On both sides of the nuchal plate elongated and cylindrical elements can be observed in dorsal view (Fig. 3A). Due to their dorsal position, they are interpreted as the scapular processes of the scapula. These are the only elements of the pectoral girdle that can be recognized.

The left forelimb is fully articulated and the right forelimb partially articulated (Fig. 3A, B). Both humeri are exposed distally but partially covered by the peripheral series proximally. The axis of the humeri presents a slightly sigmoidal shape. The radius and ulna are relatively well preserved on both sides. The radius is slightly longer, and more slender than the ulna. The ulna is dorsoventrally flattened. Only some right and left carpal elements are partially preserved. These bones are difficult to determine because of its preservation, but at least the intermedium and ulnare can be recognized in both forelimbs. Three right metacarpals are preserved. The middle and distal regions of metacarpals II to V are preserved on the left side. The metacarpals are relatively long elements. All digits are preserved on the left manus but only fragments of some bones in the right. The phalanges are exposed in ventral view. The manual phalangeal formula of this specimen is 2-3-3-3-3.

Within the xiphiplastral fontanelle two elements that might belong to the pelvic girdle can be observed (Fig. 4A). These correspond to two relatively flat bone surfaces and are interpreted as part of both pubes. Behind the xiphiplastra, are some indeterminate bones that, because of their location, may belong to other elements of the pelvis. In dorsal view, there are also elements that are difficult to interpret and which may belong to the pelvic girdle.

The hindlimbs can be identified in dorsal view through the fontanelles of the carapace and in ventral view (Figs. 3A, 4A). The condyles of the proximal end of the femur form an angle slightly less than 90°. The femoral heads are poorly developed. The femur has a sigmoidal shape, and is slightly longer than the humerus. The tibia and fibula are shorter than the femur. The tibia has an expanded proximal end. The fibula is a slender bone with a head scarcely wider than its shaft. The phalanges and metatarsals of the right foot are disarticulated and poorly preserved, but the left foot is more complete (Fig. 4B). Some toes have three phalanges, but it is not possible to establish the phalangeal formula of the pes.

Holotype of "*Salasemys pulcherrima*".—The skeleton from Tenadas del Jabalí (MDS-JTS.V.1–40) preserves many elements (Figs. 5, 6) and has been completely removed from the sediment. Its stage of ontogenetic development is more advanced than that of the holotype of *C. dumonii*, the length of the carapace being 2.5 times longer.

The preserved skull fragment (MDS-JTS.V.34) is compatible with that of the holotype and provides no additional relevant information (Fig. 5C–E). The elongated and depressed morphology of the skull, the anterodorsal position of the orbits, and the morphology of some of the bones of the dorsal skull roof are confirmed. However, sutures in ventral view are not preserved.

A poorly preserved cervical vertebra (MDS-JTS.V.34) is recognized and interpreted as procoelous. The centrum is elongate and has a ventral keel. The transverse processes are slightly anterior to the centre of the vertebra. Poorly preserved disjointed sacral or anteriormost caudal vertebrae are identified (MDS-JTS.V.9, V.10); their transverse processes are robust (Fig. 6I). Other vertebrae are preserved as well. The best preserved (MDS-JTS.V.37, V.39) are markedly procoelous (Fig. 6J, K), but it is unknown whether the whole caudal series is procoelous or only a part. The transverse processes are well developed and the neural spines are broken. The relative height of these elements is therefore unknown. A dorsal ridge is identified in the middle region of each vertebra.

The carapace shows several sutures as well as sulci that demarcate the scutes (Figs. 5A, B, 6A). We correct some problems in Fuentes Vidarte et al.'s (2003) interpretation of the ornamental pattern and reconstruction of the carapace and plastron. As with the holotype of *C. dumonii*, the external surface of the shell of the specimen from Tenadas del Jabalí (MDS-JTS.V.1, V.2) is altered, but the disturbance is less marked than in the Belgian specimen, and some grooves of the plastral scutes can be identified. This confirms Dollo's (1885) assertion that this taxon was covered by scutes in life, in contrast to the interpretation by Fuentes Vidarte et al. (2003).

The ornamentation pattern on the carapace is consistent with the holotype (Fig. 5A). However, the region that has a better defined pattern in the holotype is not preserved in the specimen from Tenadas del Jabalí. The bars converge in the rearmost point of the nuchal notch, and in four other points

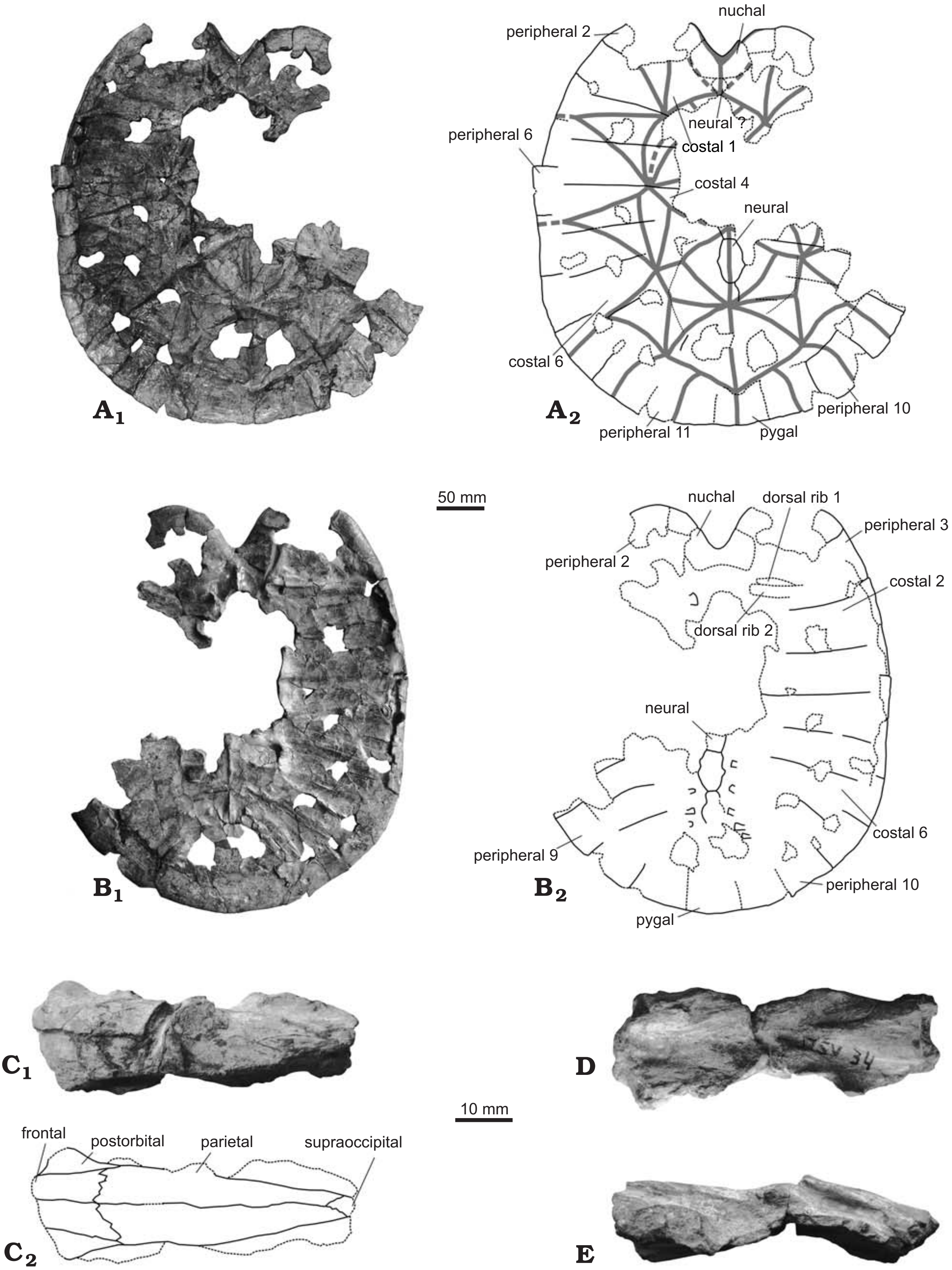

Fig. 5. Specimen of cryptodiran turtle *Chitracephalus dumonii* Dollo, 1885, MDS-JTS.V.1–40, from the Hauterivian–Barremian of Tenadas del Jabalí (Burgos, Spain). **A**, **B**. MDS-JTS.V.1. Carapace in dorsal (**A**) and ventral (**B**) views. **C**, **E**. MDS-JTS.V.34. Skull in dorsal (**C**), ventral (**D**), and rigth lateral (**E**) views. Photographs (A_1, B_1, C_1, D, E) and explanatory drawings (A_2, B_2, C_2).

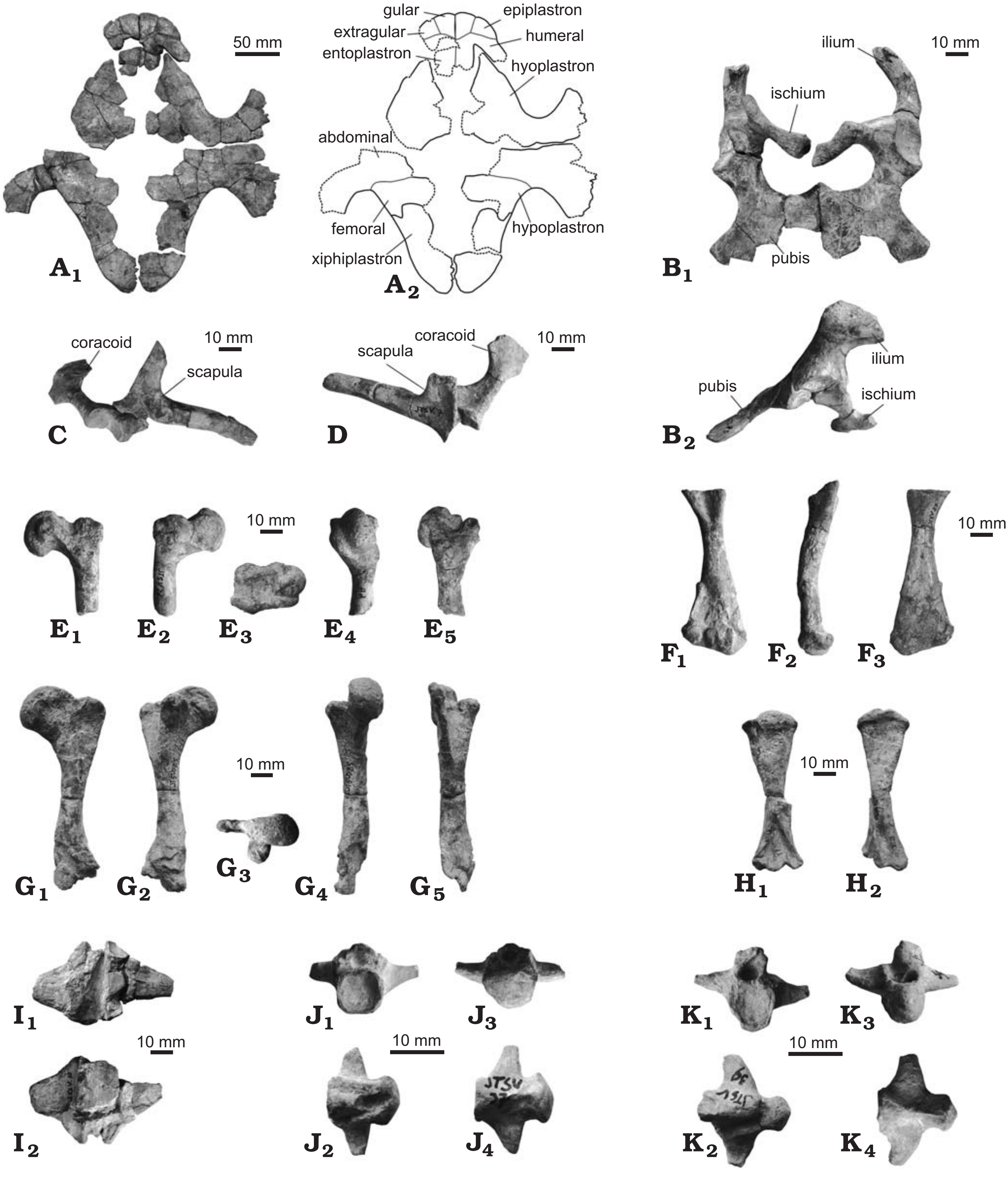

Fig. 6. Specimen of cryptodiran turtle *Chitracephalus dumonii* Dollo, 1885, MDS-JTS.V.1–40, from the Hauterivian–Barremian of Tenadas del Jabalí (Burgos, Spain). **A**. MDS-JTS.V.2, plastron in ventral view, photograph (A_1), explanatory drawing (A_2). **B**. MDS-JTS.V.4–5, pelvis in ventral (B_1) and left lateral (B_2) views. **C**. MDS-JTS.V.3, right scapula and coracoid, in anterolateral view. **D**. MDS-JTS.V.6–7, left scapula and coracoid, in anterolateral view. **E**. MDS-JTS.V.26, right humerus in distal (E_1), proximal (E_2), dorsal (E_3), medial (E_4), and lateral (E_5) views. **F**. MDS-JTS.V.27, left humerus in distal (F_1), proximal (F_2), and lateral (F_3) views. **G**. MDS-JTS.V.25, right femur in distal (G_1), proximal (G_2), dorsal (G_3), medial (G_4), and lateral (G_5) views. **H**. MDS-JTS.V.30, right tibia in medial (H_1) and lateral (H_2) views. **I**. MDS-JTS.V.10, sacral or anteriormost caudal vertebra in dorsal (I_1) and ventral (I_2) views. **J**. MDS-JTS.V.37, caudal vertebra in proximal (J_1), dorsal (J_2), distal (J_3), and ventral (J_4) views. **K**. MDS-JTS.V.39, caudal vertebra in proximal (K_1), dorsal (K_2), distal (K_3), and ventral (K_4) views.

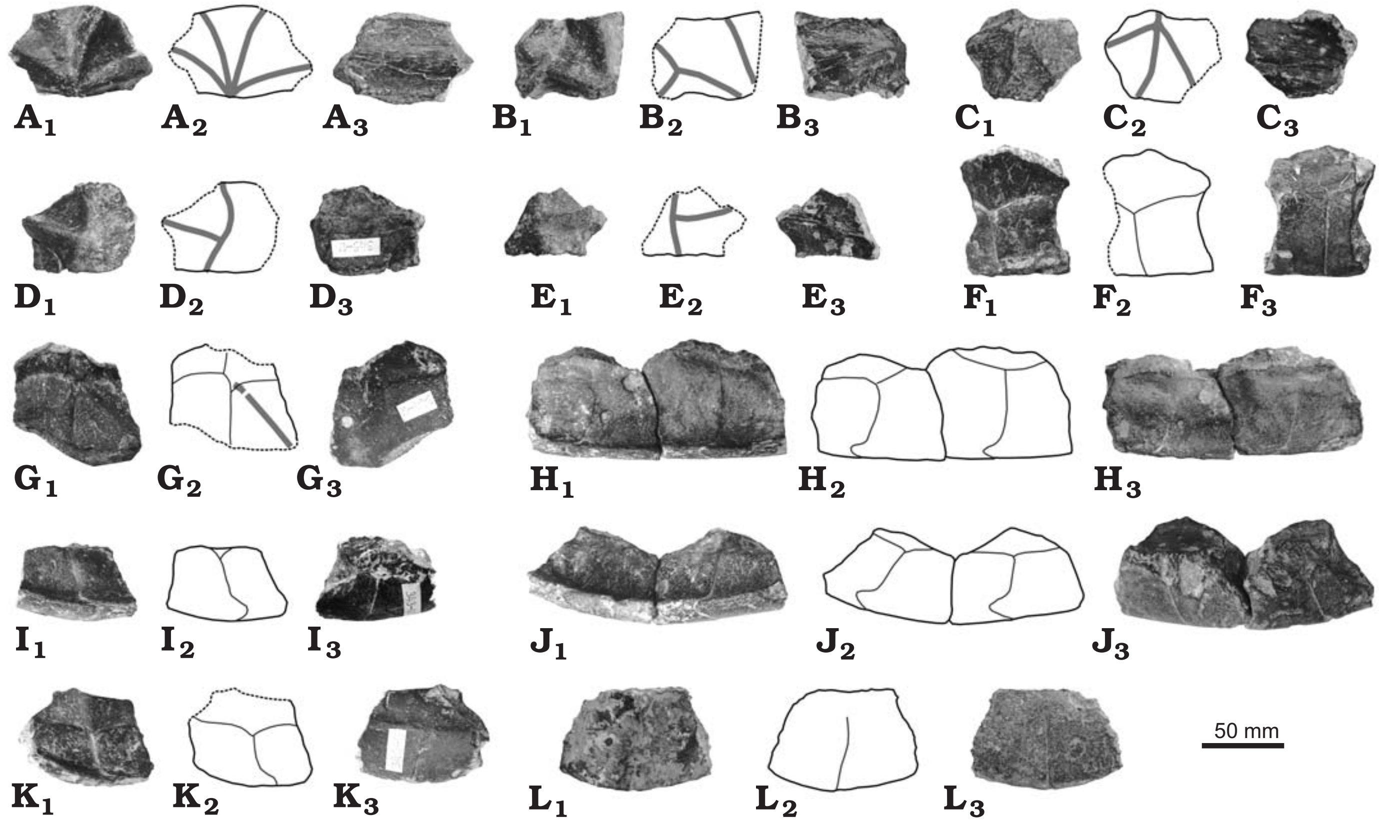

Fig. 7. Disarticulated carapace of cryptodiran turtle *Chitracephalus dumonii* Dollo, 1885, ICIPLR-1, from the Barremian–Aptian of Torremuña (La Rioja, Spain). **A**–**E**. Fragments of costal plates. **F**–**L**. Peripheral plates and fragments of these plates. All elements are represented in dorsal view (A_1–L_1), explanatory drawings in that view (A_2–L_2), and ventral view (A_3–L_3)

along the median plane. Another point of convergence was likely present within the missing portion of the carapace. Several points where the bars with several different orientations converge are present laterally. The polygons delimited by the bars have sub-triangular and sub-rhombic morphologies. This complex ornamental pattern is symmetric along the axial plane. It was not fully developed in the holotype from lack of ossification. The specimen from Tenadas del Jabalí, however, has completely ossified costal and peripheral plates and lacks carapacial fontanelles. The bone bounded by the bars is very thin, usually no more than 2 mm thick. This has contributed to breakage of some of these regions. It is possible to identify some sutures both in dorsal and ventral views (Fig. 5A, B). One of the last plates of the neural series and partial adjacent neurals are identified. The complete neural plate is elongate and sub-hexagonal. Also, the boundaries between the costal plates are identified with the exception of the posterior of the last pair. It is not possible to determine whether this specimen has one or more suprapygal plates. Eleven pairs of peripheral plates are identified, of which the most posterior pairs are considerably more slender than the first. In dorsal view, it is possible to identify the proximal area of the first and last dorsal ribs. The first is small and is articulated with the second one. A deep notch is developed in the nuchal and first pair of costals.

The specimen from Tenadas del Jabalí preserves two large median fontanelles in the plastron, but the fontanelles of the bridge are closed (Fig. 6A). These fontanelles are much larger than those of *Ordosemys leios*, being more similar to those seen in Panchelonioidea. The anterior median fontanelle is in contact with the hyoplastra and hypoplastra, and is wider than long. The posterior one, longer than wide, is situated between the proximal and medial regions of both xiphiplastra. It is not clear if both fontanelles are connected with one another or if the hypoplastra contact one another along the median plane. Considering the space between the two hyoplastra, it is likely that the entoplastron was long. The anterior region of the hyoplastra has a peculiar morphology and the contact of these plates with the limit between the epiplastra and entoplastron was ligamentous. The contact area between the hypoplastra and xiphiplastra is very like the holotype.

The sulci on the plastron indicate the morphology of several scutes (Fig. 6A). Two gular scutes (sensu Hutchison and Bramble 1981; Joyce 2007), longer than wide, and two extragulars, wider than long, are observed. The area occupied by each of these scutes is similar. The sulci marking the contacts of the abdominal and femoral scutes converge medially with the distal region of the central fontanelle and laterally with the inguinal notches.

Several elements of the appendicular skeleton are identified. Elements of the two pectoral girdles are present (MDS-JTS.V.3, V.6, V.7) (Fig. 6C, D). The scapular processes are broken. The angle formed by the two processes of the scapula is slightly less than 90°, and the acromial ridge is absent. The distal end of the coracoid is broad and flattened. The pelvis (MDS-JTS.V.4, V.5) is almost complete, except for the anteromedial area of both pubes (Fig. 6B). Its morphology and the relationship with the shell match those seen in Pancryptodira. The proximal end of the right humerus (MDS-JTS.V.26; (Fig. 6E) has a broken lateral condyle. The medial and distal areas of the left humerus are present (MDS-JTS.V.27; Fig. 6F). The right femur (MDS-JTS.V.25; Fig. 6G) is almost complete, except for its distal end. As in the juvenile specimen from Bernissart, the condyles of the proximal end of the femur form an angle slightly less than 90°. In addition to other, poorly preserved elements, it is possible to identify the right tibia (MDS-JTS.V.30; Fig. 6H). The proximal and distal ends of the preserved limb bones are more ossified than in the holotype.

Specimen of "*Salasemys pulcherrima*" from Torremuña. — The disarticulated carapace from Torremuña (ICIPLR-1; Fig. 7) comes from a larger individual than the Tenadas del Jabalí specimen. Fragments of costal plates (Fig. 7A–E), and complete or fragmented peripherals (Fig. 7F–L) are identified. The complex ornamental pattern, previously considered to be autapomorphic of "*S. pulcherrima*", allowed its identification by Pérez-García et al. (2010a). ICIPLR-1 is reassigned here to *C. dumonii*, and it sheds new light on the ontogeny of that species thanks to its preservation and level of maturity. As indicated, Dollo (1885) described sulci that delimited the scutes on the plastron and carapace in the holotype, but these can no longer be seen because of subsequent modification of the specimen. Fuentes Vidarte et al. (2003) concluded that "*S. pulcherrima*" was probably devoid of scutes. However, they may be seen on the plastron of the specimen from Tenadas del Jabalí, although the carapace preservation does not reveal whether or not they were present there. Several grooves that delimited the marginal scutes are identified on the carapace from Torremuña. Therefore, the observation of Dollo (1885) is confirmed. The marginal scutes are restricted to the peripheral plates. Some scutes cover much of the length of these plates. The outer surface of the carapace from Torremuña is better preserved than in the other known specimens of *C. dumonii*, and it is not smooth, but is roughened, a feature not identified in the other specimens.

Discussion

Current state of knowledge of *Chitracephalus dumonii*.— The original publication on *C. dumonii* (Dollo 1885) was supposed to be preliminary and the description of this turtle was therefore limited. Knowledge about fossil turtles has improved considerably since that time and, although "Thalassemydes", the group to which Dollo (1885) assigned this turtle, is no longer valid, there has been no consensus or justification on the systematic position of *C. dumonii* (Pérez-García et al. 2010b). For that reason, *C. dumonii* has usually been identified as an indeterminate turtle (Gaffney 1979; Carroll 1988; Lapparent de Broin 2001) or even as a member of groups as distantly related as Chelidae (Nopcsa 1934) or Eucryptodira (Hirayama et al. 2000; Pérez-García et al. 2010b).

Dollo's (1885) "Thalassemydes" was a group of turtles that included the European late Jurassic taxa *Thalassemys*, *Tropidemys*, *Eurysternum*, *Idiochelys*, and *Hydropelta*. Indeed, many of these taxa, or close relatives, are placed close to each other in current phylogenies, as basal representatives of Eucryptodira (e.g., Joyce 2007). However, in the analysis undertaken here, *C. dumonii* is more derived than the cited genera, being interpreted as belonging to the crown Cryptodira.

"*Salasemys pulcherrima*", a junior synonym of *Chitracephalus dumonii*.—As already noted, it is remarkable that *Chitracephalus dumonii* was largely ignored after its description, despite the fact that it is represented by one of the most complete turtle skeletons known from the Lower Cretaceous of Europe. For that reason, Fuentes Vidarte et al. (2003) could suggest that the only Mesozoic freshwater turtles with "complex" ornamentation were juvenile specimens of *Dinochelys whitei* and *Glyptops plicatulus*, not considering other groups of ornamented turtles, such as trionychids, carettochelyids, adocids, nanhsiungchelydis, and some "xinjiangchelyids". These authors named the new taxon "*Salasemys pulcherrima*", which is here synonymized with *C. dumonii* on the basis of shared ornamentation. According to the general form of the carapaces of these turtles, Karl and Reich (2009) stated that "*S. pulcherrima*" is probably a junior synonym of *C. dumonii*, but they argued that this could not be resolved because the dorsal surface of the holotype of *C. dumonii* was covered with sediment. This uncertainty has been rectified by the studies reported here.

The diagnosis of "*S. pulcherrima*" was thought to be a combination of characters not shared with any other turtle (Fuentes Vidarte et al. 2003), but most are shared with the holotype of *C. dumonii*: complex ornamental pattern, in "spiderweb" morphology, consisting of high ridges; deep notch in the nuchal region; presence of laterally expanded and recurved posterior peripherals; ligamentous attachment between the carapace and plastron; cruciform morphology of the plastron with wide axillary and inguinal notches; absence of mesoplastra; xiphiplastra narrow, lacking anal notch and with very serrated medial margins; presence of a large fontanelle, wider than long, between the hyoplastra and the hypoplastra, and of another between the xiphiplastra. Because the anterior lobe of the plastron of the holotype of *C.dumonii* is not known, some characters of the diagnosis of "*S. pulcherrima*" cannot be compared: rounded morphology of the anterior border of the epiplastra; slight epiplastral protrusion; conical and very narrow morphology of the anterior area of the hyoplastra, which lies between the epiplastra and the entoplastron, but is not sutured with them. The shape of the shell of "*S. pulcherrima*", being oval and wider in the posterior area than in the anterior, is different from the holotype of *C. dumonii*, as might be expected because they represent different ontogenetic stages. Therefore, because the diagnosis of "*S. pulcherrima*" is inadequate to distinguish this taxon from *C. dumonii*, the former is identified here as a junior synonym of the latter.

Finally, some of the characters of the diagnosis of "*S. pulcherrima*" (Fuentes Vidarte et al. 2003) are not well defined: I consider that the entoplastron and the epiplastra are independent elements, as in any other turtle. However, its preservation conceals any clear boundary between these plates, as, for example, with the suprapygal and the plates that delimit it. On the other hand, it cannot be excluded that the contact between hyoplastra and hypoplastra may represent a suture zone. The existence of a "deep groove between the first costal plates and the first peripherals" is interpreted here as a result of deformation of the carapace.

Ontogeny of *Chitracephalus dumonii*.—Comparison of the three specimens attributed to *Chitracephalu dumonii*, the holotype and the two Spanish specimens, shows that there is an ontogenetic tendency to ossify the areas bounded by the bars. In the Bernissart specimen (IRSNB R11 and IRSNB R12), bars delimited fontanelles, corresponding to unossified regions. In the Tenadas del Jabalí specimen (MDS-JTS. V.1–40 and ICIPLR-1), the space between the bars is ossified, but the thickness of the bone does not exceed 2 mm in the central areas of polygons defined by these structures. However, the thickness of these areas in the Torremuña specimen is considerably greater. These ontogenetic changes to the carapace are unique to *C. dumonii*. The holotype has a narrow peripheral ring and a complex system of bars joined together, which, along with the ribs, maintains the bone structure of the carapace. Many of them converge at a point slightly offset from the centre. As ontogeny proceeds, the fontanelles between the costal and peripheral plates disappear, as do fontanelles in the polygons bounded by the bars. When the ossified area increases, new bars are generated, making this structure more complex. The peculiar architecture of the carapace of *C. dumonii*, coupled with the way it is generated, are unique to this taxon. In *Dinochelys whitei* and *Glyptops plicatulus* (Paracryptodira), as well as in many basal members of Eucryptodira, there is a juvenile ornamentation composed of forward-radiating ridges. This pattern is preserved in adults of some basal eucryptodiran turtles, such as *Xinjiangchelys qiguensis*, *Xinjiangchelys tianshanensis*, *Xinjiangchelys radiplicatus*, and *Kirgizemys hoburensis* (Brinkman and Peng 1993b; Matzke et al. 2004). However, unlike the complex ornamentation of *C. dumonii*, which has a structural function, and whose distribution is independent of the limits of the plates and scutes, those patterns are placed on the vertebral scutes, radiating from the point where they grow and not extending beyond their margins.

The central plastral fontanelle and xiphiplastral fontanelle reduce the weight of the plastron. However, in order to maintain a robust structure, the posterior union between both xiphiplastra is very strong thanks to the presence of indentations, which are preserved throughout ontogeny. The juvenile fontanelles observed in the region of the bridge are not present in adults.

The length of the carapace of *C. dumonii* increased relative to its width during growth. This occurs in most extant turtles, but has also been observed in basal members of Eucryptodira, such as *Sinemys lens* (Brinkman and Peng 1993a). Thus, in the holotype of *C. dumonii* the width and length were almost identical to one another, but the Tenadas del Jabalí specimen is 25% longer than wide. Allometric changes are observed throughout the shell. As a result, the length of the notch of the nuchal region increases.

Systematic and palaeobiogeographic implications.—The Asian Upper Jurassic and Lower Cretaceous turtle record include numerous taxa traditionally attributed to "Macrobaenidae" and "Sinemydidae". The clade Cryptodira, which includes these taxa but also the members of Panchelonioidea, has not been confirmed in Europe until the recent description of *Hoyasemys jimenezi*, from the Barremian of Cuenca, Spain (Pérez-García et al. 2012). The identification of *C. dumonii* as a taxon belonging to this node demonstrates that, as in Asia, cryptodires were also relatively diverse in the Lower Cretaceous of Europe.

Hoyasemys jimenezi has been recognized only at its type locality. However, the synonymy between *C. dumonii* and "*S. pulcherrima*" demonstrates that the geographic range of this taxon could correspond, at least, to a wide area of Western Europe. This might be true also for other turtles from the Early Cretaceous of Western Europe. For example, in several Spanish localities, fragmentary material of a taxon that could be the British *Helochelydra* or a form closely related to it has been identified (Pérez-García 2009; Pérez-García et al. 2010c). In addition, the British taxon *Trachydermochelys* may also be present in Spain (Pérez-García, personal observation). "*S. pulcherrima*" was also reported in the Berriasian of Northwestern Germany on the basis of four fragments of plates, although these have not been figured nor has justification of this identification been given (Karl and Reich 2009).

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Appendix 1

Characters of *Chitracephalus dumnonii* scored according to the data matrix of Joyce (2007):

Frontal A, 1; parietal A, 1; jugal A, 1; quadratojugal A, 1; supratemporal A, 1; quadrate C, 2; supraoccipital B, 0; carapace A, 0; carapace B, 0; nuchal B, 0; peripheral A, 1; costal B, 0; costal C, 0; plastron A, 1; plastron B, 1; entoplastron A, 1; entoplastron C, 1; entoplastron D, 0; entoplastron E, 0; epiplastron A, 1; hyoplastron A, 0; mesoplastron A, 2; hypoplastron A, 0; xiphiplastron A, 0; xiphiplastron B, 1; plastral scutes A, 0; gular A, 0; extragular A, 0; extragular B, 0; extragular C, 1; intergular A, 0; cervical vertebra B, 1; cervical articulation A, 1; dorsal rib, 2; dorsal rib B, 0; dorsal rib C, 1; chevron A, 1; scapula B, 1; scapula C, 1; coracoid A, 1; pelvis A, 0; ilium A, 1; ilium D, 0; ischium A, 1; hypoischium A, 1; manus A, 1; manus B, 0; manus C, 0; pes A, 0.